

1 **The global contribution of soil mosses to ecosystem services**

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107 **Abstract**

108

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

125

126 **Main**

127

128 Mosses are one of the most common and ubiquitous life forms on the planet¹⁻³, contributing a
129 considerable portion of plant biomass in some of Earth's most extensive ecosystems, ranging
130 from deserts to boreal and arctic regions⁴. Yet, our knowledge of their roles in controlling soil
131 biodiversity and soil function still lags behind that of vascular plants. Vascular plants are known
132 to promote the accumulation of soil resources⁵, which are fundamental for maintaining plant
133 diversity, soil microbial communities and multiple ecosystem services. Local observational
134 studies suggest that mosses also play important roles in supporting individual ecosystem
135 attributes such as nitrogen cycling, hydrology and carbon sequestration⁶⁻⁹. Previous studies of
136 soil mosses, those growing on the soil surface, have tended to focus at local or regional scales, in
137 particular ecosystems (e.g., polar, boreal or arid)¹⁰⁻¹². The influence of soil mosses on

138 biodiversity and ecosystem functioning could depend on their specific functional traits (e.g.,
139 annual *cf.* perennial; i.e., *r- cf. K*-strategist) and taxonomies. Yet, unlike vascular plant functional
140 traits¹³, the extent to which moss traits influence the biodiversity and function of terrestrial
141 ecosystems is virtually unknown. Consequently, we still have a poor understanding of how
142 mosses, and their traits, contribute to soil biogeochemistry, biodiversity and ecosystem services
143 across global environmental gradients considering contrasting climates, vegetation types and
144 land uses. Quantifying the ecosystem role of soil mosses is essential to better understand their
145 importance for protecting soils and restoring ecosystems (e.g., drylands, degraded land),
146 particularly under changing climates or where the use of vascular plants may be inappropriate.

147
148 Here, we report results from the most comprehensive global field study of soil mosses. This
149 survey includes composite topsoil samples (uppermost ~5 cm) collected in three microsites
150 (mosses, vascular plants bare soil), from within 30 x 30 m plots at each of 123 sites across all
151 continents (Figs. 1 and S1; Supplementary Tables 1-2; Supplementary Movie 1). Our sites cover
152 the broad range of environmental conditions under which mosses occur, rather than focusing on
153 particular ecosystem types (Supplementary Table 1; Supplementary Fig. 2). Climate ranges from
154 tropical to continental, temperate, arid, and polar, vegetation types from forests to grasslands,
155 shrublands, and heathlands, and land management contexts from urban to natural
156 (Supplementary Tables 1-2).

157
158 In this study we investigated the global biogeography, magnitude and drivers of the global
159 contribution of soil mosses to 24 soil biodiversity and functional attributes linked to eight
160 ecosystem services. We aimed to: (i) determine the environmental conditions supporting
161 ecosystems with or without mosses worldwide; (ii) quantify the unique contribution of soil
162 mosses to eight ecosystem services (soil biodiversity preservation, carbon sequestration, nutrient
163 cycling, plant pathogen control, antibiotic resistance control, organic matter decomposition,
164 microbial habitat, biomass of symbiotic organisms) all across contrasting climates and compared
165 to vascular plants. We also (iii) assessed the degree of context dependency of the ecological
166 contribution of soil mosses to multiple ecosystem services across a wide range of moss traits and
167 climatic, vegetation and soil environmental conditions. Our study provides the most
168 comprehensive global study of mosses and their traits on multiple soil ecosystem services, cross-
169 validated by two global meta-analyses based on experimental work. We further compared the
170 relative importance of vascular and mosses for soil biodiversity and function and mapped the
171 global distribution of mosses.

172
173 At each site we established a 30 m × 30 m plot within which we placed three 30 m line transects
174 (Fig. 1C) wherein we assessed the cover of perennial plants, bare soil, and mosses. This allowed
175 us to calculate plot-level moss, vascular plant and bare soil cover (Methods). Our survey
176 included a wide range of mosses (19 families, 40 genera) with contrasting life histories (annual
177 to perennial), growth forms (cushions, mats, turfs) and life strategies (*r*- and *k*-strategists;
178 Methods; Supplementary Fig. 2). Deserts and urban gardens supported the largest proportion of
179 annual moss species, and tundra and wet forests a greater percentage of perennial species
180 (Supplementary Fig. 2). Most survey locations, particularly those in urban greenspaces and
181 natural grasslands, supported a sparse cover of mosses (Figs. 2A-B), but in some locations,
182 particularly polar sites, moss cover exceeded 50% (Fig. 2B). The cover of moss was positively
183 correlated with the richness of cryptogamic (moss, lichen, liverwort) species determined in the

184 field (Pearson's $r = 0.27$; $P = 0.002$, $n = 123$ sites). Mosses sampled were dominated by taxa
185 from the genera *Bryum* (12%), *Rosulabryum* (11%), *Leucobryum* (7%), *Funaria* (6%),
186 *Campylopus* (5%), *Desmatodon* (5%) and *Polytrichum* (5%; Supplementary Table 1 and
187 Supplementary Fig. 2A).

188
189 Using Structural Equation Modelling, we investigated the environmental factors associated with
190 moss cover in our global survey (Supplementary Figs. 3-5, Supplementary Table 3), and found
191 that moss cover tended to be greater in environments with low potential evapotranspiration
192 (PET) and sparse vascular plant cover, particularly in some deserts and tundra ecosystems (Figs.
193 2C and 3). In addition to PET and plant cover, precipitation and mean diurnal range temperature
194 (MDR) were also negatively associated with the proportion of moss cover when considering all
195 direct and indirect pathways in our model (Supplementary Fig. 5). Thus, after accounting for the
196 effects of vascular plant cover, mosses were significantly associated with rainfall-limited
197 environments, with low PET and MDR, likely due to specialised leaf structures that enable them
198 to capture and retain moisture, an innate ability to recover from long periods of dehydration⁹ and
199 less competition from vascular plants. The relative contribution of environmental factors in
200 explaining moss cover was maintained when conducting a simplified version of our SEM
201 (Supplementary Fig. 4). Soil moss cover was not correlated with air temperature (consistent with
202 their presence in both cold and hot deserts), ecosystem type (mosses thrive in urban and natural,
203 or forested and non-forested ecosystems), or amount of soil carbon (organic matter), pH, sand
204 content or salinity (electrical conductivity; Fig. 2C; $n = 123$) once other factors were accounted
205 for.

206

207 **Global distribution of soil moss cover**

208

209 To better visualize global hotspots of moss cover, we used Random Forest models to create the
210 most comprehensive global map of potential moss cover across contrasting regions worldwide
211 (Fig. 2D, Supplementary Fig. 5, Methods). Our analyses indicate that dry regions of the western
212 United States of America, tundra ecosystems from northern Europe, and large desert regions
213 from Australia, Asia, Africa and South America support high moss cover, compared with
214 vascular plant cover (Fig. 2D), consistent with regional studies^{11-12,14}. Earlier studies have
215 mapped the distribution of moss richness at the national level¹⁵, but there was no high resolution
216 map of moss cover. Our estimates indicate that mosses cover over 9.4M km² of Earth in the area
217 covered by the environmental conditions of our survey, and excluding areas of uncertainty
218 (Supplementary Fig. 7). This is an area similar to Canada, China or the United States of America
219 (Supplementary Appendix 1).

220

221 **The contribution of soil mosses to ecosystem services**

222

223 We collected field and laboratory information on 24 soil biodiversity and functional attributes of
224 topsoils from the 123 sites (Fig. 1) to better understand the ecological contribution of soil mosses
225 to ecosystem services (Supplementary Tables 4-5; Methods). These 24 attributes comprised a
226 wide range of soil variables associated with the maintenance of soil biodiversity (richness of
227 fungi, bacteria, protists and invertebrates), carbon sequestration (soil total organic carbon),
228 nutrient cycling (soil total N, P, Cu, Mg, Mn, Zn, Fe, K), organic matter decomposition indices
229 (soil extracellular enzyme activities related to C, N and P cycles, glucose, lignin and basal

230 respiration), microbial habitat (biomass of fungi and bacteria), plant-soil symbiosis (biomass of
231 arbuscular mycorrhizal fungi), antibiotic resistance control¹⁶ and soil-borne plant pathogen
232 control¹⁶ (Supplementary Table 4, Methods).

233
234 A relative interaction intensity index (RII¹⁷; Methods for details) was then used to calculate the
235 relative importance of soil mosses and vascular plants to the 24 soil biodiversity and functional
236 attributes at all sites (Supplementary Table 5; Methods). The index compares the differences
237 between moss (or vascular plant) and bare soil where $RII = (X_m - X_b) / (X_m + X_b)$, where X is the
238 value of a specific attribute, and X_m and X_b represent values beneath the moss (or vascular plant)
239 and in the bare soil, respectively. Positive RII values indicate an increase in the value of soil
240 biodiversity and ecosystem services beneath mosses or vascular plants compared with bare soils
241 (and *vice versa*; see Methods).

242
243 Our data show that soil mosses make significant and positive contributions to multiple ecosystem
244 services (i.e., RII moss multiservices) across the globe (Fig. 3A). The contribution of soil mosses
245 to ecosystem services is likely to be associated with their well-known capacity to influence
246 surface microclimates and their litter inputs compared with bare soils. Thus, these mechanisms
247 of moss contribution to multiple ecosystem services are likely to be similar to those of vascular
248 plants (Fig. 3A). Moreover, the contribution of soil mosses to services was also positively
249 associated with those contributions by vascular plants (i.e., RII vascular plant multiservices),
250 suggesting that the positive contributions of vascular plants and mosses to multiple ecosystem
251 services partially co-occur among terrestrial ecosystems (Fig. 3B; Supplementary Table 6). Even
252 so, further modelling effort revealed that mosses supported multiple ecosystem services in
253 locations of the planet with limited vascular plant influence (Fig. 4). Thus, even when the
254 contribution of soil mosses to function is lower than those of vascular plants (e.g., Fig. 3), the
255 large cover of soil mosses (Fig. 2D) makes this contribution significant at the global scale
256 (Supplementary Fig. 8), particularly in ecosystems with limited vascular plant contribution.
257 Together mosses played additional roles to vascular plants in supporting ecosystem services.

258
259 We further found that soil mosses were significantly and positively associated with the
260 simultaneous increase in the magnitude of soil attributes within important ecosystem services
261 such as carbon sequestration, nutrient cycling, organic matter decomposition and plant pathogen
262 control (Fig. 3). Specifically, we found greater carbon content, more essential nutrients such as
263 nitrogen, phosphorus, and magnesium, soil enzyme activities and greater control (lower
264 proportion) of soil-borne potential plant pathogens in the soils beneath mosses than in bare soils
265 (Fig. 3A). Moreover, we found multiple positive associations between the relative interaction
266 indices of 24 soil attributes under mosses compared with bare soils, particularly for those within
267 nutrient cycling and organic matter decomposition, indicating multiple co-existing positive
268 influences of mosses on soil fertility. Mosses also have a fundamental role in supporting multiple
269 ecosystem services in those boreal ecosystems within the environmental conditions represented
270 by our data (Fig. 4). Thus, our findings go beyond the well-studied effects of soil mosses on
271 individual groups of functions (e.g., nitrogen cycling) in particular ecosystems (e.g., boreal
272 forests) and in local studies, and provide a comprehensive view of the environmental
273 contribution of soil mosses across contrasting global environments.

274

275 Our findings highlight the notion that soil mosses can make a significant impact by regulating
276 global soil carbon sequestration¹⁸⁻¹⁹ because of their key role in natural environments where they
277 are the dominant vegetation (e.g., Antarctica, boreal forests and drylands)^{10,20-22} (Fig. 3). For
278 example, we estimated that worldwide, soils covered by mosses can sequester 6.43 Gt more
279 organic carbon in the top ~5 centimetres of soil than bare soils (Supplementary Appendix 1). Our
280 study largely underestimates this influence, as we limited our estimations to areas of high
281 certainty. These included ecosystems represented by our global survey (Fig. 3D), that partially
282 excluded important regions of the planet covered by mosses such as boreal forests. Nevertheless,
283 we accounted for these regions using meta-analytical data (as explained below). Soil mosses thus
284 likely play an important role in soil carbon sequestration; for example, a 15% change in moss
285 cover due to climate change or direct human land disturbance would be equivalent to about the
286 same amount of carbon emitted to the atmosphere annually from other land use changes. Mosses
287 also support extra 0.49, 0.10 and 0.06 Gt more soil N, P and Mg, respectively, worldwide,
288 boosting levels of three fundamental nutrients that often limit ecosystem productivity
289 (Supplementary Appendix 1). Therefore, our results indicate that soil mosses could play critical
290 roles in supporting some of the key Sustainable Development Goals of the United Nations
291 (<https://sdgs.un.org/goals>) including supporting life on land, and climate actions. Future studies
292 should investigate the global contributions of different species/genera to these budgets.

293

294 **Meta-analyses of the global importance of soil mosses**

295

296 In order to provide further experimental support for our global observations, and to show that
297 mosses alter soil properties rather than inhabit chemically and biologically enhanced soils, we
298 conducted meta-analyses of the effects of moss addition or removal on soil biodiversity and
299 function, compared with procedure controls (bare soils). We included manipulative studies, and
300 field and microcosm studies. Analysis of information on soil C, N, P and Mg contents, soil
301 respiration and glucose degradation (Meta-analysis #1; 36 studies from 25 papers;
302 Supplementary Appendixes 2-3) provided compelling evidence of the positive effect of mosses
303 on multiservices, soil C, N, P and Mg contents, and on soil respiration and glucose degradation
304 observed in our global survey (Meta-analysis #1; Supplementary Appendixes 2-3 and Fig. 9).
305 These results were consistent across boreal and non-boreal, and in forest and non-forest
306 ecosystems. A second meta-analysis (13 studies) showed that mosses tend to promote soil
307 function over time (Supplementary Fig. 10; Meta-analysis #2; Supplementary Appendixes 4-5).
308 The meta-analyses support our finding that mosses contribute to the build-up of critical functions
309 such as soil carbon content and respiration (Supplementary Fig. 10), and that ecosystem
310 attributes accumulate over time beneath mosses, rather than mosses selecting locations with the
311 highest function. This information is needed if we are to understand the global patterns and
312 contributions that soil mosses make in terrestrial environments. The key message from our meta-
313 analyses and observational data is that mosses are important for supporting soil services. These
314 important results will help us to argue for greater global protection of these fundamental
315 organisms.

316

317 Soil mosses had a relatively smaller influence on soil biodiversity than on carbon and nutrient
318 pools (Fig. 3B; see Supplementary Fig. 11 for soil community composition found beneath
319 mosses). Also, in general, soil mosses support a lower diversity of invertebrates than surrounding
320 bare soils. Moss tissue contains flavonoids, carotenoids and other short-chained phenolics²³ that

321 exhibit antimicrobial, antifungal, and cytotoxic activities²⁴⁻²⁵, suppressing insect activity, and
322 resulting in invertebrate mortality²⁵. However, mosses can still indirectly contribute to soil
323 biodiversity, for example, by promoting soil carbon and microbial biomass, which were
324 positively associated with their contribution to soil protists and bacterial richness
325 (Supplementary Fig. 12). Resource (e.g., organic matter and prey) availability is known to
326 regulate the diversity of soil organisms²⁶. Similarly, we found a greater positive association of
327 mosses with invertebrate richness where mosses were positively associated with micronutrients
328 (Supplementary Fig. 12). Further, mosses are important regulators of soil-borne pathogens (Fig.
329 3a), reducing the proportion of potential soil-borne pathogens associated with vascular plant
330 communities²⁷. Soils are known to be a huge reservoir of plant pathogens²⁵, and mosses could
331 help to regulate this important reservoir. Our work demonstrates that mosses regulate ecosystem
332 services in the same way as plants do, but proportionally equivalent or greater based on their
333 smaller biomass (Fig. 3). Thus, mosses play critical roles in supporting soil biogeochemical
334 cycles^{6-7,28} and multiple ecosystem services²⁹.

335

336 **The importance of environmental conditions**

337

338 To gain deeper insights into the patterns and environmental context dependencies of the
339 contribution of mosses to multiple ecosystem services, we used Random Forest modeling to
340 relate their contribution (based on average RII from 24 soil attributes) to multiple ecosystem
341 services across contrasting soil, climatic and vegetation conditions and moss traits and
342 taxonomy. Our analyses indicate that mosses can contribute to multiple services in low
343 productivity, natural ecosystems (compared with urban greenspaces; Supplementary Fig. 13), on
344 sandy, salty and low C:N soils, and in environments with low precipitation seasonality (Figs. 5A-
345 B). Thus, the magnitude of the associations between mosses with soil biodiversity and ecosystem
346 functions is environmentally context dependent. Similar associations are also found for
347 individual relative interaction indices of mosses (Figs. 5C; Supplementary Fig. 13-14). The
348 capacity of soil mosses to increase microbial biomass, and enhance nutrient and C sequestration
349 and nutrient content (compared with bare soils), was particularly notable in sandy soils (Fig. 5).
350 Sandy soils are known to have lower nutrient retention and are therefore relatively more sensitive
351 to the loss and recovery of C, nutrients and microbial biomass¹⁶. In these situations, mosses can
352 contribute markedly to retaining soil fertility, symbiotic organisms, and microbial habitat⁹. The
353 mechanisms at work likely include the capture of C- and N-rich airborne particles²² and the
354 deposition of elements such as Mg³⁰ within moss microhabitats, leading to greater soil
355 development.

356

357 Our analyses further highlight the fact that the positive contribution of mosses to multiple
358 ecosystem services is not apparent in disturbed urban greenspaces (Supplementary Figs. 13-14)
359 and regions with high precipitation seasonality (Fig. 5 and Supplementary Fig. 14). Both climatic
360 seasonality¹⁰ and physical disturbance² have been shown to limit the positive influence of mosses
361 on individual soil functions such as nitrogen availability in specific fine-scale field
362 experiments¹⁰. Our study suggests that these limitations may apply more broadly at a global
363 scale, and that inverse contributions of soil mosses to ecosystem service delivery, where moss
364 soils are relatively resource depleted, occur at locations where precipitation is highly seasonal
365 (Fig. 5). Future work should further clarify the global contribution of mosses to ecosystem
366 services in other highly managed ecosystems such as croplands.

367

368 **The role of moss traits**

369

370 We also found global evidence of the importance of moss traits (life history and growth strategy)
371 and taxonomy in driving the contribution of mosses to soil biodiversity and multiple ecosystem
372 services. Our data show that mosses support a stronger contribution to biodiversity and
373 ecosystem services in locations with a high cover of mat and turf mosses such as *Sphagnum*,
374 *Hylocomium* and *Ptilium* spp., taxa that are widely distributed in boreal forests²⁸. In systems such
375 as the boreal forest, deserts and polar regions where mosses comprise a considerable ecosystem
376 component (Fig. 2B), individual patches tend to coalesce to form a continuous moss carpet.
377 Moss traits and taxonomy also played important, yet previously undescribed, roles in driving
378 individual soil attributes such as carbon sequestration and nutrient cycling, particularly by
379 supporting soil P, N and Mg. Perennial soil mosses, for example, supported a larger content of
380 soil carbon and greater ARG control (i.e., lower abundance of ARGs) than annual mosses, and
381 could play an essential role in carbon sequestration in ecosystems such as tundra, and wet and
382 cold forests, where they are prevalent¹⁸ (Supplementary Fig. 1).

383

384 Unlike the well described associations between moss and nitrogen-fixing bacteria²⁸, the influence
385 of moss on ARGs is thus far poorly described. We posit that increases in soil carbon beneath
386 mosses might reduce microbial competition and their need to produce ARGs. This hypothesis is
387 supported by the positive significant correlation between the contribution of moss to carbon, and
388 the moss relationship with ARG control, but further experimental work is needed to develop a
389 clearer mechanistic understanding of this association. Similarly, the influence of mosses on P
390 increased with increasing cover and was particularly important for taxa with a mat-forming habit
391 (Fig. 5). This could occur because the shoots of mat-forming mosses lie close to the substrate,
392 absorbing P directly from mineral soil²². Mosses following a *K*-strategy (as defined in the
393 Material and Methods) were also more important for P cycling by supporting higher P
394 mineralization activity. Further, we found a strong positive influence of soil mosses on Mg, a key
395 macro-nutrient for metabolism and photosynthesis³⁰. Capture of intermittent pulses of organic
396 matter through stemflow and throughfall from vascular plants can contribute significant
397 quantities of Mg in large mosses²⁸.

398

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

407

408 In summary, we provide important insights into the global patterns of soil mosses and their
409 contributions to the delivery of critical ecosystem services across markedly different global
410 habitats ranging from Antarctic heaths to dry deserts. Soil mosses were positively associated
411 with greater carbon sequestration, soil P, N and Mg contents, organic matter decomposition and
412 plant pathogen control in soils globally. We provided further experimental evidence, using global

413 meta-analyses, of the effects of mosses on soil functioning. Soil mosses further contributed to
414 support multiple ecosystem services at locations where vascular plants have limited influence.
415 Moreover, we found that the contribution of soil mosses to multiple ecosystem services varied
416 among environments, and that their effects on soils likely depended on traits, and climatic and
417 soil abiotic stress (e.g., sand content and salinity). Together, our study demonstrates the global
418 importance of soil mosses, and highlights the need to conserve them to maintain important soil
419 functions as varied as carbon sequestration, fertility and pathogen control.

420

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442

443 **Author contributions**

444 M.D-B. and D.J.E. developed the original idea of the analyses presented in the manuscript.
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454

455 **Competing interests**

456 The authors declare no conflict of interest.

457

458

459 **Figure legends**

460

461 **Figure 1. A global survey of mosses to investigate soil biodiversity and function.** (A)
462 Selected pictures of the 123 sites included in this study and their global location. (B) Location of
463 study sites in relation to a global temperature and precipitation envelope. (C) Diagrammatic
464 representation of the standardized field sampling design used in the 123 investigated sites. See
465 Supplementary Table 2 for further information on these sites. See Supplementary Fig. 18 for
466 environmental context.

467

468 **Figure 2. Global distribution of soil mosses.** (A) Distribution of moss cover in our global
469 survey. (B) Moss cover across continents and ecosystem types. (C) Structural Equation Model of
470 the direct and indirect associations (red = negative, blue = positive, black = mixed) among space
471 (average distance among sites to control for spatial autocorrelation), climate, vascular vegetation,
472 land use (urban greenspaces *cf.* natural) and soil properties in driving the proportion of moss
473 cover (see Supplementary Table 3 for more details and Fig S4 for *a priori* model). MAT: mean
474 annual temperature, MAP: mean annual precipitation, PSEA: seasonal precipitation, TSEA:
475 seasonal temperature, MDR: mean diurnal temperature range, NPP: net primary productivity,
476 Prich: Vascular plant richness, Pcov: Vascular plant cover, C: soil carbon (Supplementary Table
477 3). Different categories of predictors (climate, soil, vegetation, land use and spatial influence) are
478 grouped in the same box in the model for graphical simplicity, but they do not represent latent
479 variables. Numbers adjacent to arrows are indicative of the effect size of the relationship. Only
480 significant relationships are included (*a priori* model in Supplementary Fig. 4). R^2 denotes the
481 proportion of variance explained. (D) Predicted distribution of total moss cover in ecosystems
482 across the globe (25 km / pixel), based on machine learning modelling with a $R^2 = 0.86$
483 (determined as predicted vs. observed moss cover). Locations with high uncertainty, and areas
484 not represented by environmental conditions in our study are masked in white. $n = 123$ sites in
485 all cases. An alternative simplified version of this map can be found in Supplementary Fig. 5.

486

487 **Figure 3. Contribution of mosses and vascular plants to multiple ecosystem services.** (A)
488 Contribution of moss and vascular plants to ecosystem services (average RII values based on 24
489 soil attributes; Supplementary Table 5) and the moss and plant relative interaction indices (RII)
490 for 24 individual soil attributes (mean \pm bootstrap CI 95%). * $P < 0.05$. (B) Significant ($P < 0.05$)
491 relationships between moss and vascular plant contribution to ecosystem services (average of all
492 RII) and individual RII indices based on 24 soil biodiversity and functional attributes. Moss and
493 vascular plant contribution to multiservices (RII) = 0 (e.g., vertical dashed line in Panel A)
494 indicates that values for moss or plants are equivalent to values for this bare soil. Additional
495 Spearman correlations between moss and vascular contribution to ecosystem services can be
496 found in Supplementary Table 6 ($n = 123$ sites). See Supplementary Fig. 19 for additional
497 information.

498

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

504

505 **Figure 5. Environmental factors associated with the contribution of mosses to multiple**
506 **ecosystem services.** (A and B) Environmental factors associated with moss contribution to
507 ecosystem services (average RII values based on 24 soil attributes; Supplementary Table 5). (A)
508 Random Forest predictor importance ($P < 0.05$ in red). (B) Linear regressions and mean values \pm
509 95% CI for the relationship between environmental factors and moss contribution to ecosystem
510 services (** $P < 0.01$; * $P < 0.05$; ^a $P = 0.09$). Natural ($n = 62$), Urban greenspace (61), Cushion
511 (24), Matt + Turf (99), Funariaceae (7), Others (116), Perennial (56), Ephemeral (55), Annual
512 (12): (C) Heatmap of significant ($P < 0.05$) Spearman correlations among environmental factors
513 and the moss relative interaction indices (RII) for 24 individual soil attributes ($n = 123$ sites).

514

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587
588

589 **Methods**

590 **Study sites**

591 Soils were collected from 123 sites with three microsite types (mosses, vascular plants, bare soil)
592 covering natural ecosystems and greenspaces (Supplementary Movie 1; Fig. 1; Supplementary
593 Tables 1-3) distributed across 17 countries and all continents. Our study aimed to evaluate the
594 extent to which soil mosses support soil biodiversity and multiple ecosystem services across a
595 wide range of natural (forests, heathlands, grasslands and shrublands) and urban greenspaces

596 (parks, gardens) where mosses are known to occur (Supplementary Tables 2 and 3). This
597 sampling was conducted between 2017 and 2019. Mean annual precipitation ranged between 4
598 and 1577mm. Mean annual temperature ranges between -6.7 and 26.1°C. Our sites are located,
599 on average, 8858.5km from each other (minimum average distance of 42.97 km).

600
601 At each site we established a 30 m x 30 m plot within which we placed three 30 m line transects
602 (Fig. 1C). Along each transect we recorded the cover of 1) perennial vascular plants (trees,
603 shrubs, grasses or forbs), 2) non-vascular plants (i.e., mosses) and 3) unvegetated (bare) soil
604 using a line intercept method, and used this information to calculate the percentage cover of each
605 microsite within each plot. Where mosses and lichens occurred together as a community, we
606 estimated the relative contribution of mosses within each sampled patch. Soils dominated by
607 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
608 estimate the relative cover of mosses *cf.* vascular plants across contrasting terrestrial ecosystems.
609 Moss cover ranged from 0.01 to 99.8%.

610
611
612 Within each plot, we collected composite soil samples (five cores of top ~5cm) of vegetated,
613 moss and bare microsites (Fig. 1C). Replicate samples were pooled and divided into two sub-
614 samples. One was immediately frozen (-20°C) for molecular analyses and the other air-dried for
615 chemical analyses. We focused on surface soils because this uppermost layer is typically the
616 most biologically active in terms of plant-soil interactions, microbial biomass and diversity,
617 labile nutrient pools, and C exchange with the atmosphere, and to allow direct comparison of the
618 contribution of moss and vascular plants to ecosystem services. Four of the 123 sites (three sites
619 from Antarctica and one from Chile) had samples only from bare and moss surfaces ($n = 119$ for
620 vascular plants). Thus, a total of 365 soils were analysed for attribute assessment.

621 622 **Moss traits**

623 Moss information and pictures were collected from the sites where moss soils were sampled, and
624 the dominant species identified, generally to the level of genus/species, using published keys and
625 field guides, or by consulting national and international bryological experts (Supplementary
626 Table 2). Moss taxa were characterized according to life history; those surviving for < 1 year
627 (annuals), 1-3 years (ephemeral), > 3 years (perennial). Moss growth form was characterized as
628 cushion (rounded, pincushion-shaped), mats (dense clumps, generally branched shapes), or turfs
629 (erect, lawn-like with crowded shoots³¹, and life strategy i.e., *R*-strategists (generally small,
630 rapidly growing species with annual life cycles) and *K*-strategists (larger, slower growing,
631 perennial species)³¹.

632 633 **Soil biodiversity**

634 Soil biodiversity (richness; number of phylotypes of soil bacteria, fungi, protists and
635 invertebrates) was measured via amplicon sequencing using the Illumina MiSeq platform
636 (Illumina, Inc, CA, USA) in all soils associated with mosses, vascular plants and bare soils. Soil
637 DNA was extracted from each of the 365 soil samples using the DNeasy PowerSoil Kit -
638 QIAGEN (Qiagen, Hilden, Germany) according to the manufacturer's instructions. To
639 characterize the richness (number of phylotypes) of bacteria, protists and invertebrates, a portion
640 of the prokaryotic 16S (bacteria) and eukaryotic (protists and invertebrates) 18S rRNA genes
641 were sequenced using the 515F/806R³² and Euk1391f/EukBr³³ primer sets. Bioinformatic

642 processing was performed using DADA2 as described in ref. ³⁴. Phylotypes (i.e., amplicon
643 sequence variants; ASVs) were identified at the 100% identity level. The ASV abundance tables
644 were rarefied at 5000 (bacteria via 16S rRNA gene), 1000 (protists via 18S rRNA gene) and 250
645 (invertebrates via 18S rRNA gene) sequences per sample, respectively, to ensure even sampling
646 depth within each belowground group of organisms. Protists are defined as all eukaryotic taxa,
647 except fungi, invertebrates (Metazoa), and vascular plants (Streptophyta). The richness of fungi
648 was determined via 18S-full ITS amplicon sequencing using the primers ITS9mun/ITS4ngsUni
649 and PacBio Sequel II platform in the University of Tartu, Estonia, as described in ref. ³⁵.
650 Bioinformatic processing was performed as explained above. The fungi ASVs abundance table
651 was rarefied at 1000 sequences per sample.

652

653 *Rarefaction cross-validation*

654 Rarefaction curves for the richness of bacteria, fungi, protists and invertebrates are available in
655 Supplementary Fig. 15. We also ensured that our choice of rarefaction level, taken to maximize
656 the number of samples in our study, did not influence our results. In particular, we found highly
657 statistically significant correlations between the richness of soil bacteria (rarefied at 5000 vs.
658 10,000 sequences/sample; Pearson's $r = 0.997$; $P < 0.001$), fungi (rarefied at 1,000 vs. 5,000
659 sequences/sample; Pearson's $r = 0.964$; $P < 0.001$), protists (rarefied at 1000 vs. 5,000
660 sequences/sample; Pearson's $r = 0.961$; $P < 0.001$) and invertebrates (rarefied at 250 vs. 1,000
661 sequences/sample; Pearson's $r = 0.947$; $P < 0.001$), for a subset of samples wherein high numbers
662 of sequences were available. These analyses support that our choice of rarefaction level did not
663 affect our results.

664

665 **Soil functions and ecosystem services**

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

677 The total contents of soil organic C and N were measured using a CN analyser (C/N
678 Flash EA 112 Series-Leco Truspec) after removing inorganic carbon. The total contents of P, Cu,
679 Mg, Zn, Fe, K, and Mn in the soil were determined, after nitric-perchloric acid digestion, using
680 an ICP-OES spectrometer (ICAP 6500 DUO; Thermo-Scientific, Waltham, MA, USA). The
681 activities of β -glucosidase (BG - starch degradation), N-Acetylglucosaminidase (NAG - chitin
682 degradation) and phosphatase (PHOS - P mineralization) were measured from 1 g of soil by
683 fluorometry as described in ref. ³⁶. We used the MicroRespTM technique to determine potential
684 soil respiration (basal) and the substrate-induced respiration using lignin and water as substrates
685 and measured absorbance at 570 nm after the 5 h incubation period (25°C and 60% water holding
686 capacity)³⁷.

687 The biomass of bacteria, fungi and arbuscular mycorrhizal fungi were measured using
688 microbial phospholipid fatty acids (PLFAs) according to ref.³⁸. The extracted PLFA samples
689 were quantified using an Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA,
690 USA). The peaks were identified using a Sherlock Microbial Identification System (MIDI, Inc.,
691 Newark, NJ, USA). Total biomass of fungi and bacteria were determined as the sum of bacterial
692 and fungal PLFAs, respectively. 16:1w5c was used as an indicator of the biomass of arbuscular
693 mycorrhizal fungi (AMF).

694 The abundance of the antibiotic resistance genes (ARGs) was determined using the high
695 throughput quantitative PCR³⁹ from 365 soil samples on the Wafergen SmartChip Real-Time
696 PCR system (Fremont, CA, USA). We quantified the relative abundance of 285 ARGs. This
697 method has been widely adopted to investigate the abundance of ARGs in various environmental
698 settings³⁹. Information on the primer sets used, and the type and antibiotic resistance mechanism
699 behind every ARG is available in Supplementary Table 8. We followed the PCR protocol
700 described in ref⁴⁰. In brief, the 100 nl reactions contained SensiMix SYBR No-ROX reagent
701 (Bioline, London, UK), primers, DNA, and sterilized water. We included three analytical
702 replicates for each soil sample and qPCR run. We used 5184-nanowell Smartchips (Wafergen,
703 Fremont, CA, USA) including 286 primer sets (Supplementary Table 8), calibrator (as 16S
704 rRNA gene for the same DNA sample for all the chips), and negative control. Amplification
705 conditions were 95 °C for 10 min, followed by 40 cycles of 95 °C for 30 s and 60 °C for 30 s.
706 We used the $2^{-\Delta CT}$ method, where $\Delta CT = (CT_{\text{detected ARGs}} - CT_{16S \text{ rRNA gene}})$, to calculate the
707 relative abundances of ARGs compared to the 16S rRNA gene in each soil sample according to a
708 comparative C_T method⁴⁰. The abundance of ARGs was determined as the sum of the abundance
709 of all ARGs retrieved at each sample. ARG control is determined as the inversed of the
710 abundance of total ARGs (-1 x ARG abundance) as done in ref¹⁶.

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

715

716 **Environmental factors**

717 Climatic information (mean annual temperature, seasonal temperature, diurnal temperature
718 range, precipitation, precipitation seasonality and potential evapotranspiration) were extracted
719 from the WorldClim database v2 (<https://www.worldclim.org/data/index.html>). As expected, at a
720 global scale, cross-sites mean annual precipitation and temperature were highly correlated with
721 other metrics such as land surface moisture (Pearson $r = 0.28$; $P = 0.002$; Landsat 30m
722 resolution), and recent air temperature (Pearson $r = 0.79$; $P < 0.001$; 1km resolution; within
723 sampling dates) and soil mean annual temperature (Pearson $r = 0.968$; $P < 0.001$; 1km
724 resolution), respectively. We used mean annual values because they represent the long-term
725 availability of water and levels of temperature, which are more representative and commonly
726 used at a global scale. We used NDVI (Normalized Difference Vegetation Index), from Landsat
727 satellite imagery (Landsat 8 –available from 2013–; 30m resolution –same resolution as our
728 sites) (<https://landsat.gsfc.nasa.gov>), as our proxy of net primary productivity (NPP). NDVI
729 provides a global measure of the “greenness” of vegetation across Earth’s landscapes for a given
730 composite period. NDVI data were obtained from 2013 to 2020. Plant richness (number of
731 perennial plant species) was determined in the field using three transects across 30 m x 30 m
732 plots. Vegetation (forest *cf.* no forest) and land use (natural *cf.* urban greenspaces) were

733 determined in the field. Urban greenspaces included urban forests and gardens as defined in
734 Supplementary Table 1 (see also Supplementary Table 2 for site-level information). Soil pH and
735 electrical conductivity were measured in all the soil samples with a pH meter in a 1: 2.5
736 mass:volume soil and water suspension. Sand content was also determined in the laboratory
737 using a hydrometer method.

738

739 **Statistical analyses**

740 **Patterns in moss cover distribution**

741 *Permanova*

742 We first summarized the difference in moss cover across the globe using a histogram and
743 examining potential differences in moss, plant and bare soil cover across continents (Africa,
744 Australia, South America, North America, Antarctica, Europe, Asia) and ecosystem types
745 (Supplementary Table 2) using permuted, non-metric multivariate analysis of variance
746 (PERMANOVA).

747

748 *Structural Equation Modelling*

749 We then used Structural Equation Model (SEM)⁴² to explore the direct and indirect effects of
750 climate (potential evapotranspiration [PET], mean annual precipitation [MAP], precipitation
751 seasonality [PSEA], temperature seasonality [TSEA], mean diurnal range [MDR], mean annual
752 temperature [MAT]), vascular vegetation (vascular plant cover, vascular plant richness (our
753 surrogate of diversity), NPP, whether it is forest [value = 1] or non-forest [value = 0]), plot-level
754 soil information (soil C:N ratio, soil C, pH, salinity, texture [sand content]) and land use type
755 (urban greenspaces *cf.* natural) on moss cover across the globe (Supplementary Fig. 3 for *a priori*
756 model and rationale on selected pathways). Elevation (m) and average spatial dissimilarity
757 (space) were also included in our model to account for spatial variability. Space was determined
758 as the average between-plot distance from a Euclidean distance matrix including latitude,
759 longitude (sine) and longitude (cosine; decimal degrees) aiming to account for any potential
760 influence of spatial autocorrelation. Plot-level soil information was based on three soil composite
761 samples collected at each site. We included this information to investigate whether moss cover
762 changes across sites with contrasting levels of soil organic matter (soil C), C:N ratios, texture,
763 pH and salinity.

764 Structural equation modelling allowed us to test hypothesized relationships among
765 predictors and moss cover based on an *a priori* model that constructs pathways among model
766 terms based on prior knowledge (Supplementary Fig. 3). Models showed a very good goodness
767 of fit as measured using χ^2 ($\chi^2/df = 1.45$; $df = 5$), Root Mean Error of Approximation (RMSEA =
768 0.06; $P = 0.36$) and Bollen-Stine Bootstrap ($P = 0.20$). In addition, we calculated the
769 standardized total effects of each explanatory variable to show its total effect. Analyses were
770 performed using AMOS 22 (IBM, Chicago, IL, USA) software.

771

772 **The contribution of moss and vascular plants to multiple ecosystem services**

773 *Quantifying the contribution of moss and vascular plants to ecosystem services*

774 We calculated the relative interaction index (RII)¹⁷ for each site to assess the influence of mosses
775 and vascular plants on 24 soil biodiversity and functional attributes compared with that from bare
776 soil. Previous independent studies have used the RII index to test the relative effects of plants on
777 soil attributes across climates and vegetation types including local studies of mosses⁴³.

778 The contribution of moss and vascular plants to multiple ecosystem services was
779 determined as the average RII values based on 24 soil attributes (RII moss and vascular plant
780 multiservices) (Supplementary Table 5). The RII of each soil attribute (Supplementary Table 6
781 was calculated as $RII = (X_m - X_b) / (X_m + X_b)$, where X is the value of a specific ecological
782 attributes, and X_m and X_b represent the values under the moss (or vascular plant) and in the bare
783 soil, respectively. We would like to highlight that the contribution of moss and vascular plants to
784 multiple ecosystem services was similar when this index was calculated as the average of 24
785 individual soil attribute RII (used in the main text) and when using the average of eight RII
786 ecosystem services (biodiversity preservation, carbon sequestration, nutrient cycling, plant
787 pathogen control, antibiotic resistance control, organic matter decomposition, microbial habitat
788 and biomass of symbiotic organisms) for both plants (Pearson's $r = 0.88$; $P < 0.0001$) and mosses
789 (Pearson's $r = 0.88$; $P < 0.0001$). We also analyzed the contribution of moss and vascular plants
790 to individual soil attributes (e.g., RII of soil C). The index is bounded by -1 and 1, with positive
791 values indicating greater levels of a given attribute with the soil beneath the moss (or vascular
792 plant) and *vice versa*. Soil pH, electrical conductivity and soil texture were not included as
793 services.

794
795 We calculated the mean and 95% confidence interval (CI) of the moss and vascular plant (v-
796 plants) contribution to ecosystem services (average RII values based on 24 soil attributes;
797 Supplementary Table 6), and also for each individual moss and plant relative interaction index
798 (e.g., RII for soil C) to determine the influence of the moss and plant on soils based on whether
799 the 95% CI crosses the zero line. We used a bootstrapping approach to calculate these 95% CI.

800
801 *Environmental drivers of the contribution of mosses to ecosystem services*
802 We used Random Forest (rfPermute package)⁴⁴ to investigate the relative importance of multiple
803 environmental factors in driving the distribution of moss contributions to ecosystem services
804 (average moss RII values based on 24 soil attributes; Supplementary Table 6). By doing so, we
805 aim to determine under which environmental conditions, moss provide the largest contribution to
806 multiple ecosystem services. Environmental predictors included moss cover, main taxa (each
807 individual moss family representing more than 5% in all sites [value = 1] vs. others [value = 0])
808 and traits (main reported life history, growth forms and life strategies as described above),
809 vegetation (plant cover, richness, NPP, forest [value = 1] vs. non-forest [value = 0]) and land use
810 type (urban greenspaces [value = 1] vs. natural [value = 0]), climate (potential evapotranspiration
811 [PET], mean annual precipitation [MAP], precipitation seasonality [PSEA], temperature
812 seasonality [TSEA], mean diurnal range [MDR], mean annual temperature [MAT]), plot-level
813 soil information (plot-average of soil C, C:N ratio, pH, salinity, texture), and space (as defined
814 above) and elevation. Random Forest is known to be a robust approach when working with
815 continuous and categorical variables. We included plot-level information (based on the three soil
816 composite samples collected at each site) to investigate whether the contribution of mosses to
817 nature change across sites with contrasting levels of soil organic matter (soil C), C:N ratios,
818 texture, pH and salinities.

819 We then used Spearman correlations to further investigate the relationships between
820 environmental factors (climate, land use type, soil, and plant and moss characteristics) and the
821 relative interaction indices (RII) of soil mosses on 24 individual soil attributes (Supplementary
822 Table 6). Correlation analyses were conducted in SPSS 26.0 (IBM, Chicago, IL). Figures were
823 created using 'ggplot2' packages and linear models fitted in R version 3.4.1. Spearman rank

824 correlations are a non-parametric approach which does not require normality of data or
825 homogeneity of variances and measures the strength and direction of the association between
826 two ranked variables. In addition, unlike Pearson correlations, Spearman rank correlations can be
827 used to associate two variables regardless of whether they are ordinal, interval or ratio.

828

829 *Mapping the global distribution of moss cover*

830 To predict the extent of moss cover and the contribution of moss to multiservices globally,
831 machine learning Random Forest regression analysis⁴⁵ was used with the 15 variables: Urban
832 land cover [0/1], forest [0/1], Plant cover, Net primary productivity [NDVI], C in soil, pH, C-N,
833 sand percentage, mean annual temperature, mean annual precipitation, Mean Diurnal Range,
834 Precipitation seasonality, Temperature seasonality, Potential evapotranspiration and elevation.
835 These predictors were selected based on the availability of global maps for forest and urban
836 cover types (MCD12Q1 V6 product (<https://doi.org/10.5067/MODIS/MCD12Q1.006>,
837 accessed on 4 June 2021) for 2016 derived from the IGB classification⁴⁶, plant cover
838 (<https://land.copernicus.eu/global/products/fcover>,
839 accessed on 4 June 2021), climate⁴⁷, and soil
839 information (<https://soilgrids.org>)⁴⁸ needed to map the distribution of soil mosses. We could use
840 data from all 123 sites because: (1) moss cover data were standardized globally; (2) moss cover
841 was highly correlated with key environmental factors at the global scale (Fig. 2D; Supplementary
842 Fig. 6); (3) the number of sites provided robust statistical models ($R^2 = 0.86$), given the number
843 of environmental factors considered and; (4) the large gradient in environmental conditions in
844 our global dataset covers an extensive part of the large-scale environmental variability of the
845 planet. For example, across our survey area, mean annual temperature ranged between -6.7 to
846 26.1°C, and soil pH and sand content from 4 to 9 and 16 to 95%, respectively. Further, we
847 excluded from our map (white areas) locations where environmental conditions were under-
848 represented in our survey (using the Mahalanobis approach described in Methods;
849 Supplementary Fig. 7).

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

862

863 *Identifying locations with unique and overlapping contributions of vascular plants and mosses to* 864 *multiservices*

865 We calculated a bivariate map based on the quantiles of two variables, moss multiservices and
866 vascular plant multiservices. This method⁵⁰ is used if the variables to be represented have a
867 geographic pattern or a strong correlation between the two variables. In summary, the map shows
868 the relationship between the two variables spatially located. For this analysis, we generated a

869 map to predict the contribution of vascular plants to multiservices worldwide similar to the
870 procedure for soil mosses.

871

872 **Data and materials availability**

873

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

877

878 **Methods-only references**

879

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Fig 1

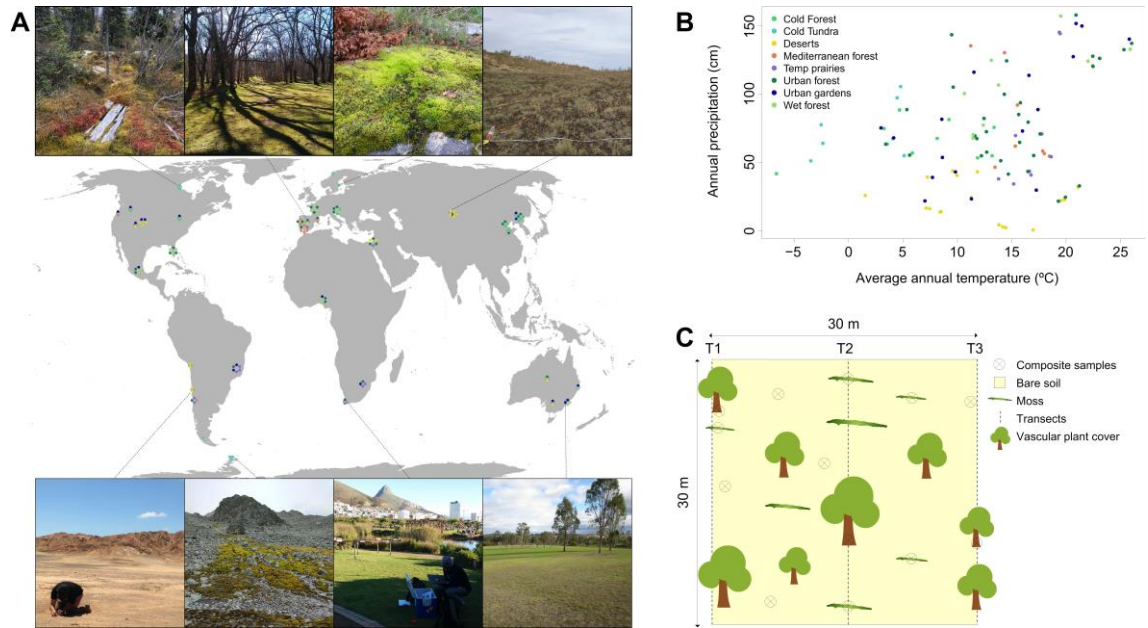


Fig. 2

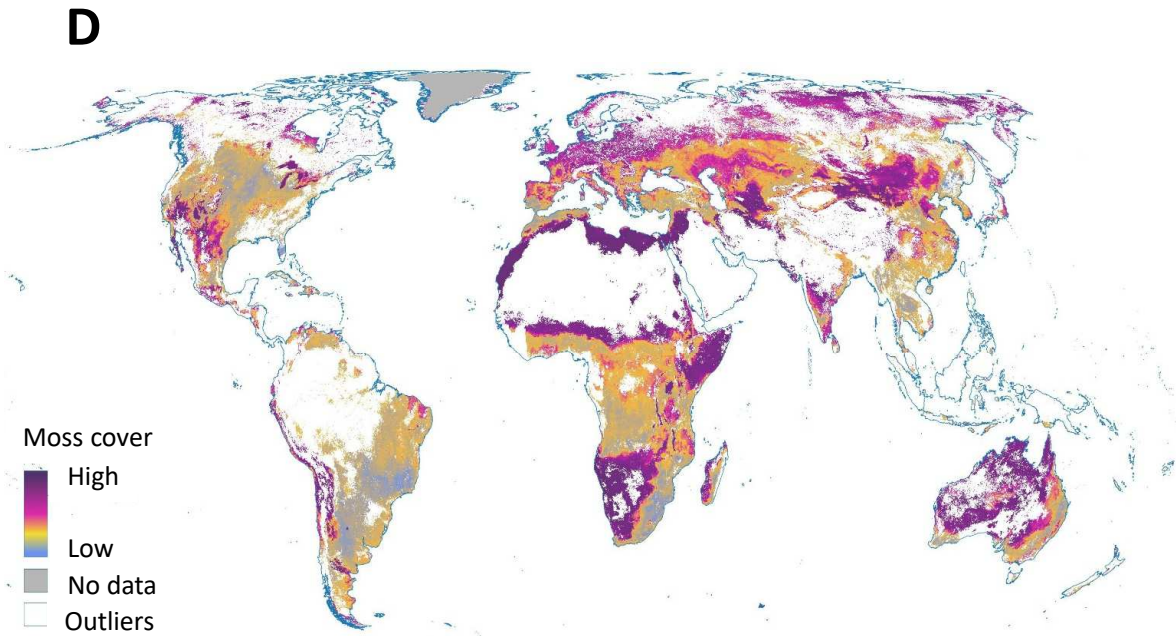
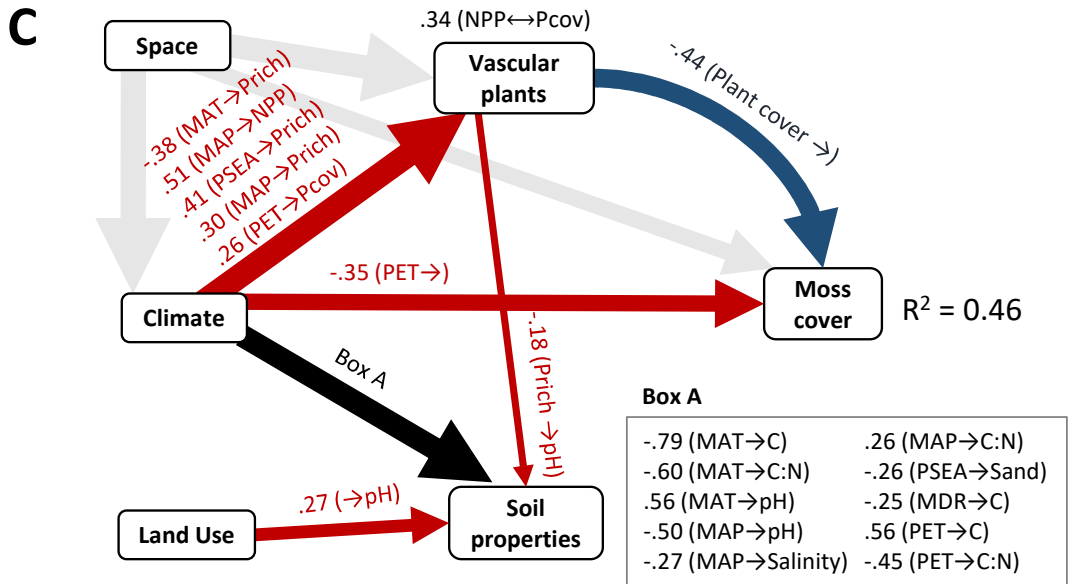
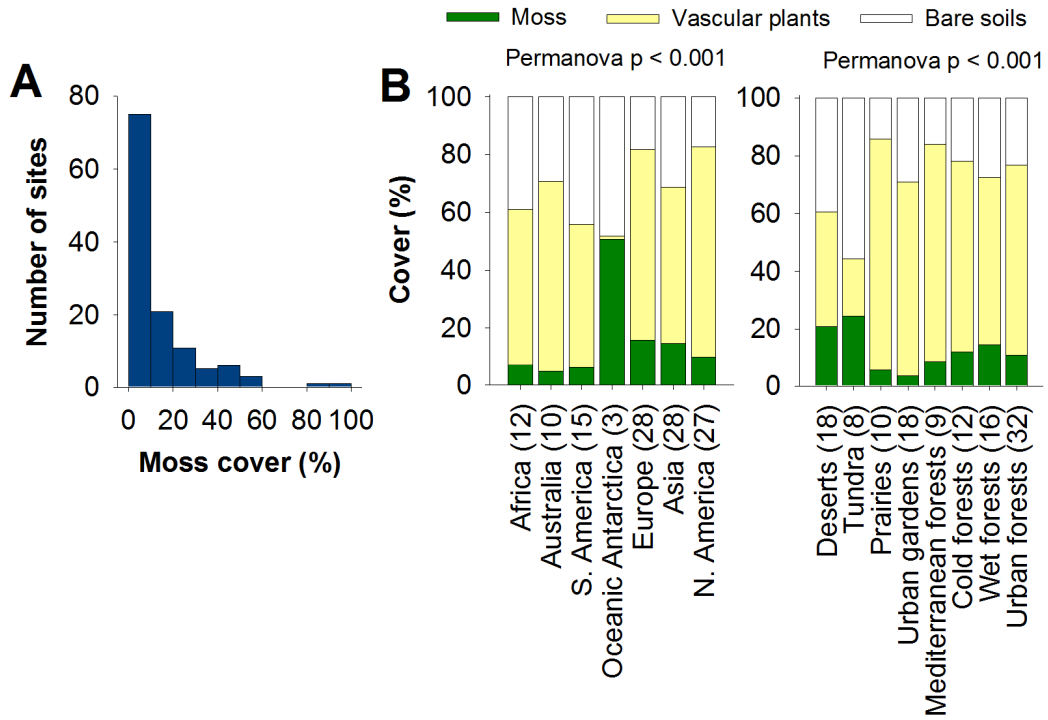


Fig. 3

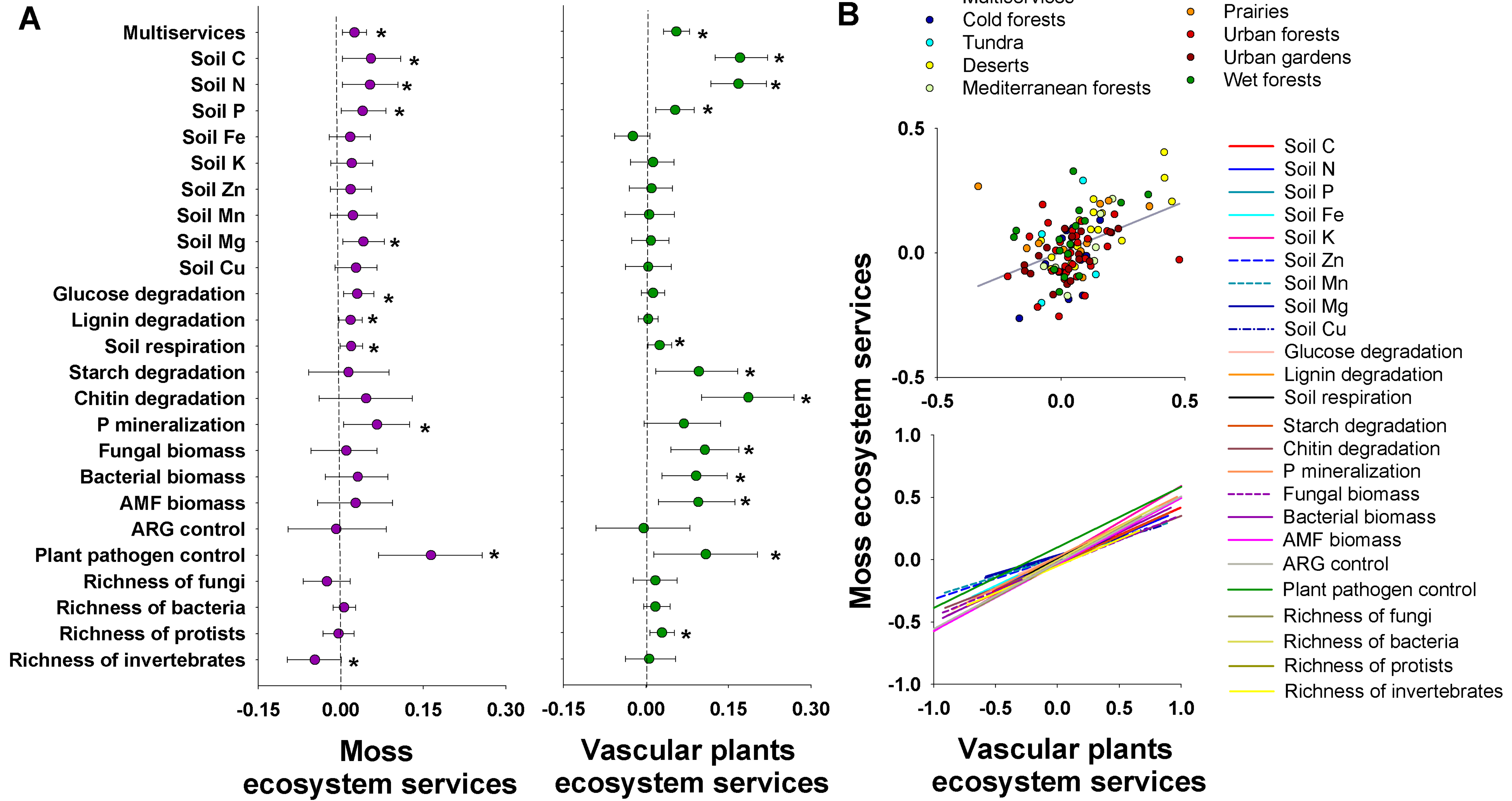


Fig.4

