Global hotspots for soil nature conservation 1

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Preprint submitted Springer Nature

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67 Abstract

68 Soils are the foundation of all terrestrial ecosystems ¹. However, unlike for plants and animals, 69 a global assessment of the hotspots for soil nature conservation is still lacking². This hampers 70 our ability to establish nature conservation priorities for the multiple dimensions supporting the 71 soil system: from soil biodiversity to ecosystem services. Here, we conducted a global field 72 survey including biodiversity (archaea, bacteria, fungi, protists, and invertebrates) and function 73 (critical for six ecosystem services) observations within 615 composite topsoil samples from a 74 standardized survey in all continents, to identify global hotspots for soil nature conservation. 75 We found that each of the different soil ecological dimensions (i.e., soil species richness [alpha 76 diversity, measured as ASVs], community dissimilarity, and ecosystem services) peaked in 77 contrasting regions of the planet, and were associated with different environmental factors. 78 Temperate ecosystems showed the highest species richness, while community dissimilarity 79 peaked in the tropics, and colder high-latitudinal ecosystems were identified as hotspots of 80 ecosystem services. These findings highlight the complexities of simultaneously protecting 81 multiple soil ecological dimensions. We further show that most of these hotspots are not 82 properly covered by protected areas (over 70%), and are vulnerable in the context of multiple 83 global change scenarios. This first global estimation of soil nature conservation priorities, 84 highlights the fundamental importance of accounting for the multidimensionality of soil 85 biodiversity and ecosystem services to conserve soils for future generations.

86 Main text:

Soils are essential to support terrestrial life on the planet ¹. They are home to diverse assemblages of organisms across all major lineages of life from bacteria to invertebrates, and provide multiple ecosystem services such as soil fertility, carbon (C) storage, waste decomposition, pest control, and water retention ^{3–5} that are critical for food production and human well-being ^{6–8}. However, soils are also highly vulnerable to anthropogenic disturbances such as climate change ^{9,10} and land use intensification (e.g., land-use change, pollution, and erosion ^{11,12}). For an adequate conservation of soils, it is critical to consider and protect the

94 multiple ecological dimensions supported by soils, from their biodiversity to the different 95 ecosystem services they support. A first step in this direction is identifying the global ecological 96 hotspots for soil nature conservation ¹³ to inform and guide policymakers and conservation 97 managers on how to extend nature conservation to the world belowground. Concurrently, 98 establishing and negotiating adequate global nature conservation policies and priorities (e.g., 99 the 2030 biodiversity targets ¹⁴) requires knowledge about the distribution of global 100 biodiversity, including identifying ecological hotspots². While these ecological hotspots were 101 established decades ago for plants and animals, this critical information for soil biodiversity 102 and ecosystem services does not exist and is therefore absent from current biodiversity 103 assessments ¹⁵. Recent developments in ecological modeling and soil macroecology have improved our understanding of the global distribution of multiple soil communities ¹⁶⁻²¹ and 104 105 their potential future trends ^{9,22}. These studies have found potential mismatches between 106 below- and aboveground biodiversity, suggesting that hotspots of plant diversity are poor proxies of belowground diversity ²³ and, therefore, are unlikely to provide sufficient protection 107 108 for life belowground. While this may be true, plant species richness, like the one found in the 109 tropics, is known to increase the diversity in soil organic matter compounds and, therefore, 110 provide resources for a diverse soil microbiological community ²⁴. This also opens the question 111 to if the hotspots of different soil ecological dimensions (e.g., diversity, community 112 composition, functions) coincide in space and how these are affected by global change, with recent studies pointing to diverging global patterns ²². Yet, many recent developments are 113 114 based on merged meta-analytical data, which are rarely measured using the same methods 115 or do not simultaneously consider multiple soil ecological dimensions in the same locations. 116 Unfortunately, we still lack globally standardized field surveys that explicitly consider the 117 ecological multidimensionality of soils that simultaneously capture information on multiple soil 118 taxonomic groups and ecosystem services, across a wide range of global environmental 119 conditions ²⁵. Closing these knowledge gaps is essential to inform the establishment of nature 120 conservation areas, steer management decisions, and set effective policy targets that address 121 the ecological conservation of soils.

122 Herein, we combined machine learning models with a standardized global field survey, 123 including 615 composite topsoil samples from all continents and climates (Supplementary 124 Fig.1) to estimate, for the first time, the extent, associated environmental factors, and climate 125 change vulnerabilities of the global hotspots of soil biodiversity and ecosystem services. Our 126 dataset is based on >11,000 individual standardized observations and including information 127 on 16 biodiversity and ecosystem service attributes (Methods; Supplementary Table 1). Our 128 study moved beyond the analysis of alpha diversity (here based on soil DNA amplicon 129 sequence variant, ASVs) and extended its scope to community dissimilarity (i.e., composition 130 heterogeneity, based on Jaccard distance from presence/absence data) of five soil groups of 131 organisms (archaea, bacteria, fungi, protists and invertebrates). Measuring the hotspots of 132 community dissimilarity and comparing them to the ones of alpha diversity allows us to identify 133 areas with high local diversity that, at the same time, contain unique communities. In addition, 134 to fully grasp the conservation potential of soil systems, soil functional properties related to six 135 key soil ecosystem services were assessed, including soil C storage (total soil organic C), 136 fertility (total nitrogen (N), phosphorus (P), potassium (K), and magnesium (Mg) contents; 137 terrestrial ecosystems in this study were not fertilized, and therefore, total nitrogen represents 138 the stocks of nitrogen in soil organic matter), organic matter decomposition (three enzymes 139 associated with starch and chitin degradation, and P mineralization), water retention (water-140 holding capacity), pest control (inverse of the proportion of soil-borne fungal phytopathogens), 141 and mutualism (i.e. plant-mycorrhizal mutualism, an ecological relationship between plants 142 and fungi that is beneficial to both partners, assessed as the proportion of mycorrhizal fungi). 143 We acknowledge that our study does not cover the entire environmental spectra found on 144 Earth, but it represents a large portion of the environmental variability found in the planet 145 (Supplementary Fig. 1). Locations showing environmental conditions under-represented in our 146 study were excluded from our spatial analyses (Figs. 1-3).

147 Our analyses revealed that the assessed soil biodiversity and ecosystem services variables 148 are associated with contrasting environmental factors at the global scale (Extended Data Figs. 149 1 and 2). For example, while soil pH was the main factor associated with alpha diversity of soil 150 fungi and bacteria, soil organic matter (soil C and N contents) was positively associated with 151 the alpha diversity of protists and invertebrates (Extended Data Figs. 2 and 3), and elevation 152 was positively correlated with the alpha diversity of archaea. In the case of the assessed 153 ecosystem services, soil pH was positively associated with soil C content, water retention and 154 pest control, whereas, temperature was associated with organic matter decomposition and 155 fertility, and precipitation seasonality with mutualism (Extended Data Figs. 2 and 3). Although 156 many of these environmental associations are well-described in the literature (e.g., ^{26,27}), the 157 fact that different soil ecological dimensions could be predicted by contrasting environmental 158 factors was much less clear due to the lack of standardized global field surveys. These 159 contrasting associations and environmental drivers explain the different global distributions 160 found for each ecological dimension and reveal that important trade-offs may exist when 161 considering nature conservation of multi-faceted soil systems. To further visualize these trade-162 offs, we used machine learning random forest spatial regression models together with 163 available current data and future projections for both climate and land-use change (2015-164 2070), to predict the distribution of soil biodiversity and ecosystem services and assess their 165 major drivers according to multiple future scenarios (shared socioeconomic pathways (SSP); 166 SSP1: global sustainability, SSP3: regional rivalry, SSP4: inequality, and SSP5: fossil-fueled 167 development ²⁸). We standardized each of these spatial distributions and used a Getis-Ord 168 Gi* spatial clustering algorithm to obtain a representation of the global hotspots (clusters of 169 statistically high values) for the modelled distribution of each single biodiversity and ecosystem 170 service variable. These were then aggregated into each soil ecological dimension (Fig. 1A, B, 171 and C). To further strength our conclusions we performed a comparison across multiple 172 methods (Supplementary Figs. 7 and 10) and an uncertainty assessment for the spatial 173 predictions (Supplementary Figs. 5, 11, 12 and 13). A rationale supporting the spatial analysis 174 from our standardized survey, and explaining the limitations of our approach, is available in 175 the Method section.

176 Further, we showed that different ecological dimensions for soil conservation peak in different 177 regions of Earth (Fig. 1A, B, C). Model fitness (measured as overall training R²) varied between 178 0.855 and 0.914 for alpha diversity and community dissimilarity (Supplementary Table 5) and 179 between 0.801 and 0.936 for ecosystem services (Supplementary Table 6). Hotspots of alpha 180 diversity tend to have a wider distribution across the world, peaking in temperate and 181 Mediterranean regions, as well as in alpine tundra (overall occupying between 30.9%, for 182 archaea, and 42.4%, for bacteria, of the world). However, hotspots of community dissimilarity 183 occur around two contrasting global conditions, tropical systems and drylands (overall 184 occupying between 35.7%, for Archaea, and 43.0%, for Fungi, of the world). For Fungi, our 185 results were further compared and validated with an independent dataset (Supplementary Fig. 186 6). While higher alpha diversity may intuitively imply a direct decrease in dissimilarity, directly 187 varying in tandem, our results show that at the global scale this is not the case (Supplementary 188 Table 15). Archaea showed the highest proportion of shared hotspot areas with 19%, with all 189 other groups obtaining less than 8% (alpha diversity and community dissimilarity for the same 190 taxa; Supplementary Table 3). Our findings further suggest the existence of important trade-191 offs in soil nature conservation priorities (Extended Data Fig. 3). For example, locations with 192 higher alpha diversity tend to be less dissimilar, and only a small proportion of locations were 193 found to support both high dissimilarity and alpha diversity (Fig. 1B). This proportion is smaller 194 for fungi (3.9%) and higher for Archaea (19.0%; Supplementary Table 2). Similarly, locations 195 with higher dissimilarity tend to have less soil C content, fertility, and higher proportion of plant 196 pathogens (Extended Data Fig. 3). Moreover, our global maps indicate that alpha diversity (Fig. 1A), community dissimilarity (Fig. 1B), and ecosystem services (Fig. 1C) have their 197 198 hotspots in mostly contrasting regions of the planet, existing only in a few locations supporting 199 high levels of more than one of these dimensions (0.1% of the evaluated areas in the world; 200 based on Fig. 1). This contrasts with results found for other biodiversity groups like plants and mammals e.g., 29,30 and supports recent findings of a mismatch between soil biodiversity and 201

other taxonomic groups (Supplementary Table 13; ²³) While globally, tropical and arid systems 202 203 were mostly classified as locations with relatively low alpha diversity across taxa, these areas 204 are hotspots for soil community dissimilarity, supporting the most unique soil community 205 assemblies (Fig. 1B). In the case of bacteria, for example, locations with high pH support a 206 higher richness (e.g., in temperate systems); however, these are always similar organisms 207 which thrive in neutral-alkaline soils. This suggests that, while local diversity in tropical 208 systems may be low (e.g., as a consequence of acidic soils), these environmentally 209 contrasting areas of the globe may harbor unique communities, which in turn may result in high gamma (regional) diversity. While this was already suggested in the past ^{16,22}, the present 210 211 study represents the first robust confirmation of this hypothesis.

212 Our results highlight the fact that preserving soils from a nature conservation perspective 213 requires a holistic approach that considers multiple soil ecological dimensions such as alpha 214 diversity, community dissimilarity, and ecosystem services in the context of a nature 215 conservation profile (Fig. 1D). Being able to position a given area within this soil nature 216 conservation profile allows to establish adequate conservation goals that effectively target the 217 preservation of soil communities and their effects on ecosystems ³¹. For example, an area that 218 falls into a community dissimilarity hotspot may focus on indicators and conservation goals to 219 track and prevent species losses, since these may be unique to its limits, while an area in an 220 ecosystem service hotspot may favor indicators that target ecosystem service supply. This 221 does not imply that conservation areas should not prioritize all soil ecological dimensions, but 222 rather that management strategies and conservation targets should be adjusted to the 223 ecological reality of each region and conservation area². Moreover, while local approaches 224 are still needed to refine the local distribution of these hotspots ³², these results also suggest 225 that no particular region can protect all dimensions of soil conservation, making a further 226 argument for global cooperation and for establishing global soil nature conservation targets.

227 Given the contrasting regions supporting the highest biodiversity and services, identifying 228 which ecological dimension is the most relevant for the conservation of soil ecological 229 conditions is not a simple task. Some ecosystems depend on a high alpha diversity while 230 others do not need such high levels of alpha diversity to properly function but rely on more 231 dissimilar soil communities (Fig. 1D; ³³). Conversely, while for microbial communities ³⁴, 232 functional redundancy driven by community composition may be more important than alpha 233 diversity per se, in general terms, ecosystems with lower alpha diversity are likely to be more 234 sensitive to ecosystem change ³⁵ and for that, more targeted conservation actions are 235 required. Although it is known that soil organisms play a crucial role in ecosystem service 236 supply ³⁶, it is not clear that it is biodiversity per se that governs this entire process. For 237 example, some specific ecosystem services may depend on the presence of only a few

species, such as specific components of the soil nitrogen cycle ³⁷, while others are the result 238 239 of the activity of many species with high levels of redundancy, such as soil respiration ³⁸. 240 Therefore, we defined priority areas for soil nature conservation as areas supporting relatively 241 high levels of either soil biodiversity or ecosystem services. We were then able to identify key 242 regions of the planet surpassing high thresholds of either biodiversity or ecosystem service 243 provision - the hotspots for soil nature conservation - (Fig. 2). Considering the areas with the 244 highest accumulation of soil biodiversity hotspots (top 5% of areas), it is possible to identify 245 tropical systems and substantial areas in North America, in Northern Europe, and in Asia as 246 having high priority for nature conservation (Fig. 2A). These areas maximize different 247 dimensions of soil ecology and may thus require integrative strategies, not only from a nature 248 conservation perspective but also considering the socio-economic appropriation of 249 belowground systems. To this respect, it is striking that ~50% of these global nature 250 conservation priority areas are not under any form of nature conservation, and that only ~10% 251 correspond to areas fully preserved (Fig. 2B). Since these global soil nature conservation 252 priority areas are the areas with the highest nature conservation relevance and given that 253 currently soils do not have any specific nature conservation targets, this is a worrisome state 254 for the conservation of soil biodiversity worldwide². This situation is also observed if we 255 consider other thresholds for the soil nature conservation potential (Fig. 2B). While soil 256 conservation may not be able to maximize all ecological dimensions at the same time, and 257 each region may have different specificities with specific research being required, a number 258 of actions may be considered. These include nature-based solutions in land management for 259 enhancing ecosystem services ³⁹, landscape-level actions like the preservation of permanent 260 forest and natural coverage in the surrounding of managed systems ⁴⁰, or nature-based 261 solutions focused on restoring or improving soil functional outputs ⁴¹. Our work provides key 262 information for regional and continental decision-makers to develop nature protection goals 263 that specifically target soil systems and biodiversity, including identifying areas with high 264 potential to establish soil-based nature conservation areas.

265 In the context of climate and land-use change, nature conservation areas and targets will need 266 to adapt to new conditions and also focus on mitigating potential impacts ^{42–44}. Thus, focusing 267 on the global soil nature conservation priority areas (top 5%), we conducted an additional 268 analysis to predict the future changes in hotspots according to four shared socio-economic 269 pathways (Fig. 3; 2015-2070). Our projections highlight the fact that the soil nature 270 conservation hotspots will change as a result of climate and land-use change linked to 271 substantial declines in both alpha diversity and ecosystem services. Globally, across 272 scenarios, net differences between 2015-2070 range from 1.5% net gains in SSP3 and -12.2% 273 net losses in SSP5. In most cases these net changes actually hide substantial losses of 274 current soil nature conservation priority areas with 7.1% (SSP4) to 17.5% (SSP5) of current 275 areas being lost globally across different future scenarios (Supplementary Table 7). Our 276 results reveal that most of the net area losses are related to declines in ecosystem services, 277 particularly C stocks (average loss across scenarios = -6.8%) and mutualism (-3.8%) and litter 278 decomposition (-3.6%), and in alpha diversity of specific groups, particularly invertebrates (-279 2.6%), fungi (-1.3%) and archaea (-1.1%). Our projections also show that new areas will 280 emerge as key areas for soil nature conservation across the world, corresponding to 281 expansions ranging from 5.3% in SSP5 (relative to the current area) to 9.5% in SSP3. 282 Surprisingly, scenarios that consider higher challenges for adaptation to climate change 283 motivated by higher regional income inequality and rivalry (SSP3 and SSP4; ⁴⁵), also show 284 the most positive effects for maintaining or expanding current nature conservation priorities 285 for soils, particularly in Africa and South America (Fig. 3). Overall, these positive effects are 286 mostly expected in the global south, with systematic negative effects in the global north across 287 scenarios. In fact, the only scenario where the global north has slight net gains (0.3-2.0%) 288 corresponds to the so-called "sustainability scenario" (SSP1). Nevertheless, in this scenario, 289 most of the rest of the world shows important net losses (-5.7% in Africa and -5.9% in Asia 290 Pacific) or just mild net gains (0.8% in South America) due to expected increases in global 291 economic development (Fig. 3). This is even more worrisome when considering recent reports 292 that show that 30% of the population across tropical countries are highly dependent on nature 293 ⁴⁶. Across all regions, the fossil-fueled economy scenario (SSP5) produces the strongest net 294 losses, with regions losing priority areas from -5.9%, for Asia-Pacific, to -31.8%, in the case of 295 North America (with most of these losses being driven by decreases in ecosystem services). 296 Furthermore, our results suggest that the current simplistic view on carbon-based targets 297 provides little protection for all soil ecological dimensions. In fact, the sustainability scenario 298 shows an overall global improvement in ecosystem services, with soil C leading these 299 improvements but with clear losses in alpha diversity. Together, these results indicate that 300 hotspots of soil biodiversity and ecosystem services are highly threatened by future climatic 301 and land-use changes, and stress the need for immediate protection of these locations. Our 302 findings also suggest that these hotspots might move in the future, with current sanctuaries of 303 soil biodiversity being subject to degradation.

In summary, based on the largest global standardized survey, including sixteen biodiversity and ecosystem service variables, our work provides the first estimate of the global hotspots for nature conservation of multiple soil ecological dimensions. Here, we identified critical unique areas for the conservation of soil biodiversity and ecosystem services at the global scale, with soil alpha diversity, dissimilarity, and services peaking in temperate, tropical, and boreal regions, respectively. While recent literature highlights the need for extending nature

conservation to ensure global sustainability and the preservation of biodiversity ⁴⁷, it also 310 311 underlines that this increased protection requires context-based solutions ⁴⁸. By unveiling 312 important trade-offs in soil biodiversity and ecosystem services, we also highlighted that no 313 particular region of the world could simultaneously protect all soil ecological dimensions. 314 Therefore, the conservation of soil biodiversity and ecosystem services requires an integrated 315 approach that probably should not focus on locally maximizing all ecological dimensions at 316 the same time. Also, the fact that we found that these three ecological dimensions do not 317 necessarily match in terms of their spatial hotspots also showed the complexity of soil 318 ecosystems and highlighted the difficulty that land managers and policymakers face when 319 designing soil conservation measures. Nevertheless, we also showed that these nature 320 conservation priority areas are currently highly unprotected, with less than ~10% of these 321 locations under adequate conservation status. We acknowledge that our study is just a first 322 step towards understanding and mapping the global hotspots of soil nature conservation and 323 that high-resolution monitoring systems and multiple time periods are needed to better guide 324 regional conservation and policy options². Still, our work suggests that current priority areas 325 of soil nature conservation are vulnerable to global change drivers in all future scenarios 326 considered, and stresses the need for immediate nature conservation targeting and protection 327 of these regions. This novel information and indicators should enable governments and 328 decision-makers to set soil nature conservation as a priority in the context of the 2030 329 Biodiversity Targets negotiations, paving the way for a more integrative view of nature.

330 Author contributions

331 C.A.G. and M.D-B. developed the original idea of the analyses presented in the manuscript. 332 M.D.-B. designed the field study and wrote the grant that funded the work. Field data were 333 collected by M.B., S.A., F.D.A., A.R.B., J.L.-B., A.d.I.R., J.D., T.G., J.G.I., Y-R.L., T.P.M., S.M., 334 M.A.M-M., A.M., T.U.N., G.F.P-B., C.P., J.P.V., A.Re., A.R., A.L.T., C.T-D., P.T., L.W., J.W., 335 E.Z., X.Z., X-Q. Z. and M.D-B. Lab analyses were done by M.D-B., H.C., F.B., J.L.M., S.P. 336 and L.T. Statistical analyses, mapping and ecological modelling was done by C.A.G., M.D-B. 337 and M.B.. Bioinformatic analyses were done by B.S. and J-T.W. The manuscript was written 338 by C.A.G. and M.D-B., edited by N.E. and D.E., with contributions from all co-authors.

339 Data and code availability

340 All the materials, raw data, and protocols used in the article are available upon request and 341 all is be made without restriction. and data publicly available in: 342 10.6084/m9.figshare.20221713

343 Competing financial interests

344 The authors declare no conflict of interest.

345 Acknowledgements

346 We thank all the researchers involved in the collection of field data. This project received 347 funding from the British Ecological Society (agreement nº LRA17\1193; MUSGONET). C.G., 348 N.E. were funded by DFG– FZT 118, 202548816; C.G. was supported by FCT-PTDC/BIA-349 CBI/2340/2020; M.D-B. was supported by RYC2018-025483-I, PID2020-115813RA-350 I00\MCIN/AEI/10.13039/501100011033, and P20_00879. M.A.M-M and S.A. was funded by 351 FONDECYT 1181034 and ANID-PIA-Anillo INACH ACT192057. J.D. and A.R. acknowledge 352 support from IF/00950/2014, 2020.03670.CEECIND, SFRH/BDP/108913/2015, and 353 UIDB/04004/2020. Y-R.L. was supported by 2662019PY010 from the FRFCU. L.T. was 354 supported by the ESF grant PRG632. F.B. and J.M. were supported by i-LINK+2018 355 (LINKA20069) funded by CSIC. C.T.D. was supported by the Grupo de Biodibersidad & 356 Cambio Global UBB - GI 170509/EF. C.P. was supported by the EU H2020 grant agreement 357 No 101000224. H.C. was supported by NSFC32101335, FRFCU2412021QD014), and 358 CPSF2021M690589. JPV was supported by DST (DST/INT/SL/P-31/2021) SERB 359 (EEQ/2021/001083) and BHU-IoE (6031).

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464 List of figures:

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465 Fig. 1 Current distribution of global soil ecological hotspots. The proportion of land occupied by hotspots 466 of alpha diversity (A), community dissimilarity (B) and ecosystem services (C) (Supplementary Table 2; 467 Extended Data Fig. 4 and 5). The top row corresponds to the proportion of global area occupied by 468 single taxa (A, B) or ecosystem services (C), and the bottom row to the global representation of 469 accumulated hotspots across taxa (A, B) or ecosystem services (C). Together, these three soil 470 ecological dimensions create a soil nature conservation profile where both areas that maximize a given 471 dimension and areas that allow for preserving a combination of global soil biodiversity hotspots are 472 identified (D). Grey areas correspond to areas that were not assessed during calculation due to high 473 uncertainty and insufficient environmental coverage (corresponding to 38.4% of the terrestrial world; 474 Supplementary Figure 5). A further estimation of spatial uncertainty for each dimension considered is 475 given in Supplementary Figures 12 and 13.

476

Fig. 2 Current distribution of the global soil nature conservation priority areas. Spatial representation of
the top 5%, 10%, 20%, and 30% areas with the highest accumulation of soil biodiversity and ecosystem
services hotspots (A), and the proportion of those areas that are under some form of nature
conservation regime (B). Grey areas correspond to areas that were not assessed during calculation.

481

482 Fig. 3 Expected changes (2015-2070) in the total area of soil nature conservation priorities (top 5%)
483 according to 4 different future shared socio-economic pathways (SSP1, SSP3, SSP4, and SSP5 ²⁸).

- 484 ECA: Europe and Central Asia, NMA: North and MesoAmerica, SA: South America, AP: Asia-Pacific,
- 485 Af: Africa. Light grey areas correspond to areas that were not assessed during calculation.

486 487

488 Methods

489

490 A global standardized survey to investigate topsoil biodiversity and function

491 We used composite topsoil samples from global field surveys which were conducted between 492 2016-2019 following standardized field protocols. This global field survey includes 151 493 locations from all continents and 23 countries, from which 615 composite topsoil samples were 494 collected, providing a large representation of all climatic and vegetation biomes in the planet 495 (Supplementary Fig. 1). The locations of the soil samples was not established following a 496 random protocol but rather were selected taking into account the local representativeness of 497 the vegetation within the ecosystem types sampled. In global terms, the approach aimed to 498 include as much climatic and edaphic variability as possible given the constraints of such a 499 sampling scheme. Between three and five composite soil (top ~0-10cm) samples (from 5-10 500 soil cores) were collected in these locations (ranging between 0.09-0.25 ha) following the 501 protocol described in Maestre et al. (2012). By including multiple composite samples within 502 each location, we aimed to account for within-location heterogeneity variation in soil 503 properties, biodiversity and services. We focused on the topsoils, because they are known to 504 hold the largest portion of soil biodiversity, and constitute the critical zone supporting key soil 505 processes from OM decomposition to plant-soil interactions. A portion of these soils was 506 frozen (-20 °C) after sampling for molecular analyses, while another portion was air-dried and 507 used for determining soil properties. We recognize that while our dataset provides a guite 508 complete coverage of global environmental conditions, an increase of sampling locations in 509 less represented regions of the globe would increase the strength of the study. To this respect, 510 we aimed at adequately representing the spatial limitations of our study by eliminating and 511 masking out all the regions that were poorly represented (Supplementary Figure 5). It is also 512 important to mention that reaching this spatial representation is not a trivial endeavor with 513 several logistic limitations (e.g., absence of local resources for sample preservation and 514 consequent material degradation; ²⁵), and overshadowed by war and current transport 515 embargos. These issues disproportionally affect these underrepresented regions and result in 516 important gaps in Africa South-East Asia. Dataset and available here: 517 figshare.com/s/fb33c5a79f cee29e70dc

518 Soil biodiversity

519 The alpha diversity (corresponding to the number of phylotypes) and community dissimilarity 520 (averaged Jaccard distance across samples from presence/absence matrices to account for 521 dissimilarity in phylotypes, measured as ASVs, rather than in their proportions) of archaea, 522 bacteria, fungi, protists and invertebrates was determined using amplicon sequencing 523 technology (Illumina Miseq platform) following the protocol in Delgado-Baquerizo et al. (2019). 524 Both these measurements are critical to understand the nature and conservation potential of 525 specific areas. While alpha diversity refers to the number of species (or ASVs in this case) 526 contained in a particular location, typically seen as priority areas for nature conservation, 527 community dissimilarity refers to the uniqueness of the community, signaling the presence of 528 specific species that are not common elsewhere. The later also represents a critical aspect for 529 the selection of new conservation areas ⁴⁹. Soil DNA was extracted using the Powersoil® DNA 530 Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's 531 instructions. A portion of the bacterial/archaeal 16S and eukaryotic 18S rRNA genes were 532 sequenced using the 515F/806R and Euk1391f/EukBr primer sets 50-52, respectively.

533 Bioinformatics processing was performed using a combination of QIIME ⁵³, USEARCH ⁵⁴ and 534 UNOISE3 55.56. Phylotypes (i.e. Amplicon sequence variant; ASVs) were identified at the 100% identity level. The ASV abundance tables were rarefied at 5000 (bacteria via 16S rRNA gene), 535 536 100 (archaea via 16S rRNA gene), 2000 (fungi via 18S rRNA gene), 1000 (protists via 18S 537 rRNA gene), and 250 (invertebrates via 18S rRNA gene) sequences/sample, respectively, to 538 ensure even sampling depth within each belowground group of organisms. Protists are defined 539 as all eukaryotic taxa, except fungi, invertebrates (Metazoa) and vascular plants 540 (Streptophyta). Note that not all samples passed our rarefaction cut-off. The total number of 541 samples included in each soil group is available in Supplementary Table 2.

542 Library preparation and Sequencing

543 Triplicate PCR reactions were performed for each of the extracted DNA samples, and we 544 included and sequenced multiple negative controls per plate to check for possible 545 contamination. Each 25µl PCR reaction contained: 12.5µl of Promega GoTaq Hot Start 546 Colorless Master Mix; 0.5 µl of each barcoded primer (bacterial 16S, 515F [5-547 GTGCCAGCMGCCGCGGTAA-37 and 806R [5'-GGACTACHVGGGTWTCTAAT-37 OR 548 eukaryotic 18S, Euk1391f (5'-GTACACCGCCCGTC-3') and EukBr (5'-549 TGATCCTTCTGCAGGTTCACCTAC-3'); 10.5 µl water; 1 µl of template DNA. 'Fusion' primers 550 also included Illumina adapters and 12-bp barcodes to enable multiplexed sequencing. PCR 551 conditions for bacterial 16S rDNA amplifications were 94°C for 3min; 35 cycles of 94°C for 552 45s, 50°C for 60s, 72°C for 90s; 72°C for 5 min. PCR conditions for eukaryotic 18S rDNA 553 amplifications were 94°C for 3 min; 35 cycles of 94°C for 45s, 57°C for 60s, 72°C for 90s; 72°C 554 for 10 min. PCR products were cleaned with the MoBio Ultra Clean PCR Clean-Up Kit. Next, 555 we performed PCR-mediated Nextera barcode ligation following the manufacturer's 556 instructions, adding unique barcodes onto amplicons, to allow for multiplexed sequencing. 557 Samples were normalized with the SequalPrep Normalization Plate Kit (Invitrogen) prior to 558 sequencing on the Illumina MiSeq platform.

559 DNA was first cleaned up using AMPure Xp beads (Beckman Coulter, California, USA) and 560 then quantified using the automated fluorescence-based PicoGreen assay (Invitrogen, 561 Massachusetts, USA). The cleaned DNA was normalized to 1.5 ng/ul and a total of 7 ng of the 562 input DNA was used for each amplicon PCR reaction. Illumina's instruction does not 563 recommend pooled three PCRs (which shouldn't be considered as technical replicates), and 564 one PCR reaction was performed per amplicon. While to minimize the PCR bias in the 565 sequencing, the number of PCR cycles was reduced to 25. In detail, the PCR conditions for 566 bacterial 16S rDNA amplification are: 95 °C for 3 min, 25 cycles of 95 °C for 30 sec, 55 °C for 567 30 sec, 72 °C for 30 sec, 72 °C for 5 min then hold at 4 °C; and PCR conditions for eukaryotes 568 18S rDNA amplification is: 94 °C for 5 min, 30 cycles of 94 °C for 30 sec, 55 °C for 30 sec, 72 569 °C for 30 sec, 72 °C for 5 min then hold at 4 °C. The Illumina forward overhang (5'-570 TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-3') and reverse overhang (5'-571 GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-3') adapters were included in the 572 amplicon PCR. Each sample was barcoded with two 8 base indices using the Illumina Nextera 573 XT Index Kit. The 15 ul reaction system was prepared with KAPA HotStart ReadyMix Kit 574 (Merck KGaA, Darmstadt, Germany). A ZymoBIOMICS Microbial Community DNA Standard 575 was used as a positive control together with the samples to assess the bias in PCR. Molecular 576 analysis of the full-length ITS region for fungi was performed using ITS9mun/ITS4ngsUni 577 primer sets and PacBio third-generation sequencing as described in ⁵⁷.Our sequencing run 578 yielded 3861042 fungal sequences (18s), 534286 invertebrate sequences (18s), 2388020

579 protist sequences (18s), 8901512 bacterial sequences (16s), and 168749 archaeal sequences 580 (16s).

581 <u>Bioinformatics</u>

582 Bioinformatic processing was performed using a combination of QIIME, USEARCH and 583 UNOISE. Briefly, data was demultiplexed and primers were trimmed before further analyses. 584 Default parameters were followed in USEARCH pipeline, except for the bases with a quality 585 score lower than 20 were end-trimmed from the forward/reverse primer reads to minimize the 586 mismatch in merging and to maximize the portion of successful mergers. A maximum of 587 expected error (ee) was set as 1.0 for the merged reads quality filtering using USEARCH 588 (Edgar 2010). zOTUs (or Amplicon Sequence Variant) were gained by denoising (error-589 correction) the dereplicated merged reads using unoise3 (Edgar 2016). Representative 590 sequences of ASVs were annotated against the Silva database (Quast et al. 2012) in QIIME 591 (Caporaso et al. 2010) using UCLUST ⁵⁴. 18S taxonomy annotation used both SILVA and 592 Protist Ribosomal Reference database (PR2, https://pr2-database.org/)58. Resultant ASV 593 tables were rarefied at 5000 (bacteria via 16S rRNA gene), 100 (archaea via 16S rRNA gene), 594 2000 (fungi via 18S rRNA gene), 1000 (protists via 18S rRNA gene), and 250 (invertebrates 595 via 18S rRNA gene) sequences/sample, respectively, to ensure even sampling depth within 596 each belowground group of organisms. They were then imported into QIIME ⁵³ for downstream 597 analysis including diversity and community composition.

598 Rarefaction resolution and primer set cross-validations

599 Rarefaction resolution

600 First, we conducted additional analyses to provide evidence that our choice of rarefaction level 601 did not affect our results or conclusions. Here, using the samples with the highest 602 sequence/sample yield, we tested for the impact of different levels of rarefaction on soil 603 biodiversity. We found highly statistically significant correlations between the diversities of soil 604 archaea (rarefied at 100 vs. 500 sequences/sample; Spearman $\rho = 0.764$; P < 0.001; n = 128), 605 bacteria (rarefied at 5000 vs. 10000 sequences/sample; Spearman ρ = 0.992; P < 0.001; n = 606 509), fungi (rarefied at 2000 vs. 10000 sequences/sample; Spearman $\rho = 0.971$; P < 0.001; n 607 = 88), protists (rarefied at 1000 vs. 5000 sequences/sample; Spearman ρ = 0.971; P < 0.001; 608 n = 287) and invertebrates (rarefied at 250 vs. 1000 sequences/sample; Spearman ρ = 0.952; 609 P < 0.001; n = 274), for a subset of samples wherein high numbers of sequences were 610 available. These results are supported by previous independent global surveys providing 611 evidence that rarefaction options do not influence global patterns in microbial communities 612 ^{59,60}. See rarefaction curves in Supplementary Figure 3.

613 Primer set cross-validation

614 Then, we provide additional evidence that primer sets are not influencing the global patterns 615 reported here. For a subset of samples, we generated additional molecular information for 616 fungal (ITS PacBio sequencing; ITS9mun/ITS4ngsUni primer sets) and bacterial (16s rRNA 617 Miseq Sequencing; 341F/805R primer sets) data. We found that the richness soil microbial 618 communities used in this study were highly significantly and positively correlated to those 619 using these alternative primer sets both for bacteria (Spearman ρ = 0.403; P < 0.001; n = 128) 620 and fungi (Spearman $\rho = 0.656$; P < 0.001; n = 228). Similarly, the community composition of 621 bacteria (Spearman ρ = 0.479; P < 0.001; n = 128) and fungi (Spearman ρ = 0.414; P < 0.001;

622 n = 228) were significantly and positively correlated to those using these alternative primer 623 sets. More importantly, we also found that the main predictors of bacterial and fungal richness 624 (soil pH in both cases; Supplementary Fig. 2) in this study followed the same pattern for 625 bacterial and fungal richness using alternative primer sets (Supplementary Fig. 4). We would 626 like to further highlight that the 18s primer sets used here to describe protists and invertebrates are the gold standard for the sequencing of these organisms ^{52,61} and have been previously 627 cross-validated in the literature ^{62–64}. We acknowledge that there are multiple alternative primer 628 629 sets, especially when specifically targeting particular groups of organisms within protists (e.g., 630 mtDNA COI gene). Nevertheless, while specific primers may deliver higher resolution for 631 specific groups, these are known to be inefficient in identifying a wide range of organisms from 632 environmental samples ⁶⁵.

633 Mapping the distribution of fungal functional guilds

634 Finally, to provide further evidence that 18s rRNA Miseq Sequencing can in this case provide 635 a solid representation of the global patterns in soil-borne mycorrhizal fungi and fungal potential 636 plant pathogens, we compared the global patterns (see mapping method below) in the 637 proportion of soil-borne mycorrhizal fungi and fungal potential plant pathogens determined 638 using 18s rRNA Miseg Sequencing with the subset of data including ITS PacBio sequencing 639 (see above). Our results showed that the proportion of soil-borne mycorrhizal fungi and fungal 640 potential plant pathogens determined using two independent methods followed similar 641 patterns and had a strong and positive correlation worldwide (Supplementary Fig. 6 and Table 642 8 and 9), allowing us to tentatively use the 18S rRNA gene as a proxy for phylotype richness. 643 The number of AMF phylotypes retrieved from ITS PacBio sequencing was not enough to 644 conduct this analysis, so we used Ectomycorrhizal fungi in our mapping comparison.

645 Soil ecosystem services

646 Six soil functions directly related to key ecosystem services were determined using highly 647 standardized methods: water retention (water holding capacity), fertility (nitrogen, phosphorus, 648 potassium, and magnesium content), carbon storage (total soil organic carbon content), mutualism (proportion of arbuscular and ectomycorrhizal fungi), pest control (inverse of the 649 650 proportion of soil-borne potential plant pathogens; as defined here ⁶⁶) and OM decomposition 651 (three enzymes associated with C, N and P cycle). Percentage of water holding capacity was 652 determined as in ⁶⁷. Soil nitrogen was determined using a CN analyzer. Soil phosphorus, 653 potassium, and magnesium concentrations were determined using ICP (Inductively Coupled 654 Plasma) Spectroscopy after acid digestion ⁶⁸. Total soil organic C content was determined 655 from CN analyzer (after removing soil carbonates) and wet-chemistry methods ⁵⁹. The 656 proportion of soil-borne fungal potential plant pathogens and fungal plant-soil mutualistic 657 organisms (arbuscular and ectomycorrhizal fungi) were determined as the sum of all taxa 658 classified as such from Funguild 69 using our 18S dataset. We found Funguild information for 659 297 ASVs of arbuscular mycorrhizal fungi, 217 ASVs of ectomycorrhizal fungi, and 165 ASVs of soil-borne potential fungal plant pathogens. Pest control was calculated as the inverse of 660 661 the proportion of soil-borne potential plant pathogens (-1 x proportion) as done in ⁶⁶. Thus, 662 locations with higher levels of pest control also have lower proportions of plant pathogens. We 663 only focused on those taxa supporting unique trophic life styles. The activity of phosphatase 664 (phosphorus mineralization), beta-glucosidase (starch degradation) and N-acetyl-β-665 glucosaminidase (chitin degradation) was determined as in ⁷⁰ using a high-throughput 666 fluorescence microplate method. The exact number of available information might differ for

667 different ecosystem services (available in Supplementary Table 2). The total number of 668 samples available for each soil attribute is available in Supplementary Table 2. We calculated 669 ecosystem services as the standardized (0-1) average of soil attributes within each ecosystem 670 service (e.g., Fertility: N, P, K and Mg; Mutualism: arbuscular and ectomycorrhizal fungi; OM 671 decomposition: phosphorus mineralization, chitin and starch degradation) using a 672 multifunctionality approach ⁷¹. Furthermore, we acknowledge that the number and type of 673 ecosystem services considered here might be limited to characterize the range of ecological 674 functions driven by soil communities. Therefore, for a subset of the data where other variables 675 are available, we correlated our ecosystem services to additional information on carbon 676 content, enzymes, nutrient availability from IEMS (a proxy of N mineralization; ⁷²) and 677 metagenomics (see Supplementary Table 10).

678 Environmental data

679 Elevation and climatic information for each location was obtained from WorldClim v2 (1 km² 680 https://www.worldclim.org/data/bioclim.html), resolution; including information on climatologies and on the seasonality of temperature and precipitation. Soil pH was determined 681 682 with a soil pH-meter from a soil-water mix ⁷³. Texture was determined as in Maestre et al. ⁷³ 683 and, in the case of missing information, this was filled using Soilgrid v2 (https://soilgrids.org; 684 as in ¹⁶). Information on dominant vegetation (forest, shrublands or grasslands) was obtained 685 as part of the field survey.

686 Drivers of soil biodiversity and services

687 To investigated the environmental factors associated with soil biodiversity and services, we 688 first used machine learning Random Forest modeling ⁷⁴. We used the R package "rfpermute" 689 to conduct these analyses. To further strengthen our results, we repeated the same analysis using XGboost algorithms ^{75,76}. XGboost allows for fine-tuning of the model outcomes, and 690 691 thus results are interesting for answering not only this comment by the reviewer but also the 692 next four comments. In brief, we used a gbtree booster using as an objective function the 693 RMSE using k-fold cross-validation. We tunned the ETA (learning rate), min chld weight, max 694 depth, resample, gamma and nfold 77 using a Bayesian optimization approach with the 695 package "ParBayesianOptimization" in R⁷⁸. This allows for efficient implementation of an 696 optimizing search. The parameter we decided to optimize was the test rmse (rather than the 697 train one), in order to prevent overfitting ⁷⁹. The number of trees fitted was also estimated on 698 this criterion using the function xgb.cv from package xgboost in R with 10% of data as 699 validation set. As feature importance, we extracted the gain obtained in predictive, using the 700 function xgb.importance (the results for this second analysis can be found in Supplementary 701 Figure 7; Supplementary Table 11 and 12). Here we chose to train the resulting models using 702 the function xgcv, which fits from 1 to 200 trees to the data and confronts trained models to 703 the cross-validation set. We chose to use the number of trees that minimized the test RMSE. 704 In general, this procedure allows to prevent overfitting (whereas train RMSE might continue 705 being improved, the point where validation RMSE is minimized corresponding to the maximum 706 learning ability without overfitting. In the new analyses, we parameterized 8 important 707 hyperparameters, including the number of trees (nroud) and the number of features 708 (colsample bytree). A full table of the resulting parameters is reported in Supplementary Table 709 11). To further strength our analysis, we compared the results obtained with our approach with 710 results obtained using a GAMM model (considering random factors). GAMMs were performed 711 by flooring coordinates (latitude and longitude) and using their combination as a random factor:

712 ("mdl=gamm(data = ddi.formula = 713 y~s(Latitude)+s(Longitude.cosine)+s(Longitude.sine)+s(s elev)+Forest+Grassland+Shrubla 714 nd+ s(s MAT)+s(s TSEA)+s(s PSEA)+s(s MAP)+s(s SOC)+s(s Texture)+s(s pH) random 715 = list(RF=~1))"; being RF the floored combination of latitude and longitude: 716 "dd\$RF=as.factor(paste(floor(coords\$long),floor(coords\$lat)))"). This approach allows to 717 control for spatial autocorrelation, apart from the nested structure of our data. Our results show 718 (Supplementary Fig. 10) that the GAMM model provided highly correlated results (Spearman 719 correlations >0.7) for all variables considered and almost identical (very aligned to 1:1 line) 720 predictions to the machine learning algorithms used in our manuscript, suggesting that the 721 type of modelling (e.g., Random Forest vs. GAMM) does not influence our results and 722 conclusions. We also conducted Spearman correlations to better describe the direction of the 723 relationship between environmental factors and soil biodiversity and services. We also 724 correlated all soil biodiversity and services attributes looking for potential trade-offs using 725 Spearman rank correlations. All the analyses in this section are non-parametric, and are 726 especially recommended when dealing with both linear and non-linear relationships. Analyses 727 were done at the sample level to account for within-location variation in soil properties, 728 biodiversity and services.

729 Global hotspots of soil biodiversity and services

730 We used spatially explicit random forest models to predict the distribution of each soil 731 biodiversity and ecosystem service variable. We were able to do these spatial analyses for 732 three main reasons: (1) the high-quality standardized biodiversity and ecosystem service 733 dataset wherein biodiversity and services are measured for the same samples, and analyzed 734 using the same protocols; (2) biodiversity and ecosystem services were highly correlated with 735 key environmental factors at the global scale (Extended Data Figs. 2-3); and (3) the large 736 gradient of environmental conditions in our global dataset covers a large portion (61.6% based 737 on a Mahalanobis analysis) of the large scale environmental variability of the planet. Note that 738 we further spatially constrained our analyses to exclude all environmental outliers ^{22,80}.

739 To map each soil biodiversity and ecosystem service variable we used spatially explicit 740 random forest models. For that, we used ArcGIS Pro that estimates random forest models by 741 using an adaptation of the random forest algorithm (a supervised machine learning regression 742 approach) proposed by Breiman et al. ^{74,81,82}. Forest-based regressions were trained based 743 on 90% of the dataset, the remaining 10% of the dataset were used for validation purposes. 744 Regression training and validation parameters are given in Supplementary Tables 5 (for Alpha 745 diversity and Community dissimilarity) and 6 (for Ecosystem services). The fitted prediction 746 model was then used to predict the unknown space using a prediction dataset that included 747 all environmental explanatory factors i.e., elevation, carbon, pH, fine texture, mean annual 748 temperature and precipitation, temperature and precipitation seasonality, forest, grassland, 749 shrubland. In the case of the analyses related to the ecosystem services, carbon was excluded 750 from all the models. All models were fitted using 1000 runs for validation and fitting. Prior to 751 prediction all variables included in the dataset and the predictors were resampled to 0.25 752 degrees using an average estimator and scaled. All predictions were made using a 0.25x0.25 753 deg. pixel size. All environmental variables used for spatial projection are listed in 754 Supplementary Table 14.

Global hotspots were then calculated using a Getis-Ord Gi* spatial clustering method ^{83–85}.
 The Getis-Ord Gi* statistic was calculated for each location (0.25x0.25 deg. pixel) in the

757 dataset. The resulting z-scores were used to estimate if a given location has statistically high 758 or low values and if these values are spatially clustered. This is done by assessing each 759 location within the context of neighboring locations. Statistically significant positive z-scores 760 indicate clustering of high values (hot spot) and statistically significant negative z-scores the 761 clustering of low values (cold spot). Values for classifying hotspots (positive z-scores) for each 762 variable were taken from the 99% confidence interval. Getis-Ord allows the use of the False 763 Discovery Rate (FDR) correction, which was also applied here, and adjusts the statistical significance of a hot-spot detection to account for multiple testing (with a confidence level of 764 765 0.95) and spatial dependency⁸⁶. This analysis resulted in a hotspot map for each combination, 766 i.e., five hotspot maps for alpha diversity, five for community dissimilarity, and six for 767 ecosystem services (Extended Data Figs. 4 and 5). We then overlayed the maps for each 768 ecological dimension (i.e., by summing the hotspot maps for each variable in each ecological 769 dimension: alpha diversity, community dissimilarity, and ecosystem services) to obtain a 770 global representation of soil biodiversity hotspots, where a high value corresponds to a 771 concentration of hotspots across multiple taxa or ecosystem services (Fig. 1A, B, and C)

772 Spatial uncertainty estimations

773 One of the difficulties of performing prediction of response variables using a new input dataset 774 is the fact that the new input environmental values might differ substantially from values used 775 to estimate the models. Therefore, estimating uncertainties on the environmental coverage of 776 the datasets as well as the estimations of both biodiversity and ecosystem services is a 777 complex but necessary requirement in such scenario modelling approaches ⁸⁷. For this, we 778 have implemented a two-stage approach to tackle both the assessment of the environmental 779 representation of the soil biodiversity and ecosystem services dataset used and the 780 uncertainty related to the estimation of each variable or group of variables. Regarding the first, 781 we calculated the Mahalanobis distance in multidimensional space (here considering the 782 twelve dimensions given by the environmental variables used for modelling (i.e., elevation, 783 carbon, nitrogen, pH, fine texture, mean annual temperature and precipitation, temperature 784 and precipitation seasonality, forest, grassland, shrubland) and centered on the known 785 distribution given by the characteristics, for the same environmental variables, of the soil 786 biodiversity and ecosystem service dataset. This analysis calculates the distance of any point 787 in space to the statistical center, given by the multivariate mean (considering all environmental 788 variables used) of the known distribution. It is often used to detect outliers in point cloud 789 distributions that are assumed to follow a multivariate Normal distribution ^{80,88}. The 790 Mahalanobis distance follows a Chi-squared distribution with d degrees of freedom, where d 791 is the dimension of the multidimensional space (d = 12 in our case). Environmental outliers 792 were estimated for a Chi-square of 0.9 (areas in grey in Supplementary Fig. 5).

793 Although this distance is an informative measure of how close a new data point is to the 794 distribution of points in space used to estimate each model, we used a second measure to 795 assess the spatial uncertainty of the estimated values for each model. In order to do this 796 analysis, for each soil biodiversity and ecosystem service variable, we calculated 1000 random 797 iterations of each random forest model and estimated the upper and lower 25% quantile of the 798 distribution of values. We then evaluated uncertainty as the difference between the upper and 799 the lower level of the iteration space for each individual variable. An average representation 800 for each dimension is given in Supplementary Fig. 5.

801 Projections of soil biodiversity and ecosystem services under global change scenarios

For the projections of soil biodiversity and ecosystem services, we used the available datasets from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) ⁸⁹ and from the Ianduse Model Intercomparison Project (LUMIP)⁹⁰ both activities from the Intergovernmental Panel for Climate Change (IPCC). The selection of scenarios followed the protocol laid out by ⁹¹.

806 In terms of climate change projections, we used a bias-corrected future projections dataset for both precipitation and temperature related variables⁸⁹. We considered three Representative 807 Concentration Pathways RCP2.6, RCP6.0, and RCP8.5⁸⁹ with forcing data from three 808 809 different general circulation models, the IPSL-cm5a-lr, gfdl-esm2m, and noresm1-m ⁹². For 810 land-use projections, we used the dataset provided by the land-use Harmonized v2.0 project 811 (http://luh.umd.edu/) ^{28,93,94}. This dataset was produced in the context of the World Climate 812 Research Program Coupled Model Intercomparison Project 6 (CMIP6) ^{28,45,95,96} and contains 813 a harmonized set of land-use scenarios that are consistent between historical reconstructions 814 and future projections. These modeled projections reproduce annual land-use reconstructions 815 for different integrated assessment models (IAMs) and shared socioeconomic pathways (SSP, 816 from 2015 to 2100) at 0.25 degrees resolution, which was developed and widely used to 817 support future biodiversity projections ^{97,98}. These shared socioeconomic pathways represent 818 a range of plausible futures based on different socioeconomic challenges for climate change 819 mitigation (low in SSP1 and SSP 4; high in SSP3 and SSP5), and potential challenges for 820 adaptation (low in SSP1 and SSP5; high in SSP3 and SSP4). While full descriptions of these 821 pathways and scenarios are given in ²⁸ we provide here a summary of the main characteristics 822 (based on 45):

823 SSP1: in SSP1 the world shifts gradually, but pervasively, toward a more sustainable path, 824 with its focus on achieving the global development goals, increasing environmental 825 awareness, and a gradual move toward less resource intensive societies. Currently, emerging 826 economies have followed the resource-intensive development model of industrialized 827 countries, but in SSP1, with the focus on equity, and the de-emphasis of economic growth as 828 a goal in high-income countries, leads industrialized countries to support developing countries 829 in their development goals, including green growth strategies, by providing access to human 830 and financial resources and new technologies.

831 SSP3: in SSP3 a resurgent nationalism, concerns about competitiveness and security, and 832 regional conflicts push countries to increasingly focus on domestic or, at most, regional issues. 833 International fragmentation and a world characterized by regional rivalry can already be seen 834 in some of the current regional rivalries and conflicts, but contrasts with globalization trends in 835 other areas. Regional conflict over territorial or national issues produces larger conflicts 836 between major countries, giving rise to increasing antagonism between and within regional 837 blocs, reducing support for international institutions and weakening progress toward the global 838 development goals, particularly in some middle-income countries.

839 <u>SSP4:</u> in SSP4 highly unequal investments in human capital, combined with increasing 840 disparities in economic opportunity and political power, lead to increasing inequalities and 841 stratification both across and within countries. Both across- and within-country inequality is 842 assumed to arise from biased technology development, generally low and highly unequal 843 investments in education resulting in increased restricted access, and reinforced wealth 844 inequality. This pathway assumes that growth is substantially smaller than it is today, but does 845 not assume that it is halted entirely. It also assumes an increased conflict over energy resources between consuming countries and producing countries, particularly if resources arefurther constrained.

848 SSP5: in SSP5 there is a foreseen acceleration in globalization and rapid development of 849 developing countries. The digital revolution enables an enhanced global discourse which may 850 lead to a rapid rise in global institutions and promote the ability for global coordination. This 851 pathway is driven by the economic success of industrialized and emerging economies to 852 produce rapid technological progress and development of human capital as the path to 853 sustainable development. Global markets are increasingly integrated, with the push for 854 economic and social development coupled with the exploitation of abundant fossil fuel 855 resources and the adoption of resource and energy intensive lifestyles around the world. All 856 these factors lead to rapid growth of the global economy. There is the ability to effectively 857 manage social and ecological systems, including by geo-engineering if necessary. While local 858 environmental impacts are addressed effectively by technological solutions, there is relatively 859 little effort to avoid potential global environmental impacts due to a perceived tradeoff with 860 progress on economic development.

All temporal changes (2070 minus 2015, using forecasting predictions) were calculated using 2015 as a baseline to which all future predictions were compared.

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864 Methods References865

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975 Extended Data Figures

976 Extended data Fig. 1 Results of Random Forest analysis to identify the main environmental
977 factors associated with soil biodiversity and ecosystem services. Random Forest analyses
978 were done using the rfPermute function of the R package with the same name. MSE = Mean
979 Square Error.

980 **Extended data Fig. 2** Spearman correlations between environmental factors and soil biodiversity and ecosystem services. N in Supplementary Table S1.

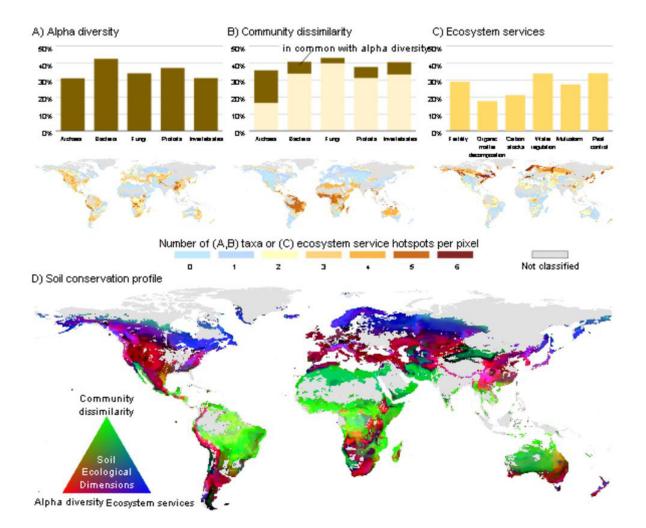
982 **Extended data Fig. 3** Spearman correlations between soil biodiversity and ecosystem 983 services. Total n-values in Supplementary Table S1.

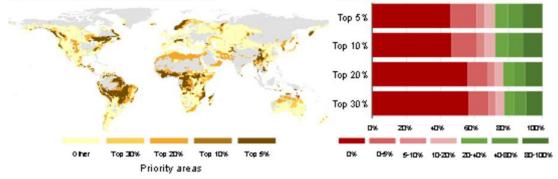
984 Extended data Fig. 4 Hotspot and coldspot maps for alpha diversity (left) and community 985 dissimilarity (right). The Getis-Ord Gi* statistic was calculated for each location (0.25x0.25 deg 986 pixel size) in the dataset 1–3. The resulting z-scores were used to estimate if a given location 987 has statistically high or low values and if these values are spatially clustered. This is done by 988 assessing each location within the context of neighboring locations. Statistically significant 989 positive z-scores indicate clustering of high values (hotspot) and statistically significant 990 negative z-scores the clustering of low values (coldspot). Values are plotted for both positive 991 (hotspots) and negative (coldspots) 99%, 95%, and 90% confidence levels.

992 **Extended data Fig. 5** Hotspot and coldspot maps for ecosystem services: soil carbon, fertility, 993 OM decomposition, pest control, mutualism, water retention. The Getis-Ord Gi* statistic was 994 calculated for each location (0.25x0.25 deg pixel size) in the dataset 1–3. The resulting z-995 scores were used to estimate if a given location has statistically high or low values and if these 996 values are spatially clustered. This is done by assessing each location within the context of 997 neighboring locations. Statistically significant positive z-scores the clustering of high 998 values (hotspot) and statistically significant negative z-scores the clustering of low values

- 999 (coldspot). Values are plotted for both positive (hotspots) and negative (coldspots) 99%, 95%,
- 1000 and 90% confidence levels.

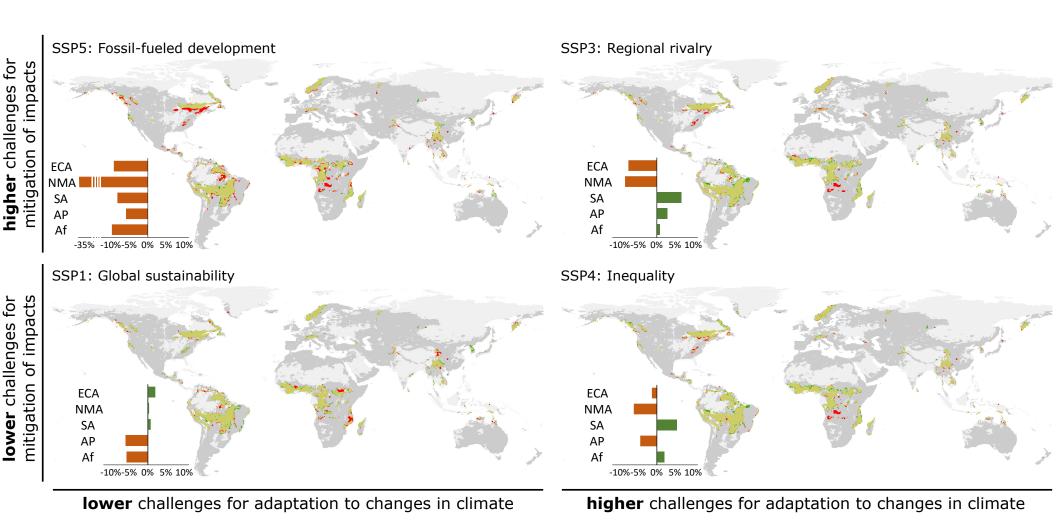
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A) Global soil nature conservation priorities

B) Proportion of protected priority areas



gains (2015-2070) in priority areas
 top 5% priority areas
 losses (2015-2070) in priority areas
 non-priority areas



ECA: Europe and Central Asia NMA: North and Meso America SA: South America AP: Asia-Pacific Af: Africa