#### Water availability creates global thresholds in multidimensional soil 1

- biodiversity and functions 2
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#### 36 Abstract

37 Soils support an immense portion of Earth's biodiversity and maintain multiple ecosystem functions which are essential for human well-being. Environmental 38 thresholds are known to govern global vegetation patterns, but it is still unknown 39 whether they can be used to predict the distribution of soil organisms and functions 40 across global biomes. Using a global field survey of 383 sites across contrasting 41 climatic and vegetation conditions, here we showed that soil biodiversity and functions 42 43 exhibited pervasive nonlinear patterns worldwide and are mainly governed by water availability (precipitation/potential evapotranspiration). Changes in water availability 44 resulted in drastic shifts in soil biodiversity (bacteria, fungi, protists and invertebrates) 45 and soil functions including plant-microbe interactions, plant productivity, soil 46 biogeochemical cycles, and soil carbon sequestration. Our findings highlight that 47 crossing specific water availability thresholds can have critical consequences for the 48 49 provision of essential ecosystem services needed to sustain our planet.

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#### 51 Introduction

Soils are the foundation of terrestrial ecosystems, supporting the delivery of multiple 52 ecosystem services that benefit human societies, from food production to carbon 53 sequestration <sup>1,2</sup>. Furthermore, soils are home to a myriad of soil organisms ranging 54 from bacteria to invertebrates <sup>2,3</sup>. However, these vital components of soil are 55 increasingly endangered by a variety of environmental disturbances, including natural 56 57 processes such as drying and warming and anthropogenic pressures such as nutrient loading <sup>4-6</sup>. Mounting evidence suggests that the ecosystem's responses to 58 environmental changes are not always gradual, and that ecosystems sometimes undergo 59 60 abrupt changes, highlighting the unpredictability of the ecological consequences. For example, recent studies have reported temperature thresholds associated with dramatic 61 declines in fungal decomposers <sup>7</sup> and ecosystem respiration <sup>4</sup>, as well as water 62 availability thresholds linked to abrupt reductions in multiple structural and functional 63 ecosystem attributes in arid regions <sup>5</sup>. However, those works have largely focused on a 64 single ecosystem attribute (e.g., organism <sup>5,7</sup> or function <sup>4,7</sup>) or environmental gradient 65 (e.g., temperature <sup>4</sup>) or accounted for specific environmental conditions (e.g., drylands 66 67 <sup>5</sup>). In the field of biogeography, a global perspective that considers contrasting 68 vegetation and climate types can sometimes reframe our understanding derived from local scales to identify more general environmental drivers <sup>8,9</sup>. Here, we understand 69 70 thresholds as points in an environmental gradient where soil biodiversity or function abruptly changes its value (discontinuous threshold or break point) or its relationship 7172 with that environmental gradient (continuous threshold)<sup>5</sup>. In this context, a unimodal 73 (or hump-shaped) relationship between soil biodiversity and environmental stress may be expected, where moderate stress promotes community species diversity through 74 niche release and mitigation of competitive exclusion or predation, but extreme 75 pressure would hinder the development of all taxa <sup>10-12</sup>. If these thresholds are preserved 76 across soil biodiversity and functions, they may be footprints of complex underlying 77 processes involving ecosystem feedbacks that may produce abrupt responses to climate 78 79 forcing <sup>13</sup>. In other cases, they may arise from inherent nonlinear mechanisms of ecosystems, which are usually disregarded in the ecological literature <sup>14</sup>. In any case, 80 unraveling the existence of these environmental thresholds on a global spatial scale and 81 carefully discussing the underlying mechanisms <sup>15,16</sup> would help develop more effective 82 83 strategies to address ongoing climate change.

84 Here, we evaluated the presence of environmental thresholds on the distribution of multiple soil biodiversity and functions across global terrestrial ecosystems. Instead of 85 86 adopting the most commonly used meta-analysis methods that are affected by heterogeneity in soil sampling and analytical methods <sup>17,18</sup>, we conducted a global 87 standardized field survey across 383 sites from six continents, representing various 88 89 climates (arid, temperate, tropical, continental, and polar) and vegetation types (forests, 90 grasslands, and shrublands) (Fig. 1). To the best of our knowledge, until now, no global 91 study has been conducted using standardized observational approaches to evaluate environmental thresholds on the distribution of multiple soil biodiversity and functions 92 93 worldwide. In this study, we obtained plot-level information on the richness of 12 soil 94 taxa across trophic levels, including bacteria, fungi, protists and invertebrates 95 (Supplementary Table 1). We used species richness (i.e., the number of zero-radius operational taxonomic units [zOTUs] generated using the marker-gene sequencing 96 97 methods) as our metric of diversity. We also obtained data for a suite of 12 proxy soil 98 functions (i.e., stocks and processes) that correspond to key components of ecosystem 99 services-water regulation, nutrient cycling, organic matter (OM) decomposition, plant

100 biomass production and plant-microbe interactions including pathogen control and mutualism (Supplementary Table 2). These variables measure either "true" soil 101 functions (that is, rates and availabilities) or key attributes/processes that constitute core 102 ecosystem functions that are both fundamental and quantifiable <sup>3,19</sup>. For example, 103 available nitrogen (N) and phosphorus (P) are nutrients that frequently limit the primary 104 production and carbon storage in terrestrial ecosystems <sup>20</sup>. Soils are a significant 105 reservoir of carbon, storing more than that held in vegetation and the atmosphere 106 combined, and thus play an important role in global carbon cycling <sup>21</sup>. Importantly, 107 these functions are more influenced by soil organisms. In this context, we hypothesize 108 109 that potential abrupt changes in soil biodiversity and functions are linked to specific environmental factors, such as temperature <sup>6</sup>, water availability <sup>5</sup>, and/or climatic 110 seasonality<sup>22</sup>. 111

#### 112 **Results and Discussion**

Our results found pervasive nonlinear relationships between broad environmental 113 gradients and multiple groups of soil biodiversity and functions worldwide. Of the 114 multiple environmental variables assessed, we found water availability to be the most 115 116 important driver, generating a series of discrete thresholds associated with abrupt changes in soil biodiversity and functions. These abrupt changes in soil biodiversity 117 were speculated to be related both directly to water limitation and indirectly to changes 118 in plant productivity and even shifts in vegetation <sup>23</sup>. Furthermore, abrupt decreases in 119 soil functions associated with reduced water availability occurred sequentially in three 120 phases characterized by abrupt declines in plant-microbe interactions, plant 121 productivity and soil biogeochemical cycles, and finally soil carbon contents. Overall, 122 the interplay between the direct effects of water limitation and the indirect effects of 123 vegetation shift governed the response behavior of soil biodiversity and functions to 124 environmental changes. It is worth mentioning that while our study does not cover the 125 entire environmental spectra found on Earth, it represents a large fraction of the planet's 126 environmental variability from arid to mesic ecosystems (Fig. 1), with a greater 127 resolution at the arid end<sup>5</sup>. We acknowledge that the abrupt changes found in this study 128 129 do not necessarily mean that these effects will translate into time; this is a future 130 research question to be solved by future studies based on temporal experiments.

#### 131 Consistent effect of water availability on soil biodiversity

132 We first discovered that a wide range of environmental variables exhibited pervasive significant thresholds related to abrupt changes in soil biodiversity across global biomes 133 of various vegetation and climate types (Extended Data Figs. 1-2, Supplementary Fig. 134 1). Biodiversity at multiple trophic levels is interconnected through the soil food web 135  $^{24}$ , as confirmed by this study (Spearman  $\rho$  ranges 0.2–0.7, Supplementary Fig. 2), 136 indicating that they may respond to environmental changes in similar ways but in 137 138 different orders. To evaluate the importance of different environmental variables in 139 controlling the abrupt change in soil biodiversity, we used the term "conservative" or "convergent" when referring to a specific environmental factor that presents the most 140 adjacent threshold in soil biodiversity (see Methods for rationale). Our results show that 141 142 water availability presented the most convergent threshold values (i.e., the smallest variability) across the diversity of all measured soil taxa (Extended Data Fig. 3). 143 Specifically, abrupt changes (or reductions) in soil biodiversity at multiple trophic 144 145 levels occurred at a small range of water availability levels of  $\sim 0.2-0.4$  (Fig. 2a). When crossing a water availability level of  $\sim 0.3$ , a potential systemic shift would occur for 146 the diversity of all groups (soil multidiversity hereafter) (Fig. 2a). The importance of 147

water availability in explaining the distribution of soil biodiversity is further supportedby a random forest analysis (Extended Data Fig. 4).

Most taxa displayed a hump-shaped pattern along the water availability gradient 150 (Fig. 2a). We speculated that such a uniform pattern across multiple groups of soil taxa 151 is attributed to their eco-physiological fitness to water limitation and the associated 152nutrient availability. Ultimately, water availability is crucial to the survival and 153154 functionality of living organisms, including the eukaryotic and prokaryotic taxa studied in this study <sup>25</sup>. Soil taxa depend on distinct optimal ranges of water availability, 155deviating from this range would impede their growth and survival <sup>25,26</sup>. Although we 156 should not assume a mechanistically simple relationship between microbial biomass or 157 growth rate and diversity <sup>11,27</sup>, moderate water stress (approaching the optimum from 158the right side of the curves, Fig. 2a) could reduce the biomass or growth rate of 159 dominant taxa, thereby freeing up more niches or alleviating competitive exclusion or 160 predation, both of which contribute to soil biodiversity <sup>11,12</sup>. In the face of strong 161 environmental stress (crossing the optimum and proceeding to extreme drought, Fig. 162 2a), however, most soil taxa no longer survive shortages, for example, in water and 163 164 nutrient availability. As evidence for the above assertion, our results further show a 165 hump-shaped relationship between soil heterotrophic respiration and water availability, with a threshold of 0.32 (Fig. 3i). Some soil organisms, such as Excavata and 166 167 Chlorophyta, did not follow this uniform pattern (Fig. 2a), which could be associated with their different eco-physiological features. For example, some members of 168 169 Chlorophyta (i.e., green algae) establish symbiotic relationships with fungi to form 170 lichens that generally prefer arid conditions <sup>28</sup>.

The observed abrupt reductions in soil biodiversity could also be linked to 171 reductions in plant productivity and essential soil nutrient availability when water 172 availability declines to approximately 0.4 (Fig. 3d-g). This notion was supported by 173174 decreases in soil fine texture (% of clay and silt; Fig. 2b), porosity (Fig. 3l), and the stability of soil aggregates <sup>5</sup>, which affect the soil's capacity to sustain inorganic 175nutrients and microbial access to water, nutrients and oxygen in soil pores <sup>26</sup>. In this 176 177regard, our results further show that larger eukaryotic taxa (mostly acting as primary 178 decomposers of plant inputs <sup>3</sup>) were more sensitive to water stress than were smaller prokaryotic bacteria (acting as nutrient miners by activating nutrients from the soil), 179 180 which may have also been linked with abrupt changes in plant community composition and soil biogeochemical cycles <sup>29</sup>. As water availability decreased to the dry end that 181 sustains forest and grassland, vegetation shifted to stress-avoidant shrub species 182 183 (Supplementary Fig. 3), which are better adapted to the infertile soil conditions and seasonal droughts characterizing these environments <sup>5,16</sup>. Accordingly, the soil 184 communities shift from larger primary decomposers that preferably degrade high-185186 quality detritus (e.g., nutrient-enriched litter and foliage) to smaller nutrient miners that are less picky for N/P-limited shrub detritus <sup>30,31</sup>. In addition, larger soil taxa (e.g., 187 Nematoda and Cercozoa in Fig. 2a) are more affected by changes in soil physical 188 connectivity for movement and access to resources in soil pores <sup>26,32</sup>, while bacterial 189 diversity is primarily controlled by soil chemical properties such as soil pH <sup>10</sup>. Soil 190 191 physical properties are more sensitive to decreasing water availability than soil pH (Figs. 2b and 3j), which may also contribute to the shift in soil biodiversity under dry 192 conditions. 193

Our analyses further revealed that climatic variables influenced soil biodiversity in
 a nonlinear way, possibly through changes in water availability. Climate change affects

196 global water availability through changes in seasonal precipitation and evaporation <sup>33</sup>. Consistently, we reported statistically inverse relationships between water availability 197 and increased seasonal variation in both precipitation (that is, PSEA, Spearman  $\rho =$ 198 -0.25, P < 0.05) and temperature (that is, TSEA, Spearman  $\rho = -0.29$ , P < 0.05) 199 (Supplementary Fig. 4). Accordingly, our results showed that high seasonal variations 200 in precipitation and temperature were also correlated with threshold behaviors in soil 201 202 biodiversity (Extended Data Figs. 1-2), which may be driven by abrupt reductions in water availability (Extended Data Fig. 5). Together with previous studies <sup>33,34</sup>, our 203 results call for more attention to the effect of extreme intra-annual climate seasonality 204 205 on soil biodiversity rather than focusing solely on interannual climate changes.

#### 206 Cascading effect of water availability on soil functions

Tipping into the response of individual soil functions to environmental gradients, we 207 also found pervasive nonlinear manners and identified environmental thresholds at 208 209 which these functions abruptly changed (Extended Data Figs. 6-7 and Supplementary Fig. 5). Using a random forest algorithm, the results revealed that water availability was 210 211 among the most important environmental drivers influencing multiple individual soil 212 functions, ranking first in five out of twelve cases (i.e., plant productivity, soil organic carbon, pathogen control, soil saprobes, and chitin degradation) and second in another 213 four cases (i.e., soil water holding capacity, soil nitrate, soil respiration and mutualism) 214 215 (Extended Data Fig. 8).

Our study demonstrated that, when specific thresholds of water availability were 216 exceeded, a sudden reduction occurred in all individual soil functions, except for 217 porosity (Fig. 3). Interestingly, the responses of soil functions to water stress could be 218 219 categorized into three distinct phases, which were characterized by orderly and abrupt 220 changes in three sets of soil functional variables (Fig. 3). The soil functional changes under water limitation commenced with a marked reduction in positive plant-microbe 221 222 interactions when water availability dropped below levels of 0.5-0.7 (Fig. 3a-c). The 223 observed decline in the relative abundance of soil saprobes (Fig. 3a) may be due to the sudden decrease in the quality of plant litter inputs (leaf nitrogen content<sup>5</sup>) into the soil, 224 225 leading to reduced substrate availability for soil decomposers. The abrupt decline in plant mutualism (Fig. 3b) could be linked to abrupt alterations in plant community 226 composition <sup>23,29</sup>. This notion was further supported by the sharp decrease in the effect 227 of pathogen control (Fig. 3c), which could be attributed to the vacancy of niches that 228 were originally occupied by pathogen competitors and the fact that pathogenic fungi 229 are more adept at surviving in dry conditions <sup>5,35</sup>. Ecosystem stability and resistance to 230 drought are positively correlated with soil saprobes and negatively related to plant 231 symbionts and pathogens <sup>35,36</sup>. Therefore, the shift to a pathogen-dominated soil fungal 232 community may occur due to weakened positive plant-microbe interactions under 233 increasingly arid conditions <sup>23</sup>, exacerbating the adverse effects on ecosystem stability. 234

235 As water availability continued to decrease to levels of ~ 0.3-0.4, we further noticed an abrupt decline in plant productivity and soil biogeochemical cycles. The 236 reductions in plant productivity could be attributed to the weakening of positive plant-237 238 microbe interactions identified above (Fig. 3a-d). The biogeochemical changes included abrupt reductions in soil nutrient transformation (including inorganic nitrate, 239 ammonium and phosphorus) and a sharp decline in organic matter (OM) decomposition, 240 241 characterized by chitin degradation and soil heterotrophic respiration (Fig. 3e-i). The 242 observed reductions in soil available nutrients linked to decreased plant-derived organic 243 inputs into the soil, which were driven by the abrupt reduction in plant productivity (Fig.

244 3d) and by the sharp decline in the relative abundance of soil saprobes (Fig. 3a). This was further supported by the decrease in OM decomposition, which is the primary 245 source of readily-available inorganic nutrients in soil <sup>37</sup>. The available N and P are good 246 surrogates of soil nutrient availability for soil organisms <sup>19</sup>. Accordingly, our results 247 showed that there were sharp declines in the diversity of most soil organisms, especially 248 larger-size eukaryotic taxa, when water availability dropped to the level of abrupt 249 250 reductions in soil inorganic nutrients (Fig. 2a). Other changes observed at this level of water availability include a decline in soil water holding capacity (Fig. 3i), which was 251 a key driver affecting the soil's capacity to store soluble inorganic nutrients <sup>38</sup>. 252

With a further decrease in water availability below 0.25, a sharp decline in the soil 253 carbon sink was ultimately detected (Fig. 3k). The reductions in soil carbon content 254 could be attributed to a decrease in the diversity of soil taxa (Fig. 2a), which are crucial 255for maintaining ecosystem functioning and soil fertility<sup>3</sup>. In addition, drastic reductions 256in soil nutrients (Fig. 3e-g), which are essential for plant productivity and soil carbon 257 storage <sup>20</sup>, may have contributed to the reduction in soil organic carbon content. The 258 drastic reduction in the terrestrial carbon sink adds to other abrupt changes that occurred 259 260 under drier conditions, such as the decline in plant cover (Fig. 2b) and species richness 261 <sup>5</sup>, implying that most plant species may not survive shortages of both water and 262 nutrients once this threshold of water availability is crossed.

#### 263 Conclusions

By presenting pervasive nonlinearity in multiple soil taxa and functions along gradual 264 changes in broad environmental gradients, our results greatly extend the current 265 framework of abrupt shifts for terrestrial ecosystems. We identified a series of water 266 267 availability threshold values associated with abrupt declines in soil biodiversity starting 268 from larger eukaryotic organisms to smaller prokaryotic bacteria. Additionally, we 269 found that soil functions under water stress undergo a three-phase disruption, 270 characterized by abrupt declines in plant-microbe interactions, plant productivity and 271 soil biogeochemical cycles, and soil organic carbon content. Furthermore, we propose 272 that such threshold behaviors are governed both directly by water stress and indirectly 273 by vegetation shifts along the way. Overall, our global survey highlights the fundamental importance of water availability in governing soil biodiversity and 274 functions worldwide and suggests that further water limitations are likely to shift the 275276 ecological functions provided by soil organisms and may potentially result in ecosystem collapse in some cases. 277

## 278 Methods

## 279 Field survey and soil sample collection

280 The global field survey aimed to cover a wide range of environmental contexts, soil biodiversity, and functions. To achieve this goal, a total of 383 soil samples were 281 282 collected from natural sites across all continents except Antarctic, to include globally 283 distributed regions that span a wide range of climatic and vegetation types. Coordinates 284 for each site were recorded in situ with a portable GPS, and vegetation type was annotated on-site based on the dominant vegetation. Specifically, the surveyed locations 285 286 encompassed tropical, temperate, continental, polar, and arid regions, including 287 grasslands, shrublands, forests, and moss heaths (ecosystems entirely covered by soil 288 mosses). It provides a good representation of the most common environmental 289 conditions found on Earth, with the mean annual precipitation and temperature, and 290 plant cover ranging between 17 and 2161 mm, -6.7°C and 29.2°C, and 0.1% and 100%, respectively. The range of estimated environmental variables can be found in Extended Data Fig. 1. This method has been used in previous global studies, which have shown its effectiveness in biome classification <sup>3,39</sup>.

294 Between 2016 and 2019, we conducted a sampling campaign specifically designed 295 to evaluate soil biodiversity and functions at the plot level. A representative plot was 296 established at each site, reflecting the vegetation present in that area. To ensure 297 consistency and minimize confusion arising from sampling annual communities at different times of the year or years, we focused only on perennial plant species <sup>19,39</sup>. To 298 299 account for spatial heterogeneity in the plot, five soil cores (the uppermost ~10 cm 300 depth with surface litter removed) were collected from both under the dominant perennial plant species (e.g., trees, shrubs, grasses) and in open areas devoid of 301 perennial vegetation <sup>19</sup>, and then were homogenized into a composite soil sample 302 (weighing over 250 g) in the field. We selected topsoil because it is the most commonly 303 304 used depth in comparable studies and is typically biologically the most active in terms of plant roots, microbial biomass, and nutrient pools <sup>39</sup>. After field sampling, the soils 305 were sieved (< 2 mm) in laboratory and separated into two portions: one portion was 306 307 air-dried for one-month and stored for soil biochemical analyses, and the second portion 308 was immediately frozen at -20 °C for molecular analyses. We do not expect seasonality 309 to affect our results, as global patterns in nutrient availability are expected to be more 310 consistent over time, and seasonality is known to have a reduced impact on large scale patterns in ecology <sup>40</sup>. 311

## 312 Environmental context

In this study, we represented the environmental context with a range of variables that 313 314 included climatic factors, such as the temperature and precipitation, biological factors, such as plant cover and productivity, as well as soil physical property and chemical 315 conditions, such as soil fine texture and pH. These variables were chosen due to their 316 significance as environmental predictors of soil biodiversity and functions, and the 317ability to influence their responses to environmental change <sup>3,5,39</sup>. The cover of 318 perennial vegetation was measured in situ at each site using the line-intercept method 319 <sup>19</sup>. Soil properties were determined using standardized protocols <sup>19</sup>. In brief, for all soil 320 321 samples, pH was measured with a pH meter in a 1:2.5 mass:volume suspension of dry 322 soil and deionized water, and salinity was measured with a conductivity meter in a 1:5 mass:volume suspension. Soil fine texture, which is defined as the percentage of clay 323 324 + silt, was determined using a simplified method combining sieving and sedimentation steps <sup>41</sup>. Soil pH and fine texture ranged between 3.77 and 9.54, and 0.49% and 88.22%, 325 326 respectively.

We obtained climatic data from the Worldclim database (www.worldclim.org) at a 327 1 km resolution <sup>42</sup>. Specifically, mean annual temperature (MAT) and temperature 328 seasonality (TSEA, defined as the standard deviation of the monthly mean temperatures 329 expressed as a percentage of the annual mean temperature) as well as precipitation 330 seasonality (PSEA, defined as the coefficient of variation of the monthly precipitation 331 332 estimates expressed as a percentage of the annual mean precipitation) were extracted. 333 For assessing climatic water availability, the aridity index (precipitation/potential 334 evapotranspiration) was used instead of mean annual precipitation, as it reflects the balance between water received by the land surface (precipitation) and that demanded 335 by the atmosphere (potential evapotranspiration, PET, calculated using the FAO 336 Penman-Monteith equation <sup>43</sup>). This is a widely used water-availability related metric 337 338 at a global scale <sup>5</sup>. The Global Potential Evapotranspiration database (V3) <sup>43</sup>, which is based on interpolations provided by WorldClim  $^{44}$ , was used to estimate water availability, with values ranging from 0.01 to 2.12 in this study.

#### 341 Soil diversity measures

In this study, the diversity of soil taxa, including bacteria, fungi, protists, and 342 invertebrates, was measured using an Illumina MiSeq platform for amplicon 343 sequencing. Soil DNA was extracted with the Powersoil DNA Isolation Kit (MoBio 344 345 Laboratories) following the manufacturer's instructions. The 16S rRNA gene for 346 bacteria and the 18S rRNA gene for eukaryotes were sequenced using the 341F/805R <sup>45</sup> and Euk1391f/EukBr <sup>46</sup> primer sets, respectively. The bioinformatic analysis were 347 performed using a combination of QIIME<sup>47</sup>, USEARCH<sup>48</sup>, and UNOISE3<sup>49</sup>. The 348 sequences were clustered into soil phylotypes - zero-radius operational taxonomic 349 units (zOTUs) – at a 100% identity level. The representative sequences of zOTUs were 350 annotated against the SILVA (16S rRNA gene)<sup>50</sup> and PR2 and SILVA (18S rRNA 351 gene)<sup>51</sup> databases. Before estimating the richness of soil organisms, the zOTU 352 abundance tables were rarefied at 10,000 (for bacteria) and 4,000 (for eukaryotes) 353 354 sequences per sample to ensure an even sampling depth within each group of soil 355 organisms. Protists were defined as eukaryotic taxa, except fungi, Metazoa (invertebrates and vertebrates), and vascular and non-vascular plants (Streptophyta). 356357 Algae were classified as protists in this study. Fungal guilds were characterized using 358 the FUNGuild <sup>52</sup>.

Here, we employed species richness, which represents the number of phylotypes, 359 as a measure of soil diversity since it is widely used and straightforward <sup>39</sup>. We used the 360 zOTU tables to estimate the richness of 12 of the most common prokaryotic and 361 362 eukaryotic taxa found in our soil samples: bacteria, fungi, protists (Apicomplexa, 363 Cercozoa. Ciliophora, Chlorophyta, Excavata, Ochrophyta, Oomycota) and invertebrates (Arachnida, Nematoda, Rotifera). To generate a composite diversity index 364 365 (i.e., multidiversity), we normalized the richness of each taxon to a 0-1 scale using the 366 formula (rawDiversity – min(rawDiversity)) / (max(rawDiversity) – min(rawDiversity)) and then calculated the mean value<sup>3</sup>. Nevertheless, we acknowledge that quantification 367 368 of soil invertebrate biodiversity using sequencing techniques may have limitations, as 369 larger soil organisms may be underrepresented by this approach<sup>3</sup>.

#### 370 Soil functions

This study included 12 surrogates of soil functions that are regulated by soil organisms 371 372 and are associated with a diverse range of ecosystem services. These surrogates include 373 aboveground plant productivity (estimated using satellite data to measure average plant 374 biomass), soil carbon storage (evaluated by measuring the content of total soil organic 375 carbon), soil water regulation (measured using soil water holding capacity and porosity), organic matter decomposition (evaluated using an enzyme related to chitin degradation, 376 377 the proportion of saprotrophic fungi, and soil heterotrophic respiration), nutrient 378 cycling (assessed by measuring the contents of soil Olsen-P, ammonium and nitrate), and plant-microbe interactions (evaluated by mutualism and pathogen control). These 379 variables measure either "true" functions (e.g., element cycling) or key 380 381 properties/processes (e.g., soil enzyme activity), which together provide a good proxy for biogeochemical cycles, productivity, and the buildup of terrestrial ecosystems <sup>3,19</sup>. 382 383 We discussed the ecological significance of these variables individually below and in 384 the Supplementary Table S2.

385 Plant productivity is of great importance in regulating the functioning of terrestrial

386 ecosystems, given that nearly all aboveground and belowground life forms rely on it as their ultimate source of energy, directly or indirectly <sup>3,53</sup>. To quantify plant productivity, 387 we used the Normalized Difference Vegetation Index (NDVI) from the Moderate 388 Resolution Imaging Spectroradiometer aboard NASA's Terra satellites 389 (https://modis.ornl.gov/data.html) at a resolution of 250 m, which provides a global 390 measure of vegetation greenness across Earth's landscapes, serving as a proxy of 391 photosynthetic activity and vegetation distribution <sup>54</sup>. Here, we obtained averaged 392 NDVI values obtained from the month before, during, and after the sampling dates of 393 394 the surveyed plots. Previous work has shown that the choice of productivity period 395 should not alter our results<sup>3</sup>.

Other eleven soil functions listed above, except for plant productivity, were analyzed with air-dried soil samples. Previous studies have found that air drying and further storage of soils does not appreciably alter the functions of interest in this study, and these methods are commonly used when analyzing physical and chemical soil properties in natural terrestrial ecosystems worldwide <sup>19</sup>. Furthermore, it is also important to note that most of the sampled soils were collected when they were in a dry state, minimizing the potential bias induced by our drying treatment <sup>3,19</sup>.

403 Soil water regulation was assessed through the measurement of two important soil physical properties, namely soil water holding capacity and soil porosity. Soil water 404 405 holding capacity - the amount of water that a given soil can retain - is relevant to several aspects of soil water management <sup>55</sup> and crucial in determining aboveground 406 plant productivity via regulating plant-water provision <sup>56,57</sup>. On the other hand, soil 407 porosity – the percentage of the soil volume occupied by pore spaces – is an important 408 physical property that controls various key soil hydrological properties, including water 409 storage capacity and infiltration <sup>58,59</sup>. Soil water holding capacity was determined in the 410 lab using the funnel method <sup>38</sup>. Soil porosity was quantified as  $100 \times (1-$  (bulk 411 density/particle density)), where bulk density was measured for each sample using the 412 cylindrical core method <sup>38</sup>, and particle density was estimated using a constant value of 413  $2.65 \text{ g/cm}^3$ . 414

415 Regarding soil nutrient cycling, we obtained the availability of inorganic N (ammonium and nitrate) and P (Olsen P) from K<sub>2</sub>SO<sub>4</sub> and NaHCO<sub>3</sub> (pH: 8.5) extracts, 416 respectively, for all samples, using colorimetric assays <sup>19</sup>. The contents of available N 417 and P are reliable indicators of their availability to plants and microorganisms in 418 terrestrial ecosystems globally <sup>19</sup>. Soil organic C (SOC) is a significant terrestrial carbon 419 reservoir and plays a crucial role in atmospheric CO<sub>2</sub> sequestration <sup>60,61</sup>. SOC 420 421 concentration was determined in ball-milled soils by dry combustion, gas 422 chromatography and thermal conductivity detection Thermo Flash 2000 NC soil analyzer (ThermoFisher Scientific, Waltham, Massachusetts, USA), after the removal 423 of carbonates by acid fumigation <sup>19</sup>. Soil organic C varied from 0.45 to 378.1 g/kg in 424 this study. Extracellular enzymes are responsible for the breakdown of organic matter 425 <sup>62</sup>, and  $\beta$ -N-acetylglucosaminidase (NAG) provides a major source of mineralizable 426 nitrogen in the soil by catalyzing chitin breakdown to amino sugars <sup>63</sup>. The activity of 427 NAG was measured using the fluorometry method from 1 g of soil <sup>64</sup>. 428

Soil heterotrophic respiration is an important process that contributes to carbon losses through the decomposition of litter, detritus and soil organic matter by soil microorganisms, and it plays a crucial role in the global carbon cycle <sup>65</sup>. The estimation of soil heterotrophic respiration was carried out using a high-throughput colorimetric method (Microresp <sup>66</sup>). Dried soil samples were incubated at 20° C for 10 hours (short-

434 term incubation). Soils were then transferred to the 96-well deep microtiter plates by adding approximately 0.5-1 g soil per well. The soil moisture was adjusted to 60% of 435 its water-holding capacity using sterile deionized water, which is optimal for microbial 436 activity<sup>3</sup>. First, the soil samples were pre-incubated for 5 hours in growth chambers 437 under dark conditions, while being covered with polyethylene film to prevent soil 438 drying and allow gas exchange. Our approach aims to allow the microbial community 439 to settle after the initial disturbance <sup>67</sup> and to avoid rapid initial CO<sub>2</sub> flush as a 440 consequence of rewetting dry soils (i.e., Birch effect <sup>68</sup>) without compromising the re-441 adaptation of microbial communities to new incubation conditions <sup>69</sup>. Subsequently, the 442 443 samples were incubated for 5 hours with colorimetric detection plates. The Microresp protocol utilizes a CO<sub>2</sub> detection solution containing cresol red indicator dye, which 444 445 changes due to the pH variation that occurs when respired CO<sub>2</sub> reacts with the 446 bicarbonate of the detection solution. The absorbance of the detection plate was measured immediately before and after use at 595 nm. To ensure accuracy, three 447 analytical replicates were performed per sample, and the average of these replicates per 448 assay temperature was used as the observed potential respiration rate for each sample. 449

450 Plant roots interact closely with beneficial symbionts (arbuscular and 451 ectomycorrhizal fungi) that enhance nutrient acquisition and pathogens that cause root necrosis or plant death <sup>36,70</sup>. In this study, plant-microbe interactions were evaluated by 452 considering mutualism and pathogen control. Mutualism specifically refers to the 453 relationship between plant and mycorrhizal fungi, which provide benefits to both 454 455 partners, and was quantified by determining the relative abundance of mycorrhizal 456 fungi in overall fungal community. Pathogen control, on the other hand, refers to the ability of an ecosystem to reduce the incidence of fungal diseases <sup>70</sup>, and was calculated 457 as the inverse of the relative abundance of soil-borne fungal phytopathogens in overall 458 fungal community. 459

#### 460 Statistical analyses

#### 461 **Partial correlations**

462 Partial correlations were used to assess the relationships among individual variables in 463 soil biodiversity or environmental context, with the two-sided Spearman's *rho* ( $\rho$ ) used 464 as the measure of strength and direction of the association. We used a false discovery 465 rate approach to determine adjusted P values to control for spurious correlations (false 466 positives). The statistical analysis was conducted using the R package 'psych' <sup>71</sup>.

#### 467 Threshold identification

468 In this study, we employed the Akaike information criterion (AIC) in two steps to identify the most suitable model that describes the relationship between soil 469 biodiversity/functional attributes (y) and environmental gradients (x) <sup>5</sup>. The first step 470 involved fitting linear and nonlinear models, including quadratic (the simplest case of 471 472 nonlinear trend) and generalized additive models (GAM, more complex trend through smoothing parameters), to the data <sup>5</sup>. The linear model is the null hypothesis that 473 assumes a gradual x-y relationship, while a lower AIC value for either nonlinear model 474 475 implies the presence of a threshold point.

In the second step, we tested for the presence of threshold only when nonlinear regressions were a better fit to the data. We considered a threshold as the point in x where y changes abruptly its value (discontinuous threshold or break point) or its relationship with x (continuous threshold). In the latter case, the incidence of abrupt

change in slope is regarded, but also more subtle and continuous changes that may involve high degree polynomials (usually better fitted by GAM models where changes in the slope do not involve a breakpoint of a sudden change but indicate a point of maximum curvature). Both cases, despite being continuous, are still thresholds and may indicate important information for management: the value of x signaled is the most obvious point where one should stop assuming the previous x-y relationship.

486 In this study, we examined both continuous and discontinuous thresholds, which involved evaluating the performance of three threshold models. Continuous thresholds 487 can be effectively detected using segmented regression (i.e., a linear regression that 488 489 modifies its slope at the threshold) or more complex GAM regression. On the other hand, discontinuous thresholds require an overall change in both intercept and slope, 490 and can be well-fitted to either step (i.e., a linear regression that changes only the 491 intercept at the threshold) or a combination of step and segmented regressions (called 492 493 stegmented, which involve changes in both intercept and slope at the threshold). All these models, except for GAM, generate a threshold value as part of their parameters. 494 The best model among segmented, step, and stegmented regressions was chosen using 495 496 the AIC values. If GAM regression was found to be the best model compared to 497 threshold models, the threshold yielded by segmented regression was reported to indicate the point of maximum curvature of the regression. Detailed AIC values for 498 499 each regression model are provided in Supplementary Table 3.

Threshold detection is sensitive to influential points or outliers. We used the 500 Mahalanobis distance method to remove outliers (points scoring a Mahalanobis 501 distance higher than 12<sup>72</sup>) and restricted the search of threshold to the 0.05 and 0.95 502 quantiles of x gradient. We performed 1000 bootstrap samplings on each case to 503 identify a set of 1000 plausible thresholds for each case and obtained the mean value as 504 the final threshold. To further test whether the identified threshold significantly affected 505 the slope and/or intercept of the fitted regressions, we bootstrapped linear regressions 506 at both sides of the threshold and used the unpaired two-sided Mann-Whitney U test to 507 compare the slopes. In almost all cases where nonlinear regressions were the better fit, 508 509 we found significant differences in slopes of both sides of the threshold (Extended Data Figs. 2 and 7). This approach followed the method in ref. <sup>5</sup>]. We used the chngpt <sup>73</sup> and 510 gam <sup>74</sup> packages in R to fit nonlinear regressions. 511

#### 512 Convergence of environmental thresholds

We evaluate the conservatism or convergence of environmental variables in driving 513 abrupt changes in soil biodiversity by measuring the variability of the threshold values 514 identified. A smaller variability indicates a higher conservatism of environmental 515 factors, or a higher convergence of corresponding identified thresholds. The underly 516 assumption is that when a series of thresholds detected across soil biodiversity converge 517 within a narrow range of a given environmental gradient, there is a fundamental and 518 519 insurmountable difference separating responses of soil biodiversity. This may be due to strong convergence in environmental limits, such as a physiological trigger that is equal 520 across soil taxa, or due to interactions across ecological dimensions typical of feedback 521 that amplify responses to the environmental factor, such as low carbon leading to low 522 decomposition, low fungal diversity, and even less decomposition and less carbon <sup>16</sup>. 523 The threshold variability is evaluated using the average variation degree (AVD)<sup>75</sup>, 524 525 which quantifies the deviation degree from the mean of identified environmental threshold of multiple groups of soil taxa. In this respect, only those soil taxa that 526 respond nonlinearly to a given environmental factor are included in estimating the 527

528 threshold variability for that environmental factor. The AVD is calculated using the 529 following equation:

530 
$$a = \frac{\sum_{i}^{n} |t_{i} - \bar{t}|}{\delta * n}$$

531 where *a* is the variation degree,  $t_i$  is the threshold identified for ecosystem attribute *i*, 532 *n* is the number of ecosystem attributes that respond nonlinearly to a given 533 environmental factor, and  $\bar{t}$  and  $\delta$  is the average value and standard deviation of all 534 thresholds identified across ecosystem attributes, respectively.

#### 535 Data availability

All the materials, raw data, and protocols used in the article are available upon request and without restriction, and all data that support the main findings of this study will be made publicly available in Figshare <sup>76</sup> upon publication.

#### 539 Code availability

540 The data in this study were analyzed with publicly available tool packages in R and

the figures were produced with R. The R code used in the analysis presented in this paper is available in Figshare  $^{76}$ .

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#### 561 Author contributions

M.D.-B., M.B., and Y.F. developed the original ideas. F.T.M., M.D-B., and B.K.S.
provided the original data. M.D-B., F.T.M., B.K.S., T.S-S., L.G-V., and J.W. contributed
to lab analyses. J.Z., Y.F., M.B., M.D.-B., and C.C. conducted statistical analyses. J.Z.,
Y.F., and M.D.-B. wrote the first draft of the manuscript, and all authors contributed
substantially to revisions.

## 567 **Competing interests**

568 The authors declare no competing interests.

## 569 Figure legends

Fig. 1 | Map showing locations of the 383 soil sampling sites included in this study.
Sites are colored based on the Köppen climate classification of biomes <sup>77</sup>. Map is
displayed using the Robinson projection.

Fig. 2 | Nonlinear relationships between water availability and the diversity of soil 573 taxa as well as other environmental factors. The y axes represent the diversity of 574 multiple groups of soil taxa and the multidiversity of all of the groups (a) and other 575 576 environmental properties that are influenced by water availability (b). Regression models represent the linear regressions before and after the water availability threshold. 577 Black dashed lines represent the smoothed trend fitted by a generalized additive model, 578 and blue solid lines represent the linear fits at both sides of each threshold. Inset 579numbers and vertical dashed lines describe the water availability threshold identified. 580

Fig. 3 | Relationships between soil functions and water availability. Threshold 581 values of water availability were identified for (a) soil saprobes, (b) plant-mycorrhizal 582 583 mutualism, (c) plant-pathogen control, (d) plant productivity, contents of soil (e) nitrate, (f) ammonium, and (g) available phosphorus, (h) enzyme activity of chitin degradation, 584(i) soil heterotrophic respiration rate, (j) soil water holding capacity, and (k) content of 585 586 soil organic carbon. The relationship between (i) soil porosity and water availability was better fitted by a linear regression over nonlinear model. Many functional variables 587are log-transformed to improve normality. The rest of the information is the same as 588589 Fig. 2.

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