Blind spots in global soil biodiversity and ecosystem function research

Carlos A. Guerra [1,2], Anna Heintz-Buschart [1,3], Johannes Sikorski [4], Antonis Chatzinotas [5,1], Nathaly Guerrero-Ramírez [1,6], Simone Cesarz [1,6], Léa Beaumelle [1,6], Matthias C. Rillig [7,8], Fernando T. Maestre [9,10], Manuel Delgado-Baquerizo [9], François Buscot [3, 1], Jörg Overmann [4,11], Guillaume Patoine [1,6], Helen R. P. Phillips [1,6], Marten Winter [1,6], Tesfaye Wubet [12,1], Kirsten Küsel [1,13], Richard D. Bardgett [14], Erin K. Cameron [15], Don Cowan [16], Tine Grebenc [17], César Marín [18,19], Alberto Orgiazzi [20], Brajesh K. Singh [21,22], Diana H. Wall [23], Nico Eisenhauer [1,6]*

Affiliations

[1] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[2] Institute of Biology, Martin Luther University Halle Wittenberg, Am Kirchtor 1, 06108 Halle(Saale), Germany

[3] Helmholtz Centre for Environmental Research - UFZ, Department of Soil Ecology

[4] Leibniz-Institut DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen, Braunschweig, Germany

[5] Helmholtz Centre for Environmental Research - UFZ, Department of Environmental Microbiology

[6] Institute of Biology, Leipzig University, Germany

[7] Freie Universität Berlin, Institut für Biologie, Altensteinstr. 6, 14195 Berlin, Germany

[8] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany

[9] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Calle Tulipán Sin Número, Móstoles 28933, Spain.

[10] Departamento de Ecología and Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef", Universidad de Alicante, Carretera de San Vicente del Raspeig s/n, 03690 San Vicente del Raspeig, Alicante, Spain

[11] Microbiology, Braunschweig University of Technology, Braunschweig, Germany

[12] Helmholtz Centre for Environmental Research - UFZ, Department of Community Ecology

[13] Institute of Biodiversity, Friedrich Schiller University Jena, Dornburger-Straße 159, 07743 Jena, Germany

[14] School of Earth and Environmental Sciences, The University of Manchester, Manchester, M13 9PT, UK

[15] Department of Environmental Science, Saint Mary's University, Halifax, NS, Canada

[16] Centre for Microbial Ecology and Genomics, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria, South Africa

[17] Slovenian Forestry Institute, Večna pot 2, SI-1000 Ljubljana, Slovenia

[18] Instituto de Ciencias Agronómicas y Veterinarias, Universidad de O'Higgins, Rancagua, Chile.

[19] Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile.

[20] European Commission, Joint Research Centre (JRC), Ispra, Italy

[21] Hawkesbury Institute for the environment, Western Sydney University, Penrith, NSW, 2751, Australia

[22] Global Centre for Land-Based Innovation, Western Sydney University, Penrith, NSW, 2751, Australia

[23] School of Global Environmental Sustainability and Department of Biology, Colorado State University, Fort Collins, CO 80523-1036 USA

* Corresponding author

Abstract

Soils harbor a substantial fraction of the world's biodiversity, contributing to many crucial ecosystem functions. It is thus essential to identify general macroecological patterns related to the distribution and functioning of soil organisms to support their conservation and governance. Here we identify and characterize the existing gaps in soil biodiversity and ecosystem function data across soil macroecological studies and >11,000 sampling sites. These include significant spatial, environmental, taxonomic, and functional gaps, and an almost complete absence of temporally explicit data. We also identify the limitations of soil macroecological studies to explore general patterns in soil biodiversity-ecosystem functioning relationships, with only 0.6% of all sampling sites having a non-systematic coverage of both biodiversity and function datasets. Based on this information, we provide clear priorities to support and expand soil macroecological research.

Keywords: Soil ecology, Macroecology, Soil fauna, Soil microbes, Ecosystem functions

1. Introduction

Soils harbor a large portion of global biodiversity, including microbes (e.g., Bacteria), micro- (e.g., Nematoda), meso- (e.g., Collembola), and macrofauna (e.g., Oligochaeta), which play critical roles in regulating multiple ecosystem functions and services, including climate regulation, nutrient cycling, and water purification[1–6]. Accordingly, recent experimental[7,8] and observational[9,10] studies, based either on particular biomes (e.g., drylands) or local sites, have shown that soil biodiversity is of high importance for the maintenance of multifunctionality (i.e. the ability of ecosystems to simultaneously provide multiple ecosystem functions and services[11]) in terrestrial ecosystems.

Nevertheless, with few exceptions[9,12], global soil biodiversity-ecosystem function relationships have not yet been studied in depth, with macroecological studies evaluating the patterns and causal mechanisms linking soil biodiversity to soil ecosystem functions only emerging in the last decade[10,13–15]. By comparison, albeit with important limitations[16], there is a plethora of studies describing the global distribution and temporal patterns of aboveground biodiversity[17], ecosystems[18], and biodiversity-ecosystem function relationships[12,19–23], something that is currently mostly absent (but see[24]) in soil macroecological studies due to the lack of temporally explicit data for soil biodiversity and soil related functions.

Despite the mounting number of soil ecology studies, significant gaps and/or geographic and taxonomic biases exist in our understanding of soil biodiversity[25]. Although the existing gaps in global soil biodiversity data are consistent with gaps in other aboveground biota[16,26,27], these are further exacerbated when described across specific ecological gradients (e.g., differences across altitudinal gradients) and taxa (e.g., Collembola, Oligochaeta)[28]. Further, and almost nothing is known about the temporal patterns in soil biodiversity at larger spatial scales and across ecosystem types. Identifying and filling these gaps on soil species distributions and functions is pivotal to identify the ecological preferences of multiple soil taxa, assess their vulnerabilities to global change drivers, and understand the causal links between soil biodiversity, ecosystem functions and their associated services[16,29]. Despite growing scientific and political interest in soil biodiversity research[25] , little to no attention has been given to the governance of soil ecosystems (Fig. S1), which has resulted in a lack of inclusion of soil biodiversity and functions in decision making regarding land management debates, conservation, and environmental policy[30].

In contrast to groups of organisms from other realms (e.g., aboveground terrestrial[31]) for which the Global Biodiversity Information Facility (GBIF) constitutes already the main global data hub[32,33], soil organisms are poorly represented, with distribution data on soil species spread across the literature and a number of platforms (e.g., the global Ants database[34], the Earth Microbiome project[35]). Across all available soil biodiversity data, major issues remain regarding the spatial and temporal representativeness (e.g., absent data in most tropical systems) of data, and coverage of taxonomic groups of soil biota (e.g., most focus on fungi and Bacteria), which limits our capacity to comprehensively assess and understand soil systems at multiple temporal and biogeographic scales. More importantly, both the lack of representativeness and the distribution of gaps in global soil biodiversity and ecosystem function research hampers the prioritization of future monitoring efforts[16]. Such a knowledge deficit in soil biodiversity also prevents stakeholders from taking appropriate management actions to preserve and maintain important ecosystem services[36], such as food and water security, for which soils are the main provider. Therefore, it is both timely and relevant to identify these blind spots in global soil macroecological knowledge and research. By doing so, we can assess their main causes and line up potential solutions to overcome them.

Here, we identify fundamental gaps in soil macroecological research by analysing the distribution of sampling sites across a large range of soil organisms and ecosystem functions. In a review of current literature, we collected sample locations from most existing studies focused on soil macroecological patterns. The studies were then organized according to different soil taxonomic groups and ecosystem functions studied (nine and five categories, respectively, see Methods for more details). Since the mere accumulation of data will not significantly advance ecological understanding[37,38], it is important to identify how well the current studies cover the range of existing environmental conditions on Earth, including soil properties, climate, topography, and land cover characteristics[39,40]. Finally, we examined how these macroecological studies have captured the diversity of global environmental conditions to identify critical ecological and geographical "blind spots" of global soil ecosystem research (e.g., specific land use types, soil properties, climate ranges; see Methods for more detail). By identifying the environmental conditions that have to be covered in future research and monitoring to draw an unbiased picture of the current state of global soils as well as to reliably forecast their futures, our synthesis goes a significant step beyond recent calls to close global data gaps[25]. Therefore, our comprehensive spatial analysis will help researchers to design future soil biodiversity and ecosystem function surveys, to support the mobilization of existing data, and to inform funding bodies about the allocation of research priorities in this important scientific field.

2. Results and Discussion

2.1. Biogeographical biases

From our literature search, we collected details on locations of 11,065 individual sampling sites representing studies on soil biodiversity [N=7,631; 68.9% of the total number of sites] and ecosystem functions [N=3,497; 31.6% of the total number of sites] (Fig. 1). Bacteria, fungi, and soil respiration (Fig. 1a) were the best-represented soil taxa and functions in our literature survey, respectively. The total number of sites across all studies is quite low when compared with many aboveground macroecological databases that can individually surpass the numbers found here (e.g., the PREDICTS database[41] contains ~29,000 sites across the globe).

Globally, soil biodiversity and ecosystem function data are not evenly distributed. Bacteria [N=3,453], fungi [N=1,687], and Formicoidea [N=3,024] (which together concentrate 71.6% of all soil biodiversity records) have comparatively large and geographically balanced distributions when compared to Nematoda [N=149], Rotifera [N=41], Collembola [N=27], and Acari [N=10], which have a substantially lower number of sampling sites and more scattered distributions (see Fig. S2a for more detail). In the case of Bacteria and fungi, the relatively high number of sampling sites reflects a community effort to assemble databases based on collections from different projects[10,42]. In the case of Formicoidea, the availability of data reflects the outcome of systematic global sampling initiatives[43] or a combination of both[44].

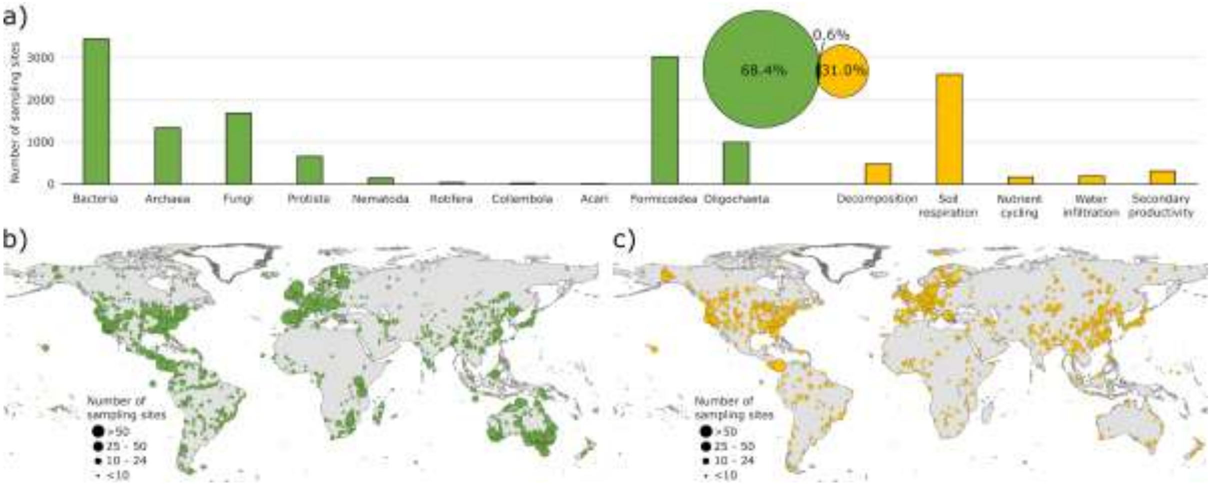

Fig. 1 Global distribution of sampling sites for soil taxa and soil ecosystem functions. (a) corresponds to the global number of individual sampling sites for each soil taxon (on the left - in green) and ecosystem function (on the right - in orange). The venn diagram indicates the proportion of sampling sites for soil taxa (in green) and functions (in orange), and the 0.6% [N=63] of overlap between biodiversity and function data points (this number does not mean that soil biodiversity and function were assessed in the same soil sample or during the same sampling campaign; i.e., there could still be a thematic or temporal mismatch), relative to the total number of sampling sites covered by the studies. The maps show the overall spatial distribution of sampling sites for all taxa (b) and soil ecosystem functions (c). The size of the circles corresponds to the number of sampling sites within a 1-degree grid ranging from <10 to >50.

Soil ecosystems are by nature very heterogeneous at local scales[45]. Having a small and scattered number of sampling sites, for both soil functions and taxa, limits the power of current global analyses to evaluate macroecological relationships between soil biodiversity and ecosystem function, particularly for nutrient cycling and secondary productivity, which have strong local inter-dependencies[46]. In fact, from the five functions assessed here, there is a clear concentration of studies on soil respiration, accounting for 69.1% [N=2,616] of all function records (see Fig. S2b for more detail). Thus, our study provides evidence for a lack of matching data for soil biodiversity and multiple ecosystem functions in current global datasets. Due to the dependency of these and other soil functions on biodiversity[2,47], being able to deepen our understanding of the strength and distribution of expected biodiversity and ecosystem function relationships is critical to better inform management and policy decisions[48]. In this context, only 0.6% of all sampling sites have an overlap between biodiversity and function datasets (corresponding to 63 sampling sites), with a non-systematic coverage of just a few taxa and functions across sites. Nowadays, macroecological studies on aboveground biodiversity and ecosystem functioning[19,41,49–52] rely on data mobilization mechanisms that allow for data to be often reused to address multiple research questions. By contrast, apart from some taxonomic groups (i.e., Bacteria and fungi) soil macroecological studies based on observational data have a very small degree of overlap and still remain conditioned by poor data sharing and mobilization mechanisms[53–55].

We also discovered that most studies are based on single sampling events, i.e., without repeated measurements in time for the same sampling sites. Being able to study how communities and functions change over time is essential for assessing trends in key taxa and functions, and their vulnerability to global change[17]. Our global survey suggests that such information is almost nonexistent in large-scale soil biodiversity and ecosystem functions studies. Thus, for most soil communities and functions, although local studies exist[56,57], understanding the global trends and the implications of global change drivers and scenarios is difficult and limited by the absence of globally distributed and temporally explicit observational data.

2.2. Ecological blind spots

Overall, both soil biodiversity and ecosystem function variables reveal a high degree of spatial clustering across global biomes: temperate biomes (especially broadleaved mixed forests and Mediterranean) contain more sampling sites than tundra, flooded grasslands and savannas, mangroves, and most of the tropical biomes, with the exception of moist broadleaf forests (Fig. S3). This spatial clustering is even more pronounced in studies of ecosystem functions, with temperate systems being overrepresented with 62% of all sampling sites, while the rest of the globe has scattered information on soil conditions. This likely reflects differences in funding availability and research expertise across countries[27,58]. In fact, for taxa like Collembola and Nematoda, most of sampling sites are concentrated in temperate regions, with very few being documented in other regions. Further, the availability of soil biodiversity and function data is especially scarce, and in some cases non-existent: in tropical and subtropical regions (see Fig. S3 for more details), which are among the most megadiverse places on Earth, montane grasslands, and deserts. In many cases, local experts may exist, although their contributions are often not included in macroecological studies. At the same time, for many of the best-represented regions in the globe, there is rarely a complete coverage of soil taxa and functions, with records often being overinflated by one or two densely sampled taxa (e.g., Bacteria and fungi) or functions (e.g., soil respiration).

The range of environmental conditions currently described within soil macroecological studies is critical to understand the relationship between soil biodiversity, ecosystem functions, and key environmental conditions (e.g., the known relationship between Bacteria richness and pH[59] or the dependence of soil respiration on temperature[60,61]). In this context, the complete range of soil carbon levels existing on Earth is not well covered, with soils of very high and low carbon contents (Fig. 2a) being underrepresented compared with their global distribution. The same applies to soil type, with only a fraction of soil types being well covered (i.e., acrisols, andosols, cambisols, kastanozems, luvisols and podzols), while others are significantly underrepresented or completely absent (e.g., durisols, stagnosols, umbrisols; Fig. 2o). In contrast, our study identified over- and underrepresented environmental conditions in soil biodiversity and function studies (Fig. 2). For example, some soil properties are well represented across studies, such as soil texture (i.e., sand, silt, and clay content) and pH, with the exception of extreme ranges (e.g., pH > 7.33 or silt content < 19%).

In contrast to to soil conditions, climate variability is systematically poorly covered in soil biodiversity and function studies, with significant climatic ranges being almost completely missing (Fig. 2f-k). These include low and high potential evaporation and aridity areas, areas with high climate seasonality, low precipitation and extreme temperatures (i.e., very hot and very cold systems), with no overall significant differences between biodiversity and ecosystem function studies. Drylands, for example, cover ~45% of the land surface[62] and have been shown to be highly diverse in terms of soil biodiversity and with strong links to specific ecosystem functions[24,63], but are often underrepresented. Climatic conditions (current and future) have strong influences on both soil organisms[57] and functions[60,64]; as such, assessing a wide range of these conditions, including climatic extremes, is fundamental to describe the complex dynamics of soil systems. This issue is further exacerbated when looking at specific climate combinations (Fig. 3c), where 59.6% of the global climate is not covered by any of the studies considered.

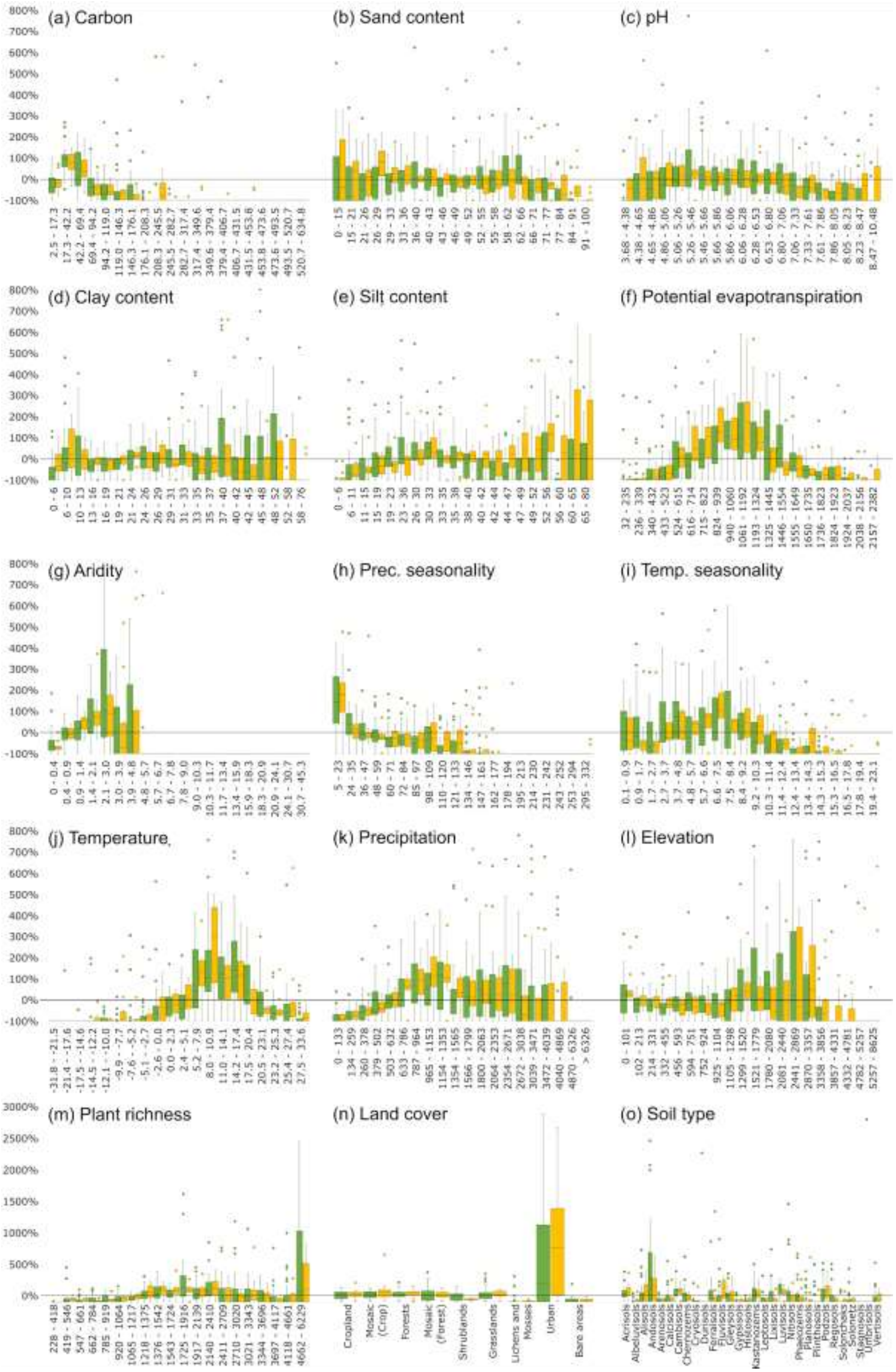
800%
700%
600%
500%
400%
300%
200%
100%
0%
-100%
(a) Carbon
2.5 - 17.3
17.3 - 42.2
42.2 - 69.4
69.4 - 94.2
94.2 - 119.0
119.0 - 146.3
146.3 - 176.1
176.1 - 208.3
208.3 - 245.5
245.5 - 282.7
282.7 - 317.4
317.4 - 349.6
349.6 - 379.4
379.4 - 406.7
406.7 - 431.5
431.5 - 453.8
453.8 - 473.6
473.6 - 493.5
493.5 - 520.7
520.7 - 634.8
(b) Sand content
0 - 15
15 - 21
21 - 26
26 - 29
29 - 33
33 - 36
36 - 40
40 - 43
43 - 46
46 - 49
49 - 52
52 - 55
55 - 58
58 - 62
62 - 66
66 - 71
71 - 77
77 - 84
84 - 91
91 - 100
(c) pH
3.68 - 4.38
4.38 - 4.65
4.65 - 4.86
4.86 - 5.06
5.06 - 5.26
5.26 - 5.46
5.46 - 5.66
5.66 - 5.86
5.86 - 6.06
6.06 - 6.28
6.28 - 6.53
6.53 - 6.80
6.80 - 7.06
7.06 - 7.33
7.33 - 7.61
7.61 - 7.86
7.86 - 8.05
8.05 - 8.23
8.23 - 8.47
8.47 - 10.48
800%
700%
600%
500%
400%
300%
200%
100%
0%
-100%
(d) Clay content
0 - 6
6 - 10
10 - 13
13 - 16
16 - 19
19 - 21
21 - 24
24 - 26
26 - 29
29 - 31
31 - 33
33 - 35
35 - 37
37 - 40
40 - 42
42 - 45
45 - 48
48 - 52
52 - 58
58 - 76
(e) Silt content
0 - 6
6 - 11
11 - 15
15 - 19
19 - 23
23 - 26
26 - 30
30 - 33
33 - 35
35 - 38
38 - 40
40 - 42
42 - 44
44 - 47
47 - 49
49 - 52
52 - 56
56 - 60
60 - 65
65 - 80
(f) Potential evapotranspiration
32 - 235
236 - 339
340 - 432
433 - 523
524 - 615
616 - 714
715 - 823
824 - 939
940 - 1060
1061 - 1192
1193 - 1324
1325 - 1445
1446 - 1554
1555 - 1649
1650 - 1735
1736 - 1823
1824 - 1923
1924 - 2037
2038 - 2156
2157 - 2382
800%
700%
600%
500%
400%
300%
200%
100%
0%
-100%
(g) Aridity
0 - 0.4
0.4 - 0.9
0.9 - 1.4
1.4 - 2.1
2.1 - 3.0
3.0 - 3.9
3.9 - 4.8
4.8 - 5.7
5.7 - 6.7
6.7 - 7.8
7.8 - 9.0
9.0 - 10.3
10.3 - 11.7
11.7 - 13.4
13.4 - 15.9
15.9 - 18.3
18.3 - 20.9
20.9 - 24.1
24.1 - 30.7
30.7 - 45.3
(h) Prec. seasonality
5 - 23
24 - 35
36 - 47
48 - 59
60 - 71
72 - 84
85 - 97
98 - 109
110 - 120
121 - 133
134 - 146
147 - 161
162 - 177
178 - 194
195 - 213
214 - 230
231 - 242
243 - 252
253 - 294
295 - 332
(i) Temp. seasonality
0.1 - 0.9
0.9 - 1.7
1.7 - 2.7
2.7 - 3.7
3.7 - 4.8
4.8 - 5.7
5.7 - 6.6
6.6 - 7.5
7.5 - 8.4
8.4 - 9.2
9.2 - 10.3
10.3 - 11.4
11.4 - 12.4
12.4 - 13.4
13.4 - 14.3
14.3 - 15.3
15.3 - 16.5
16.5 - 17.8
17.8 - 19.4
19.4 - 23.1
800%
700%
600%
500%
400%
300%
200%
100%
0%
-100%
(j) Temperature
-31.8 - -21.5
-21.4 - -17.6
-17.5 - -14.6
-14.5 - -12.2
-12.1 - -10.0
-9.9 - -7.7
-7.6 - -5.2
-5.1 - -2.7
-2.6 - 0.0
0.0 - 2.3
2.4 - 5.1
5.2 - 7.9
8.0 - 10.9
11.0 - 14.1
14.2 - 17.4
17.5 - 20.4
20.5 - 23.1
23.2 - 25.3
25.4 - 27.4
27.5 - 33.6
(k) Precipitation
0 - 133
134 - 259
260 - 378
379 - 502
503 - 632
633 - 786
787 - 964
965 - 1153
1154 - 1353
1354 - 1565
1566 - 1799
1800 - 2063
2064 - 2353
2354 - 2671
2672 - 3038
3039 - 3471
3472 - 4039
4040 - 4869
4870 - 6326
> 6326
(l) Elevation
0 - 101
102 - 213
214 - 331
332 - 455
456 - 593
594 - 751
752 - 924
925 - 1104
1105 - 1298
1299 - 1520
1521 - 1779
1780 - 2080
2081 - 2440
2441 - 2869
2870 - 3357
3358 - 3856
3857 - 4331
4332 - 4781
4782 - 5257
5257 - 8625
3000%
2500%
2000%
1500%
1000%
500%
0%
(m) Plant richness
228 - 418
419 - 546
547 - 661
662 - 784
785 - 919
920 - 1064
1065 - 1217
1218 - 1375
1376 - 1542
1543 - 1724
1725 - 1916
1917 - 2139
2140 - 2410
2411 - 2709
2710 - 3020
3021 - 3343
3344 - 3696
3697 - 4117
4118 - 4661
4662 - 6229
(n) Land cover
Cropland
Mosaic (Crop)
Forests
Mosaic (Forest)
Shrublands
Grasslands
Lichens and Mosses
Urban
Bare areas
(o) Soil type
Acrisols
Albeluvisols
Alisols
Andosols
Arenosols
Calcisols
Cambisols
Chernozems
Cryosols
Durisols
Ferralsols
Fluvisols
Gleysols
Gypsisols
Histosols
Kastanozems
Leptosols
Lixisols
Luvisols
Nitisols
Phaeozems
Planosols
Plinthosols
Podzols
Regosols
Solonchaks
Solonetz
Stagnosols
Umbrisols
Vertisols

Fig. 2 Global soil ecological blind spots. Values (y-axis) correspond to the percentage of sites per study per class when compared with the global proportional distribution of each class within each variable defining soil ecosystems (soil biodiversity studies in green and ecosystem function studies in orange): (a) soil carbon [g/soil kg][65]; (b) sand content [%][65]; (c) soil pH[65]; (d) clay content (%)[65]; (e) silt content (%)[65]; (f) potential evapotranspiration[66]; (g) aridity index[66]; (h) precipitation seasonality[67]; (i) temperature seasonality[67]; (j) mean annual temperature[67]; (k) mean total precipitation[67]; (l) elevation[68]; (m) vascular plant richness[69]; (n) land cover[70]; (o) soil type[65]. The zero black line corresponds to a situation where the proportion of sites in a given class within a study matches the global proportional representation of the same class. Although outliers were not eliminated, for representation purposes these were omitted >800% between panels a to l and <3000% for panels m to o.

Although representing a major driver of soil biodiversity and function[4], land-cover based studies have shown different responses across groups of soil organisms[56,71,72] and specific functions[73,74]. While, in general, land cover types are well covered, sites in the proximity of urban areas are disproportionately represented (Fig. 2n). Lichens, mosses, and bare areas have been neglected, and shrublands are not well represented in ecosystem function assessments. These gaps may have important implications, particularly when they correlate with understudied ecosystems like drylands or higher latitude systems that may harbor high biodiversity[63], but for which patterns are mostly unknown. In this context, the present analysis indicates that low diversity areas (here represented as plant richness[69]) are absent from most studies or poorly represented, with the focus being mostly on higher diversity areas. Concurrently, it has been suggested that there may be important mismatches between above- and belowground biodiversity across the globe[75], i.e., there are huge areas where aboveground biodiversity does not well predict belowground biodiversity.

When looking at how belowground studies cover the combinations of aboveground diversity (Fig. 3a) and of soil conditions (Fig 3b), important mismatches are observed. We also looked at combinations of environmental gradients. Here, although most soil-related environmental combinations (Fig. 3b) are well covered across studies, the same does not apply when looking at the aboveground diversity (Fig. 3a), which shows a very good coverage in forest and crop areas with above average plant richness in mid to low elevations, while other environmental combinations are underrepresented. Overall, while it is unreasonable to expect all macroecological studies to cover all possible soil conditions, the systematic underrepresentation of many soil characteristics observed here may undermine our capacity to generalise results given that they do not capture the full ecological space of soil organisms.

Many of the reasons and drivers of existing data gaps have already been illustrated in recent literature for aboveground systems[16] (e.g., accessibility, proximity to large cities, etc.). In the case of soil biodiversity and ecosystem functions, these blind spots are further reinforced because of the lack of standardized protocols for acquiring biodiversity and ecosystem function data. This translates into an absence of comparable data, which is even more pronounced than in other systems[16,76]. Nevertheless, there is a continuous movement towards improving data mobilization and international collaborations that could help overcome these issues if steered in the direction of underestimated taxa and/or functions identified here[77].

In a changing world where soil biodiversity shifts are being systematically reported[78–80], and where current forecasts are pointing to increases in land-use intensity[81,82], desertification[83], and rapid climate change[84–87], understanding if and to what extent biodiversity changes are happening in soil communities is of high importance. This is particularly relevant to assess causal effects between changes in biodiversity and ecosystem function (e.g., are changes in biodiversity occurring because of changes in function, paired with them, or despite them, and *vice versa*), which is even more relevant if key ecosystem functions (e.g., carbon sequestration) are the subject of evaluation.

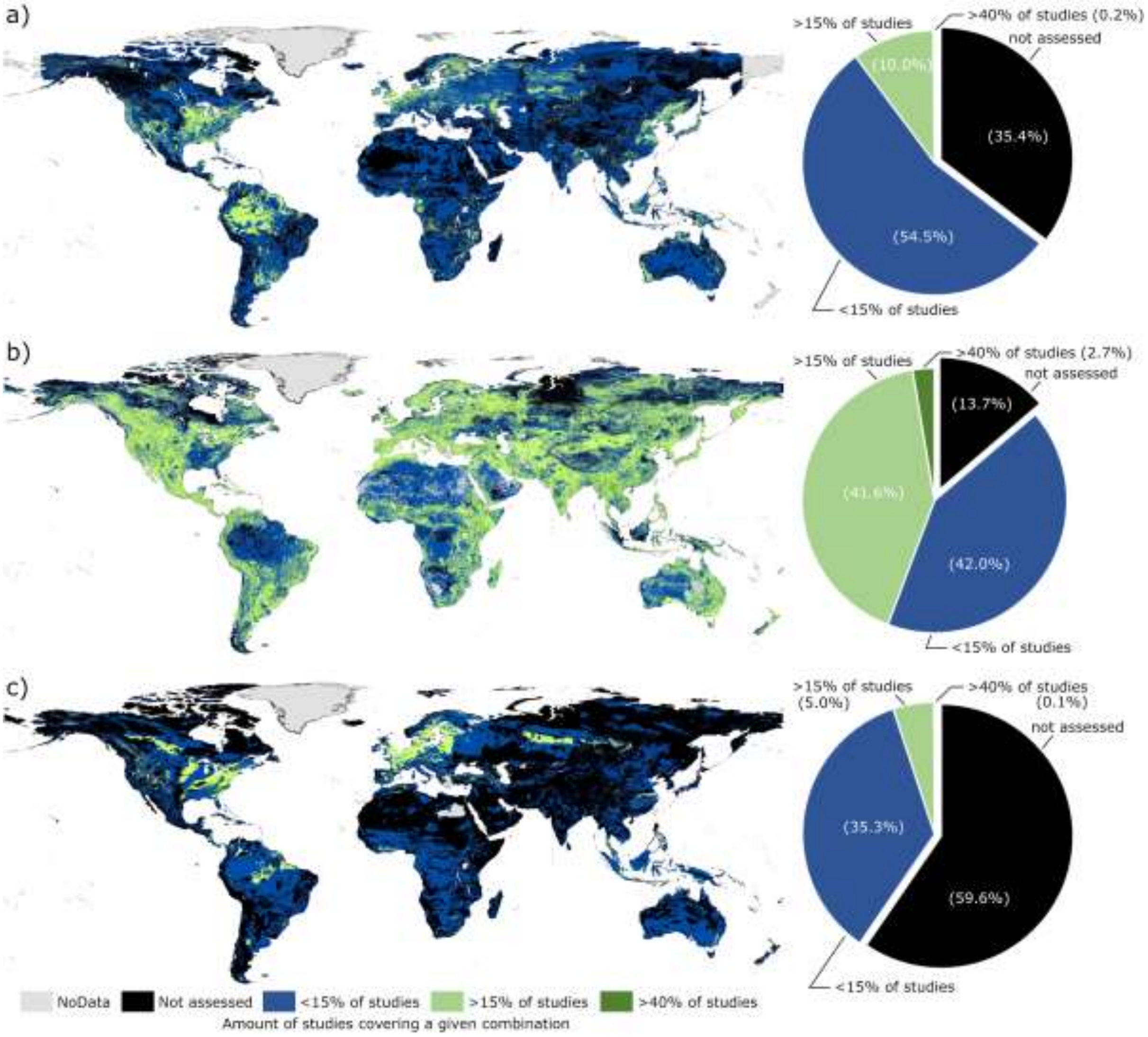

Fig. 3 The extent to which main soil environmental characteristics are assessed across macroecological studies. Colours correspond to the amount of studies covering a given combination of characteristics (see Methods for more details) within: a) land cover (including the combination of land cover, plant diversity and elevation); b) soils (including the combination of organic carbon content, sand content and pH); and c) climate (including the combination of mean precipitation and temperature, and their seasonality). Black corresponds to combinations that were not assessed by any of the studies here included; in blue are the combinations assessed by less than 15% of the studies (N= 7); in light green the variable combinations assessed by less than 40% of the studies (N=18); and in dark green, the variable combinations assessed by more than 40% of the studies. All combinations were created by a spatial overlap using the same class distribution of each variable as in Fig. 2 (see Methods and Fig. S4a-e for more details).

Filling the knowledge gap on large-scale temporal trends in soil biodiversity and ecosystem function cannot be achieved without spatially explicit studies based on resampled locations. This could be done with a proper global monitoring framework that is recognized and supported by a large number of countries, which currently does not exist. In this context, given the strength of recognized soil taxa interactions[88], biodiversity and ecosystem function relationships[24], and above-belowground interactions[89], these large-scale monitoring activities and research studies should consider going beyond traditional single taxa/function approaches and collect information on the multiple dimensions of soil ecosystems[28], while at the same time expanding/supporting surveys to cover the blind spots of soil macroecological research (Fig. 3).

2.3. Challenges to move beyond blind spots

Across all soil taxa and functions, the geographical and ecological blind spots identified here often emerge from a number of obstacles specific to soil ecology[77] (see summary in Table 1). Soil macroecologists face many challenges and constraints spanning from a lack of methodological standards and scientific expertise in different taxonomic groups[90–92], to limitations caused by the current implementation of the Convention for Biological Diversity (CBD) and the Nagoya Protocol[93,94]. While the first has more immediate, albeit non-trivial solutions (e.g., by expanding the language pool of the researchers and studies included[16,95] and by applying common standards for sampling, extraction, and molecular protocols[96–99]), the latter contains systemic issues that go beyond soil ecology alone. In this context, although the CBD and the Nagoya Protocol were created to protect countries while making the transfer of biological material more agile, numerous states have either not yet implemented effective national Access and Benefit Sharing (ABS) laws or have implemented very strict regulations[100,101]. Yet, even after 25 years of the CBD and the ABS framework being in place, the major motivation for a strict national regulation - the anticipated commercial benefits and high royalties from the "green gold" - has not yet materialized[93,102].

Table 1 Summary of the main obstacles soil ecologist face to create a global soil biodiversity monitoring network and the priority actions to overcome them.

Challenges	**Priority Actions**		
	Researchers	**Institutions**	**Policymakers**
Legal issues regarding the transport and sharing of soil samples and biological data	• Raise the awareness of institutions and decision-makers about the importance of these legal bottlenecks for the development of	Develop a legal understanding of the implications of material transfer mechanisms for soil samples and provide support to	Establish global multilateral solutions and International Treaties focused on soil biodiversity and ecosystem

	international research programs.	researchers also by promoting knowledge and expertise exchange. Support and facilitate the establishment of international consortia and bilateral institutional agreements particularly with developing countries	function research. Establish knowledge transfer mechanisms for soil-related research together with the classification of soil samples for research purposes.
Scattered literature and lack of mobilization/ systematization of local studies	Invest in data harmonization, synthesis, meta-analysis approaches, data collation, and proper metadata to improve currently available datasets (e.g., through GBIF for soil biodiversity). Define and publish data standards that allow for better data transfer focussing on the methods, reporting in standard units, and best practices for data availability. Increase the focus on understudied soil groups (e.g., collembola, acari, protists, mammals) and functions (e.g., soil aggregate stability, bioturbation, nutrient cycling). Establish effective coordination of current networks to support the development of integrated ecological assessments of the soil realm	Adoption of available data and methods standards[99,103–107] and support the establishment and maintenance of data repositories and open access policies.	Support open access partnerships (e.g., the German DEAL[108]) to facilitate knowledge transfer and collaboration across countries and researchers from different backgrounds and expertise. Improve the digitally available data on soil biodiversity and ecosystem function by supporting the expansion of current global databases (e.g., GBIF) or the creation of interoperable data infrastructures on soil function data.
Lack of temporally explicit information on soil biodiversity and functions	Identify relevant sites - e.g., sites covering a wide range of taxa or functions and/or a high degree of standardization - for resampling. Revisit already sampled sites to obtain temporal measurements of soil biodiversity and ecosystem function.	Institutional support of long-term databases and collections of soils, soil functional data, and soil biological material.	Create funding schemes for strategic long-term research projects on soil monitoring and research (e.g., using the LTER framework as an example[109]).
Lack of globally distributed expertise, research funding and infrastructures	Promote knowledge transfer mechanisms and capacity building, especially with developed countries that might see little advantage of being involved in a global network that only offer co-authorship as the main benefit. Setup international workshops, summer schools, or classes with a focus on educating the next generation of scientists on different aspect of soil ecology.	Build on or expand current networks to include knowledge transfer activities, namely on education, methods calibration, sharing research facilities, and taxonomic expertise.	Promote funding flexibility to train and empower researchers across countries and/or regions, also allowing local scientists, particularly in the developing world, to conduct soil biodiversity and ecosystem function research. Establish soil health as a research priority beyond farming areas and with a special focus on ecological conservation of soil organisms and ecosystem functions.

Researchers have yet to coordinate a global effort to characterize the multiple aspects of soil biodiversity and function in a comprehensive manner, with the current literature being dominated by scattered, mostly local studies focused on specific soil organisms and/or functions. Although here we do not assess the potential of local studies to overcome the current blind spots, other studies[34,35,64] have shown that, with a significant effort in standardization and data mobilization, local and regional studies add fundamental knowledge and empower local researchers to participate in global initiatives. In fact, several studies not included in this assessment can provide a finer-scale resolution in many areas of the globe[71,110,111].

Nevertheless, their spatial extent systematically coincides with overrepresented areas (e.g., temperate areas), and their taxonomic and functional focus is mostly on the already prevailing taxa (i.e., Bacteria and fungi) and functions (i.e., soil respiration), potentially increasing existing biases. This increases the relevance of facilitating data mobilization from regions and, more importantly, environmental conditions that are systematically not covered by macroecological studies.

In parallel, and given the nature of global change drivers, understanding their influence on local soil communities and ecosystem functioning requires global macroecological approaches that can provide context, predictions, and concrete suggestions to policymakers across the globe. Yet these macroecological approaches will be less effective in providing relevant outputs at national scales if they are based on data extrapolated from other countries; they would be strongly improved if local data were made available[25,112]. Without more comprehensive studies seeking answers to large-scale soil ecological questions - often involving dealing with multiple scales (temporal and spatial) and a number of thematic and taxonomic depths[75] - it is difficult to deepen soil macroecological knowledge[113]. This is particularly relevant in testing biodiversity and ecosystem function relationships at the global scale, or trying to address specific societal issues (e.g., the attribution of climate and land-use change as drivers of soil ecological change or general biodiversity trends)[17].

Another major challenge is associated with the fact that currently ABS agreements are bilateral. This hinders global soil ecology initiatives as it requires that providers and receivers need limited individual material transfer agreements. Thus, for a global initiative, this can amount to hundreds of material transfer agreements. However, there is an increasing quest for global solutions and multilateral systems, such as the International Treaty on Plant Genetic Resources for Food and Agriculture (IT PGRFA; www.fao.org/3/a-i0510e.pdf), or other harmonized best practices examples like the Global Genome Biodiversity Network[94]. As the commercial value of soil organisms is regarded to be zero *in situ*[114], and as these are mostly ubiquitously distributed at the highest taxonomic level (e.g., Bacteria and fungi), soil *per se* has no commercial value as it does not match the criteria that "provider countries host unique and unmatched biodiversity" of the Nagoya Protocol[115]. Therefore, a global multilateral solution, similar to the examples listed above (e.g., the IT PGRFA), but focused on facilitating the exchange of soil samples to drive basic research on soil biodiversity, taxonomy, and ecosystem functioning, while still safeguarding against the spread of foreign genotypes, is pressingly needed. At the same time, as long as bilateral ABS agreements are required, researchers should engage with local policymakers to enable unrestricted soil biodiversity and ecosystem function research, as was the case for Brazil from 2006 to 2016[116].

2.4. Looking for solutions to unearth global observations

Globally, soil habitats are under constant pressure from major threats, such as climate change, land use change and intensification, desertification, and increased levels of pollution. Here, we argue for a global monitoring initiative that systematically samples soil biodiversity and ecosystem functions across space and time. Such a global initiative is urgently needed to fully understand the consequences of ongoing global environmental change on the multiple ecosystem processes and services supported by soil organisms (Table 1). This requires that current and future funding mechanisms include higher flexibility for the involvement of local partners from different countries in global research projects. Given that soil ecological research requires cross-border initiatives[77] and expensive infrastructure, there is a need for flexible funding with proper knowledge transfer mechanisms to sustain global soil macroecological research. Such knowledge will in turn contribute to advancing our understanding of macroecological patterns of soil biodiversity and ecosystem function, thereby fulfilling national and global conservation goals[114,117,118].

Considering the current pool of literature, improving the digitally available data on soil biodiversity and ecosystem function should be a top priority that could be made possible by systematically mobilizing the underlying data[119] in already existing open access platforms (e.g., GBIF). Achieving this goal on shared knowledge and open access data will return benefits beyond making global soil biodiversity surveys possible. It will allow local researchers to expand their own initiatives, create a more connected global community of soil ecologists, bypassing publication and language limitations, and potentially open doors in countries that may otherwise be reluctant in sharing their soil biodiversity data[27].

In parallel, coordinated sampling strategies based on standardized data collection and analysis are needed to improve soil macroecological assessments. From our results, it is clear that most, if not all, studies look at only a fraction of the soil realm without much spatial and thematic complementarity of global environmental conditions. Also, the significantly small overlap between biodiversity and functional studies indicates that most community assessments disregard the ecosystem functions that these provide and *vice versa*, prompting a call for more complex approaches that can show potential links and global ecosystem services. Our study helps to identify global target locations and biomes which need to be given priority in future surveys. Future sampling strategies would greatly benefit from coordinated sampling campaigns with biodiversity and function assessments at the same locations and ideally from the same soil samples to improve the current spatial-temporal resolution of data on soil biodiversity and ecosystem functions.

These two complementary pathways (i.e., data mobilization and sharing of current literature and a globally standardized sampling) if done in a spatially explicit context, and following standardized protocols, could ultimately inform predictive modelling frameworks for soil ecosystems to track the fulfilment of global/national biodiversity targets, policy support, and decision making. Taken together, our study shows important spatial and environmental gaps across different taxa and functions that future macroecological research should target, and a need to collect temporal datasets to explore if current aboveground biodiversity declines are also seen in belowground taxa. With the identification of global spatial, taxonomic, and functional blind spots, and the definition of priority actions for global soil macroecological research[75], our synthesis highlights the need for action to facilitate a global soil monitoring system that overcomes the current limitations.

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