

New Global Species Biodiversity: Soil soars, Ocean flounders

Robert J. Blakemore PhD

VermEcology, 101 Suidomichi, Nogeyama, Kanagawa-ken 231-0064, Japan.

C/- Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa-ken 247-0007.

Email: rob.blakemore@gmail.com

ABSTRACT

Based on topographic field data, an argument is advanced that Soil houses $\sim 2.1 \times 10^{24}$ taxa and supports >99.9% of global species biodiversity, mostly Bacteria or other microbes. Contradictory claims that Soil is home to only a quarter of biota while Ocean harbours 80-99% of Life on Earth are both dismissed. Earlier guesstimates of ~ 8.8 million taxa (~ 2.2 million or 25% marine), of 1-6 billion, or up to over a trillion species worldwide are likely underestimations. Recent studies show $>10^{12}$ microbial OTUs (just 10^{10} or $\sim 1\%$ in Ocean) soon raised to 10^{12} - 10^{14} and speculated as high as 10^{22} - 10^{23} species. Scaling of simple topsoil samples herein ups the total taxa. Biomass at 2×10^{-13} g of all 2.1×10^{30} soil cells totals $\sim 4 \times 10^{17}$ g or ~ 400 Gt (= ~ 200 Gt carbon).

INTRODUCTION

An honest inventory of our global biotic stock is vitally important in order to estimate biodiversity and track extinctions. False claims that soil has “*more than 25% of our planet's biodiversity*” (Ref.) and simultaneously ocean has 80% (Ref.) or “*97 percent of life in the world, maybe in the universe*” (Ref.) or “*99% of the habitable space on this planet*” (Ref.) are clearly misguided.

Table 2. Currently catalogued and predicted total number of species on Earth and in the ocean.

Species	Earth			Ocean		
	Catalogued	Predicted	$\pm SE$	Catalogued	Predicted	$\pm SE$
Eukaryotes						
Animalia	953,434	7,770,000	958,000	171,082	2,150,000	145,000
Chromista	13,033	27,500	30,500	4,859	7,400	9,640
Fungi	43,271	611,000	297,000	1,097	5,320	11,100
Plantae	215,644	298,000	8,200	8,600	16,600	9,130
Protozoa	8,118	36,400	6,690	8,118	36,400	6,690
Total	1,233,500	8,740,000	1,300,000	193,756	2,210,000	182,000
Prokaryotes						
Archaea	502	455	160	1	1	0
Bacteria	10,358	9,080	3,470	652	1,320	436
Total	10,860	10,100	3,630	653	1,320	436
Grand Total	1,244,360	8,750,000	1,300,000	194,409	2,210,000	182,000

Predictions for prokaryotes represent a lower bound because they do not consider undescribed higher taxa. For protozoa, the ocean database was substantially more complete than the database for the entire Earth so we only used the former to estimate the total number of species in this taxon. All predictions were rounded to three significant digits.
doi:10.1371/journal.pbio.1001127.t002

Figure 1. Mora *et al.* (2011: tab. 2) Earth's taxa has ~ 8.8 million (~ 2.2 million or 25% marine!).

In a highly biased survey range of 3–100 million taxa (10^6 – 10^8), Mora *et al.* (2011: tab. 2) chose a mere ~8.8 million (~2.2 million or 25% marine). Whereas Larsen *et al.* (2017) proposed a new Pie of Life projected for >1–6 billion (10^9) species on Earth dominated by Bacteria (~70–90% of total) which they mainly considered for insect hosts. Mundanely, they also found on average six cryptic species per morphologically described arthropod taxon (their [tab. S1](#)) quite counterbalancing approximately 20% of published eukaryote names that are synonyms (Ref.).

Subsequently, Louca *et al.* (2019) claimed only “about 2.2–4.3 million full-length OTUs [unique taxa] worldwide” (10^6) refuting predictions that billions or trillions of prokaryotic OTUs exist. Wiens (2021) explained how Louca *et al.* (2019) had made entirely avoidable underestimation errors whilst also revising Larsen *et al.*'s (2017) projected 1–6 billion estimate downwards to 0.183 to 4.2 billion (10^8 – 10^9) species with 58–88% Bacteria, again most of these in insect hosts.

Bahram *et al.* (2018) concluded soils are Earth's most diverse biomes, but fail to give figures.

High-throughput genomic sequencing and bioinformatics studies allow scaling values based on Locey & Lennon (2016: fig. 3 below) showing Earth with $\sim 10^{12}$ microbial OTU taxa (just 10^{10} or ~1% in global Ocean). These totals were later raised to 10^{12} – 10^{14} microbial taxa by Lennon & Locey (2020) and then by Fishman & Lennon (2022) who had “a soft upper constraint of 10^{22} – 10^{23} due to neutral drift”. Most of these taxa at any time are likely dormant (Ref.) and/or unculturable as fewer than 1% of the soil species are culturable (Schloss & Handelsman, 2006).

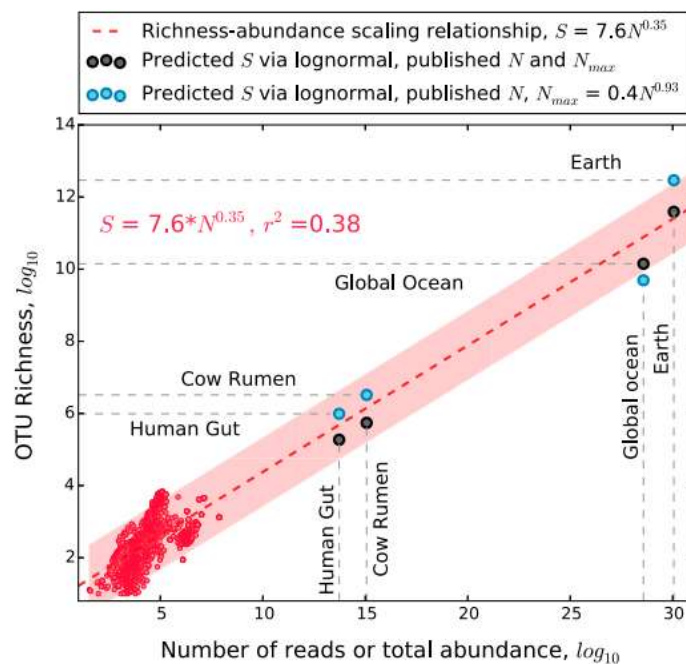


Fig. 3. The microbial richness-abundance scaling relationship (dashed red

Figure 2. From Locey & Lennon (2016: fig. 3) with Earth's 10^{12} taxa (just 10^{10} or 1% Oceanic).

However, to date, none of the estimates of terrestrial biodiversity have considered terrain that may easily double soil surface area (Blakemore, [2018b](#)). All estimates based upon planimetrically flat land areas are manifestly deficient since land is hilly and soil bumpy. Thus this study aims to estimate soil microbial totals taking terrain into consideration for the first time.

As Blakemore ([2018b](#)) stated: "A single gramme ($\sim 1 \text{ cm}^3$) of fertile topsoil may have three billion microbes (Bacteria, Actinomycetes, Archaea, Fungi, Protozoa, etc.), up to 60 km of fungal hyphae, with 10,000 to 50,000 microbial species having 1,598 km of DNA some dating to the beginning of life four billion years ago." Average soil carbon is $\sim 1\text{--}2\%$ and global soil organic carbon (SOC) alone amounts to $>10,000 \text{ Gt}$, thus if one g of soil has $>10,000 \text{ spp}$, its total biodiversity must be truly astronomical and lower values or figures above are likely most modest.

METHODS

Two main steps to determine the status of soil biota are to review sample surveys to obtain a consensus per gram then to determine the soil matrix extent to give an overall estimate of totals.

How many species per gram or tonne of soil?

Curtis *et al.* ([2002](#)) stated: "the entire bacterial diversity of the sea may be unlikely to exceed 2×10^6 , while a ton of soil could contain 4×10^6 different taxa" (or 4 million taxa) which seems a substantial underestimation error as "species of bacteria per gram of soil vary between 2,000 and 8.3 million" (Gans *et al.*, [2005](#); Roesch *et al.* [2007](#)) ($= 10^4\text{--}10^6 \text{ spp/g}$ or $10^{10}\text{--}10^{12} \text{ spp/t}$ that, if all unique taxa, is equivalent to twenty billion up to a trillion spp per ton of topsoil). [Discrepancies in Gans *et al.* are samples of 10 g soil so strictly $0.83 \times 10^6 \text{ spp/g}$, yet their fig. 4 shows total species number computed as up to 10^7 thus a million or so spp per g seems correct].

Raynard & Nunan ([2014](#)) had: "densities commonly found in bulk soil ($10^8 \text{ cells g}^{-1} \text{ soil}$)" or "a single gram of soil can harbour up to 10^{10} bacterial cells and an estimated species diversity of between 4×10^3 [1] to 5×10^4 species [2]" ($= 10^{14}\text{--}10^{16} \text{ cells/t}$ and $4 \times 10^9\text{--}5 \times 10^{10} \text{ spp/t}$).

Bickel & Orr ([2020](#)) found: "bacterial phylotypes ranges between 10^2 and 10^6 per gram of soil^{1,2,4}, with high values similar to the diversity in all of earths environments³" ($= 10^8\text{--}10^{12} \text{ spp/t}$).

Madison James *et al.* ([2022](#)) summarize: "Soil microorganisms are the largest biodiversity pool on earth, with more than 10^{30} microbial cells [total surely!], $10^4\text{--}10^6$ species, and nearly 1,000 Gbp of microbial genome per gram of soil (Vogel *et al.*, [2009](#); Mendes and Tsai, [2018](#))".

Soils naturally include root-zone Rhizosphere: "the most diverse microbiomes on Earth, containing up to 10^{11} microbial cells and $\sim 30,000$ bacterial species per gram of root [1]. The rhizosphere microbiome exists through an interwoven tapestry of bacteria, viruses, archaea,

protists, fungi, nematodes, and small arthropods interacting directly with plant roots and each other" (White *et al.*, 2021). McNear (2013) has " 10^{10} – 10^{12} cells per gram rhizosphere soil".

Thus soil has up to 10^8 – 10^{12} cells/g or 10^{14} – 10^{18} cells/t, there being 10^6 grams in a tonne.

Soil biodiversity ranges 10^2 – 10^6 spp/g or 10^8 – 10^{12} spp/t, there being 10^6 grams in a tonne.

How many tonnes of topsoil on Earth?

Estimates by Whitman *et al.* (1998: tab. 2 below) cites 2.6×10^{29} prokaryotic cells in 1.2×10^{14} m² soil. They footnote 1 m of topsoil ranges from 10^7 to 10^9 cells per gram (median 10^8 /g) with 1.3 t per cubic metre to give a global total of (1.2×1.3) = **$\sim 1.6 \times 10^{14}$ t of topsoil to 1 m depth.**

Table 2. Number of prokaryotes in soil

Ecosystem type*	Area, $\times 10^{12}$ m ²	No. of cells,† $\times 10^{27}$
Tropical rain forest	17.0	1.0
Tropical seasonal forest	7.5	0.5
Temperate evergreen forest	5.0	0.3
Temperate deciduous forest	7.0	0.4
Boreal forest	12.0	0.6
Woodland and shrubland	8.0	28.1
Savanna	15.0	52.7
Temperate grassland	9.0	31.6
Desert scrub	18.0	63.2
Cultivated land	14.0	49.1
Tundra and alpine	8.0	20.8
Swamps and marsh	2.0	7.3
Total	123.0	255.6

*From ref. 73.

†For forest soils, the number of prokaryotes in the top 1 m was 4×10^7 cells per gram of soil, and in 1–8 m, it was 10^6 cells per gram of soil (16). For other soils, the number of prokaryotes in the top 1 m was 2×10^9 cells per gram of soil, and in 1–8 m, it was 10^8 cells per gram of soil (18). The boreal forest and tundra and alpine soils were only 1 m deep. A cubic meter of soil was taken as 1.3×10^6 g.

Figure 3. From Whitman *et al.* (1998: tab. 2).

Conversely, Blakemore (2018b: fig. 4; tab. 5) has "habitable land" of 104×10^6 km² presumably with rich humic topsoil, say ~ 1 m deep (and ~ 1 t per m³), there being 10^6 m² in a km², thus 1.04×10^{14} t or 104,000 Gt. Doubled for terrain is about 208,000 Gt or **$\sim 2.1 \times 10^{14}$ t global topsoil.**

RESULTS

If 10^{14} – 10^{18} cells/t soil $\times 2.1 \times 10^{14}$ t the range is 2.1×10^{28} – 10^{32} cells (median $\sim 2.1 \times 10^{30}$).

A range of 10^8 – 10^{12} spp/t $\times 2.1 \times 10^{14}$ t gives 2.1×10^{22} – 10^{26} spp total (median $\sim 2.1 \times 10^{24}$).

Biomass carbon content Whitman *et al.* (1998) took as half the average soil prokaryotic cell dry mass of 2×10^{-13} g, thus 2.1×10^{30} cells would total $\sim 4 \times 10^{17}$ g or ~ 400 Gt (= ~ 200 Gt carbon).

DISCUSSION

Properly allowing for terrain, Earth's surface as exposed to Sun, air and rain of Land vs. Ocean from Blakemore (2018b) is 64:36%; so Soil has by far the largest area and supports most biota.

Whitman *et al.* (1998) initially estimated microbial prokaryotes cell numbers in Soil vs. Ocean as 2.6×10^{29} vs. 1.2×10^{29} , respectively (68% vs. 32%); biomass soil carbon was 26 vs. 2.2 Gt C (92% vs. 8%). Soil was to 1 or 8 m depth, Ocean included open water and 10 cm of sediment. My present value of 2.1×10^{30} soil cells to just 1 m increases their Soil tally by about ten times.

For global biodiversity, a reasonable status summary by Fishman & Lennon (2022) had: “*the present number of bacterial and archaeal taxa $S_{present}$ is between 10^6 and 10^{23} .*” My present estimate of $\sim 2.1 \times 10^{24}$ soil species increases their upper value by a factor of about twenty times but a lower $\sim 2.1 \times 10^{20}$ soil species—as calculated below—is within their range. Adding weight to the argument, the methods to achieve these similar conclusions were calculated independently.

Whereas terrain doubles area at metre scale, at cm–mm sampling scale it is likely quadrupled. Blakemore (2018b: tabs. 5–6) had x1, x2 and x4 soil as 162,000 Gt (agreeing with Whitman *et al.*, 1998: tab. 2), 324,000 and 648,000 Gt, respectively; or 1.6, 3.2 and 6.5×10^{14} t soil. My median scaling estimate of around $\sim 2.1 \times 10^{24}$ soil microbial taxa is therefore likely a low value that may be readily doubled (see - <https://vermecology.wordpress.com/2022/08/04/different-f3/>). Accounting for neglected terrain & topography at cm–mm scale, may double soil microbial tallies again to $\sim 4.2 \times 10^{30}$ cells, $\sim 4.2 \times 10^{24}$ spp and biomass total of ~ 800 Gt (= ~ 400 Gt C).

Accepting $\sim 2.1 \times 10^{30}$ soil microbial cells with $\sim 2.1 \times 10^{24}$ taxa implies one unique taxon per million microbial cells. Albeit if as many as 99% of soil microbes were eventually proven ubiquitous “species”, $\sim 2.1 \times 10^{22}$ different genetic phylotypes would remain. Soils are often deeper than 1 m, but if such high species richness occurred in only the top 10 cm of 10% of Earth's topsoils, it would yet total in the order of $\sim 2.1 \times 10^{20}$ species. Higher values seem reasonable as random samples separated by up to 9,000 km had only <1.5% bacterial taxa in common to all, the majority of 88% OTUs unique to just one soil (Fulthorp *et al.*, 2008). A similar figure of 80% wholly endemic taxa per soil sample was found by Schloss & Handelsman (2006). Moreover, Operational Taxonomic Units often apply to Genera comprising many species. Such findings attest to and support a massive Soil microbial biodiversity, orders of magnitude above the cold, dark, depleted and ever-mixing Ocean's.

For the Ocean, Ferrer *et al.* (2019) categorically state: “*It is estimated that the ocean.. hosts the largest population of microbes on Earth. More than 2 million eukaryotic and prokaryotic species are thought to thrive both in the ocean and on its surface.*” Hoshino *et al.* (2020) claim: “*Global marine sedimentary taxonomic richness predicted by species–area relationship models is 7.85×10^3 to 6.10×10^5 for Archaea and 3.28×10^4 to 2.46×10^6 for Bacteria as amplicon sequence*

variants, which is comparable to the richness in seawater and that in topsoil [!]” also “the global diversity of marine prokaryotes (Archaea and Bacteria) in the near-surface ocean (0 to 1,000 m below sea level [mbsl]) was estimated (3.75×10^4 operational taxonomic units)”.

Remarkably, a couple of grams of topsoil has an equivalent to all Ocean’s total 10^4 – 10^6 taxa!

Furthermore, Whitman *et al.* (1998) had 5×10^{19} cfu (colony forming units) in the atmosphere, and, since only 1% of Bacteria are culturable, this likely equates to 5×10^{21} cells. That is about 500 times the estimate of Curtis *et al.* (2002) who said: “The atmosphere is thought to have an NT [total “individuals” (sic for microbes with binary fission!) of aerobiotic cells] value of 10^{19} , which is sufficient to accommodate 4×10^6 taxa” or 4 million species (most taxa shared with soils?). This is also twice the Ocean’s best tally whilst also exceeding it as the Earth’s largest biome. Aquatic taxa totals are proportionately infinitesimal. Prior to latest microbial totals, mainly in soil on land was already shown to support 99.7% of biomass and 98.0% of biodiversity (Blakemore, 2020: fig. 2; - <https://vermecology.wordpress.com/2020/05/27/realms-of-the-soil/>).

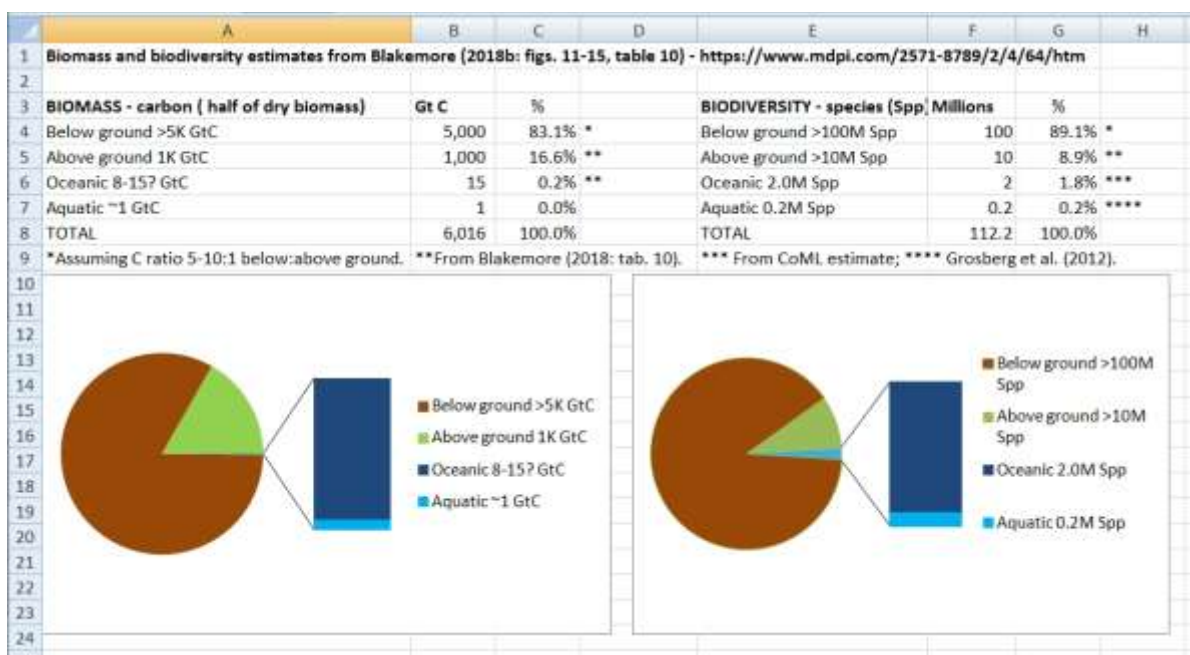


Figure 4. Blakemore (2020: fig. 2) Global soil biomass & biodiversity (~90% now upped >99.9%).

How much soil biota is currently known and why is it so important?

Soil provides 99.7% human food (Pimental & Burgess, 2013), all our fibres and building materials, many of our medicines (such as Penicillin, Streptomycin or Ivermectin), filters and stores most of our freshwater supplies, and supports >99.9% of biodiversity albeit we know <0.0001% of soil fauna, fungi or flora (my estimate is just 310,000 soil species currently

described, mostly microbes or invertebrates such as earthworms). Furthermore, an argument may be made to include all plants that seed or root in soils as soil flora (~4–500,000 spp - [Ref.](#)).

Table 3: Abundance and biodiversity estimates for common soil Invertebrates [from Brusaard *et al.* 1997; Wall & Moore 1999; Chapman 2009; Turbe *et al.* 2010; Tab. 1; Blakemore, 2012; and Wikispecies ([Ref.](#)) sources and pers. obs.]. Note: all species have many unique symbionts/parasites too *

Soil Invertebrate Group	Individuals (approx.)	m ²	Biomass g m ²	Known species	% Known
Bacteria and Archaea	10 ¹²		20-500*	3,200	<<1%?
Fungi	(500+km)		20-500*	80,000	0.5%
Protozoa	10 ¹⁰		6-30	1,500	8%
Rotifera (Bdelloid soil rotifers)	10 ⁵		?	300	?
Nematoda	10 ⁸		1-30	25,000	~1.3%
Lobopodia (Onychophora, Tardigrada)				-1,200	<<50%
<i>Lobopodia (Onychophora)</i>	?		?	<200	50%
<i>Lobopodia (Tardigrada)</i>				-1,000	?
Arachnida, Opiliones				6,300	?
Arachnida, Pseudoscorpionida				3,300	?
Acari (mites)	10 ⁴		0.2-4	45,200	4%
Hexapoda (totals)	10⁴		0.2-4	-9,000	17%
<i>Hexapoda (Collembola)</i>	Up to 100,000			6,500	
<i>Hexapoda (Diplura)</i>				800	
<i>Hexapoda (Protura coneheads)</i>				731	
Soil Insecta and their larvae	50-500		4.5	55,000+?	20%?
Myriapoda (centi-, millipedes)	100-1100		1.5-22.5	18,000	20%
<i>Myriapoda (Symphyla)</i>				160	
<i>Pauropoda (Myriapoda relative)</i>				500	
Isopoda (slaters, woodlice, etc.)	Up to 1800		<4	5,000	?
Isoptera (Termites)	Colonies		?	2,600	60%?
Blattodea (Cockroaches)	?		?	4,500	?
Ants (Hymenoptera: Formicidae)	Colonies		?	13,000	50%
Molluscs (Soil Gastropods)	?		?	24,000	40%?
Terrestrial Turbellaria (Planarians)	?		?	830+	?
Terrestrial Polychaeta	?		?	?	?
Oligochaeta (Mega-, Microdriles)	50-2,000		20-500	10,000	20%?
<i>Microdriles (Enchytraeidae)</i>	1,000-300,000		1-53	~700	?
<i>Microdriles (excluding enchytraeid)</i>	?		?	1-2,300??	?
<i>Megadriles (true earthworms)</i>	50-2,020		20-305*	7,000	<20%?
Total species (approx.)				310,000	?

* Sub-surface biomass (even excluding plant roots and tubers) exceed those above-ground. Highest earthworm values are from Lee (1985: tab. 7) in NZ pastures (mean 2,020 m² with 305 gm² from McColl & Lautour, 1978). Enchytraeid maxima are from Springett (1967: fig. 24)/Gragg (1963: tab. 2) from Moor House, UK (mis)quoted by Spain & Lavelle (2001) *

Figure 5. Soil biota table (from Blakemore, 2016: tab. 3; see also - <https://vermecology.wordpress.com/2022/08/04/different-f3/>).

Blakemore (2016: tab. 3) compiled list of 310,000 known of many millions soil species is greater than a \$1 billion, 10 yr Census of Marine Life of 230,000 spp ([Ref.](#)). After this CoML survey completed, Mora *et al.* (2011: tab. 2) totalled just 194,409 catalogued Ocean spp; both predicted only ~2 million total taxa. The current study substantially increases Soil taxa totals.

As biodiversity estimates grow so too they decline as soil erosion and species extinctions take their toll (Blakemore, 2018a; [Ref.](#)). Despite vital importance and massive biodiversity inventory, not a single **SOIL ECOLOGY INSTITUTE** yet exists anywhere on Earth (except perhaps on my humble office desk – see <https://vermecology.wordpress.com/2015/12/10/isei-international-soil-ecology-institute-and-soil-ecology-exchange-yokohama-sexy-open-day-5th-december-2015-for-unfao-international-soil-day/>). This major soil research deficiency requires urgent redress.

REFERENCES

- Bahram, M., Hildebrand, F., Forslund, S.K. *et al.* (2018). Structure and function of the global topsoil microbiome. *Nature*, **560**, 233–237. <https://doi.org/10.1038/s41586-018-0386-6>.
- Bickel, S. & Or, D. (2020). Soil bacterial diversity mediated by microscale aqueous-phase processes across biomes. *Nat Commun*, **11**, 116. doi.org/10.1038/s41467-019-13966-w.
- Blakemore, R. J. (2016). *Cosmopolitan earthworms*. (6th Edn.). VermEcology, Yokohama, Japan, 1,250 pp. + 150 figs.
- Blakemore, R.J. (2018a). Critical Decline of Earthworms from Organic Origins under Intensive, Humic SOM-Depleting Agriculture. *Soil Syst*, **2**, 33. <https://doi.org/10.3390/soilsystems2020033>.
- Blakemore, R.J. (2018b). Non-Flat Earth Recalibrated for Terrain and Topsoil. *Soil Syst*, **2**, 64. <https://doi.org/10.3390/soilsystems2040064>.
- Blakemore, R.J. (2020). *Realms of the Soil (vs. Solar Lunacy)*. Online: <https://vermecology.wordpress.com/2020/05/27/realms-of-the-soil/>.
- Curtis, T.P., Sloan, W.T. & Scannell, J.W. (2002). Estimating prokaryotic Diversity and Its Limits. *Proc Natl Acad Sci USA*, **99**, 10494-10499. <http://dx.doi.org/10.1073/pnas.142680199>.
- Ferrer M., Méndez-García C., Bargiela R., Chow J, Alonso S, García-Moyano A, Bjerga GEK, Steen IH, Schwabe T, Blom C, Vester J, Weckbecker A, Shahgaldian P, de Carvalho CCCR, Meskys R, Zanaroli G, Glöckner FO, Fernández-Guerra A, Thambisetty S, de la Calle F, Golyshina OV, Yakimov MM, Jaeger KE, Yakunin AF, Streit WR, McMeel O, Calewaert JB, Tonné N, Golyshin PN; INMARE Consortium. (2019). Decoding the ocean's microbiological secrets for marine enzyme biodiscovery. *FEMS Microbiol Lett*, **366(1)**, fny285. doi: 10.1093/femsle/fny285.
- Fishman, F.J. & Lennon, J.T. (2022). Macroevolutionary constraints on global microbial diversity. *bioRxiv*, <https://doi.org/10.1101/2022.06.04.494835>. <https://www.biorxiv.org/content/10.1101/2022.06.04.494835v1.full>.
- Fulthorpe, R., Roesch, L., Riva, A. *et al.* (2008). Distantly sampled soils carry few species in common. *ISME J*, **2**, 901–910. <https://doi.org/10.1038/ismej.2008.55>.
- Gans, J., Woilinsky, M. & Dunbar, J. (2005). Computational improvements reveal great bacterial diversity and high metal toxicity in soil. *Science*, **309**, 1387–1390. <https://www.science.org/doi/10.1126/science.1112665>.
- Hoshino T, Doi H, Uramoto GI, Wörmer L, Adhikari RR, Xiao N, Morono Y, D'Hondt S, Hinrichs KU, Inagaki F. (2020). Global diversity of microbial communities in marine sediment. *Proc Natl Acad Sci USA*, **117(44)**, 27587-27597. doi: 10.1073/pnas.1919139117.
- James, Madison T., Farrisi, S.T., Shah, S. & Shah, V. (2022). Identification of Major Organisms Involved in Nutritional Ecosystem in the Acidic Soil From Pennsylvania, USA. *Front Env Sci*, **10**, doi:10.3389/fenvs.2022.766302.
- Larsen, B.B., Miller, E.C., Rhodes, M.K. & Wiens, J.J. (2017). Inordinate fondness multiplied and redistributed: the number of species on Earth and the new pie of life. *Q Rev Biol*, **92(3)**, 229–65. doi: 10.1086/693564.
- Lennon, J.T. & Locey, K.J. (2020). More support for Earth's massive microbiome. *Biol Direct*, **15**, 5. www.ncbi.nlm.nih.gov/pmc/articles/PMC7055056/. doi: 10.1186/s13062-020-00261-8.

- Locey, K.J. & Lennon, J.T. (2016). Scaling laws predict global microbial diversity. *Proc Natl Acad Sci USA*, **113**, 5970–5975. <https://www.pnas.org/doi/pdf/10.1073/pnas.1521291113>.
- Louca, S., Mazel, F., Doebeli, M. & Parfrey, L.W. (2019). A census-based estimate of earth's bacterial and archaeal diversity. *PLoS Biol*, **17**, e3000106.
- McNear, D.H., Jr. (2013) *The Rhizosphere - Roots, Soil and Everything In Between*. Nature Education Knowledge, **4(3)**, 1.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How many species are there on earth and in the ocean? *PLoS Biol*, **9**, e1001127.
- Pimentel, D. & Burgess, M. (2013). Soil Erosion Threatens Food Production. *Agriculture*, **3**, 443-463. <https://doi.org/10.3390/agriculture3030443>.
- Raynaud, X. & Nunan, N. (2014). Spatial ecology of bacteria at the microscale in soil. *PLoS ONE*, **9**, e87217. DOI: 10.1371/journal.pone.0087217.
- Roesch, L., Fulthorpe, R., Riva, A. *et al.* (2007). Pyrosequencing enumerates and contrasts soil microbial diversity. *ISME J*, **1**, 283–290. <https://doi.org/10.1038/ismej.2007.53>.
- Schloss P.D. & Handelsman J. (2006). Toward a census of bacteria in soil. *PLoS Comput Biol*, **2(7)**, e92. doi: 10.1371/journal.pcbi.0020092.
- White, R.A., III, Rosnow, J., Piehowski, P.D., Brislawn, C.J. & Moran, J.J. (2021). In Situ Non-Destructive Temporal Measurements of the Rhizosphere Microbiome 'Hot-Spots' Using Metaproteomics. *Agronomy*, **11**, 2248. <https://doi.org/10.3390/agronomy11112248>.
- Whitman, W.B., Coleman, D.C. & Wiebe, W.J. (1998). Prokaryotes: The unseen majority. *Proc Natl Acad Sci USA*, **95**, 6578–6583. <https://www.pnas.org/doi/pdf/10.1073/pnas.95.12.6578>.
- Wiens, J.J. (2021). Vast (but avoidable) underestimation of global biodiversity. *PLoS Biol*, **19**, e3001192. <https://doi.org/10.1371/journal.pbio.3001192>.