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Defending Earth's terrestrial microbiome

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Microbial life represents the majority of Earth's biodiversity. Across disparate disciplines from medicine to forestry, scientists continue to discover how the microbiome drives essential, macro-scale processes in plants, animals and entire ecosystems. Yet, there is an emerging realization that Earth's microbial biodiversity is under threat. Here we advocate for the conservation and restoration of soil microbial life, as well as active incorporation of microbial biodiversity into managed food and forest landscapes, with an emphasis on soil fungi. We analyse 80 experiments to show that native soil microbiome restoration can accelerate plant biomass production by 64% on average, across ecosystems. Enormous potential also exists within managed landscapes, as agriculture and forestry are the dominant uses of land on Earth. Along with improving and stabilizing yields, enhancing microbial biodiversity in managed landscapes is a critical and underappreciated opportunity to build reservoirs, rather than deserts, of microbial life across our planet. As markets emerge to engineer the ecosystem microbiome, we can avert the mistakes of aboveground ecosystem management and avoid microbial monocultures of single high-performing microbial strains, which can exacerbate ecosystem vulnerability to pathogens and extreme events. Harnessing the planet's breadth of microbial life has the potential to transform ecosystem management, but it requires that we understand how to monitor and conserve the Earth's microbiome.

Global estimates of the Earth's biodiversity include 5 million to 7.7 million unique species of animals[1,2], 500,000 plants[3], 6 million to 8 million terrestrial fungi[4,5] and up to 1 trillion species of prokaryotes[6]. The Earth microbiome—the full complement of pro- and eukaryotic microbial life—represents the majority of Earth's biodiversity. Microbial life was the first to inhabit our planet[7] and will probably be the last. Microbes regulate the major biogeochemical cycles on Earth, to the extent that signatures of microbial biogeochemical activity underpin efforts to discover extraterrestrial life[8]. By regulating global nutrient cycles, greenhouse gas exchange, and disease transmission and protection, the Earth microbiome provides an essential life-support system to our planet. A functioning Earth without a functioning microbiome is nearly unimaginable.

Yet, like all other domains of life, there is increasing evidence that the Earth microbiome is under threat. Early indicators come from soil fungi, which live a dual life as both micro- and macrobiological organisms[9]. A century of monitoring shows a remarkable 45% decline in mushroom-forming mycorrhizal fungi across Europe, probably due to land conversion and intense nitrogen pollution[10,11]. Anecdotal reports of fungal species extinctions around the world are increasingly pervasive[12] but require additional and repeated monitoring efforts. One example includes the link between extensive forest harvesting in Norway and

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Conserve

Protect microbial biodiversity within intact ecosystems

Restore

Incorporate microbial biodiversity into ecosystem restoration

Manage

Enhance microbial biodiversity within managed food and forest landscapes

Fig. 1 | Three strategies to protect microbial life. We propose three actions to conserve, restore and manage terrestrial microbial diversity. First, 'conserve' refers to the need to protect existing microbial biodiversity within intact ecosystems, which includes documenting and mapping microbiome data. Second, 'restore' involves incorporating microbial biodiversity into the practice of ecosystem restoration. Finally, 'manage' proposes that managed ecosystems can act as reservoirs of microbial diversity.

extinctions of key wood-decay fungi[13]. Furthermore, microbes, which can evolve extremely specialized symbiotic networks of interactions with their plant hosts, are threatened by accelerated co-extinction, as their hosts face increasing population declines[14,15]. Along with the direct impacts on ecosystem health and functioning, these microbial extinctions directly threaten human well-being through their role in disease transmission and protection, food security and regulating global climate[16–18].

More broadly, microbial life is sensitive to nearly all aspects of environmental change[19–24], and recent work shows that while global change can increase local microbial richness, it will ultimately homogenize this pool of biodiversity[25–28], leading to a decline in global-scale gamma diversity—the total number of microbial species on Earth. As anthropogenic pressure homogenizes local biodiversity, we lose landscape level beta-diversity—the organisms that make different geographical locations microbiologically and functionally distinct. The global homogenization of soil microbial biodiversity impacts all major taxonomic and functional groups of microorganisms[27], regardless of soil habitat[29]. Given the prominent contribution of microbes to total ecosystem biodiversity and functioning[30], these emerging patterns of microbial homogenization and extinction suggest that the scale and consequences of the planet's sixth mass extinction event may be orders of magnitude higher than previously anticipated[31]. If levels of macrobiological diversity on the planet serve as a warning[32], we need to consider the possibility that microbial extinction events can, will and are already happening.

Here we start from the basis that microbial biodiversity is under threat, whether from biodiversity homogenization or full-blown global extinctions, and that this microbial biodiversity is critical for human survival[16]. Building on this, we discuss recent advances and future avenues to (1) conserve, (2) restore and (3) manage microbial biodiversity to improve ecosystem functionality and sustainability (Fig. 1). First, we discuss the need to quantify and map the existing terrestrial microbiome, in particular the soil fungal microbiome, so we can identify the most urgent threats and knowledge gaps, to facilitate effective conservation of microbial biodiversity. Second, we explore current opportunities to restore microbial biodiversity in natural systems, which can likewise facilitate the restoration of macrobiological diversity. Finally, we identify emerging research avenues that are beginning to reveal how managed lands represent a vital and underappreciated avenue to promote microbial biodiversity. While we are not the first to call for microbiological conservation[33,34], here we highlight the broader opportunities to incorporate microbial diversity in ecosystem restoration and the diversification of managed landscapes.

Conserve: documenting terrestrial microbial biodiversity to prioritize conservation efforts

You cannot manage what you do not measure. Over the past decade, massive adoption of DNA sequencing to characterize microbial communities has led to the first global inventories of microbial biodiversity, identifying hotspots as well as mismatches between micro- and macrobiogeography[35–38]. Here we suggest that at least three key principles should guide molecular-based surveys designed to monitor and conserve the terrestrial microbiome. First, we must constantly work to expand the spatial and geographic coverage of datasets to minimize uncertainties, particularly in less disturbed regions that are the last strongholds of biodiversity—areas that will serve as important conservation and restoration targets and baselines. Where possible, researchers should make use of longer read amplicon or metagenomic sequencing approaches that can resolve microbial taxa to species and strain level. Cultivation could also be prioritized where feasible for follow up work and potential inclusion in synthetic communities[39]. Second, surveys need to be repeated through time where possible, to understand where biodiversity is declining the fastest. Temporal surveys in particular need to be designed using existing knowledge to capture key moments in time where rates of change are potentially the fastest and most concerning, that is, with more frequent sampling in periods of more rapid change[40,41]. This will be essential to prioritize limited conservation resources. Third, and perhaps most urgently, we must work to share this information broadly, in fully open-access and transparent ways[42].

Ultimately, large-scale temporal monitoring of microbial diversity is both critical to understanding threats and identifying strategies to protect microbial diversity on our planet[33]. However, such a global repeated survey of the terrestrial Earth microbiome has unique logistical challenges. We cannot extract this information from satellites, fly a plane or charter a ship. We must take a distributed, decentralized approach—connecting scientists and communities on the ground, around the world. There are already impressive efforts underway to either execute large-scale sampling[36,38,43–45] or synthesize existing data[46]. The African Microbiome Initiative[47], The Australian Microbiome Initiative[48], the China Soil Microbiome Initiative[49], SoilBON[33] and the European LUCAS soil survey[50] have already undertaken the first of their kind continental-scale, high-spatial-resolution sampling efforts. The US National Ecological Observatory Network manages a high-temporal-frequency sampling effort across its >40 continental monitoring sites[51]. Synthesis efforts such as Global Fungi[52], The Society for the Protection of Underground Networks[53] and the Earth Microbiome Project[54] have begun compiling data from these efforts, as well as work to extract the enormous amounts of data available from primary literature focused on the local scale. However, while data availability is exploding, there are clear and persistent sampling gaps in our global picture of the Earth microbiome.

By synthesizing data across such large-scale data repositories, we can approximate the regions of our planet that are well represented in terms of microbial monitoring data. In doing so, we also identify the regions that require concerted focus if we are going to represent the full diversity of microbial life. To assess this, we used statistical approaches to identify under-sampled regions of the global soil fungal microbiome using ~10,000 observations from the Global Fungi Database (Supplementary Methods), visualized in Fig. 2. We focus on fungi as the Global Fungi Database is a leader in data synthesis, representing the largest compilation of fungal microbiome diversity so far. Using these data, we asked which environmental conditions have been under-sampled on Earth (for example, places with combinations of climate and soil factors that have never been sampled; Fig. 2a), and which regions are furthest from our current sampling in absolute geographic distance (Fig. 2b). By averaging these two pictures of under-sampling, we can begin to visualize where sampling is most needed (Fig. 2c). While coverage is broad, there are clear and persistent gaps in the high latitudes of Canada and Russia, the Amazon, southeast Asia and the entire continent of Africa. While this analysis is limited to soil fungi, databases are generally less well developed for other microbial groups[38,46].

Ultimately, we still need additional data synthesis leadership—organizations to facilitate data generation, analysis and distribution, invested in generating new data in partnership with scientists who live and work within hotspots of sampling priority. These efforts might follow the approaches of national and international plant inventory datasets (for example, National Forest Inventory datasets), many of which represent public resources that have transformed our understanding of aboveground vegetation dynamics. Armed with key microbial biodiversity metrics and threats, conservation organizations can identify diversity hotspots that are critical for active conservation. Guerra et al. highlighted the urgent need to incorporate such microbial information into national and international conservation frameworks, not only to preserve the diversity of life on Earth, but also to maintain key functions provided by individual endemic species[33]. As specific actions, we recommend prioritizing the following.

1. Extending the International Union for Conservation of Nature (IUCN) Redlist, a list of species in need of urgent conservation, to include a wider range of threatened microbial species or consortia where possible, while recognizing that the inherent challenges will mean that this cannot be comprehensive, given the limited availability of historical data to differentiate native versus invasive species.
2. Incorporating microbial biodiversity into conservation planning.
3. Incentivizing land management practices that support microbial biodiversity. For example, retention forestry, the practice of retaining large trees during forest harvest, can 'lifeboat' key aspects of fungal biodiversity[55]; cover cropping, which ensures plants are grown on agricultural fields during non-productive rotations, and adoption of no-till agriculture can have substantial effects on soil microbial biodiversity[56].
4. Sharing of key meta-data, at a minimum date and location.

Despite the importance of conservation in the protection of the global terrestrial microbiome, extreme degradation of global landscapes is accelerating: current trends suggest that more than 90% of the Earth's soil will experience significant erosion by 2050[57]. This means that both natural and assisted microbial restoration will probably be essential to restore the functional capacity of terrestrial ecosystems across the globe. Indeed, the small size and rapid turnover rates of individual microbes can allow for rapid production of microbial inocula. As a result, microbial restoration may provide a scalable, and previously underappreciated, avenue for accelerating the rates of ecosystem restoration and biodiversity recovery across the globe.

Restore: rebuilding the ecosystem microbiome

We are witnessing surging global interest in ecosystem restoration. The United Nations has declared this decade the 'UN Decade of Ecosystem Restoration[58]. The World Economic Forum's 1t.org programme aims to conserve and restore 1 trillion trees by 2030 to both rebuild biodiversity reservoirs and combat climate change[59]. Initiatives such as '30 by 30' are motivating governments around the world to set aside 30% of land surface for conservation and restoration[60]. Ecosystem restoration, when done in an ecologically and socially responsible way, in combination with conservation, is a critical component of protecting global biodiversity. In many cases, this involves merely protecting degraded land, allowing the natural regeneration of ecosystems, while in some cases, this can also involve the introduction of local vegetation while also promoting the economic sustainability of local people[61]. Without appropriate consideration of ecological context, mass restoration projects can fail[62]. However, when we restore ecosystems, for example by planting trees, we rarely think to 'plant' the associated microbiome. There is increasing evidence that active microbiome restoration through whole microbiome transplant can increase the speed, resilience and overall success rates of ecosystem restoration efforts around the world, above and beyond protecting key intact refugia[63,64].

Soil transplants—moving soil and associated microbial communities from one location to another—are a low-tech method for introducing intact microbial communities surviving in nearby refugia. An emerging body of work suggests that explicit soil microbiome restoration can facilitate the creation of more diverse, stable and functioning ecosystems[64,65]. Pioneering soil transplant work has demonstrated that native plants in restored American Midwest prairies grow more vigorously and are more likely to survive when inoculated with soil microbial communities from intact prairie remnants[64,66]. Introduction of native soil-derived arbuscular mycorrhizal fungi accelerates regeneration of species-rich vegetation in previously barren post-mining landscapes in Estonia[67]. Hawaiian fungal reintroduction efforts have enhanced native plant recovery and disease resistance[68]. Recent restoration work in high-latitude grasslands could only achieve aboveground plant diversity similar to native systems when soil from those same native systems was also introduced at the time of seeding[69]. In Finland, where >40% of polypore fungal species are on the Red List, reintroduction of threatened species using inoculated decaying logs efficiently promoted mycelia and mushroom growth[70]. All of these examples demonstrate how active microbiome restoration can be essential for restoring entire ecosystems.

To test this hypothesis more quantitatively, we performed a literature synthesis, identifying studies quantifying plant biomass response to inoculation with 'wild microbiomes', either using live soils from reference ecosystems or live spores extracted from those ecosystems ($N = 81$ from 27 studies). Across all studies, plant growth was stimulated by an average of 64% with a strong positive skew, with effects reaching as

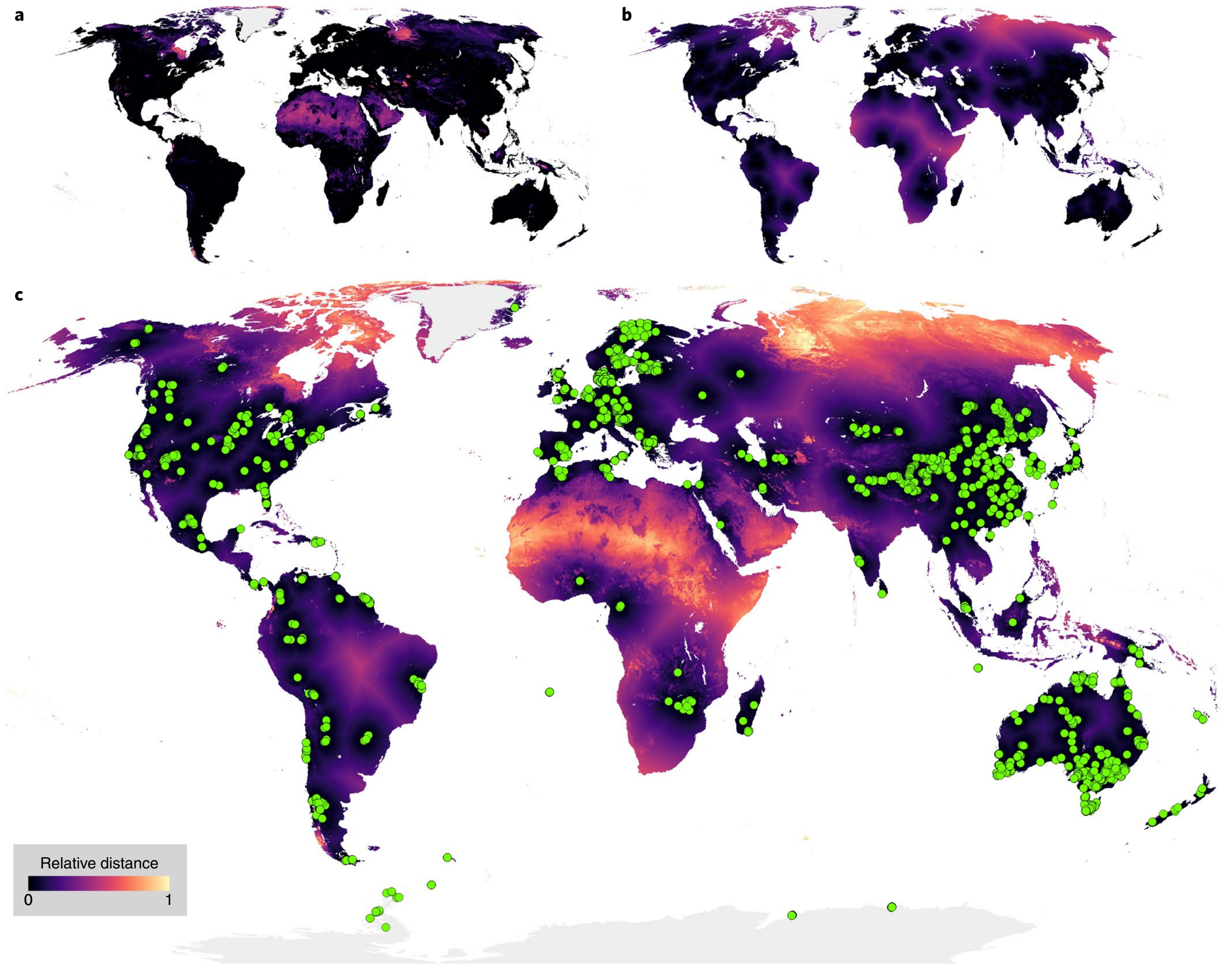

Fig. 2 | A map of sampling priorities for the soil fungal microbiome. Lighter colours indicate areas of greater urgency. **a**, Sampling priorities based on environmental conditions that have not yet been captured by existing observations. **b**, Sampling priorities based on absolute geographic distance from existing observations. **c**, An averaging of the two sampling priority maps. Green points indicate locations of existing soil samples in the Global Fungi Database, release version 3.

high as a ~700% stimulation (Fig. 3, analysis performed on log-response ratios, further detail available in Supplementary Methods). Plants growing with wild microbes generally outperform those that are not. Importantly, past work has shown that the effects of natural soil microbiome transplants far outweigh those associated with commercially available soil microbial mixtures[63,71,72]. At the same time, it is important to emphasize that these approaches are not universally successful as the ecological context will probably determine the likelihood of success in any region. Furthermore, soil transplants can often fail to introduce key members of the phyllosphere microbiome, which are also key for ecosystem health, as well as root-associated microorganisms that are missing from bulk soil[73]. Future work will probably reveal when and where these approaches are most effective, as well as new techniques to maximize the likelihood of positive outcomes.

While the effects reported so far show remarkable impacts on plant regeneration, they may be unsurprising given the fundamental role of soil microbes in governing aboveground plant growth. For example, most plants on Earth form an essential symbiosis with mycorrhizal fungi[74]. These fungi have been repeatedly implicated in plant drought tolerance, pathogen protection and nutrient acquisition[74]. However, these fungal communities are also particularly sensitive to fertilization and soil disruption, which are common in agriculture and mining[67,74–76]. Active soil transplants may allow these fungi to overcome dispersal or establishment limitation, and the same may be true for other soil organisms[77], particularly in areas that have proven resistant to natural regeneration. There are a wealth of studies showing positive responses of plants to inoculation with mycorrhizae[72,78–81], and meta-analysis shows that plant responses to inoculation are more positive when the soil community is more complex[82]. Pine forestry in particular cannot be established at all if key ectomycorrhizal symbionts are not present[83,84]. While mycorrhizal fungi provide a well-studied example, in principle these phenomena probably extend to the entire microbiome, inclusive of all fungi, bacteria, viruses, soil animals and their respective interactions. Taken together, this body of work suggests that restoration efforts must move toward encompassing microbial ecosystems.

While soil transplant work is extremely promising, it is also important to recognize the potential challenges and risks. For example, it is still unclear how the extent to which soil transplants can scale without doing irreparable harm to 'donor' sites as the amount of soil in a donor system is finite, and mass excavation will destroy microbial habitat. It would be incredibly valuable to develop ways to introduce wild microbial communities without destructive soil excavation. The history of

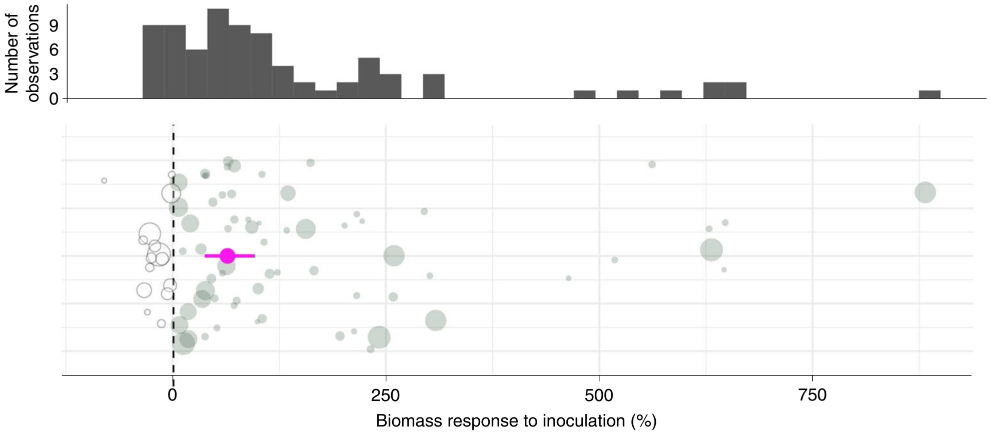

Fig. 3 | Response of plant biomass to inoculation with soil organisms from intact reference habitats relative to control (N = 81). Filled circles indicate significantly positive responses while open circles indicate non-significant or negative responses. The pink circle and associated error bar represent the overall analysis mean, a ~64% plant biomass increase in response to inoculation. Point sizes are linked to the inverse of study variance, with larger circles reflecting greater confidence and associated weight in our statistical analysis. The top panel is a histogram of observations reporting each observed effect size. Additional details on how this analysis was performed can be found in Supplementary Methods.

ecological manipulation is rife with unintended consequences. Before these approaches can be scaled up widely, microbiologists need to carefully document the effects of these transplants using modern molecular surveys to ensure that we are not creating more problems than we solve.

Manage: managed ecosystems as reservoirs of microbial diversity

Managed landscapes which include food and forest agriculture, dominate terrestrial ecosystems and currently cover ~50% of the global habitable land surface[85]. By adopting large-scale monocultures, applying massive amounts of synthetic fertilizers and pesticides, and restricting gene pools through selective breeding, cloning and genetic modification, humans have significantly increased the productivity and efficiency of the global agricultural system[86–88]. However, as these ecosystems reach unprecedented scale, the limitations of a reductionist approach to ecosystem design are becoming clear: systems with incredibly low ecological and genetic diversity are more susceptible to extreme climate events[89]. This is worrying as these events are becoming increasingly frequent in the face of global climate change[90]. Monoculture systems are likewise more susceptible to pathogens and pests, creating a need for regular and substantial applications of pesticide to remain viable[91]. In some cases, this has caused entire crop varieties to become imperilled—for example, coffee in Latin America[92] and potato during the Irish potato famine[93], or removed from the food system entirely (for example, Gros Michel banana[94]).

Biodiversity–ecosystem stability relationships are some of the most reproducible patterns in ecology[95–99]. As a result, there is mounting effort to increase the aboveground macrobiological diversity of our managed landscapes. Despite these lessons from aboveground ecosystems, there is increasing danger of repeating the mistakes of macrobiological agriculture at the micro scale, with consequences for indigenous microbial taxa[100]. For example, given the potential of microbial inoculations to promote plant productivity, there is an exploding landscape of microbial inoculant companies advocating for the large-scale application of single species or very low-diversity non-native microbial consortia. Most recently, a startup has announced ambitions to inoculate over 1 million hectares of agricultural land primarily with a single species of arbuscular mycorrhizal fungus[101]. While some microorganisms are present across many ecosystems, mass application of single species may result in a loss of genetic and ecological diversity, and is unlikely to account for ecosystem-specific requirements, for example, in types and rates of soil processes[38,102]. The proliferation of low-diversity microbial inoculant solutions in agriculture is a missed opportunity to embrace a more holistic approach to ecosystem design. We emphasize that there are notable exceptions. The 'Effective Microorganisms' initiative began over 40 years ago in Japan, and has built native and biodiverse consortia of bacteria and yeasts, which have been shown to enhance crop productivity in most cases[103,104]. Essentially, a particular combination of functional groups of microorganisms is sourced from the local environment, grown in co-culture, and then applied as a solution directly to plants or soil[103]. This work has been replicated in multiple environments, using locally sourced microbial communities to enhance agricultural outcomes[105,106]. Ultimately, we should move towards approaches that can use locally sourced, native and biodiverse communities of soil organisms to achieve outcomes.

These approaches are possible and may have greater potential than reductionist ones[107]. There is increasing evidence that microbes are locally adapted to particular environmental conditions[108–110], implying that native, locally sourced communities may outperform introduced, exotic communities[108,111–113]. Manipulative experiments and meta-analysis have demonstrated that microbiome diversity and network complexity can enhance multiple ecosystem functions, generating fundamentally more stable and productive ecosystems[114–118]. These findings suggest that embracing native microbial biodiversity and complexity within managed ecosystems may allow for greater production, while also allowing these systems to remain reservoirs of significant microbial diversity. But how can this be achieved? Here we offer three actions that, if taken, we believe could fundamentally change how the world values and applies microbial biodiversity, in particular for managed ecosystems.

(1) Define a healthy soil microbiome. What does a 'wild', intact microbiome look like in different regions of the planet? Which microbial communities are 'high-performing', generating positive outcomes for managed landscapes, such as carbon capture, erosion control or plant nutrition? When and where do these 'wild' and 'high-performing' microbiomes overlap the most, and which agriculture practices can support these communities? Answering these questions will enable the development of agricultural microbiome management that creates positive outcomes for farmers and foresters, as well as for fungi and bacteria. We emphasize that the widespread introduction and invasion of certain microbial taxa complicates the definition of intact microbial communities, and where possible, efforts should be

made to distinguish native versus introduced taxa. Furthermore, analogous efforts in medical microbiology have yielded remarkable successes but are still far from complete. We should expect this to be a community-wide effort that will continue to evolve with our understanding of ecosystem health. Ultimately, what a healthy soil microbiome looks like will probably vary significantly within and across ecoregions. Maximizing biodiversity impact will probably require significant 'personalization' to the particular location.

(2) Communicate potential outcomes with all stakeholders. Our community has demonstrated that microbiome manipulation can create positive outcomes for biodiversity and ecosystem health, with notable examples coming from restoration ecology[64,68,69] and mycorrhiza in forestry[119]. In many ways, we already know that microbiome management for ecosystem services is both possible and can be massively beneficial[120]. Yet, this work is sometimes seen as overly complicated but more frequently simply unknown to farmers, foresters and restoration practitioners. We must make clear that these microbiome interventions: (1) are already possible using low-tech approaches such as soil transplants, (2) may assist in transitioning away from intensive use of chemical fertilizers and (3) can be as or more effective than reduced complexity applications of individual microbial species or strains[101]. These messages can accelerate attempts to build microbial biodiversity back into our managed landscapes. There will of course be variation in uptake of new practices, hence we must identify early adopters to demonstrate these approaches at scale. Furthermore, it is essential that this work is done in partnership with scientific organizations that can monitor source and sink environments, to ensure microbiome management is done responsibly. Finally, these efforts would benefit from additional research on how to scale the introduction of native microbial communities beyond soil transplants, in ways that will allow land managers to feasibly rewild microbes at landscape scale.

(3) Scale the science. The academic community is exceptional at challenging old paradigms and discovering fundamentally new ways to understand the world. Yet, most academic programmes are not capable of, nor designed for, building massively collaborative efforts that can implement new discoveries at scale. Many of the ideas we have proposed—a global monitoring network, changing the practice of agriculture—are far beyond the capacity of any single academic lab. This is where we must build partnerships with existing non-governmental organizations and companies, or establish entirely new ones. This is where our programme officers must consider new models for supporting translational science. Importantly, these must be science first initiatives, open to changing and adapting as the scientific community continues to discover how the Earth microbiome functions.

Conclusion

The world is at a scary precipice. As we enter a sixth mass extinction event[31], some of the most vulnerable components of the Earth's biodiversity may be those we cannot see. Microbial organisms represent key fundamental life support mechanisms for our planet. As we erode this biodiversity, we close doors on novel ways to support our managed food and forest landscapes. More profoundly, we lose billions of years of evolutionary insight. Action is needed now to defend the Earth microbiome. We need global mapping and monitoring, with an emphasis on locations that have been chronically under-sampled, to guide and prioritize conservation efforts. Armed with this information, we need to integrate microbial diversity into our concept and practice of biodiversity conservation and restoration. Finally, we must identify ways to build microbial biodiversity into our managed agricultural and forestry landscapes. Covering the largest proportion of the vegetated area on Earth, managed landscapes provide a unique opportunity to enhance biological diversity while also promoting yields. Capitalizing on this opportunity is critical as we face the challenge of feeding an ever-growing human population while also preserving and promoting the biodiversity Earth depends on. By taking these actions now, we may slow the extinction of Earth's unseen, biological majority.

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Author contributions

C.A. and T.W.C. conceived the project. C.A., E.H., F.F. and G.R.S. conducted the meta-analysis. C.A. and J.v.d.H. performed all mapping analyses. C.A., M.A.A., P.B., P.K., F.F., J.v.d.H., T.K., E.H., G.R.S. and T.W.C. contributed to the writing and revising of the manuscript.

Competing interests

T.W.C. is the founder of Restor, a non-governmental organization that facilitates the global restoration movement. T.K. and C.A. are the founders of the Society for the Protection of Underground Networks, an organization that advocates for the protection of belowground network forming fungi. C.A. is the founder of Funga, an organization that facilitates the restoration of belowground fungal biodiversity.

Additional information

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