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OPINION

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Frontiers in soil ecology—Insights from the World Biodiversity Forum 2022

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Abstract

Global change is affecting soil biodiversity and functioning across all terrestrial ecosystems. Still, much is unknown about how soil biodiversity and function will change in the future in response to simultaneous alterations in climate and land use, as well as other environmental drivers. It is crucial to understand the direct, indirect and interactive effects of global change drivers on soil communities and ecosystems across environmental contexts, not only today but also in the near future. This is particularly relevant for international efforts to tackle climate change like the Paris Agreement, and considering the failure to achieve the 2020 biodiversity targets, especially the target of halting soil degradation. Here, we outline the main frontiers related to soil ecology that were presented and discussed at the thematic sessions of the World Biodiversity Forum 2022 in Davos, Switzerland. We highlight multiple frontiers of knowledge associated with data integration, causal inference, soil biodiversity and function scenarios, critical soil biodiversity facets, underrepresented drivers, global collaboration, knowledge application and transdisciplinarity, as well as policy and public communication. These identified research priorities are not only of immediate interest to the scientific community but may also be considered in research priority programmes and calls for funding.

KEYWORDS

biodiversity change, ecosystem functioning, scenario modelling, soil biodiversity, soil macroecology

1 | INTRODUCTION

The theme of the second World Biodiversity Forum 2022 (WBF2022) was *Inspiration for Action* with the goal to connect researchers across all disciplines of biodiversity science with practitioners and societal actors, to develop actions and solutions to conserve biodiversity, as well as envision a path towards a sustainable future (https://www.worldbiodiversityforum.org/en/welcome). Already the first WBF in 2020 had a strong participation from soil ecologists and raised questions regarding the extrinsic and intrinsic value of soil organisms (Phillips et al., 2020). In this year's meeting, the participation of soil ecologists was even more pronounced with two dedicated sessions on *Soil biodiversity for global welfare* and *Soil biodiversity and function scenarios* (see Word Cloud of contributions in Figure 1), as well as multiple contributions to other sessions.

Notably, this paper is not intended to represent a comprehensive assessment of the most important research questions in soil ecology (see e.g., Crowther et al., 2019; Eisenhauer et al., 2017; Geisen et al., 2019; Tedersoo et al., 2020; White et al., 2020), but to highlight emergent frontiers that were identified during discussions at the WBF2022, mostly with respect to soil macroecology (e.g., across scales; Shade et al., 2018) and drivers of biodiversity and ecosystem function change. In addition, recent research on soil microbiomes delivered keys to understanding soil functioning across a diversity of contexts and global change scenarios (Berg & Cernava, 2022; Rillig et al., 2019). We structured the research topics into frontiers in (1) data integration, (2) causal inference, (3) soil biodiversity and function scenarios, (4) critical soil biodiversity facets (variables), (5) underrepresented drivers, (6) global collaboration, and (7) knowledge application and transdisciplinarity, as well as (8) policy and public communication (Figure 2). These identified research priorities are not only of immediate interest to the scientific community but may also be considered in research priority programmes and calls. As such, they reflect the theme of the WBF and represent *Inspiration for Action* in soil biodiversity research.

2 | FRONTIERS IN SOIL ECOLOGY

2.1 | Frontiers in data integration

Soil biodiversity data is rapidly accumulating (White et al., 2020). A number of recent initiatives produced global data sets that represent the distribution of soil microbial diversity (Aslani et al., 2022; Bahram et al., 2018b, 2022; Delgado-Baquerizo et al., 2018; Egidi et al., 2019;

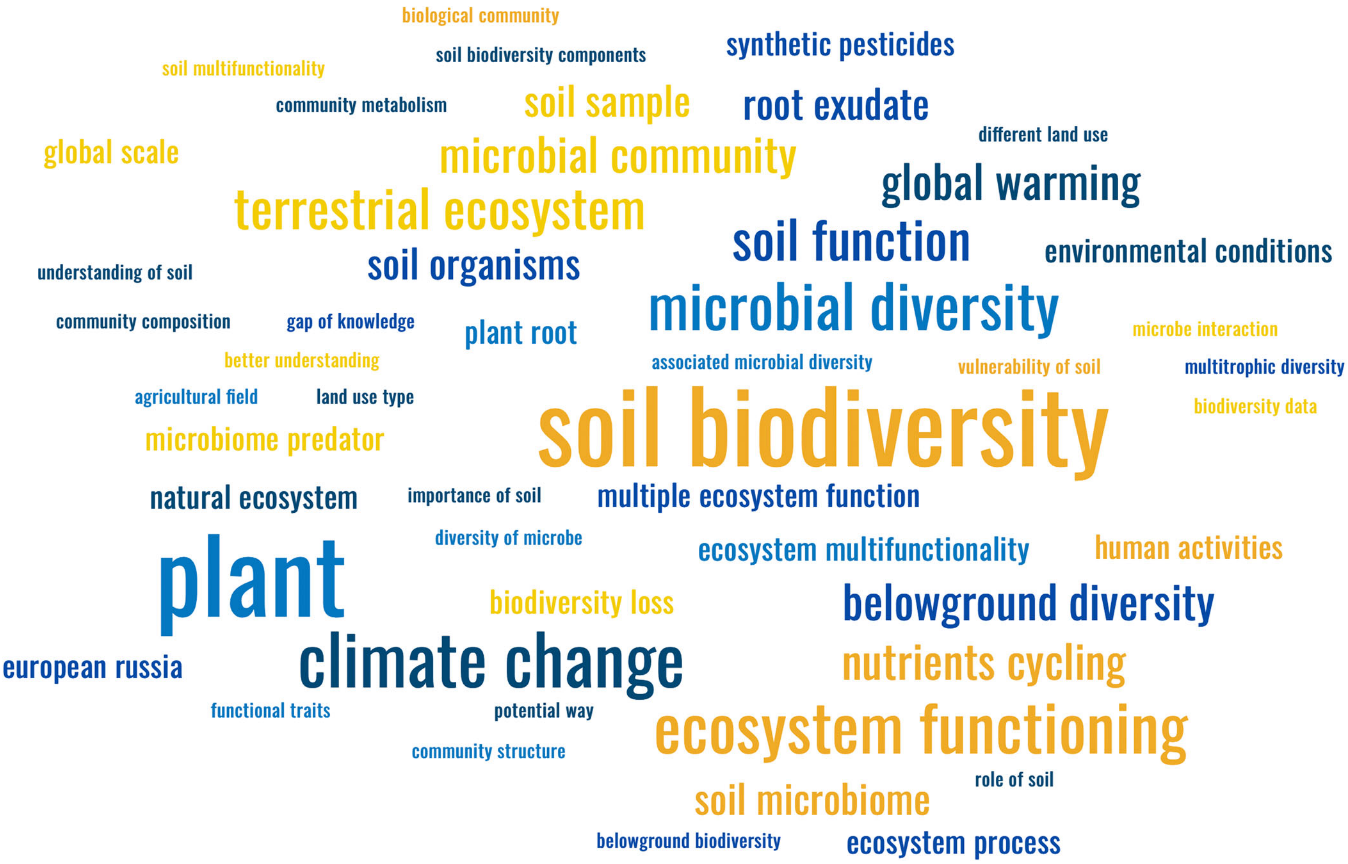

FIGURE 1 Word cloud based on the 22 abstracts of the oral contributions to soil-related sessions at the World Biodiversity Forum 2022 in Davos. The size of the words is proportional to their occurrence. This figure was produced using a free WordCloud Generator (https://monkeylearn.com/word-cloud/).

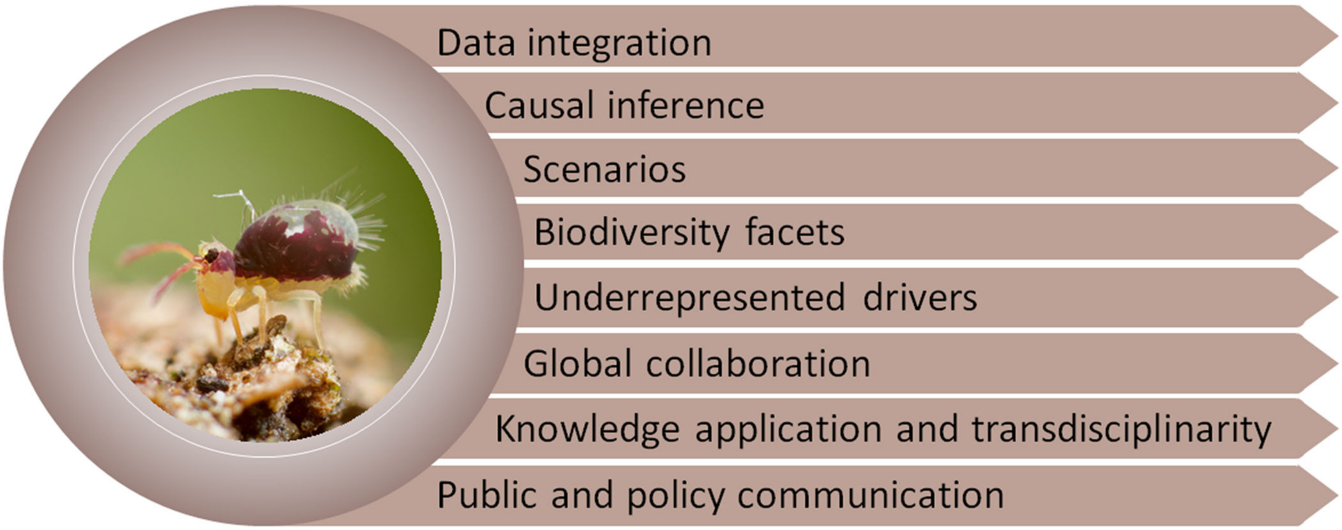

FIGURE 2 Frontiers in soil ecology identified at the World Biodiversity Forum 2022. Photo credit: Andy Murray.

Maestre et al., 2015; Tedersoo et al., 2014). Other initiatives compiled already existing data on the abundance and diversity of soil animals (van den Hoogen et al., 2019; Lavelle et al., 2022; Phillips et al., 2019; Potapov, 2022), soil microbial biomass (Patoine et al., 2022; Xu et al., 2013), fungal communities (*GlobalFungi*) and guilds (FungalTraits; Põlme et al., 2020), and plant mycorrhization types (FungalRoot; Barceló et al., 2019; Soudzilovskaia et al., 2020). This opens exciting opportunities for data integration for a holistic description of the soil biosphere. Yet, accumulated data are not easy to integrate, as it was produced using different methodological approaches (e.g., classical taxonomy vs. next-generation sequencing), collected with different sampling designs and spatial and temporal resolution. Meta-analytical approaches have allowed to advance our knowledge about global patterns in soil biodiversity (Delgado-Baquerizo et al., 2016; van den Hoogen et al., 2019; Phillips et al., 2019; Potapov et al 2020); however, these approaches are also very 'noisy' and rarely use directly comparable data. Existing integrative studies linked environmental DNA (eDNA) with functional indicators and showed an overall positive relationship between soil multidiversity and multifunctionality (Delgado-Baquerizo et al., 2020b), and how trophic regulation shapes soil functioning (Martinez-Almoyna et al., 2022), while others emphasized the importance of rare taxa for specific processes (Bahram et al., 2022). Recently, new suggestions for unified data infrastructure and metadata entries, which would strongly improve retrieving and reusing data and biobanking, were published by the European Microbiome Support Consortium (Cernava et al., 2022; Ryan et al., 2021). There are a number of prominent research frontiers in this context:

- *Linking existing data and producing new standardized data*: We need better practices in data management. This includes standardizing existing data through common databases (Burkhardt et al., 2014; Ramirez et al., 2015) and ontologies (Le Guillarme et al., 2021), linking biodiversity data/facets (e.g., sequencing data with abundance data; Geisen et al., 2018), as well as standardization and automatization of data collection via common and easily reproducible protocols and data templates in traditional (Guerra et al., 2021c; Potapov et al., 2022a) and molecular tools (Calderón-Sanou et al., 2020; Knight et al., 2018; Mathon et al., 2021; Tedersoo et al., 2022a), and image analysis approaches (Schneider et al., 2022). An example for linking multiple types of standardized data is found in Myriatrix, a virtual research environment for Myriapoda and Onychophora proposed by Martínez-Muñoz (2019), based on Scratchpads (Smith et al., 2011). The platform uses a consolidated classification (taxonomic backbone) and several application programming interfaces to find, aggregate and visualize literature, images, genetic sequences and conservation data. The platform can further feed into the Global Biodiversity Informatics Facility (GBIF) and into the Global Biotic Interactions (GloBI) infrastructure (Poelen et al., 2014). Overall, it does not seem that the data linking and standardization limitation lies in the existing technology, but in the adoption of rapidly developing digital tools by the research community. Progress could be made by supporting emerging research infrastructures with permanent positions, training and capacity building.
- *Integrating data across disciplines*: Establishing links among soil functions, microbial diversity, soil animal diversity, and aboveground plant and animal diversity requires the collection of comprehensive data sets and the creation of open platforms (for communication and infrastructure). The first approximation is achievable with the data in hand by overlaying extrapolation maps in macroecological studies. However, this method may result in high uncertainty and would not be very informative to infer functional interactions (Eisenhauer et al., 2021; Guerra et al., 2020). Novel monitoring initiatives, such as soil biodiversity observation network (BON) and the Global Initiative of Crop Microbiome and Sustainable Agriculture (https://www.globalsustainableagriculture.org/), intend to address this frontier via the simultaneous assessment of multiple components of soil life, parameters and functions in terrestrial ecosystems (Guerra et al., 2021a; Potapov et al., 2022a). While multiple previous works have focused on DNA sequencing of taxonomic markers, studies based on metagenomics, metatranscriptomics or metaproteomics can also provide the fundamental basis between soil biodiversity and ecosystem function.
- *Establishing a long-term monitoring system*: Soil ecosystems are dynamic in space and especially in time (Eisenhauer et al., 2021; Kuzyakov & Blagodatskaya, 2015). To understand the mechanisms linking biodiversity and ecosystem functioning in soil, and to extrapolate them in the future, we need temporal analysis of trends in soil organisms and functions (e.g., Körner et al., 2022). This requires knowledge integration across different microhabitats (Eisenhauer et al., 2021), and putting soil biodiversity in the landscape context (Le Provost et al., 2021). Moreover, it is important to identify the appropriate spatial (and temporal) grains for multitrophic studies in soil, which intend to link organisms spanning from microorganisms to macrofauna (Eisenhauer et al., 2021; Thakur et al., 2020). Such repeated assessments across and within years are of particular importance in highly dynamic systems like croplands (Eisenhauer et al., 2021).
- *Uncovering the unknown soil biodiversity*: Multiple gaps of knowledge limit our capacity to protect soil biodiversity and function and to further reduce current uncertainty in soil biodiversity. First, understanding prokaryotic functional diversity is highly challenging, as 85 out of the currently established 118 phyla have not had a single species described to date (Overmann et al., 2019). This issue needs to be addressed by gathering meaningful taxonomic and functional information for both dominant and not-yet cultured prokaryotes. Targeted culturing efforts are needed to further identify new taxa and link them to sequencing data. Identifying those locations of the planet wherein unknown taxa are most likely to exist could also help in this fundamental endeavour (Delgado-Baquerizo, 2019). A recent assessment showed numerous gaps in soil biodiversity knowledge globally (Guerra et al., 2020), which should be covered with joint efforts and capacity building in the 'global south'. Although we have detailed information on the status of conservation of many plants and aboveground animal species, this information as well as

taxonomic expertise is largely lacking for soil organisms (Eisenhauer & Hines, 2021; Phillips et al., 2017). We know that there are important global mismatches in soil and plant biodiversity across space (Cameron et al., 2019; Tedersoo et al., 2014) and time (Delgado-Baquerizo, 2019; Eisenhauer et al., 2019); thus, we cannot protect soil organisms just by protecting aboveground plant and animal biodiversity (Cameron et al., 2019).

2.2 | Frontiers in causal inference

Soil biodiversity and functions are particularly complex to assess comprehensively, and a mechanistic understanding of their dynamics requires a combination of observational, experimental and modelling approaches. Soil communities are composed of interacting organisms (Eisenhauer et al., 2021; Wardle et al., 2004) that are difficult to analyse separately because of these interdependencies (Brose & Scheu, 2014). Moreover, some soil organisms function as ecosystem engineers (e.g., earthworms and ants) and thus strongly influence the environmental conditions for the other species (Jones et al., 1994). A better understanding of the dynamics in soil biodiversity, properties, and functions, their drivers and making progress in linking observed trends with mechanistic models is thus particularly challenging and should be one of the key research foci in soil macroecology. Novel technologies like metagenomics, metatranscriptomics or metaproteomics will help to establish links between biodiversity and function across spatial and temporal scales. We highlight here three research areas that we believe could foster our understanding of soil biodiversity and function dynamics at large spatial scales:

From predictive models to causal inferences: A traditional tool kit to analyse the relationship between a response variable (e.g., species richness) and few environmental predictors are regressions, with some penalizations (e.g., akaike information criterion) to rank the most 'important' drivers of the response variable. Despite the simplicity of the approach, there are two shortcomings that are often overlooked. First of all, any variable selection in a regression is for predictive inference (i.e., which model best predicts the response variable) and not for causal inference (i.e., which is the effect of pH on bacterial richness) (see Arif& MacNeil, 2022). In other words, interpreting variable importance from a predictive model is a risky game. Second, when considering soil biodiversity, which comprises highly interlinked organisms, it is crucial to take a holistic vision to consider the interdependencies between species or groups of species when making inferences about potential drivers or responses to specific environmental variables. Indeed, some relationships between a given taxon and an environmental variable might actually be driven by another taxon feeding on the first taxon and directly responding to the environmental variable. There is, thus, a lot to gain by jointly analysing multiple groups of soil biota in response to multiple environmental drivers and to assess the conditional dependencies between groups of soil biota and the environment (Eisenhauer et al., 2021). With no prior knowledge of the system, probabilistic graphical models are promising tools for such an inference and have proven powerful in identifying important links between groups of species and environmental variables (e.g., Ohlmann et al., 2018). These inference models are not directed and only represent partial dependencies between a set of variables. Alternatively, directed acyclic graphs (DAGs) allow for such causal inference (Pearl, 2009). Structural equation models (e.g., Eisenhauer et al., 2015; Martinez-Almoyna et al., 2022) are particular cases of DAG, but other implementations are less constrained and better designed for causal inference. Causal models should include all relevant groups of soil biota and variables of the studied ecosystem and should be carefully constructed, based on theoretical and empirical knowledge (although graphical models could be used first to get a rough idea of the partial dependencies between all variables). Since soil biodiversity contains many dozens of major taxonomic and functional groups (Potapov et al., 2022b) with many thousands of distinct taxonomic units, with even rare ones potentially being functionally relevant (Jousset et al., 2017), causal models would hardly provide true causal inferences. An option to increase the chance of finding true causal links is the combination of multiple observational approaches with different methods (e.g., environmental DNA, classical soil animal extraction) and scales, such as showing the importance of body size in the biogeography of soil microorganisms and microfauna, as conducted across China and the globe (Aslani et al., 2022; Luan et al., 2020).

With the ever-increasing availability of regional, continental or global soil biodiversity data, we believe the next grand challenge will be to build such causal inference models across multiple species groups and carefully selected environmental variables (e.g., soil temperature, in situ soil physicochemical properties). Other exciting avenues will consider ecosystem functioning variables at large spatial scales to assess the direct and indirect effects of environmental variables on soil biodiversity, soil food webs and soil functioning. Initiatives like Soil BON (Guerra et al., 2021b, 2021c; Potapov et al., 2022a) will likely provide the quality and completeness of data to achieve such a goal.

Scaling-up experimental data across space: Despite the use of causal inference based on observational data, the mechanisms at play are difficult to tease apart. For this, experimental setups are the tool of choice. They allow dissecting specific mechanisms at play and are important to reveal and understand feedback loops. It is one of the drawbacks of most causal inference models discussed above that they rely on DAGs: feedback loops are pervasive in ecology and notably in soil (e.g., plant soil feedbacks; Mariotte et al., 2018; Pernilla Brinkman et al., 2010), and they have been revealed through manipulations and mesocosm experiments (Pernilla Brinkman et al., 2010). These experiments are, however, limited in the spatial and temporal scale they consider. Therefore, manipulative experiments could be better harnessed in combination with observational studies to benchmark or validate their revealed relationships (Delgado-Baquerizo et al., 2020a, 2020b). Another strong advantage of manipulative experiments is to make a proper quantification of impacts; for instance, to measure the energy flux in soil food webs in response to a disturbance (e.g., Schwarz et al., 2017), something hardly achievable with observational data that remain more descriptive on those aspects (e.g., Barnes et al., 2014; Calderón-Sanou et al., 2021; Potapov et al., 2019a).

Manipulative experiments are relevant at the local scale, such as to understand the functioning of specific soil food web configurations (e.g., Bradford et al., 2002; Eisenhauer et al., 2012; Guerra et al., 2020; Heemsbergen et al., 2004; Wagg et al., 2014) or how soil biodiversity responds to environmental changes (e.g., Blankinship et al., 2011; Eisenhauer et al., 2012; Phillips et al., 2019; Rillig et al., 2019). However, manipulative experiments even at the local scale are also pivotal to study general ecological hypotheses, such as biodiversity–ecosystem functioning relationships (e.g., Eisenhauer et al., 2016; Jochum et al., 2020; Tilman et al., 2014) or interactions between groups of soil organisms (Heemsbergen et al., 2004; Potapov, 2022). This fundamental knowledge is the basis for functional macroecology. We also believe that the assessment of soil biodiversity in various initiatives of global networks of experiments that have recently emerged (e.g., BugNet, Drought-Net (Knapp et al., 2017), Nutrient Network (Borer et al., 2014), WARM) would allow scaling-up experimental data to better understand the mechanisms by which soil organisms respond to environmental pressures and how they influence (or are influenced by) ecosystem processes (Mathieu et al., 2022). Both observational and experimental approaches are needed to foster our knowledge of soil macroecology (Eisenhauer et al., 2021). We believe that finding ways to combine or analyse them together would lead to a stronger inference. For instance, manipulative experiments can be conducted along elevational gradients (Delgado-Baquerizo et al., 2020a; Sundqvist et al., 2013) to contrast the effect of a single parameter modification (e.g., drought) on soil biodiversity with the continuous ‘normal’ variation along the gradient (e.g., across Drought-Net sites; Knapp et al., 2017). Moreover, soil biodiversity drivers and consequences identified based on observational data can be experimentally tested in targeted experiments (Delgado-Baquerizo et al., 2020a, 2020b).

Additional perspectives on combining experimental and observational data are to build meta-models that allow using simplistic (but ground-truth) relationships from experiments (e.g., fungal survival under several droughts or warming treatments) to constrain causal inference models based on observational data. As far as we are aware, this approach is not yet available, but similar attempts have been carried out like using experimental data to constrain species distribution models (Talluto et al., 2016). More information is definitely needed on the niche volumes and tolerances of soil organisms, and stronger collaborations in data collection and with the field of statistical ecology and causal inference will be required to make this happen. Combining global observational data with global experimental work will open a new area of research to predict soil biodiversity and functioning across spatial and temporal scales.

2.3 | Frontiers in soil biodiversity and function scenarios

Our understanding of soil biodiversity and functioning relationships has significantly advanced in the past decades. Most notably, we now know that functional dissimilarity between soil organisms underlies the relationship between soil animal species richness and functioning (FAO, ITPS, Global Soil Biodiversity Initiative [GSB], SCBD, EC, 2020; Heemsbergen et al., 2004), which has been taken as an explanation for the *seemingly* high functional redundancy of soil biodiversity, especially for broad processes like decomposition (e.g., Liiri et al., 2002; Schimel, 1995). The rise of DNA-based methods has significantly advanced our mechanistic understanding of, in particular, the role of specific groups of microbes in biogeochemical cycles, and there is plentiful evidence that disturbance-induced changes in soil communities lead to changes in soil functioning (e.g., Allison & Martiny, 2008; de Vries et al., 2012). Yet, despite these advances, we still lack a generalized framework of when and where and which aspects of soil biodiversity matter for ecosystem functioning (Mathieu et al., 2022). We identify a few key areas that may advance our fundamental understanding of soil biodiversity–ecosystem functioning links in the real world and allow for incorporating aspects of soil biodiversity in global climate and biogeochemical models. Moreover, this will allow us to develop predictive models for future changes in soil biodiversity (Delgado-Baquerizo et al., 2020a; Guerra et al., 2021b), ecosystem functioning (Delgado-Baquerizo et al., 2020a) and high-priority conservation areas (Guerra et al., 2022):

Trait-based approaches for global predictions: A deeper understanding of the functional traits of animals, microorganisms and plants that matter for ecosystem functioning will help us focus and synchronize efforts of describing soil communities, and incorporate these traits into global climate and biogeochemical models (Bergmann et al., 2020; Guerra et al., 2021a). Identifying key traits and ascribing them to specific taxa will help us predict the occurrence of those traits through quantitative PCR or amplicon sequencing (Delgado-Baquerizo et al., 2018). Easy-to-measure community-level traits, such as biomass and metabolism, may be crucial for routine measurements and incorporation into global climate models (Crowther et al., 2019;

Patoine et al., 2022; Smith et al., 2019). Understanding how these traits, and associated process rates, link to specific soil properties and plant species or traits will ease their incorporation into global models and improve their accuracy (Crowther et al., 2019; Manning et al., 2015; Smith et al., 2019). As we unlock new insights into the diversity and functional trait composition of soil communities, we have begun to gain improved knowledge of the biogeographic patterns underlying these trends. For example, predictable variation in fungal community composition has been found to drive considerable variation in forest tree growth rates across Europe, with microbial traits explaining more variation than climate and edaphic conditions (Anthony et al., 2022). Similarly, the large-scale variation in saprotrophic fungal traits has been found to explain almost 30% of the variation in wood decomposition rates across North American soils (Lustenhouwer et al., 2020), highlighting the critical importance of fungal functional biogeography in determining soil carbon dynamics (Maynard et al., 2019). As such, the functional composition of soil biodiversity can help us to capture considerable proportions of unexplained variation in carbon turnover that can improve our mechanistic understanding of global biogeochemistry. This mechanistic information about the role of soil microbial traits is going to be particularly important for predicting the effects of extreme climatic events on ecosystem C cycling processes and greenhouse gas emissions (e.g., Williams & de Vries, 2020), which are currently not included in dynamic global vegetation models that form a submodel of global climate models (Pörtner et al., 2022).

Changing biotic interactions under global change: Interactions between soil organisms and plant traits, in particular, root traits and root exudation, which are a major mechanism of plant–microbial communication and a precursor of the formation of mineral-associated soil organic matter, have only been studied in controlled experiments and in a few, mostly crop or model, species (e.g., de Vries et al., 2019; Zhalnina et al., 2018). Such dynamics in real-world ecosystems and their implications for ecosystem functioning are a major gap in our understanding (Bergmann et al., 2020; Williams & de Vries, 2020). In addition, interactions between soil organisms are continuously updated (Bahram et al., 2018b; Bradford, 2016; Geisen, 2021; Guo et al., 2022), again mostly using controlled experiments. Expanding this growing understanding to real-world conditions, as well as understanding their context-dependence and response to global change, will be fundamental for understanding and predicting the impacts of global change on ecosystem functioning, including climate feedbacks (Crowther et al., 2019; Guerra et al., 2021b). For instance, it has been shown that trophic interactions between soil animals can change with warming temperatures (Thakur et al., 2017). Expanding both our mechanistic understanding of interactions between soil organisms, how these link to plant traits, what their relevance is in the real world, how this varies across ecosystems and with environmental change and how these interactions link to ecosystem functioning will require coordinated global networks of field experiments (see above) as well as linked experiments under controlled conditions (e.g., Delgado-Baquerizo et al., 2020a). For this to succeed, the global soil biodiversity community will need to come together to forge and tighten links with ecosystem ecologists, biogeochemists and atmospheric scientists. Moreover, it will require concerted and consistent funding streams focused on describing soil biodiversity across time and space, and a mechanistic understanding of its role in ecosystem functioning in a changing world

2.4 | Frontiers in critical soil biodiversity facets

Considering multiple diversity metrics (e.g., alpha-, beta- and gamma-diversity) is needed to develop a comprehensive understanding of how biodiversity is changing in the Anthropocene (Guerra et al., 2020, 2022; McGill et al., 2015), as different biodiversity metrics may have different determinants across large spatiotemporal scales (Guerra et al., 2020; Potapov et al., 2022; Soudzilovskaia et al., 2015), or across environmental and disturbance gradients (Potapov et al., 2019a). For instance, integrating various metrics could be useful to understand the mechanisms behind community turnover, species loss and ecosystem functions (Eisenhauer et al., 2021; Guerra et al., 2022). Most soil biodiversity studies observed changes in abundance and alpha-diversity, for example, the number of species of specific taxa, as an indicator of soil biodiversity change, while beta-diversity, that is, species turnover, remains an understudied biodiversity metric (Guerra et al., 2020, 2022, but see Thakur et al., 2017). The combined assessment of multiple biodiversity facets is critical to understand drivers and effects of biodiversity (Eisenhauer et al., 2021; Potapov et al., 2022). A recent study shows, for example, that the abundance of microbes may be a better indicator of some ecosystem functions, rather than their biodiversity (Bahram et al., 2022). We consider it important to integrate abundance and beta-diversity into large-scale studies to identify endemicity and vulnerability of soil organisms to global change (Tedersoo et al., 2022b), and to evaluate the relevance of 'conserved' areas in protecting soil biodiversity (e.g., not only protecting highly diverse areas but also those ones with certain combinations of drivers and thus unique community composition and functioning; Guerra et al., 2022). Regarding the relationship between soil biodiversity and ecosystem functioning, it is largely unexplored which metric is more informative under different contexts. The abundance of organisms performing particular functions in soil, that is, functional or trophic groups, may be more appropriate to predict specific soil functions in the ecosystem (i.e., functional identity and diversity of soil organisms). Yet, the richness of soil organisms has been positively related to multifunctionality at large scales, when measured both within a trophic level and across trophic levels, that is, multitrophic diversity (Delgado-Baquerizo et al., 2020b; Schuldt et al., 2018; Soliveres et al., 2016). Changes in the functional composition of soil communities (functional beta-diversity) have also been related to changes in ecosystem functions across different trophic levels (Martinez-Almoyna et al., 2022; Steinwandter et al., 2018). Particularly representative functional metrics can be community metabolism or energy flux (Barnes et al., 2018; Jochum & Eisenhauer, 2022; Mathieu et al., 2022). Metabolism scales nonlinearly with body mass, and thus metabolic approaches allow for a direct comparison of functional contributions across size classes of soil organisms, where abundance, biomass and diversity all are poorly comparable. Thus, different soil biodiversity facets (e.g., genetic, phylogenetic, taxonomic, functional, interaction and trophic diversity at different spatial scales) can provide complementary information on how soil biodiversity responds to global change and how it is related to soil functioning, which is why they have been proposed to be assessed in future soil biodiversity monitoring frameworks (Eisenhauer et al., 2021). Here, we summarize the critical frontiers in soil biodiversity research concerning the use of key biodiversity facets:

Using functional traits and trait diversity as a proxy of a potential function: In recent decades, plant ecology studies embraced the concept of traits being proxies for the impact of species on ecosystem functioning (Violle et al., 2007), as well as species responses to soil and climate environmental drivers (van Bodegom et al., 2014; van Ommen Kloeke et al., 2012; Ordoñez et al., 2009; Soudzilovskaia et al., 2013). The functional traits concept allows making a critically important step from species identity to species' roles in an ecosystem, and facilitates the operational reduction of highly multi-dimensional species diversity data, to quantitative data related to functions featured by an ecosystem. Given the enormous taxonomic diversity of soil organisms, the assessment of the soil communities from a functional point of view has a great potential (see also Section 2.3). Yet, while for plants it is widely recognized that the use of the functional trait concept allows making an important step in linking community composition to function (e.g., van Bodegom et al., 2014, but see van der Plas et al., 2020), the concept of functional traits of soil organisms is still in its infancy (Pey et al., 2014). It has been suggested that functional traits, such as body size and niche breadth, contribute to the community assembly of soil organisms (Aslani et al., 2022). Yet, despite important single efforts to conceptualize traits of soil biota (Pey et al., 2014; Põlme et al., 2020), we still lack a unified and inclusive framework that would (i) define key universal functional traits of soil organisms (going beyond body size and broad categories in feeding more) and (ii) link these traits to soil functioning. As a consequence, we also lack protocols for trait assessments of soil organisms, similar to those available for plants (Cornelissen et al., 2003).

Studying soil interaction networks and spatial associations: Soil organisms are involved in a multitude of interactions below and above the ground (Bahram & Netherway, 2022; Potapov, 2022). The use of complementary molecular methods like stable isotope analysis, fatty acid and amino acid analysis, as well as eDNA barcoding, can unravel trophic interactions in soil food webs (Jochum & Eisenhauer, 2022; Potapov et al., 2019b; Traugott et al., 2013). Community metabolism, which is a very important but understudied biodiversity facet, can be directly measured from heuristic food webs combined with measures of abundance and linked to functioning by reflecting the total activity and consumption rates of organisms (Barnes et al., 2018). Community metabolism may not correlate with community biomass (or diversity) across large environmental gradients (Potapov et al., 2020), which is why it may provide unique information about soil biodiversity. Moreover, it is now recognized that trophic interactions play a major role in shaping the diversity of ecological communities over large spatial scales that should be accounted for in macroecological studies (Eisenhauer et al., 2021). Such biotic interactions result in nonrandom co-occurrences and affect species–environment relationships, which makes disentangling community interactions from environmental associations a challenge, especially at large scales. Advanced molecular methods, such as metagenomics and transcriptomics, across large scales, could provide further insights into the spatial association between species (exemplified in Bahram et al., 2018b) or trophic or functional groups (Martinez-Almoyna et al., 2022; Ohlmann et al., 2018).

Assessing the distribution of functional genes to measure ecosystem functioning: The distribution of functional genes may better reflect ecosystem functions compared to taxonomic diversity (Bahram et al., 2022; Beugnon et al., 2021, see in oceanic studies, Louca et al., 2016). Metagenomics and transcriptomics analyses now allow us to profile nearly all potential and realized functional genes existing in a single sample in a high-throughput manner, respectively. Rapid advances in high-throughput methods, such as metagenomics, metatranscriptomics, proteomics and metabolomics analyses, besides high-throughput physicochemical analyses, will continue to unravel the taxonomic, functional and interaction diversity of soil organisms.

Uncovering rare microbes and hidden biodiversity: Rare microbial groups like specific Archaea may play key roles in ecosystem processes (Jousset et al., 2017), while they may show stronger associations with climate change factors (Bahram et al., 2022). Understanding the ecology of such rare groups (rare biosphere) holds great promise in soil protection and restoration, and can also be the target for novel biotechnological processes. We now have an unprecedented opportunity to develop primers for such groups by leveraging growing PCR-free, metagenomics-based databases (Bahram et al., 2018a). The investigation of the hidden biodiversity in deeper soil layers will be a critical component of future soil biodiversity monitoring (Eisenhauer et al., 2021), given that differences in fungal community composition at a few cm of depth can be greater than the biogeographic differences across a landscape (Feinstein & Blackwood, 2013). This affects how soil communities function at different depths and how they respond to global change (Li et al., 2020). Moreover, a recent study revealed that microbial life in groundwater can be as productive as in some ocean waters (Overholt et al., 2022).

Understanding the relationship between functional diversity and stability: Biodiversity within soil functional groups may be important for the stability of ecosystem functioning; that is, a high number of coexisting species that perform similar functions under dissimilar environmental conditions provides stability of this function under environmental change. Yet, despite the past attempts to link functional diversity with stability in soil (e.g., Griffiths & Philippot, 2013; Philippot et al., 2021; Preston et al., 1999), the biodiversity–stability relationship remains to be established for soil organisms. Studying soil biodiversity as interaction networks, for example, food webs, can provide insights into the stability of soil communities under global change (de Castro et al., 2021). This is facilitated by advanced network tools for disentangling indirect from direct associations (e.g., Xiao et al., 2022).

2.5 | Frontiers in underrepresented drivers

A good understanding of soil biodiversity drivers and functions starts with good baseline data on the environmental conditions these organisms live in (Lembrechts et al., 2020b). Indeed, many—if not all—assessments of regional and global patterns in biodiversity, as well as assessments of soil ecosystem functioning, rely on spatially explicit information on the environmental conditions and stressors affecting the ecosystem. Nevertheless, even for the most fundamental variables, such as soil type, texture, temperature, moisture and pH, high-resolution and sufficiently accurate global data are still limited (e.g., Entekhabi et al., 2010; Lembrechts et al., 2020a; de Sousa et al., 2020). Global products are increasingly emerging, yet often remain at coarse spatial resolutions, are based on data with insufficient global coverage or lack the necessary accuracy. Indeed, especially soil microbial diversity operates at the scale of micrometres, while physicochemical data is often extrapolated at 100 × 100 m resolution at best (Lembrechts et al., 2020b). Furthermore, the recent surge in high-resolution remote-sensing products has been less expansive for soil properties, due to the inherent issues related to assessing belowground conditions from space. For several other, less common drivers, such as pesticides (Beaumelle et al., 2021; Edlinger et al., 2022; Riedo et al., 2021), antibiotics, other—often new—chemical substances, such as PFAS (perfluoroalkyl and polyfluoroalkyl substances), heavy metals and microplastics (Rillig et al., 2019; Steiner et al., 2022), global coverage is even lower:

Assessing and predicting underrepresented drivers: Importantly, while assessment of the current levels and implications of most of these environmental conditions is scattered at best, many of them are also rapidly changing under global change. Assessments of ongoing changes, let alone predictions of future changes or reconstructions of past changes, are rare even for soil temperature (Lembrechts & Nijs, 2020) and nonexistent at the large scale for most of the other environmental parameters covered above. Widespread monitoring of soil environmental conditions, and especially soil contamination, is therefore needed (Hou & Ok, 2019). Especially rare and often overlooked contaminants should become part of government monitoring programmes, and be analysed across biomes and along elevational and latitudinal gradients, in different land-use types and including nature-protection areas, where they are not applied (Beaumelle et al., 2021). Indeed, limited but important data on soil organisms show that latitudinal and altitudinal patterns of aboveground biodiversity are often in opposite directions compared to belowground ones (e.g., Decaëns, 2010; van den Hoogen et al., 2019; Phillips et al., 2019; Tedersoo et al., 2014).

Interactions of drivers and context dependencies: Regardless of the availability of data, the relative importance (relative to other drivers, such as vegetation, climate and soil properties, such as pH) of many soil-related parameters or contaminants (e.g., microplastics, antibiotics, new compounds) for driving soil community composition and soil functioning is still poorly understood (Rillig et al., 2019). Indeed, for many specific groups of soil biota, we have very little understanding of how they respond to changes in these parameters. The remaining key questions are (i) if these compounds impair (or improve) the functioning of specific groups or soil biodiversity and functioning as a whole, (ii) if and how multiple contaminants interact (Rillig et al., 2019; Thakur et al., 2018), (iii) how they interact with climate change (Beaumelle et al., 2021) and (4) what (often nonlinear) shapes these relationships take (Saleem et al., 2019)?

2.6 | Frontiers in global collaboration

International collaborations on soil biodiversity and ecosystem change are currently being used successfully to record scientific names, gather past data and develop new experiments to test hypotheses across temporal and spatial scales (see examples in Frontier I). Similarly, the encouraging use of soil biodiversity as indicators or including soil organisms in existing indicators for monitoring changes across lands or temporal scales can serve as a platform for additional hypotheses related to change and status of soils (Guerra et al., 2021b; Orgiazzi et al., 2018):

Taxonomic expertise: To improve the scientific understanding of soil biodiversity change across scales, a broader approach for future collaborations might involve more experts integrating across and within other (soil) disciplines (Kühl et al., 2020). This relates in the first place to the experts in taxonomy and soil sciences. The few soil biota taxonomists accumulated the bulk of knowledge in species characteristics that is useful and necessary information for other disciplines, to understand the mechanisms and consequences of observed biodiversity patterns and changes. Yet, expertise for each taxonomic group in soils is not represented equally across the globe, with fewer experts available to participate in today's multidisciplinary soil ecology. However, open online identification platforms (e.g., https://araneae.nmbe.ch) and involvement of citizen scientists (Pfingstl et al., 2022) can become resources for expertise exchange and for enlarging equitable participation in soil biodiversity assessmen.

Capacity building and inclusive global initiatives: A bonus of linking more experts and components of soil biodiversity and ecosystem functioning in research is capacity building—the opportunity and responsibility to include and promote in all future collaborations, the new generations of soil biodiversity scientists. It is particularly important to actively engage and train contributors in lower- and middle-income countries, so they can have meaningful research careers and participate equally in knowledge sharing (Maestre & Eisenhauer, 2019), such as having free access to taxonomic identification in international collaborations. Contributors must be aware that country-based collaborator involvement is preferred over 'helicopter' collaborations (Maestre & Eisenhauer, 2019), where scientists fly into countries to sample and leave without involving local scientists (Parker & Kingori, 2016, 2022). A further point noted for international collaborations is understanding the costs (e.g., communication load and formats) and benefits (e.g., added scientific value, networking, joint publications) of large consortia and the necessity of everyone understanding the benefits, goals and ethics of a large project (Muscarella & Poorter, 2022; Scholz et al., 2022). Volunteer scientists in developing countries may need funding to participate, such as with the cost of shipping soils and other samples. Legal challenges in soil, taxa and data exchange persist (Overmann & Scholz, 2017) and may continue, as countries plan how to deal with 'one health'—plant, animal and human diseases. Nevertheless, as we work through the benefits and challenges of international collaborations in soil biodiversity, we are excited about the potential for providing scientific information on soil habitats and soil biodiversity across ecosystems.

2.7 | Frontiers in knowledge application and transdisciplinarity

Soil knowledge has been increasingly available in global reports (e.g., FAO, ITPS, GSBI, SCBD, EC, 2020; Orgiazzi et al., 2016), in databases (see Frontier I) and through events, such as the UN International Year of Soil 2015, the Global Soil Week or the World Soil Day. Its application has already started since urban green areas are becoming more biodiverse (e.g., wildflower strips, nature and urban gardening), and soil organisms like earthworms (as key detritivores and ecosystem engineers) or microbes (in soil inocula) are being increasingly recognized to improve soil quality and therefore productivity. However, there is more knowledge to be gained and applied, especially in agriculture. Current frontiers in knowledge application are (i) limited scientific evidence for the benefits of soil-knowledge-based approaches in practice-relevant settings, (ii) hypothesis-driven research that lacks focus on application potential and (iii) the missing link between research and real-world challenges of land managers. Farmers and scientists usually aim for the same goals (i.e., healthy soils; Wall et al., 2015), but 'talk a different language' that leads to decreasing interest or even to misunderstandings and conflicts. Collaboration with diverse stakeholders at the beginning of a project will allow for joint hypothesis building. As such, joint stakeholder workshops, social events and knowledge transfer (e.g., presentations or colloquia open to the public) will bring the parties closer together, and research outputs will become more targeted and relevant for application.

Promising approaches that are based on soil knowledge need to be validated in experiments at a suitable scale. Many approaches that render promising results in lab or greenhouse experiments are challenged by the complexity of real-world systems and result in high context-dependency of the aimed-for benefits, complicating large-scale application (Bender et al., 2019). Fostering calls that include both science and industry as funded parties will make knowledge utilization immediate, such as realized in calls from the EU or specific national funding schemes. In addition to basic research, existing knowledge has to be directly linked to current and future challenges, such as those in food security, nature conservation or climate change mitigation (Pörtner et al., 2022). Examples of knowledge that can be more widely applied are manifolds. Seed coating with (compost) microbiomes (Qiu et al., 2020) is a currently underrepresented approach to protect seeds and ease plant establishment (Pedrini et al., 2017). Engineering soil microbiomes may be more extensively used to support agricultural production (e.g., Bender et al., 2016; Panke-Buisse et al., 2015). The success of adding external microbes and microbial consortia needs to be monitored, as their survival and functional roles are dependent on the environmental and physical–chemical properties of each soil. For novel, ecology-based approaches, adequate and independent quality control is crucial, since products with unsatisfactory quality can undermine the confidence of practitioners in such approaches (Salomon et al., 2022). Monitoring soil biodiversity can guide improvements in soil fertility. At the political interface, soil models can be used to predict public strategies (Mao et al., 2021). The discovery of mechanisms within the soil system will only be useful when effectively applied across multiple sectors, such as agricultural production and policymaking.

2.8 | Frontiers in public and policy communication

Knowledge of soils and the biotic interactions therein, as well as on global patterns of soil biodiversity and functioning, have been advancing quickly during the last two decades, bringing soil-related topics from a niche subject into a regular subject in high-impact scientific journals (e.g., Bardgett & van der Putten, 2014; Rillig et al., 2019; Wall et al., 2015; Wardle et al., 2004). Public awareness of the extent of soil biodiversity and the fundamental importance of soils for the planet's functioning and human existence, however, is lagging behind. This lack of awareness is also reflected by the widespread neglect of addressing soil biodiversity in most existing environmental policies, where soils are merely considered with respect to the functions they provide, their role in mitigating climate change or even only as part of the abiotic environment, providing habitat for aboveground species (Zeiss et al., 2022). The awareness of soils being living systems, where organisms perform essential functions that supply humans with critical everyday services, such as food, fodder, or clean water and harbour a substantial part of global biodiversity (Orgiazzi et al., 2016), is only starting to enter public discussions beyond that of land managers (Guerra et al., 2021a). The inherent complexity of soils combined with the small size of many soil organisms and the methodological limitations of studying them make it much harder for soil ecologists to reach a similar prominence for soil-related issues compared to aboveground biodiversity (Cameron et al., 2019; Phillips et al., 2017). The fact that a vast fraction of soil organisms has yet to be described (Eisenhauer et al., 2019; Orgiazzi et al., 2016) and that we are only beginning to understand their global, landscape-scale and local distribution patterns makes it difficult to provide similar arguments for soil biodiversity protection than for aboveground biodiversity. Notably, there is no time to wait until the belowground data situation matches aboveground biodiversity data. Soil scientists have to find other ways to bring soil biodiversity to the table and implement adequate protection strategies (Guerra et al., 2022). Policymakers do not operate in a vacuum; they represent us, are part of society and react to their environment, including the values and beliefs of their potential voters. This implies that raising the awareness of soils as living systems in the general public may be equally important in causing change at the policy level. The goal must be to implement an awareness of living soils in all parts of society. We consider the following measures and considerations as the most promising for turning science into action:

(a) The most obvious way is certainly by scientists connecting and campaigning directly to policymakers and stakeholders, as a range of initiatives, such as the Global Soil Biodiversity Initiative (GSBI), are currently doing. In communicating to policymakers, quantifying the monetary value of soil biodiversity-derived ecosystem functions and the financial consequences for society of potentially losing them becomes crucial, since financial considerations are part of almost all policy measures. Moreover, direct outreach to stakeholders, such as land managers, farmers and the general public is important.

(b) Communication channels and the language used matter since the information provided needs to directly relate to the experience realm of the information receiver. Not only the way the information is presented but also who is presenting the information is crucial. Identifying multiplicators and facilitating peer-to-peer learning or on-farm demonstrations can be effective ways of knowledge dissemination and inducing action, for example, for farmers (Sutherland & Marchand, 2021; see the concept of lighthouse farms as an example: www.lighthousefarmnetwork.com).

(c) (Include essential information on soil life and health into curricula of Kindergartens, schools, University and professional education (e.g., for farmers, architects, city planners, etc.). Scientists can contribute by helping to produce easily accessible teaching materials (see e.g., https://bodenreise.ch/). Given the fundamental importance of healthy soils for human societies, it is unjustifiable that such information is currently often not taught.

(d) Cognitive science tells us that motivation for action, for example, for climate change or biodiversity, is best triggered by emotions and that emotions are generated through experiences, not statistics. Create sensual experiences of soil biodiversity (touching, smelling, seeing, hearing soil). Prominent examples are Citizen science projects, such as 'Sounding Soil' or 'Soil your undies' challenges, where one can listen to sounds soil organisms make or see their activity by burying cotton underpants and retrieving them after a while when they have been decomposed, respectively, creating direct sensual experiences. Such efforts can also help to bring soils into mainstream media (e.g., media coverage of the Citizen Science project 'Beweisstück Unterhose' was recorded in 24, countries and reached all media channels, including boulevard newspapers, children's news, and science documentaries; www.Beweistueck-unterhose.ch). Policymakers, for example, are facing various demands and information from several stakeholders, and their decisions cannot be fully based on rationality and evidence (Cairney & Kwiatkowski, 2017). Emotions and moral beliefs play an, at least, equally important role, and such approaches can also help to elicit political action.

(e) Use of novel digital tools to create virtual reality experiences can also facilitate soil experiences (see *'Adventure Soil Life'—A virtual journey through an unknown world*; ViMM (vi-mm.eu) as an example). Digital tools can also bring the public to engage with soil, such as through the soil animal identification app www.bodentierhochvier.de (Neu et al., 2022) and can even contribute to advancing scientific knowledge (Pfingstl et al., 2022).

(f) Training early-career scientists to be involved in soil biodiversity and science policy in local and global scientific organizations. This should also include communication training and psychological aspects of communication theory.

3 | CONCLUSIONS AND OUTLOOK

In this conference report, we identified emergent frontiers in soil ecology that were the in focus of the WBF2022 in Davos (Figure 2). We identified a wide range of frontiers in soil biodiversity and function, from data integration to knowledge application, which will need to be overcome to ensure the conservation of soils for the next generations. These research priorities extend on the strong interdisciplinary work in soil ecology, call for more transdisciplinary approaches and thus represent *Inspiration for Action* in soil biodiversity research and nature conservation. In line with the saying related to the health of the human skin '*The skin never forgets*', protecting the soil as the Earth's thin skin and the biodiversity therein needs to be a top priority to protect global biodiversity. Soils are experiencing an increasing number and severity of anthropogenic stressors (FAO, ITPS, GSBI, SCBD, EC, 2020; Geisen, 2021), but represent the basis for human nutrition and health (Banerjee & van der Heijden, 2022; FAO, ITPS, GSBI, SCBD, EC, 2020; Wall et al., 2015), calling for immediate action to maintain these essential nature's contributions to people. This has been known for decades, but little has been done since then ('*The nation that destroys its soil destroys itself*', Franklin D. Roosevelt, 1937).

Accordingly, the significance of soils has moved more and more into the scientific focus, changing from a niche topic with many specialized journals and conferences to a mainstream topic in ecology, earth-system sciences, and nature conservation over the last two decades. The fate of soils is specifically mentioned in the Resolution of the WBF2022: 'Foster soil management, which encourages landscape heterogeneity through incentivized biodiversity-friendly agricultural practices and educational programmes about the critical value of soil biodiversity' (https://policykitchen.com/system/files/2022-07/WBF%20Davos%20Resolution%202022.pdf). To further facilitate this process, however, it may be questionable if future conferences like the WBF should have soil-centred sessions, or if contributions might be better integrated into broad topics, such as biodiversity change, biodiversity monitoring, biodiversity–ecosystem functioning, macroecology, and science-policy connections. This may foster a more integrated and holistic appreciation of biodiversity change in terrestrial ecosystems as well as connections to other realms.

Founded in 2020 in response to the World Economics Forum, the location was predetermined and coincided with the beautiful landscape of the Swiss mountains and their biodiversity (Figure 3). However, biodiversity research needs to fully embrace the global community of researchers, practitioners, representatives from different sectors, decision-makers and societal actors (Isbell et al., 2022), which may require considering a rotating system of subsequent meetings in different countries around the globe, including the global south. Alternatively, or in addition, a travel stipend programme could support contributors without sufficient funding.

Moreover, to reach out to policymakers and the public, it may be considered to present and discuss the contents, implications, and applications of contemporary biodiversity research highlighted by the Conference Resolution during targeted policy and public events. There is an urgent need to build more direct bridges between science and policy-making and specifically invite politicians, advisors, and companies to attend the next WBF. We are happy that so many soil scientists joined this meeting and about their active engagement, to halt and reverse the degradation of ecosystems and to provide nature-based solutions for living in harmony with nature is a necessity for discussions at future meetings and for a sustainable world.

AUTHOR CONTRIBUTIONS

Nico Eisenhauer, Carlos A. Guerra, and Anton Potapov led the workshop and discussions. Nico Eisenhauer led the paper writing. Nico Eisenhauer, S. Franz Bender, Irene Calderón-Sanou, Franciska T. de Vries, Jonas J. Lembrechts, Wilfried Thuiller, Diana H. Wall, Romy Zeiss, and Anton Potapov wrote first drafts of subsections. All authors contributed to discussions during the workshop. All authors contributed to paper writing.

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FIGURE 3 Meeting location of the World Biodiversity Forum 2022 in Davos, Switzerland. Left: Local biodiversity of an alpine pasture. Photo: Nico Eisenhauer. Right: Landscape heterogeneity and diversity of ecosystem types. Photo: Michael Steinwandter.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

ETHICS STATEMENT

The authors confirm they have adhered to the journal policies regarding ethics.

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