Opinion Paper

Priorities for research in soil ecology

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Abstract

The ecological interactions that occur in and with soil are of consequence in many ecosystems on the planet. These interactions provide numerous essential ecosystem services, and the sustainable management of soils has attracted increasing scientific and public attention. Although soil ecology emerged as an independent field of research many decades ago, and we have gained important insights into the functioning of soils, there still are fundamental aspects that need to be better understood to ensure that the ecosystem services that soils provide are not lost and that soils can be used in a sustainable way. In this perspectives paper, we highlight some of the major knowledge gaps that should be prioritized in soil ecological research. These research priorities were compiled based on an online survey of 32 editors of Pedobiologia – Journal of Soil Ecology. These editors work at universities and research centers in Europe, North America, Asia, and Australia. The questions were categorized into four themes: (1) soil biodiversity and biogeography, (2) interactions and the functioning of ecosystems, (3) global change and soil management, and (4) new directions. The respondents identified priorities that may be achievable in the near future, as well as several that are currently achievable but remain open. While some of the identified barriers to progress were technological in nature, many respondents cited a need for substantial leadership and goodwill among members of the soil ecology research community, including the need for multi-institutional partnerships, and had substantial concerns regarding the loss of taxonomic expertise.

Keywords

Aboveground-belowground interactions; biodiversity–ecosystem functioning; biogeography; chemical ecology; climate change; ecosystem services; global change; microbial ecology; novel environments; plant-microbe interactions; soil biodiversity; soil food web; soil management; soil processes

Introduction

Many, if not most, of the ecosystems on Earth are dependent on, or substantially influenced by, interactions and processes occurring within and among the planet's soils (including sediments). The remarkable biodiversity harbored in soil provides essential ecosystem services (Bardgett and van der Putten, 2014; Wall et al., 2015), and the sustainable management of soils has attracted ever-increasing scientific attention (Wall et al., 2015). Soil organisms and how they drive the processes that underlie essential ecosystem services have fascinated and challenged soil ecologists for decades (Powell et al., 2014). Their importance and complexity are increasingly arousing public and political interest in soil, such as that exemplified by the International Year of Soils in 2015 (Powell and Eisenhauer, 2015) and the annual celebration of World Soil Day (every December 5th, since 2002). Many policy makers and land managers are realizing that soil ecological knowledge is key for sustainable environmental management, for the protection and conservation of soils, and for the nutrition and health of an increasing human population (Wall et al., 2015; Keith et al., 2016). However, despite these points, many knowledge gaps still exist and hinder researchers from making specific recommendations about soil conservation issues (Phillips et al., 2017) to maintain soil processes linked to ecosystem services under increasing human pressure and global change. As a consequence, soil ecology will remain an extremely important field of research into the future and requires a coordinated global effort to address the most important issues facing the sustainability of soils and gaps in soil ecological knowledge.

In this perspectives paper, we highlight what we have identified as the most crucial and emerging questions in soil ecological research. These research priorities were compiled based on an online survey of 32 editors of Pedobiologia – Journal of Soil Ecology. Thus, this list of questions may not be exhaustive and certainly contains some geographical biases (Fig. 1), but we are confident that they will serve as a constructive collection of ideas to target future research and facilitate progress in soil ecology.

Survey

Thirty-two editors of Pedobiologia – Journal of Soil Ecology participated in the online survey in September and October of 2015. These editors work at universities and research centers in Europe, North America, Asia, and Australia (Fig. 1) and cover many different disciplines in soil ecology (Fig. 2). All of them provided responses to the following five questions/requests:

1. Please list 5-10 outstanding research questions in soil ecology that, in your opinion, should be prioritized.
2. Which of these priorities are currently achievable given available technological or analytical resources?
3. For the achievable priorities, please state, in your opinion, why these have not been achieved.
4. For the priorities that are not currently achievable, what technological or analytical advances are required to facilitate research into these priorities?
5. Which research themes/keywords best represent the majority of your research?

Overall, we received 214 responses to question #1. Questions were screened, similar questions were merged, and then questions were grouped in the following four categories: (1) soil biodiversity and biogeography, (2) interactions and the functioning of ecosystems, (3) global change and soil management, and (4) new directions. In total, 117 questions were identified, and we then asked all editors to vote for the most pressing questions to be addressed in each category. The questions that were supported by at least six of the 23 respondents (>25%) to this second survey are presented below. Within each section, the questions are proposed in order of decreasing support; all proposed questions and their level of support are provided in the supplementary online material. Responses to questions/requests 2–5 of the initial survey are summarized in the sections "New directions" and "Conclusions".

1. Soil biodiversity and biogeography

Currently, there is a focused and highly dynamic research effort to understand how biodiversity, in general, is changing and what is driving this change (Vellend et al., 2013; Dornelas et al., 2014; Wright et al., 2014; McGill, 2015; Gonzalez et al., 2016; Vellend et al., 2017). Remarkably, information on soil biodiversity is lagging behind compared to the diversity of other groups of organisms, and the underlying databases and analyses are largely lacking comprehensive information pertaining to soil biodiversity (Phillips et al., 2017). This gap is probably due to limited and patchy data on soil biodiversity, particularly the absence of surveys with explicit temporal and spatial perspectives (Phillips et al., 2017), and difficulties comparing studies using different methodologies. Soil ecologists are still trying to determine the main drivers of soil biodiversity patterns (Fierer and Jackson, 2006; Powell et al., 2015a) and the fate of soil biodiversity in the face of global environmental change (Maestre et al., 2015; Veresoglou et al., 2015).

According to the Global Soil Biodiversity Atlas (2016), remarkably few species of soil taxa have currently been described, with estimates ranging from <1% for protists, <1.5% for bacteria, <7% for fungi, 17% for Collembola, 23% for earthworms, to 55% in mites. These values are much less than what has been described for other taxa (e.g., ~88% of vascular plants have already been described). In addition, even when taxonomic information is available, much less is known about the functional roles of the great majority of these organisms within the ecosystems in which they occur (e.g., Janion-Scheepers et al., 2016). On top of this, bridging the vast gap in the spatial and temporal scales at which soil ecology is usually studied (e.g. small-scale biodiversity descriptions, short-term experiments in the laboratory) and scales at which ecosystems are managed in the real world (e.g. spanning from months to decades and from hectares to continents) remains a challenge (Jiang et al., 2016). Moreover, there has been little exploration of the roles that evolution has played in shaping soil biodiversity, and this has largely been biased towards a small subset of mutualistic or parasitic soil biota (Blaxter et al., 1998; Masson-Boivin et al., 2009; Tedersoo et al., 2010). As such, we are greatly limited in our abilities to address even the most basic questions, such as how much of the world's biodiversity is found in soils, and answers to questions relating to the main driving factors behind microbial biogeography are highly context-dependent. Further, while we are starting to address the questions of whether communities of certain organisms assemble in fundamentally different ways in soils due to the massive interchange that occurs among these communities (Rillig et al., 2016), there may be additional consequences for the evolution of soil biota that are not being addressed (Antwis et al., 2017).

The following section summarizes research questions that relate to the drivers of soil biodiversity, the study of underlying evolutionary processes, and linkages to ecosystem responses at larger spatial scales.

Drivers of soil biodiversity

1. How important are root and litter traits in determining the diversity and abundance of soil organisms?

2. Are there ecological assembly rules that determine community composition and structure, and what are the important mechanisms underlying these rules (dispersal limitation, species sorting, competition, facilitation, etc.)?

3. To what extent does niche differentiation occur for soil organisms, and what are the important mechanisms that contribute to this differentiation?

4. How do climatic conditions, parent material, vegetation type, and the distribution of mineral and organic surfaces in soil interact in shaping communities of soil biota?

5. What are the drivers of the phenology of soil organisms and processes, and how do we develop robust sampling strategies to effectively take these into account?

6. What consequences do dispersal limitations of soil organisms have for the

genetic structure and adaptability of populations of soil organisms?

7. How prevalent is endemism in soil biota?

Evolution

8. How frequent is horizontal exchange of genetic material among viruses, animals, plants, and microbes in soil, and does this differ from what is observed in aquatic systems?

9. What is the reason for the high frequency of parthenogenesis in some soil animal species and its absence in certain lineages, and what is its consequence for the evolution of these species?

10. How important is epigenetic regulation of gene expression for evolutionary and ecological processes in soil?

Scaling up

11. What is the degree of functional redundancy of soil communities, and does it

vary among ecosystem types?

12. Can biogeochemical process models be improved by including information regarding the soil organisms present?
13. Are there emergent properties at the landscape scale that arise from processes measured at much smaller scales, and can these properties be predicted from known soil ecological principles?
14. Are there general patterns that can be inferred from spatial associations between resources and consumers in soil?
15. Are genomic measures of functionality in soil useful predictors of ecosystem process rates and stability?
16. How large is the flux of greenhouse gases from soil environments, and what are the ecological controls of these quantities?

2. Interactions among soil organisms and the functioning of ecosystems

Despite their functional significance, trophic and non-trophic interactions among soil organisms are still poorly understood (Bardgett and van der Putten, 2014). There is increasing awareness of the need to explore species interactions in complex food webs to understand the provisioning of multiple ecosystem services (Thompson et al., 2012, Hines et al., 2015; Soliveres et al., 2016). In this context, a perspective that encompasses the whole soil ecosystem, from soil aggregates and the interactions within (Maaß et al., 2015) to the interactions between aboveground-belowground food webs (Eisenhauer et al., 2015; Hines et al., 2015) and involving ecosystem engineers (Jones et al., 1994), is needed to connect different compartments.

For trophic relationships, major advances can be made by better connecting the microbial utilization of plant-derived substrates to the movement of elements through faunal energy and nutrient pathways in soil, which are then linked to aboveground communities by plants and epigeic generalist predators (Scheu, 2001; Wardle et al., 2004; Scherber et al., 2010). Non-trophic relationships also play important roles, such as during the chemical mediation of species interactions in soil (van Dam and Bouwmeester, 2016), and behaviors arising during quorum sensing and swarming by soil microorganisms with subsequent effects of soil biota on plant growth (Phillips et al., 2003). Both trophic and non-trophic relationships can serve to link above- and belowground compartments, such as plant defenses against herbivores and pathogens being influenced, partly, by changes in belowground plant chemistry (Johnson et al., 2016) or *vice versa*. Central to these phenomena is the observation that complex networks of interactions can have emergent properties that influence network and ecosystem stability (Rooney et al., 2006; Neutel et al., 2007; Hines et al. 2015). We know about trophic networks in soil (Moore et al., 2005), but mostly at low taxonomic resolution and relatively little with regards to networks of mutualists in soil and the specificity of mutualistic interactions. Also, those networks are not well placed to determine whether the structure of mutualistic networks belowground can be inferred from knowledge generated during the study of aboveground mutualisms.

The following section summarizes questions related to interactions within soil food webs, whether direct (through trophic interactions) or indirect (through chemical interactions or *via* effects on soil physical characteristics); how these interactions are linked to aboveground communities; and what the consequences are of soil biodiversity and interactions among soil organisms for ecosystem processes.

Soil food webs and interactions therein

17. How important is facilitation among soil organisms, and what are the underlying mechanisms (e.g., chemical/physical) of facilitative interactions?

18. What is the relative contribution of top-down *versus* bottom-up control within soil food webs, and does their importance vary among food web compartments?

19. How important are mutualists, parasites, and viral diseases in regulating the functioning and assembly of soil communities?

20. What is the role of info-chemicals for microbe–plant, microbe–animal, and animal–plant interactions in soil, and how are chemical signals transmitted

effectively in a humus-rich environment?

21. How important are interactions among soil microorganisms for energy flows in food webs relative to interactions among soil fauna?

22. Do saprotrophic microorganisms and soil animals compete for resources, and do these interactions affect energy flows and nutrient stoichiometry?

23. How temporally stable are soil microbial communities, in terms of both taxonomic and functional community structure, and which community members are active at any one time?

24. Does functional redundancy in the traits expressed by multiple species lead to predictable outcomes from species interactions in soil despite differences in species composition?

Linking ecosystem compartments

25. How can we link belowground to aboveground food webs in dynamic models?

26. How does biodiversity in soil affect the diversity of other, connected environments in aquatic systems, and how important are temporarily flooded soils/sediments in linking diversity in these environments?

27. Are microbial communities in plant and animal tissues aboveground, in the litter layer, and in the soil functionally linked?

28. Do effects of landscape composition (diversity and composition of different adjacent ecosystems) and fragmentation on aboveground taxa lead to cascading effects on soil biota?

29. Is the weak link between biodiversity above- and belowground due to soil organisms being limited more by resources arising from belowground sources (e.g., minerals arising from weathering) compared with aboveground sources (e.g., carbon from photosynthesis)?

30. What is the relative contribution of above- and belowground plant residues for the nutrition of soil food webs?

Soil biodiversity–ecosystem functioning

31. Can ecosystem functions be predicted from the trait composition of soil communities?

32. Does intraspecific genetic diversity contribute to variation in ecosystem functioning?

33. What are the tipping points, with respect to species losses or disturbances to

ecosystems, that result in loss of soil functions?

34. How do soil biodiversity and ecological interactions in soil contribute to multiple ecosystem services, such as carbon sequestration, disease suppression, and maintenance of aboveground biodiversity?

35. How active are rare species in soil ecosystems, and do they provide significant contributions toward ecosystem functions?

36. What is the relative importance of biotic and abiotic drivers for decomposition and the subsequent cycling of elements in different soil types and ecosystems?

3. Global change and soil management

Anthropogenic environmental change is altering the composition and biodiversity of ecosystems at an unprecedented rate (Millennium Ecosystem Assessment, 2005; Ceballos et al., 2015) with poorly understood consequences for the functioning of ecosystems. While biodiversity–ecosystem functioning research has provided compelling evidence regarding the significance of biodiversity for the functioning of ecosystems (e.g., Hooper et al., 2005; Cardinale et al., 2012), the role of soil biodiversity (Bardgett and van der Putten, 2014) and the ways in which soil communities will change in response to altered environments (Veresoglou et al., 2015) are less clear (but see e.g., Blankinship et al., 2011 and Powell et al., 2015b). Environmental change may have substantial direct impacts on soil organisms and ecological processes that have consequences for soil fertility (Maestre et al., 2015), which may then result in feedbacks by which fertility shifts go on to impact those communities of soil organisms (Leff et al., 2015). How soils are physically and chemically managed has also been the focus of several studies, and while these types of environmental change are likely strong determinants of soil biodiversity and compositional shifts, the context-dependence (Deng et al., 2015; Hewins et al., 2015) and temporal nature (Venter et al., 2016; Eisenhauer, 2016; Jiang et al., 2016) of these shifts are poorly understood. And with apparent increases in the uses of commercial microbial inoculants in soil during ecosystem management, there is a greater need to assess and mitigate any associated risks (Schwartz et al., 2006; Antunes et al., 2009).

While the drivers of soil biodiversity and the ecosystem consequences are addressed in sections 1 and 2, respectively, questions related to the belowground consequences of global environmental change and implications for soil management are summarized in this section.

Global environmental change and biotic exchange

37. What roles can soil biota play in ecosystem resistance and adaptation to global

change, and what are the mechanisms underlying these contributions?

38. Is soil biodiversity currently undergoing an extinction crisis and, if so, to what extent is soil biodiversity being lost?

39. What is the role of soil organisms in plant range expansion, and to what degree can soil organisms migrate to favorable regions in response to climate change?

40. How resistant and resilient are ecosystems to changes in the composition and structure of soil communities?

41. What are the effects of land use change on trait composition and species composition of soil communities?

42. What is the relative importance of current *versus* historical processes in shaping species composition of belowground communities?

Managing soils for ecosystem service provisioning

43. How feasible is it to restore extensively degraded soil ecosystems to a functional state, and, if so, what roles can soil biota and ecological theory play in developing best practices for doing so?

44. What is the status and future of the generation of 'designer soils' that can

provide a selected suite of ecosystem services in new (e.g., terraforming) or existing (e.g., restoration) environments?

45. Can we alter soil microbial communities to impart desired characteristics to plant products used in food, beverage, and materials production?

46. What advances in our understanding of soil ecology can lead to significant increases in agricultural production and sustainability?

47. How can research and knowledge from soil ecologists be better integrated with the social and economic sciences?

48. Are practices used in plant breeding for pest and disease resistance unintentionally selecting against mutually beneficial symbioses with microbes?

49. Can the value of soil quality and its effects on ecosystem services be quantified?

4. New directions

Many of the questions posed in response to the survey took the form of a 'wish list' for soil ecologists or a list of challenges that the discipline is facing from a practical perspective. While the responses indicated that there were many issues that would need to be addressed to ensure progress on the questions that were posed, the general mood was that most priorities were achievable. In total, 72% of the priorities raised were identified as achievable based on available technologies and analytical resources. However, in the responses, there was much more of a focus on the need for broad collaboration, stable funding for research, and innovation by soil ecologists in the ways that the above problems are thought about. Many respondents cited a greater need for coordinated approaches to research, engagement with the public and industry, and ensuring resources are available for advances to be made in the future. For instance, many open questions cannot be answered on a global scale because the necessary data is not available in central databases (Phillips et al., 2017), but several soil ecologists already have started initiatives to establish such databases, such as on soil biodiversity (Burkhardt et al., 2014; Ramirez et al., 2015; Cameron et al., 2016) or trait data (Pey et al., 2014; Nguyen et al., 2016). The rapid development and advancement of DNA-based analyses of soil biota is only one prominent example that offers new opportunities to disentangle links of biodiversity/species assemblages within or between different organization levels, such as among clades, functional groups, or trophic levels. However, merging the respective data in global databases in a way that allows straightforward data extraction and usage will require big collaborative and interdisciplinary efforts.

The respective list of questions is summarized in this section and may guide future research activities proposed above. Our aim here is to reflect current attitudes about the advances that need to be made to progress soil ecology as a discipline. Although some, or even all, of the topics below might not sound entirely new to certain soil ecology practitioners or to specialists developing new techniques, nor be issues that are only important to soil ecologists, we think that a broader discussion on these topics would be beneficial to the wider community of soil ecologists.

New techniques and measurements

50. Can we better integrate soil fauna into high-throughput analyses of soil biodiversity, perhaps through more effective approaches to sampling environmental DNA from soil and better designed primers for eukaryotic organisms?

51. How do we effectively characterize functional diversity and capacity in soil ecosystems instead of relying mainly on DNA sequencing?

52. Can we develop a comprehensive index of soil health that is a reliable and informative measure of soil quality?

53. Is it possible to visualize, *in situ*, soil processes (soil aggregate formation, interactions between biota etc.) in space and time at a level of resolution at which these processes are occurring?

54. Can we take a trait-based approach to biodiversity in soil ecology, and what

would that look like?

55. Are there particular soil taxa that can be used as an indicator to assess the degree of impact associated with particular environmental stressors and perturbations?

56. How can we manipulate microbial communities to evaluate their functional roles without substantially altering the abiotic environment?

New ways of thinking and working

57. Can we establish long-term soil ecological observatories to track important issues, such as biodiversity loss and gradual environmental change?

58. How can we encourage open data sharing among soil ecologists (e.g., in open databases) in a way that ensures progress can be made without concerns arising with respect to the unethical use of these data?

59. Can we reverse the decline in taxonomic studies and recruit a new generation of taxonomists that are capable of integrating morphological evidence with an informed use of solid molecular databases?

60. How do we place soil biodiversity within a conservation perspective given the challenges we face with this 'enigmatic' system, such as extremely high

diversity with much of it being cryptic or undescribed?

61. How can the public be engaged to appreciate the value of soil biodiversity?

62. How can we ensure that emerging soil ecologists receive the right training to address the questions identified in this paper?

63. Can we prevent soil ecology as a discipline from becoming too focused on technological tools and ensure an appropriate emphasis on addressing fundamental and applied questions in soil ecology?

Conclusions

The present survey identified sixty-three prioritized questions that may serve as a guide for soil ecological research. While some of the barriers to progress were technological in nature, many respondents cited a greater need for elements that can only be achieved with substantial leadership within and goodwill among members of the soil ecology research community. These include reversing the loss of important taxonomic expertise for many, if not all, groups of soil organisms; negotiating meaningful collaborative endeavors among researchers across many institutions in multiple countries; and securing funding for investigating the relevance of soil ecology to processes at large spatial and temporal scales. Global efforts such as the

Global Soil Biodiversity Initiative (https://globalsoilbiodiversity.org/) suggest that this could be possible and may represent a starting point from which to build this concerted effort to address these questions. In addition, while the sample represented soil ecological researchers from 15 countries, there are large regions that still need to be canvassed, such as South and Central America, Africa, and several regions in Asia (Fig. 1), to ensure appropriate priorities are put in place for soil ecological research. Tackling the pressing questions listed above will not only be essential to advance basic soil ecological research, but will also generate crucial information for land managers and decision makers for a sustainable treatment of the soils that humankind relies on.

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Figure

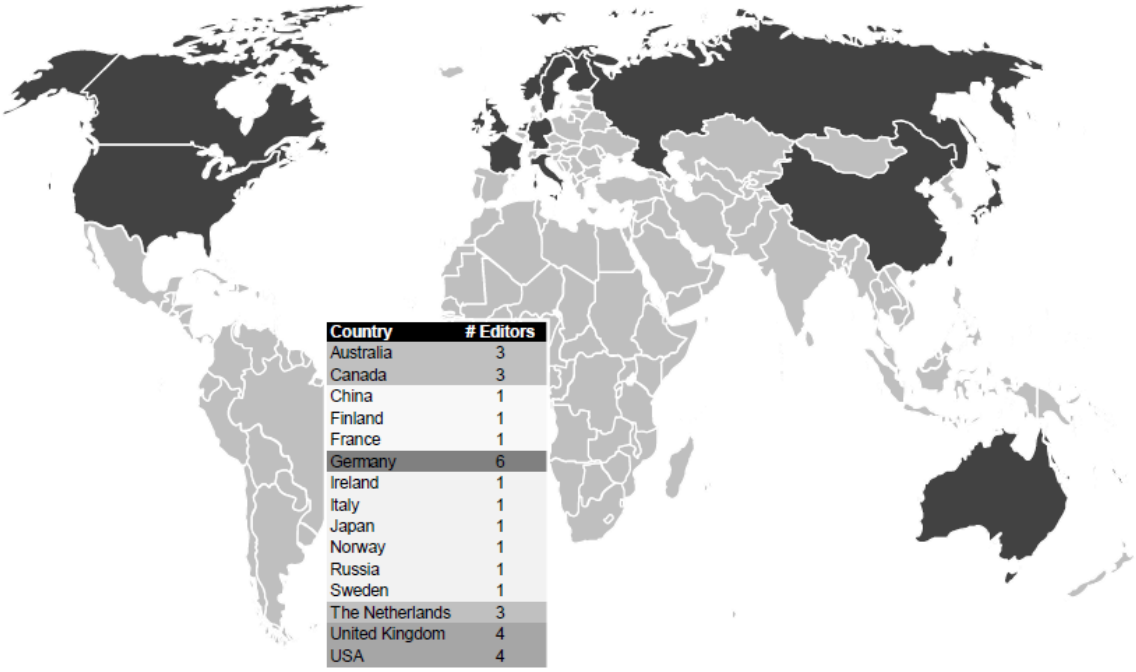


Figure 1. Geographic location of home institutes of the 32 Pedobiologia editors who participated in the present survey. In the map, countries represented by one or more editors are given in dark gray. In the table, different countries are given in alphabetical order, and countries represented by more than one editor are highlighted with different shades of gray.

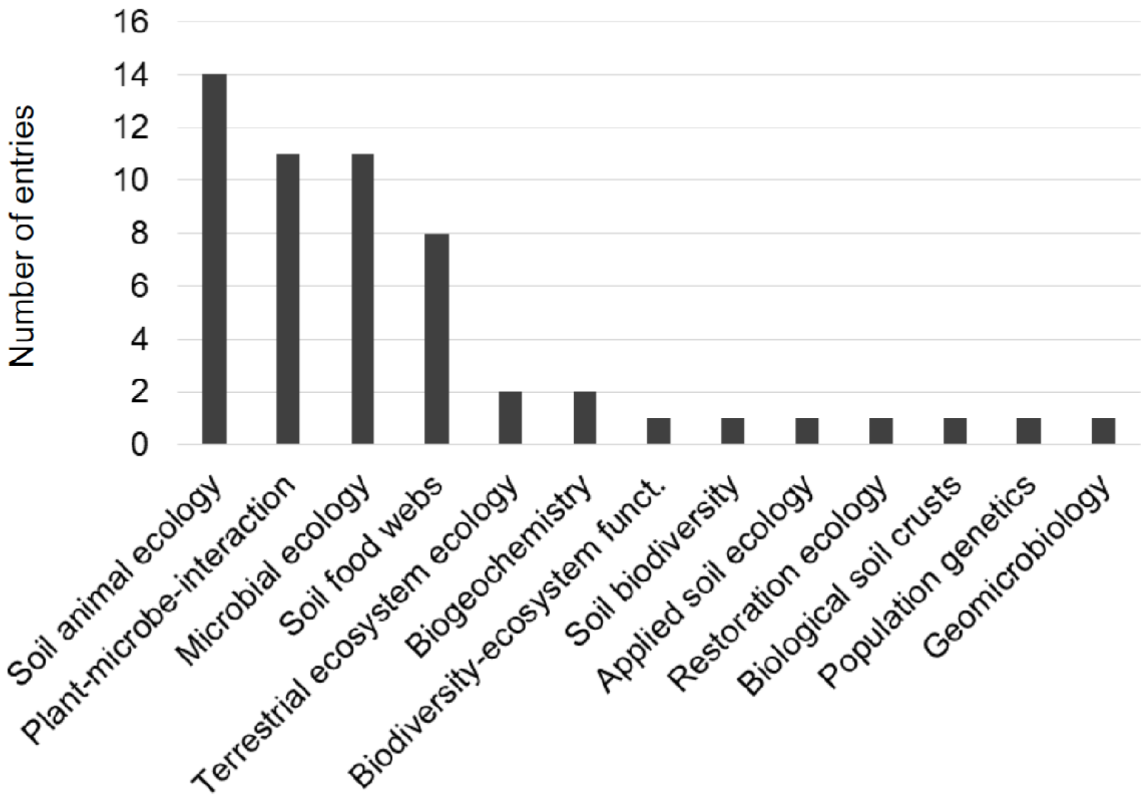
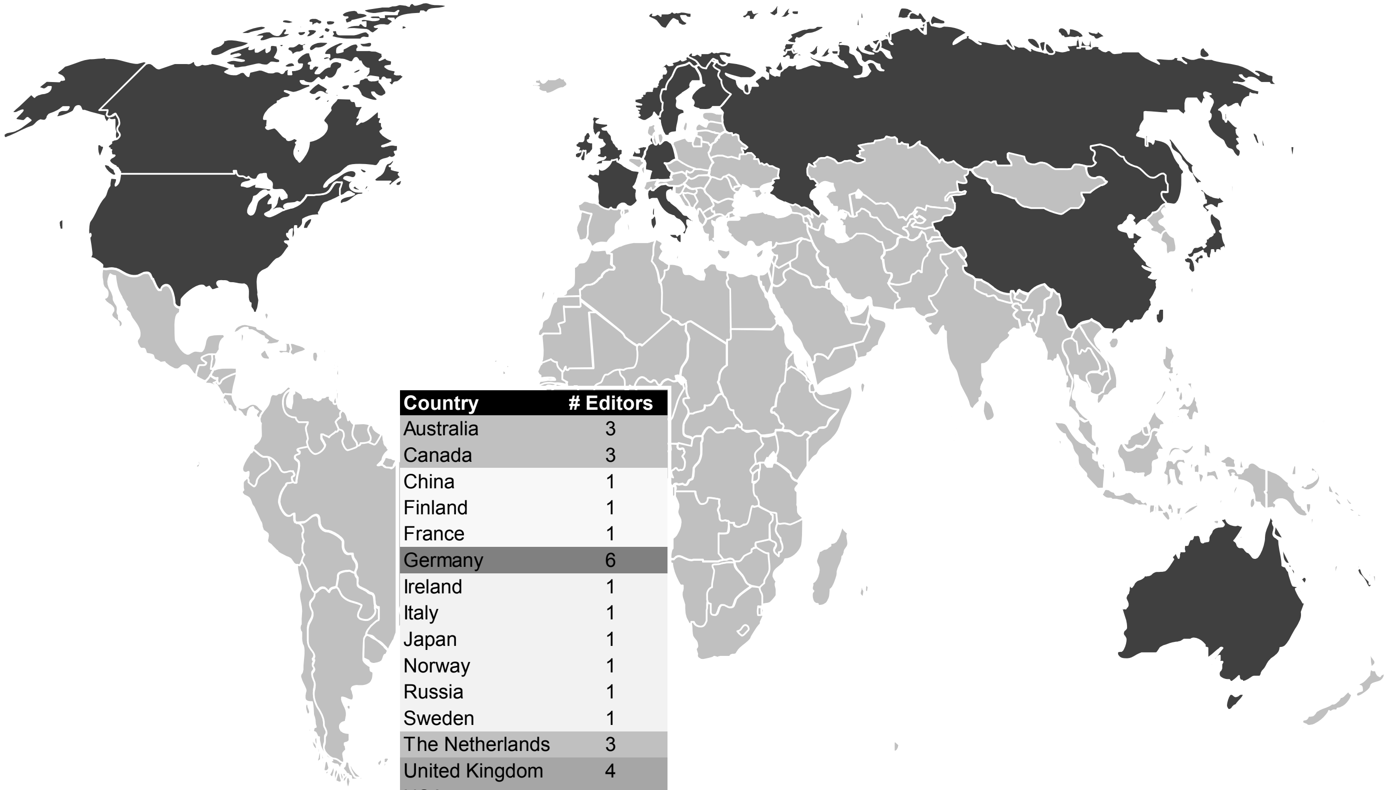
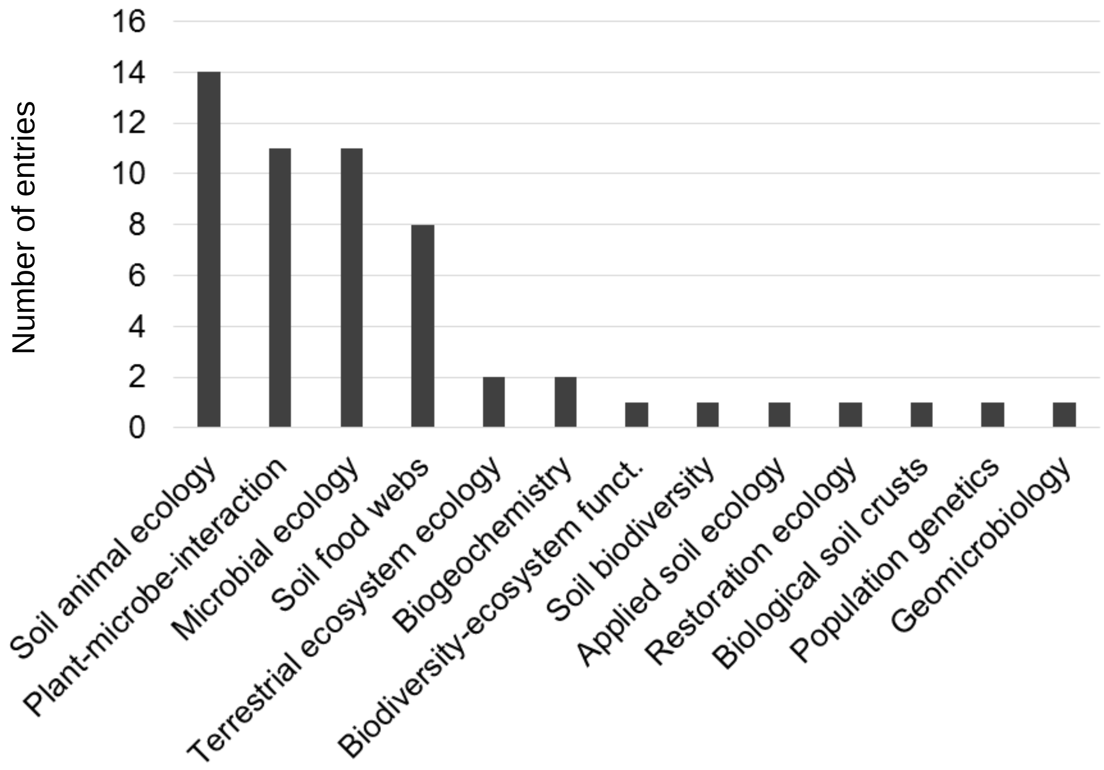


Figure 2. The 32 Pedobiologia - Journal of Soil Ecology editors who participated in the present survey represent different disciplines in soil ecology (multiple entries per editor were possible).



Country	# Editors
Australia	3
Canada	3
China	1
Finland	1
France	1
Germany	6
Ireland	1
Italy	1
Japan	1
Norway	1
Russia	1
Sweden	1
The Netherlands	3
United Kingdom	4
USA	4



Number of entries
16
14
12
10
8
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2
0
Soil animal ecology
Plant-microbe-interaction
Microbial ecology
Soil food webs
Terrestrial ecosystem ecology
Biogeochemistry
Biodiversity-ecosystem funct.
Soil biodiversity
Applied soil ecology
Restoration ecology
Biological soil crusts
Population genetics
Geomicrobiology

Highlights

- There still are fundamental aspects that need to be better understood in soil ecology.
- Here we highlight major knowledge gaps that should be prioritized in soil ecological research.
- Research priorities were compiled based on an online survey of 32 Pedobiologia editors.
- Major themes are: (1) soil biodiversity and biogeography, (2) interactions and the functioning of ecosystems, (3) global change and soil management, and (4) new directions.
- There is a need for substantial leadership and goodwill among members of the soil ecology research community

Supplementary Table 1. All questions identified by the 32 respondents in the in

Section

1. Soil biodiversity and biogeograpy
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2. Interactions among soil organisms and the functioning of ecosystems
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3. Global change and soil management
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4. New Directions
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itial survey, after revising to combine similar questions and grouping

Subsection	Votes in support
Drivers of soil biodiversity	15
Drivers of soil biodiversity	14
Drivers of soil biodiversity	11
Drivers of soil biodiversity	11
Drivers of soil biodiversity	11
Drivers of soil biodiversity	10
Drivers of soil biodiversity	6
Drivers of soil biodiversity	3
Evolution	15
Evolution	13
Evolution	7
Evolution	5
Evolution	3
Evolution	2
Scaling up	12
Scaling up	12
Scaling up	11
Scaling up	10
Scaling up	8
Scaling up	7
Scaling up	5
Linking ecosystem compartments	17
Linking ecosystem compartments	13
Linking ecosystem compartments	11
Linking ecosystem compartments	10
Linking ecosystem compartments	6
Linking ecosystem compartments	6
Linking ecosystem compartments	4
Linking ecosystem compartments	3
Linking ecosystem compartments	3
Soil biodiversity and ecosystem functioning	17
Soil biodiversity and ecosystem functioning	14
Soil biodiversity and ecosystem functioning	14
Soil biodiversity and ecosystem functioning	8
Soil biodiversity and ecosystem functioning	7

Soil biodiversity and ecosystem functioning	6
Soil biodiversity and ecosystem functioning	4
Soil biodiversity and ecosystem functioning	3
Soil biodiversity and ecosystem functioning	3
Soil biodiversity and ecosystem functioning	2
Soil biodiversity and ecosystem functioning	2
Soil biodiversity and ecosystem functioning	2
Soil biodiversity and ecosystem functioning	0
Soil food webs and interactions therein	14
Soil food webs and interactions therein	10
Soil food webs and interactions therein	10
Soil food webs and interactions therein	9
Soil food webs and interactions therein	8
Soil food webs and interactions therein	8
Soil food webs and interactions therein	8
Soil food webs and interactions therein	7
Soil food webs and interactions therein	5
Soil food webs and interactions therein	4
Soil food webs and interactions therein	4
Soil food webs and interactions therein	2
Soil food webs and interactions therein	1
Global environmental change and biotic exchange	16
Global environmental change and biotic exchange	11
Global environmental change and biotic exchange	11
Global environmental change and biotic exchange	6
Global environmental change and biotic exchange	6
Global environmental change and biotic exchange	6
Global environmental change and biotic exchange	5
Global environmental change and biotic exchange	5
Global environmental change and biotic exchange	5
Global environmental change and biotic exchange	4
Global environmental change and biotic exchange	4
Global environmental change and biotic exchange	3
Global environmental change and biotic exchange	3
Global environmental change and biotic exchange	2
Global environmental change and biotic exchange	0
Managing soils for ecosystem service provisioning	12
Managing soils for ecosystem service provisioning	11
Managing soils for ecosystem service provisioning	11
Managing soils for ecosystem service provisioning	9

Managing soils for ecosystem service provisioning	8
Managing soils for ecosystem service provisioning	7
Managing soils for ecosystem service provisioning	6
Managing soils for ecosystem service provisioning	5
Managing soils for ecosystem service provisioning	4
Managing soils for ecosystem service provisioning	3
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Managing soils for ecosystem service provisioning	3
Managing soils for ecosystem service provisioning	2
Managing soils for ecosystem service provisioning	2
Managing soils for ecosystem service provisioning	1
Managing soils for ecosystem service provisioning	1
New techniques and measurements	13
New techniques and measurements	12
New techniques and measurements	8
New techniques and measurements	8
New techniques and measurements	7
New techniques and measurements	6
New techniques and measurements	6
New techniques and measurements	5
New techniques and measurements	4
New techniques and measurements	4
New techniques and measurements	4
New techniques and measurements	2
New techniques and measurements	0
New ways of thinking and working	14
New ways of thinking and working	12
New ways of thinking and working	10
New ways of thinking and working	9
New ways of thinking and working	6
New ways of thinking and working	6
New ways of thinking and working	6
New ways of thinking and working	4
New ways of thinking and working	4
New ways of thinking and working	4
New ways of thinking and working	3
New ways of thinking and working	3
New ways of thinking and working	2
New ways of thinking and working	1
New ways of thinking and working	1
New ways of thinking and working	1

g into categories, and the number of votes for each question by the 23 respo

Question

How important are root and litter traits in determining the diversity and a
Are there ecological assembly rules that determine community composition an
To what extent does niche differentiation occur for soil organisms and what
How do climatic conditions, parent material, vegetation type, and the distr
What are the drivers of the phenology of soil organisms and processes and h
What consequences do dispersal limitations of soil organisms have for the g
How prevalent is endemism in soil biota?
What are the main driving factors of microbial biogeography?

How frequent is horizontal exchange of genetic material among viruses, anim
What is the reason for the high frequency of parthenogenesis in some soil a
How important is epigenetic regulation of gene expression for evolutionary
What special adaptations were required to evolve prior to colonization of t
How does the diversity of reproductive systems in soil organisms compare wi
Are evolutionary processes in soil different from those above the ground?

What is the degree of functional redundancy of soil communities and does it
Can biogeochemical process models be improved by including information rega
Are there emergent properties at the landscape scale that arise from proces
Are there general patterns that can be inferred from spatial associations b
Are genomic measures of functionality in soil useful predictors of ecosyste
How large is the flux of greenhouse gases from soil environments and what a
What is the fate of high molecular weight phenolic compounds in different s

How can we link belowground to aboveground food webs in dynamic models?
How does biodiversity in soil affect the diversity of other, connected envi
Are microbial communities in plant and animal tissues aboveground, in the l
Do effects of landscape composition (diversity and composition of different
Is the weak link between biodiversity above- and below-ground due to soil c
What is the relative contribution of above- and belowground plant residues
Are networks of mutualisms and trophic interactions belowground fundamental
How important are organisms other than plants in controlling energy and nut
To what extent does the spatial turnover in soil animal and microbial commu

Can ecosystem functions be predicted from the trait composition of soil com
Does intraspecific genetic diversity contribute to variation in ecosystem f
What are the tipping points, with respect to species losses or disturbances
How do soil biodiversity and ecological interactions in soil contribute to
How active are rare species in soil ecosystems and do they provide signific

What is the relative importance of biotic and abiotic drivers for decomposi
What are the relative interactive contributions of bacteria, fungi, protist
Do the outcomes of community assembly processes affect the variability of p
What are the contributions of microbial-mediated weathering in the critical
What is the relationship between soil carbon and nitrogen dynamics and plan
To what extent is the functioning of soil biota affected by the composition
What are the mechanisms by which mycorrhizal fungi interact with heterotrop
How do we link functional aspects of soil to population dynamics of soil or

How important is facilitation among soil organisms, and what are the underl
What is the relative contribution of top-down versus bottom-up control with
How important are mutualists, parasites, and viral diseases in regulating t
What is the role of infochemicals for microbe-plant, microbe-animal, and an
How important are interactions among soil microorganisms for energy flows i
Do saprotrophic microorganisms and soil animals compete for resources, and
How temporally stable are soil microbial communities, in terms of both taxo
Does functional redundancy in the traits expressed by multiple species lead
Is competition a dominant regulating factor in soil animal communities?
How does resilience vary among trophic levels and how does this variation i
To what extent is plant secondary metabolite production driven by rhizosphe
How do soil organisms of different body size interact within soil food webs
What is the extent of the plant extended phenotype and do soil organisms al

What roles can soil biota play in ecosystem resistance and adaptation to gl
Is soil biodiversity currently undergoing an extinction crisis and, if so,
What is the role of soil organisms in plant range expansion and to what deg
How resistant and resilient are ecosystems to changes in the composition an
What are the effects of land use change on trait composition and species co
What is the relative importance of current vs. historic processes in shapin
How can we conduct realistic experiments to study the effects of multiple,
Are microplastics harmful in soil ecosystems?
To what extent can differences in life history and other traits of soil fau
How much carbon can be stored in the world's soils and how can this be max
What are the important mechanisms by which non-native species introductions
What are the long-term fates and ecological consequences of xenobiotic comp
What are the major limitations to soil fertility and agricultural productio
What are the molecular and physiological mechanisms that allow acclimation
Do microbes inhabiting mineral surfaces respond differently to perturbation

How feasible is it to restore extensively degraded soil ecosystems to a fun
What is the status and future of the generation of 'designer soils' that ca
Can we alter soil microbial communities to impart desired characteristics t
What advances in our understanding of soil ecology can lead to significant

How can research and knowledge from soil ecologists be better integrated wi
Are practices used in plant breeding for pest and disease resistance uninte
Can the value of soil quality and its effects on ecosystem services be quan
Can productivity gains be achieved by improving the abilities of plants to
How can we better exploit soil ecological interactions during ecosystem man
Can we manage soil carbon sequestration processes through the use of princi
Is it possible to manage soils sustainably, from either an environmental or
Under what circumstances is the addition of biochar and other amendments be
Can continued advances in our understanding of symbiotic and endophytic mic
Are commercial inoculants as effective as indigenous soil biota in achievin
Are the ecological means of protecting ecosystems from soil pests feasible?
Are invasive practices used in managed ecosystems ultimately incompatible w

Can we better integrate soil fauna into high-throughput analyses of soil bi
How do we effectively characterize functional diversity and capacity in soi
Can we develop a comprehensive index of soil health that is a reliable and
Is it possible to visualize, in situ, soil processes (soil aggregate format
Can we take a trait-based approach to biodiversity in soil ecology, and wha
Are there particular soil taxa that can be used as an indicator to assess t
How can we manipulate microbial communities to evaluate their functional ro
Can we develop methodologies that allow the simultaneous identification of
Can we develop more effective methods for assessing population and communit
How can we exploit modern molecular methods to resolve issues such as the s
How reliable are our molecular markers at differentiating among different m
What are the key measurements that could be made to link cellular and organ
Are there more meaningful experimental model organisms (besides Caenorhabdi

Can we establish long-term soil ecological observatories to track important
How can we encourage open data sharing among soil ecologists (e.g. in open
Can we reverse the decline in taxonomic studies and recruit a new generatio
How do we place soil biodiversity within a conservation perspective given t
How can the public be engaged to appreciate the value of soil biodiversity?
How can we ensure that emerging soil ecologists receive the right training
Can we prevent soil ecology as a discipline from becoming too focused on te
Can we use genomic information obtained from the environment to culture lar
Can we make substantial advances in our understanding of soil ecology throu
What types of experiments can be established to look at multiple and intera
Can we focus more research on understudied and 'non-charismatic' soil biota
How can we encourage soil biologists to work with soil chemists to better u
How do we convince funding bodies and industry that long-term, large-scale,
Is it reasonable to expect that individuals from different research organiz
How can we facilitate the technological advances that are required to simul
How can we ensure that ecologists working above- and below-ground, as well

Can we have a "meeting of the minds" on halting the rapid decline of soil b ondents to the follow-up survey.

abundance of soil organisms?
nd structure, and what are the important mechanisms underlying these rules (
; are the important mechanisms that contribute to this differentiation?
ribution of mineral and organic surfaces in soil interact in shaping communi
how do we develop robust sampling strategies to effectively take these into
genetic structure and adaptability of populations of soil organisms?

nals, plants, and microbes in soil, and does this differ from what is observ
animal species and its absence in certain lineages, and what is its conseque
and ecological processes in soil?
terrestrial systems by soil microbes and invertebrates?
ith that of organisms existing aboveground?

; vary among ecosystem types?
arding the soil organisms present?
sses measured at much smaller scales, and can these properties be predicted
between resources and consumers in soil?
em process rates and stability?
are the ecological controls of these quantities?
soil types under different environmental conditions?

ironments in aquatic systems, and how important are temporarily flooded soil
litter layer, and in the soil functionally linked?
; adjacent ecosystems) and fragmentation on aboveground taxa lead to cascadi
organisms being limited more by resources arising from belowground sources (
for the nutrition of soil food webs?
ly different from those aboveground, and why?
trient flows between aboveground and belowground food webs?
unities differ compared with that observed for aboveground animals and micro

mmunities?
functioning?
s to ecosystems, that result in loss of soil functions?
multiple ecosystem services such as carbon sequestration, disease suppressi
cant contributions toward ecosystem functions?

.tion and the subsequent cycling of elements in different soil types and ecc
:s, viruses, and animals to soil ecosystem functioning?
)rocesses linked to ecosystem services?
. zone and other soil biotic processes during pedogenesis and organic matter
ıt life form, soil type, and soil food web structure ?
ı of the soil atmosphere (e.g. organic volatiles, air humidity)?
)hic fungi and what are the consequences for soil organic matter turnover?
:ganisms?

.ying mechanisms (e.g., chemical/physical) of facilitative interactions?
ıin soil food webs, and does their importance vary among food web compartmen
:he functioning and assembly of soil communities?
ıimal-plant interactions in soil, and how are chemical signals effectively t
.n food webs relative to interactions among soil fauna?
do these interactions affect energy flows and nutrient stoichiometry?
)nomic and functional community structure, and which community members are a
l to predictable outcomes from species interactions in soil despite differen

.nfluence nutrient stoichiometry?
ɔre interactions?
;?
.so have extended phenotypes?

.obal change, and what are the mechanisms underlying these contributions?
to what extent is soil biodiversity being lost?
;ree can soil organisms migrate to favorable regions in response to climate
ıd structure of soil communities?
)mposition of soil communities?
ıg species composition of belowground communities?
temporally variable perturbations on soil communities?

ına explain current responses and predict future effects of climate change?
:imized to attenuate increasing atmospheric CO2?
; impact soil ecological processes, and are the effects different for invasi
)ounds in soil, and how do environmental conditions affect these fates and c
)n in the medium- to long-term?
of soil biota to pollution?
ı than those found elsewhere in the soil (for example, due to a greater capa

ıctional state and, if so, what roles can soil biota and ecological theory p
ın provide a selected suite of ecosystem services in new (e.g., terraforming
:o plant products used in food, beverage, and materials production?
increases in agricultural production and sustainability?

.th the social and economic sciences?
entionally selecting against mutually beneficial symbioses with microbes?
ıtified?
selectively interact with particular soil organisms in the rhizosphere?
ıagement and when tackling global challenges?
.ples learned from soil ecological research?
a financial perspective, given current and future practices in resource cc
eneficial to soil fertility and biology?
croorganisms further reduce the need for synthetic N fertilizers?
ıg desirable outcomes?
?
vith achieving benefits from soil ecological processes?

.odiversity, perhaps through more effective approaches to sampling environme
.l ecosystems instead of relying mainly on DNA sequencing?
informative measure of soil quality?
tion, interactions between biota etc.) in space and time at a level of resol
ıt would that look like?
the degree of impact associated with particular environmental stressors and
oles without substantially altering the abiotic environment?
organisms and characterisation of their traits from diverse environments?
ty structure for soil biota that better reflect an actual species concept?
species concept for taxa that do not exhibit sexual reproduction, or the dri
microbial taxa?
nismic responses of soil biota and their activities to processes that occur
.tis elegans and Tertahymena thermophila) that would help us build quantitat

issues such as biodiversity loss and gradual environmental change?
databases) in a way that ensures progress can be made without concerns aris
on of taxonomists that are capable of integrating morphological evidence wit
the challenges we face with this 'enigmatic' system, such as extremely high
?
to address the questions identified in this paper?
echnological tools and ensure an appropriate emphasis on addressing fundamen
rge numbers of difficult-to-isolate organisms from these samples?
ıgh quantitative modelling?
ıctive effects of important drivers of global change?
ı?
understand the processes that go into the formation of recalcitrant organic
and secure funding is needed to address these challenges?
zations and supported by different funding bodies can work together in an ef
.taneously study geochemical and biochemical processes on mineral and organi
as ecologists more generally collaborate effectively to maximize knowledge

biological fertility worldwide, between scientists and corporate interests?

(dispersal limitation, species sorting, competition, facilitation, etc.)?

ties of soil biota?
account?

ved in aquatic systems?
ence for the evolution of these species?

from known soil ecological principles?

s/sediments in linking diversity in these environments?

ng effects on soil biota?
(e.g., minerals arising from weathering) compared with aboveground sources (

obes?

ion, and maintenance of aboveground biodiversity?

›systems?

: formation?

ıts?

:ransmitted in a humus-rich environment?

ıctive at any one time?
ıces in species composition?

change?

.ve soil biota than for invasive plants and other aboveground organisms?
:onsequences?

ıcity to acquire nutrients through mineral weathering)?

›lay in developing best practices for doing so?
;) or existing (e.g., restoration) environments?

›nsumption by humans?

›ntal DNA from soil and better designed primers for eukaryotic organisms?

.ution at which these processes are occurring?

perturbations?

.vers of population dynamics for modular organisms?

at the scale of entire ecosystems?
.ive models accounting for the high biodiversity in soils, extensive interpl

sing with respect to the unethical use of these data?
:h an informed use of solid molecular databases?
diversity with much of it being cryptic or undescribed?

ıtal and applied questions in soil ecology?

matter?

:ficient and meaningful way given constraints that are put upon those resear
.c surfaces?
gained from individual studies?

(e.g., carbon from photosynthesis)?

ay between trophic and non-trophic interactions, and the fracta

chers by those agencies?