Time-lagged responses of soil biota are pervasive and require new approaches

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Abstract

When land-use changes, soil biodiversity is typically assumed to respond immediately. Nonetheless, soils are inherently slow systems. We argue that soil communities often remain in a transient state for decades to centuries, generating persistent ecological legacies. These lags can arise through two interacting mechanisms: environmental inertia, as the physical and chemical properties of soils change slowly, and source limitation, as habitat loss erodes species pools at the landscape scale. We synthesize evidence that these processes generate long-term ecological memory in soils. As a consequence of time-lagged effects, soil systems may commonly exhibit extinction debt and recovery credit. While these concepts are well established in metapopulation theory, they remain underdeveloped for belowground biodiversity. Our perspective challenges static interpretations of soil biodiversity patterns and suggests that contemporary observations often reflect past land use more strongly than present conditions. To quantify these dynamics, we outline a research agenda integrating large-scale soil biodiversity data, historical land-use trajectories, and modelling approaches to separate legacy effects from contemporary drivers. Identifying where and when soil legacies persist, and when management or restoration can offset them, is essential for generating realistic projections of soil biodiversity under global change.

1 Introduction

Anthropogenic land-use change is widely recognized as the primary driver of modern biodiversity loss (Jaureguiberry *et al.* 2022). Nonetheless, the temporal dynamics of biodiversity responses within soil communities remain less understood. Because soil health and functioning underpin critical ecosystem services such as food production, climate regulation, and habitat provisioning (Lehmann *et al.* 2020; Smith *et al.* 2021), soil has become a central focus of international collective agreements (Lal 2024). At the same time, our understanding of soil responses to anthropogenic change largely mirrors that of aboveground ecosystems (Hooper *et al.* 2000), potentially distorting our perception of processes occurring belowground.

Soil biodiversity change is commonly conceptualized and modelled as an immediate response to land-use modifications. This assumption overlooks the fact that soils are inherently slow systems, characterized by high inertia. Indeed, soils contrast with aboveground communities in many respects: aboveground communities are dominated by mobile and short-lived organisms, which may respond rapidly to environmental shifts (Khaliq *et al.* 2024; Zhu *et al.* 2024). Soil communities, however, inhabit a matrix defined by slowly changing variables such as soil organic matter, pH, hydraulic properties and physical structure (Zajícová & Chuman 2019). These abiotic lags can reflect historical management and continue to modulate assembly processes long after land-use has changed (Navarrete-López *et al.* 2025). At the same time, the persistence of soil communities can also be driven by metapopulation processes, such as the availability of source pools and dispersal vectors in increasingly fragmented landscapes (Vahter *et al.* 2022).

The assumption currently dominating soil ecology is not that soil communities lack history, but that history is sufficiently weak that contemporary communities primarily reflect contemporary conditions. We argue that this assumption is often incorrect. Specifically, we propose that the ecological memory of soils to historical events could persist for extended periods, creating legacies where soil community shifts tied to past disturbances remain detectable today. If such delayed responses are the norm rather than the exception, then both observational and experimental studies may systematically misinterpret the drivers of present-day soil biodiversity patterns. To address this possibility, we propose a paradigm shift in soil ecology, synthesizing evidence for the central concept of soil ecological memory.

2 Environmental and demographic dimensions of memory in soils

The phenomenon of soil ecological memory will manifest itself as two well known and complementary time-lagged processes: extinction debt and recovery credit. Delayed extinction, or extinction debt, represents a future commitment to biodiversity loss that has not yet been realized (Kuussaari *et al.* 2009). This can arise either through demographic and dispersal processes (e.g., it takes time for species to disappear or immigration to cease) or through buffered environmental conditions that temporarily mask the effects of habitat degradation (e.g., it takes time for resources and soil conditions to change; Ewers & Didham 2005; Helm *et al.* 2006). Recovery credit, often termed colonization credit, represents the delayed gain of species following the return to suitable habitat conditions, constrained by dispersal limitation or the slow amelioration of chemical and physical soil properties (Török & Helm 2017; Watts *et al.* 2020).

Which of these processes dominates depends on the direction of habitat change: extinction debt will arise during habitat degradation, whereas recovery credit will occur during restoration (**Figure 1**). Importantly, both processes can be generated by different mechanisms, including demographic and abiotic lags, while producing analogous community-level responses (**Figure 1**).

Metacommunity theory expands these processes by highlighting movement-based mechanisms, such as immigration and emigration (Brown & Kodric-Brown 1977; Ovaskainen & Hanski 2002), and ultimately colonization and extinction. The rescue effect posits that immigration from neighbouring patches prevents local populations from going extinct despite unfavorable site conditions (Brown & Kodric-Brown 1977). Conversely, when habitat area in the landscape is reduced, local species richness can exceed the equilibrium predicted by species-area relationships for some time, creating a measurable debt (Wu *et al.* 2020).

In soils, the general mechanisms of debt and credit will have their direct counterparts. When a soil community experiences habitat degradation and begins shifting towards a novel equilibrium, both environmental conditions and metapopulation processes are expected to change. With respect to the former, slow changes in abiotic conditions can buffer species against extinction by providing a temporary refugium (Negrete-Yankelevich *et al.* 2007; Zajícová & Chuman 2019). With respect to the latter, both local demographic processes and landscape-level dynamics may contribute to time lags in community change (Mennicken *et*

al. 2020). Although soil organisms are typically short-lived, increased mortality under stressful conditions can trigger compensatory demographic responses that delay local extinctions (Villellas *et al.* 2015). At the landscape scale, rescue effects may arise when surrounding source pools replenish local communities following extinction events, provided that habitat conditions remain permissive enough for at least temporary establishment (Jackson & Sax 2010). Once soil abiotic conditions and source pools have changed sufficiently that immigration can no longer compensate for local extinction, the debt will be paid and soil memory lost.

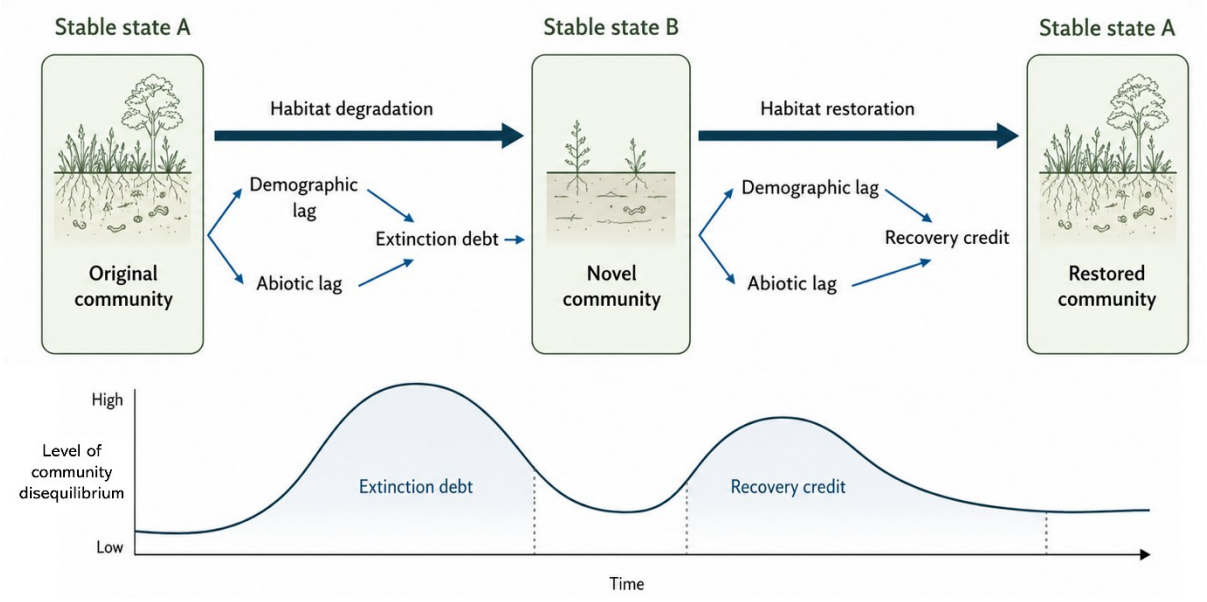

Figure 1. Conceptual causes of soil ecological memory. Depicted is a scenario where a soil community A undergoes habitat degradation via land use change and is developing towards a novel equilibrium community B. When the habitat is restored, the community will return towards its original state. During these processes, both demographic and abiotic lags can cause delayed community responses, resulting in extinction debts during degradation and recovery credit during restoration. We also foresee that the level of disequilibrium and duration of soil memory is proportional to the period of stable conditions that preceded perturbation.

For simplicity, we do not consider restoration dynamics separately. Instead, we assume that community responses during restoration broadly mirror those observed during habitat degradation (but for more nuanced views, see Gawecka & Bascompte 2023 and Moreno-Mateos *et al.* 2017). In terms of changes in both directions, we expect the strength and duration of soil ecological memory to depend not only on the magnitude of environmental change, but also on the period of prior community development and historical contingency preceding land-use change (Chang & Turner 2019). Consequently, the successional stage preceding disturbance is likely to affect memory length, with climax communities potentially

exhibiting longer time lags than successional or periodically disturbed communities. In addition, the relaxation time required to reach a new equilibrium may vary both with the mechanisms generating the lag, and with species life histories, the size and proximity of remnant habitats, and local site characteristics (Figueiredo *et al.* 2019). These hypotheses require explicit testing in a soil context.

Beyond general determinants of relaxation times, soil communities may also exhibit alternative stable states (Bardgett & Caruso 2020; Pausas & Bond 2020). If these alternative equilibria are stable, then a disturbed community may settle in a new state and never return from it due to hysteresis. Here again, a shortsighted focus on current conditions will disguise the impact of history, since a contemporary snapshot will only reveal drastically different communities under similar current conditions, without exposing the impact of past disturbance in determining these states.

3 Evidence of soil ecological memory

3.1 Literature review

To date, few studies have explicitly targeted the presence, nature and duration of land use legacies on soil biota (but see section below). This does not imply that long-term legacy effects have been fully overlooked, but rather that research has been scattered and that the vocabulary needed to describe it remains underdeveloped. To assess the extent of evidence for delayed responses of soil biota to land-use change, disturbance, and restoration, we conducted a systematic literature search in Scopus (accessed May 2026). Search terms were designed to capture three components: i) soil organisms and communities, ii) ecological legacies and time-lagged responses, and iii) land-use change, habitat loss, disturbance, and restoration. We restricted the search to peer-reviewed articles published in English between 2005 and 2025. The complete search string is provided in **Supplementary Table 1**.

3.2 Results

Our initial search yielded 161 articles. All articles retrieved were screened based on their content, and studies conducted primarily in laboratory or greenhouse settings were excluded. Of the 161 articles identified, 140 met the inclusion criteria of presenting empirical field data and were retained for further analysis. The articles included, the topics they addressed, and the reasons for exclusion of non-retained studies are provided in **Supplementary Table 1**.

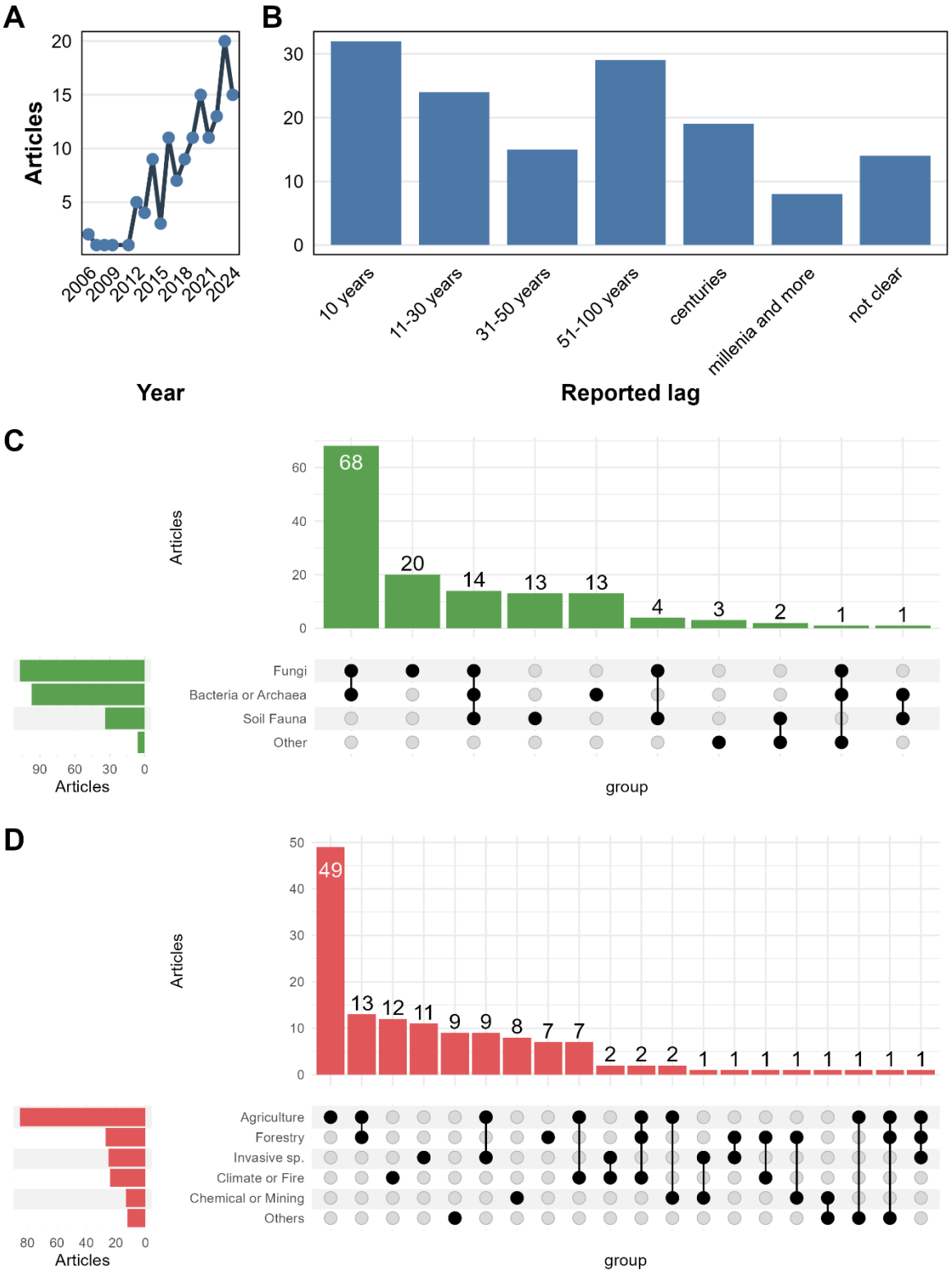

Figure 2. Number of studies showing delayed responses of soil communities over the past 20 years (A), as split per time lag reported (B), organism group(s) (C; with different combinations resolved along the x-axis) and type of perturbation (D; with combinations along the x-axis). Marginal distributions to the left of (C) and (D) show the total number of studies per organism group and disturbance type, respectively.

Our literature search revealed a marked increase over time in studies discussing delayed responses in soil communities (**Figure 2A**). Most of the studies retained focused on microbial communities (particularly fungi, bacteria, and archaea), whereas comparatively few studies examined soil animals or other groups (**Figure 2C**). Across taxa, agricultural land use was the most frequently studied driver of delayed responses (**Figure 2D**). The time lags reported ranged from less than a decade to millennia (**Figure 2B**). However, this variation appeared to reflect differences in the temporal scales examined rather than genuine differences in the duration of ecological memory. Most studies simply investigated responses over periods ranging from a few years to approximately a decade. Against this backdrop, it is notable that many studies still reported extensive delays in community change. Methodologically, studies documenting longer lags were typically based on space-for-time substitutions (as comparing contemporary habitats with contrasting histories), whereas true time-series studies rarely extended beyond a decade.

3.3 Explicit demonstrations of soil memory

In compiling the research above, we did not restrict ourselves to studies where ecological memory was the central focus of the paper itself. Instead, we included any study reporting patterns indicative of ecological memory that met our search terms. Among the subset of studies which did identify long-term soil legacies, extinction debt or delayed responses as their key focus, we still find a versatile representation of different habitats, organism groups and historical perturbations. Below, we will highlight selected case studies.

In agricultural soils, contemporary arbuscular mycorrhizal fungal richness has been better explained by the availability of natural habitats in the late nineteenth century than by present-day habitat conditions (Zárate Martínez *et al.* 2024). During agricultural intensification, changes in plant functional traits have been observed to precede shifts in the structure and functional activity of soil microbial communities, revealing a cascading time lag across trophic levels (Boeddinghaus *et al.* 2019). In forests, soil macro-invertebrate communities have been shown to continue declining for more than 15 years following selective logging (Negrete-Yankelevich *et al.* 2007). In planted forests of *Pinus radiata*, the ability of the soil microbiome to respond to modern disturbances like added nutrients may be overshadowed by legacies of past pastoral farming (Addison *et al.* 2021). Similarly, forest soils that experienced clear-cutting and agricultural conversion some six decades ago will still exhibit altered bacterial responses to modern drought, resulting in reduced network connectivity and impaired recovery of diversity (Osburn *et al.* 2021).

The influence of history can be so strong that some soil characteristics, including pH, nematode richness, and specific enzymatic activities, may be attributable primarily to historical land use rather than current management (Negrete-Yankelevich *et al.* 2020). In oak forests, farming practices from more than a century ago continue to shape microbial biomass, enzymatic activity, and community structure (Fichtner *et al.* 2014), whereas fungal communities in tropical secondary forests exhibit altered species evenness and reduced beta diversity more than 80 years after farming and logging have ceased (Bachelot *et al.* 2016). Historical human migrations have also introduced lasting biological legacies. For example, the nineteenth-century introduction of non-native earthworms through alpine farming continues to influence soil bioturbation in the Arctic today (Jerand *et al.* 2023).

Among long-term legacies, the literature also demonstrates strong effects of past climates. At a global scale, conditions during the Last Glacial Maximum continue to shape contemporary soil bacterial richness and composition (Delgado-Baquerizo *et al.* 2017). On a shorter timescale, historical precipitation regimes have been found to dictate how contemporary microbial communities respond to severe drying and rewetting stress (Evans & Wallenstein 2012). These findings are crucial to understanding the effects of current stressors, as they suggest that historical land use and modern climate can interact to shape ecosystem resilience.

Together, our review of the evidence suggests that soil ecological memory is pervasive, widespread and can persist from years to millennia, depending on the ecosystem, disturbance type and organism group under consideration. At the same time, it points to a scattered literature, where generalities are hard to establish and analogous phenomena are referred to by heterogeneous vocabulary. This is an untenable *status quo*. If the effects of history are masking effects of contemporary conditions and management, studies focusing on the latter will fail to acknowledge the former, yielding a major risk of causal misinterpretations. How then may we incorporate both contemporary and historical contexts into the same framework?

4 From concepts to predictive models

To resolve the drivers of soil communities, we should adopt an analysis framework which allows simultaneous effects of both contemporary and historical factors. Where past approaches have typically asked whether the current community is better explained by past or present conditions (e.g., Lalechère *et al.* 2025; Zárate Martínez *et al.* 2024), we should

resolve the importance of both historical and modern disturbances going forward and then compare their relative effects. This is no trivial task, but adopting the framework outlined in **Figure 1** allows us to pinpoint some of the key elements.

A key starting point is in recognizing that soil ecological memory can arise through time lags in both abiotic conditions and resources, as well as in the demographic responses of soil communities. Importantly, we note that an abiotic lag effect on species is fundamentally different from a demographic lag effect (**Figure 1**), since under an abiotic lag, species occurrence will be more attuned to contemporary conditions (minus demographic lag), but still subject to continued change over time. A myopic focus on a single pathway may then overlook the contribution of the other, risking the false conclusion that a community has reached equilibrium. For example, the observation of stable local soil conditions may create an illusion of community stability even when landscape-scale metacommunities are becoming impoverished. Conversely, the effects of changing soil conditions may be temporarily buffered by persistent metacommunities.

As a first step, we will thus want to quantify the relation between current conditions and time since disturbance. If source pools and soil abiotic conditions continue to change throughout the time period assessed, we can infer that the community is still in a transitory state and that changes will continue even in the absence of further environmental change. Indeed, this is the essence of a debt to be paid or a credit to be recovered.

4.1 Carriers of memory

At their core, both extinction debt and recovery credit can be captured through community completeness (Pärtel *et al.* 2013), i.e., the relationship between the contemporary community encountered at a site and the habitat specific species pool (**Figure 1**; **Figure 3**). This completeness can then be characterized from two perspectives: either we may focus on the species pool or we may also include interactions between species (Genes & Dirzo 2022). Importantly, the latter perspective will frequently convey a more complex view of extinction debts and recovery credits.

To assess soil ecological memory, we therefore need to define what makes a good response proxy for delayed effects. Simple community characteristics like species richness or diversity indices would only prove informative if the richness of stable states between modified and pristine habitats are markedly different. Therefore, depending on the perturbation, the metric of richness may not be informative enough to reflect true time lags (Hillebrand *et al.* 2018).

For example, in a grassland-to-forest transition, bacterial richness might remain relatively similar throughout the conversion, whereas community composition shows marked change (Wang *et al.* 2019). Using species richness alone as a response proxy for soil memory could then lead to both false positives and false negatives, i.e. the inference of no lag when a lag exists, or the inference of a lag when no lag exists. To reduce the risk of such errors, we should examine *both* species richness *and* composition.

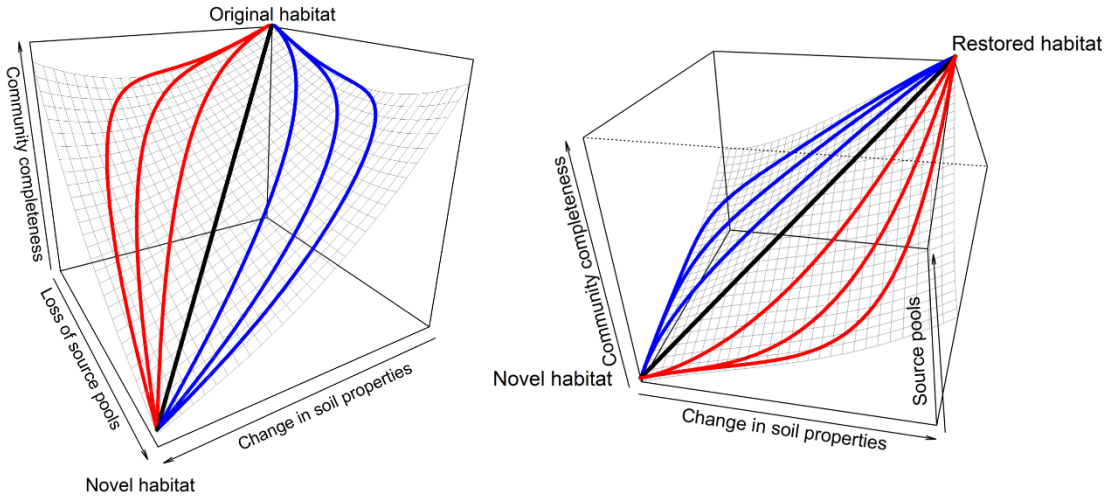

Figure 3. We hypothesize that reduction in community completeness during habitat degradation (left panel) and restoration (right panel) follows different trajectories depending on the relative timing and magnitude of shifts in availability of source pools and local habitat conditions. Trajectories of different colour represent different scenarios: When land-use change is accompanied by strong changes in habitat connectivity and dispersal source pools, then we expect slow change in the physico-chemical environment of soil to cause an abiotic memory (blue trajectories). However, if soil properties change, but surrounding landscapes still offer dispersal sources for soil biota, then we expect extinction debt to be generated by the rescue effect (red trajectories). The black trajectory represents the (perhaps unlikely) scenario where changes at the level of abiotic soil conditions and landscape-level processes are tightly linked over time. Such a scenario will generate more linear change towards a new equilibrium community, with no bias towards either origin of lag.

Community completeness, defined as the ratio between the observed community and the species pool, may provide a more informative proxy, but only when constrained to species for which the conditions at the focal site are actually suitable (*sensu* Trindade *et al.* 2026). For example, while grassland and forest soils share some species, others are largely restricted to forests. The latter will therefore belong to the forest species pool but not the grassland species pool (Li *et al.* 2025). Estimating community completeness, however, requires substantially more information than simpler metrics such as species richness, including knowledge of which species occur under which conditions. Community dissimilarity (or beta-diversity) between pristine and perturbed habitats may be a more approachable metric in the short term.

Still, metrics of community dissimilarity, community completeness and species suitability all require substantial knowledge of species-specific ecology, for us to assess what taxa could be present but are missing, or what taxa are there in excess.

4.2 Inference of soil ecological memory

While selecting an appropriate metric for biotic community change will be essential for detecting both contemporary and historical imprints, we should remind ourselves about what our predictions concern: the hallmark of an extinction debt is the continued loss of species over time, and the hallmark of a colonization credit is the continued gain of species over time – both in the explicit absence of further habitat modification. As a result, we might probe for two imprints: if we have access to species occurrence data across a wide set of conditions, then an extinction debt should be seen as the occurrence of species not predicted by current abiotic conditions. If, on the other hand, we have access to time series data, then debt should be evidenced by the loss of species without any further habitat modification. *Vice versa*, a recovery credit should be seen as the lack of species whose occurrence is predicted by current environmental conditions and/or the gain of species without any further habitat modification. Both considerations will naturally apply to species interactions, too.

Combining these aspects (**Figure 3**), we can generate several predictions about the origin of soil ecological memory. If degraded habitats differ from pristine habitats in abiotic conditions but exhibit similar community completeness, then delayed community responses are more likely to arise from metacommunity processes such as the rescue effect. However, if degraded habitats retain their abiotic conditions and exhibit similar community completeness, memory may instead reflect soil abiotic changes yet to materialise. During restoration or following the cessation of disturbance, convergence in abiotic conditions and community completeness towards pristine habitats would indicate habitat recovery. However, if dissimilarities in community completeness remain, they could analogously be explained by divergent soil abiotic conditions or metacommunity composition at the landscape scale.

Testing these predictions will call for extensive data, since a mismatch between predicted vs observed occurrence of species can only be interpreted if we have access to adequately parameterized and well-calibrated models of species occurrence. Quantifying the lack or excess in predicted occurrences of species will then offer a proxy of local extinction debt and can further be dissected into contributions from species traits, landscape features, time-since-disturbance, current land-use etc. By comparison, time-series data will arguably offer a simpler currency, since such data will make it possible to relate species loss or gain to time

since disturbance, and thereby estimate the duration of lags for different species. Here, the rate of decline in species occupancy will directly inform us about the length of biotic lags, conditional on the absence of further changes in the environment.

5 Challenges and future directions

Any field of research is more likely to advance if it focuses on testing explicit hypotheses rather than the *ad hoc* explanation of observational patterns (Popper 2007). To define a set of stringent predictions to address, we may first consider what types of soil ecological memory to expect in different habitats with different histories (**Figure 4**). Going forward, we may look beyond general mechanisms and towards community assembly, aiming to understand how species ecologies, bioclimatic regions and the ecological context affect the generation of memory.

With regards to general mechanisms and processes behind soil ecological memory, we can hypothesize that:

i) Local soil disturbance or land-use change will primarily result in demographic lags of soil communities, given that metapopulations remain intact.
ii) When metapopulations deteriorate, habitat buffering by soil will primarily generate abiotic lags.
iii) The length of time lags depends on the magnitude of change in either soil abiotic properties or metapopulations.
iv) The length of time lags depends on the duration of preceding community development, due to hysteresis.
v) Time-lagged responses of soil communities are least pronounced when local disturbance is accompanied by erosion of metapopulations.
vi) The processes and mechanisms of soil ecological memory are analogous during degradation and restoration.

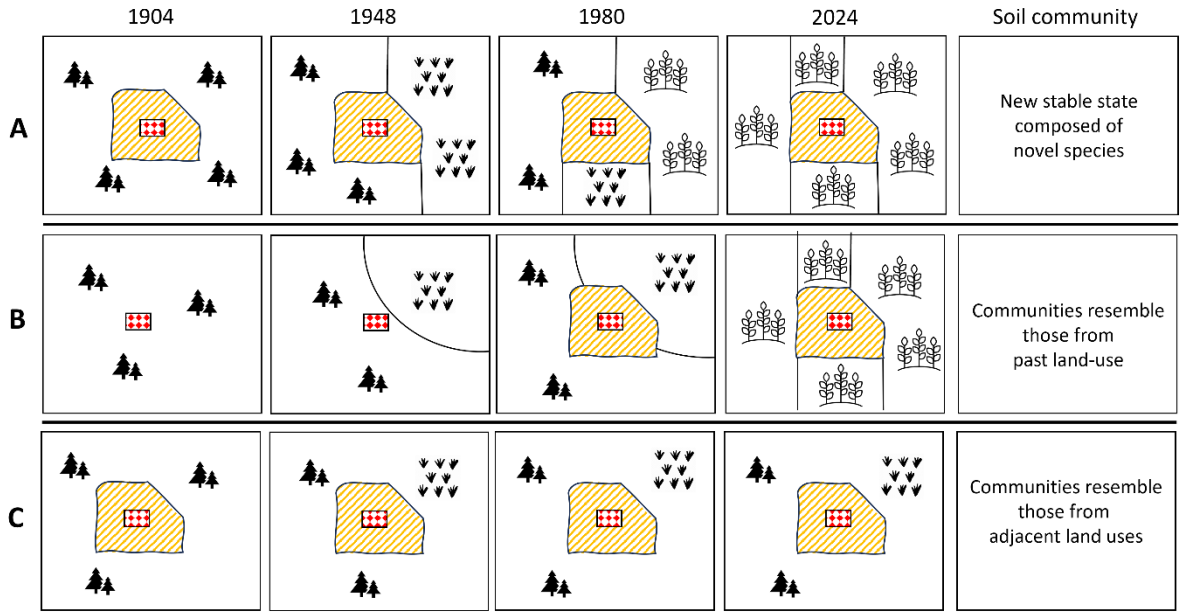

Figure 4. Theoretical expectations regarding the structure of soil communities at sampling sites (in red) with different histories. We expect arable croplands (in orange), which were converted from natural habitats long ago and also have eroded metapopulations, to exhibit no lags (A). Sites derived from similar landscapes but converted more recently (B) are expected to exhibit legacies due to abiotic lags. Demographic legacies like the rescue effect are expected to be stronger with a higher proportion of remnant habitat around the site (C).

Beyond mechanisms of memory generation, we can hypothesize that:

i) Interacting species, e.g., mutualists and pathotrophs, are more likely to exhibit lagged responses to change.

ii) Interacting species, e.g., mutualists and pathotrophs, are also more likely to exhibit co-extinction and co-establishment.

iii) The generation and persistence of soil ecological memory will, among other things, depend on the bioclimatic region, being less pronounced in high-energy environments like the tropics.

Testing these hypotheses is a task for a community of scientists and practitioners. While hypothesis-driven experiments would generate the most robust knowledge, natural experiments may yield similar explanatory capability if they are planned carefully. First, however, we should start with acknowledging the possibility that soils are indeed inherently prone to time-lagged community responses and we may have to rethink the way we approach change going forward.

6 Conclusions

Here, we argue that present-day soil biodiversity assessments may be systematically skewed, as soils likely carry substantial, unrecognized ecological memory that reflects historical inertia rather than true resilience. By understanding where soil communities are constrained by historical debt and where recovery is limited by credit, we can begin to identify landscapes where management and restoration can yield rapid gains in soil biodiversity and soil health, and those where long time horizons or alternative interventions are required.

Understandably, it is no easy task to switch to an even more complex approach to community assembly, especially when considering that the processes affecting soils can easily reach beyond an individual's science career. At the same time, we may find that the integration of soil ecological memory could provide explanations to findings previously counterintuitive, frustratingly uninformative or even left in the drawer altogether. To catalyze development in the field, we have advanced a series of hypotheses regarding what mechanisms are likely to be generating time lags and where we might expect them. We hope that the field will follow – and we will be delighted to be proven wrong.

Author contributions

T.V conceived the original idea of the research. All authors worked to refine the concepts and approach presented here. T.V wrote the original draft and all authors contributed to reviewing and editing the manuscript and approved the final submitted version.

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Data Availability

All data used in this study is publicly available. R code to generate figures 2 and 3 is available at https://doi.org/10.6084/m9.figshare.32717415

Supplementary information

Literature search string and references of articles used for the systematic literature survey are available in Supplementary Table 1.

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