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Persistence of soil organic carbon caused by functional complexity

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First paragraph

Soil organic carbon management has the potential to aid climate mitigation through drawdown of atmospheric carbon dioxide. To be effective, such management must account for processes influencing carbon storage and re-emission at different space and time scales. Achieving this
40 requires a conceptual advance in our understanding to link carbon dynamics from the scales at which processes occur to the scales at which decisions are made. Here, we propose that soil carbon persistence can be understood through the lens of decomposers as a result of functional complexity derived from the interplay between spatial and temporal variation of molecular diversity and composition. For example, co-location alone can determine whether a molecule is
45 decomposed, with rapid changes in moisture leading to transport of organic matter and constraining the fitness of the microbial community; while greater molecular diversity may increase the metabolic demand of, and thus potentially limit, decomposition. This conceptual shift accounts for emergent behavior of the microbial community and would enable soil carbon changes to be predicted without invoking recalcitrant carbon forms that have not been observed
50 experimentally. Functional complexity as a driver of soil carbon persistence suggests soil management should be based on constant care rather than one-time action to lock away carbon in soils.

55 Soils contain the largest active reservoir of terrestrial organic carbon, which has the potential to exacerbate global warming, but is also believed to offer a viable strategy for climate change mitigation. The wide range of soil management and land use change proposed to increase soil carbon sequestration¹ for the long term requires global-scale prediction of soil organic carbon persistence and vulnerabilities under novel climate conditions². Such a global effort also requires
60 the ability to quantify and accurately predict carbon retention at local to regional scales, while assessing the global potential and future risk from environmental change. However, we lack the theoretical framework to bridge the gap between the fine scales where carbon accrues and large scales relevant for carbon management policy³. This deficiency in understanding manifests itself in projections of soil carbon dynamics at regional to global scales that diverge greatly from each
65 other and from observations⁴.

We propose that soil organic carbon persistence can be understood based on functional complexity in the following three aspects: (1) molecular diversity, (2) spatial heterogeneity, and (3) temporal variability of the soil system. Understanding the responses of decomposition to
70 changes in environment, soil properties, and management through the lens of functional complexity may provide the basis for developing models that explain and quantify soil carbon persistence without invoking the existence of organic carbon forms with very long residence times prevalent in current approaches^{5,6}. Rather, the proposed conceptual approach builds on and harmonizes known reactions of soil organic matter decomposition that result from interactions of
75 organic carbon with soil biota, minerals, and environment⁷. It can inform the design of field experiments and new types of observations. New models should also identify directions to better manage soils to sequester carbon and thereby mitigate climate change. To be successful, these

models should borrow advances in scaling and modeling from engineering and material science in combination with new and growing soil datasets that capture decomposition responses to
80 changes in land use and cover, soil properties or climate. Such an approach would fulfill the policy need for what we propose to call ‘models with intent’ that enable us to raise organic carbon levels in soils where they are currently undersaturated, and to maintain maximal carbon levels in soil systems in ways that contribute to functional ecosystems and a healthy biosphere.

85 **Molecular diversity**

Until recently, the chemical and physical characteristics of plant litter were perceived as the main control over decomposition in addition to moisture and temperature⁷; hence, predictions of decomposition are typically based upon litter nitrogen or lignin contents^{5,6}. Meanwhile, in mineral soils, the concept of “chemical recalcitrance” of plant and microbial material causing
90 slow turnover times has been replaced in favor of a continuum model for soil organic carbon compounds⁸. Here we propose that the molecular diversity of the organic compounds (Fig. 1) rather than the material properties of individual compounds controls decomposition. For large molecules and particulate organic matter requiring extracellular enzymes for microbial uptake and metabolism, producing enzymes is energy intensive and is only sustainable if the payoff is
95 energetically worthwhile⁹. Even metabolizing smaller and soluble molecules that can be taken up directly, such as root exudates, may require diverse metabolic investments. Different requirements for metabolizing different molecules result not only from large differences in molecular structures (e.g., lignin vs. cellulose) but sometimes for molecules that are structurally similar (e.g., ortho- vs. para-benzoic acid)¹⁰.

Consequently, beyond a certain point, a greater diversity of molecules increases the cost of metabolism. Investments to use molecules that are rare in the soil solution, because of low production rates or rapid adsorption, are energetically less rewarding¹¹; thus such molecules may remain in soil even if they are potentially easily metabolized. The magnitude of additional cost
105 incurred with every additional microbial metabolic system depends on how closely related the metabolic pathways are^{10,11}. Therefore, the greater the molecular diversity of available substrates, the greater the cost:benefit ratio associated with their assimilation¹². Molecular diversity can increase decomposition rates, however, if one compound provides the energy or nutrients needed to decompose another one, often referred to as priming. How to quantify diversity to predict
110 whether changes in concentration of specific molecular groups increase or decrease persistence of other molecules is not sufficiently understood. Equally uncertain is which molecular properties best capture the diversity characteristics that are relevant to organic carbon persistence, since elemental composition, oxidation state and molecular diversity do not increase in the same ways during decomposition¹³. In addition, the diversity of organic carbon binding to minerals also
115 increases persistence¹⁴.

A focus on molecular diversity may reconcile the divide between the scientific communities studying organic and mineral horizons¹⁵. This reconciliation is based on the increasing diversity of molecular configurations from plants to litter to topsoil to subsoil¹⁶. Plant material comprises
120 many copies of closely related molecules that make up structures of leaves or wood and dominate the substrate available to decomposers in litter and at the top of the mineral soil. Here, lower molecular diversity coupled to high concentrations of individual compounds facilitates both specialization and more efficient “investment strategies” for soil biota¹⁷, which we argue

supports faster decomposition (Fig. 1). With increasing decomposition and consumption of the
125 most common molecules, molecular diversity increases¹⁸ and enhances the persistence of the
remaining organic carbon^{14,19}.

Spatial heterogeneity and temporal variability

Large tracts of the soil-pore network are practically devoid of decomposers²⁰, and the distribution
130 and forms of organic matter are equally patchy at this scale²¹. Physical separation has for some
time been invoked as an important stabilization mechanism²², emphasizing occlusion within
aggregates or encapsulation of easily mineralizable organic matter within large organic
molecules rather than the spatial distance between decomposer and substrate *per se*²³. Here we
propose that spatial heterogeneity alone can limit decomposition (Fig. 1): for decomposition to
135 proceed, degraders or their enzymes must come into contact with substrate. This aligns with
observed carbon turnover times on the order of months²⁴, shorter than the assumed long-term
sequestration of carbon within soil aggregates and may therefore not be the sole reason for
carbon persistence. Aggregation (as well as adsorption) may also help in promoting spatial
heterogeneity²¹, which is consistent with observations that aggregation increases organic carbon
140 persistence²⁴.

Predicting and managing decomposition is then not only a question of when a compound
becomes soluble but rather the likelihood that decomposer and substrate are co-located²⁵.

Bacteria are relatively immobile because water films in hydrologically unsaturated soil are not
145 thick enough for the complete immersion of bacterial cells²⁶, and even with full immersion in
water, bacteria are energetically limited to move long distances. Fungal growth over short

distances is slower than the rate of substrate diffusion, except in nutrient-rich environments^{27,28}.

Therefore, the likelihood of contact between substrate and decomposer should be examined and to what extent it depends on short-distance transport of organic carbon rather than microbial

150 mobility that is typically invoked.

In addition to spatial heterogeneity, temporal variations of soil moisture, temperature, nutrients, and organic carbon can cause non-linear decreases or increases in decomposition, even unexpected access to very old carbon²⁹, reflecting biogeochemical thresholds of ecosystem

155 properties (Fig. 1). It is typically assumed that microbes change their activity in tandem with moisture and temperature fluctuations, and their response is independent of how extreme or

frequent environmental fluctuations are^{5,6}. This view is not sufficient for guiding management and predictions of soil organic carbon dynamics, because high temporal variation causes two

additional, as yet unrepresented processes: (i) not only solubility of substrate but transport within

160 soil pores changes the amount of organic carbon that can be assimilated by microorganisms³⁰;

and (ii) adaptation of microbial communities to rapid changes in environmental and substrate

conditions contributes to their ability to utilize organic carbon³¹. Mounting evidence suggests that

not only current but also historical environmental conditions may significantly alter rates and

pathways of carbon transformations³². For example, adaptation to high soil temperatures were

165 shown to decrease the sensitivity of decomposition to changing temperatures³². The responses

that allow microbes to tolerate or adapt to environmental stress therefore lead to characteristic

life history traits and physiological trade-offs³³ that shape microbial community composition,

activity, and function over the long term.

170

Interactions of molecular, spatial, and temporal complexity

Interaction among molecular diversity, spatial heterogeneity, and temporal variability increases the uncertainty that decomposers must confront and adapt to, compared to facing each of these complexities individually. Spatial heterogeneity and temporal variability may exacerbate the
175 consequences of molecular diversity. The cost of having the capability to decompose diverse organic matter is already high^{11,34} and, in patchy and unreliable resource landscapes, enzyme production may further decline due to low as well as fluctuating concentrations of specific organic molecules or nutrients³⁵. This can even result in the loss of the capacity to use substrates for growth³⁶ and the development of metabolic flexibility, including dormancy³⁴. This loss of
180 microbial capacity may ultimately reduce organic carbon decomposition even when resources become available. Adaptation of the biotic community to this pulsed nature of the environment has significant effects on the dynamics of carbon in soil, as a reduced ability of an individual decomposer to utilize a certain type of molecule would diminish the probability of contact between substrate and competent decomposer.

185

In turn, molecular diversity may influence spatial heterogeneity when certain molecules adsorb to iron oxides while others adsorb to silicates or accumulate in pores^{8,14}. Therefore, the combination of spatial heterogeneity and molecular diversity likely further reduces organic carbon decomposition, as also suggested by theory²⁵. It remains an interesting question whether
190 spatial heterogeneity poses a more important constraint on decomposition than does molecular diversity and how these complexities interact.

Emergent behavior of soil organic carbon decomposition

195 The described functional complexity is expected to cause ‘emergent behavior’ as in other complex systems³⁷, in which fine-scale interactions among individual parts of the system lead to the emergence of a behavior with a quality that cannot be inferred from the behavior of these parts³⁷. Even though the concept of emergent behavior and self-organization is well-established in theoretical ecology³⁷, it has only rarely been applied to soil systems³⁸. Rather, organic carbon
200 decomposition is traditionally described from a large-scale perspective, as the sum of individual behavior of microbes and substrate (Fig. 2a).

Recognizing soil as a complex system opens up possibilities to describe persistence as an emergent behavior arising from nonlinear interactions among decomposers, their diverse organic
205 substrates, and their heterogeneous and changing local soil environment (Fig. 2b). While laboratory experiments have shown the potential of spatial self-organization in microbial communities³⁹, studies on microbial self-organization in soil interacting with its environment are limited²⁰. Modeling individual microorganisms in soil decomposer communities^{40,41} demonstrated the potential significance of emergent behavior for soil organic carbon turnover. The next steps
210 include (i) obtaining better representation of how emergent behavior affects soil organic carbon persistence, (ii) translating these insights into model structures that capture essential insights at the pore scale as well as further translate these to the global scale⁴² that may also include machine-learning approaches⁴³, and (iii) implementing these insights into management-relevant recommendations as part of policy-relevant decision support systems.

215

Implications for Management and Policy

We propose to integrate soil functional complexity into the development of management and prediction, as this complexity mediates the effects of land use and cover, soil properties and
220 climate on soil carbon sequestration (Fig. 3). Carbon persists in soil when many different molecules with individually low concentrations are distributed throughout a heterogeneous landscape of pores interacting with different minerals under variable environmental conditions. Soil management will therefore need to focus on ongoing care to manipulate the intricate balance between carbon inputs and losses, rather than rely on locking away carbon in soil for the long
225 term. Promoting functional complexity consistent with a mixture of inputs and a diversity of plant species^{44,45} (which will stimulate a diverse microbial community⁴⁵ and rhizodeposits¹⁴), and with lower soil mixing (by tillage), should therefore be explored to increase soil carbon persistence and sequestration (Fig. 4). Specifically, it is important to better understand how to sequester carbon in soil by increasing persistence based on functional complexity in comparison
230 to merely increasing organic carbon inputs.

Using predictive models to explore soil carbon behavior under different scenarios can be the basis for substantial policy and industry investment⁴⁶. We propose to combine soil functional complexity — molecular, spatial, temporal — with multi-scale modeling to optimize such global
235 efforts in soil carbon sequestration²⁵. The concept of functional complexity also avoids the pitfall of invoking stable carbon forms with long⁶ or infinite⁵ turnover times that relay a false policy and extension message of irreversible carbon storage in soil. Such ‘models with intent’ need to operate regionally to globally, at scales large enough to justify policy interventions but local

enough to exhibit emergent properties reflective of the known functional complexity of soils. In
240 contrast to traditionally employed upscaling approaches for such decision-support tools, we
propose multi-scale modeling approaches that combine ‘microscale’ and ‘macroscale’ models,
either concurrently or by extrapolating over time with broad macroscale assumptions. The most
complex and highly resolved model (in space, process, and time) should serve as the basis model
for the macro-scale projections. By integrating results from the basis model into the macro-scale
245 model through responses in decomposition that reflect soils’ underlying functional complexity
rather than static properties (Fig. 2), processes occurring at the finer scales are accounted for.
Examples of multi-scale modeling are found in chemical engineering and material science⁴⁷, in
atmospheric science to describe cloud physics⁴⁸, in reactive transport in groundwater⁴⁹, and may
be combined with artificial intelligence⁴³.

250
Quantifying soil functional complexity to parameterize such models will not be easy, particularly
for global applications. In the near term, this challenge may be resolved by measuring carbon-
relevant responses to a change in land cover or use, soil properties, or climate, because these
responses reflect the underlying soil functional complexities. Engaging with temporal, spatial or
255 molecular complexity may motivate a new generation of scientific experiments such as those
increasingly done in soil microbial ecology⁵⁰. Initially, such microbial responses may be used to
define soil functional types⁵¹, or rather what we may call “soil functional response types”, to
distinguish them from types based on static soil properties. The multi-scale models we envision
could then be used to predict functional response types based on fine-scale information; a
260 convergence of theory and empirical evidence would build confidence in the new models’
predictive power. The functional response types would ideally be further integrated into dynamic

geospatial models, because they are expected to change over time, with management, land cover, or climate. Contemporary efforts in developing new soil sensor technology⁵² must be intensified to provide the capacity to quantify these responses through laboratory measurements and
265 eventually through real-time and high-resolution field measurements.

In what way soil functional complexity will guide global soil management and prediction of climate-carbon feedbacks will and should vary among locations and land-uses. Likewise, different next-generation carbon modeling approaches will allow testing the robustness of scaling
270 assumptions. As already implemented for global climate models, prediction tools for soil carbon sequestration operating at the global scale should also be compared within a common testbed⁵³. Such an ensemble approach will allow rigorous comparison of their behavior without biases resulting from other assumptions being made, such as boundary or initial conditions. Soil organic carbon models based on measured functional complexity and upscaling using soil response types
275 have the potential to generate policy-relevant soil management recommendations that are required to underpin international programs needed to address global change challenges.

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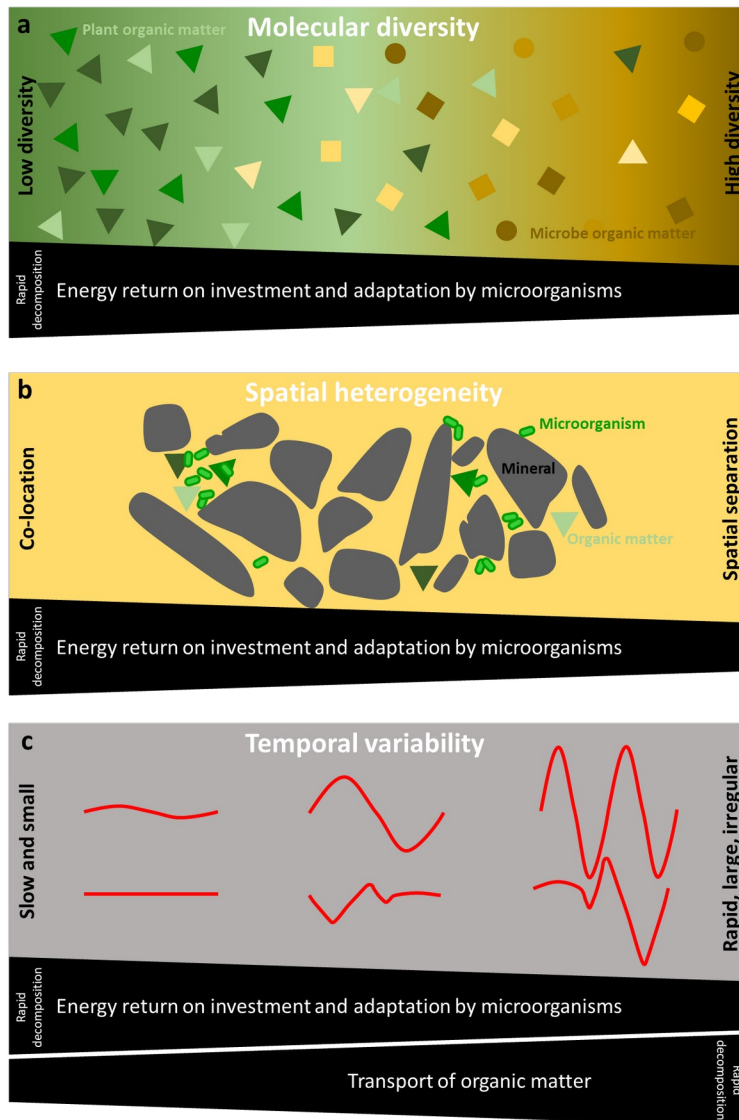
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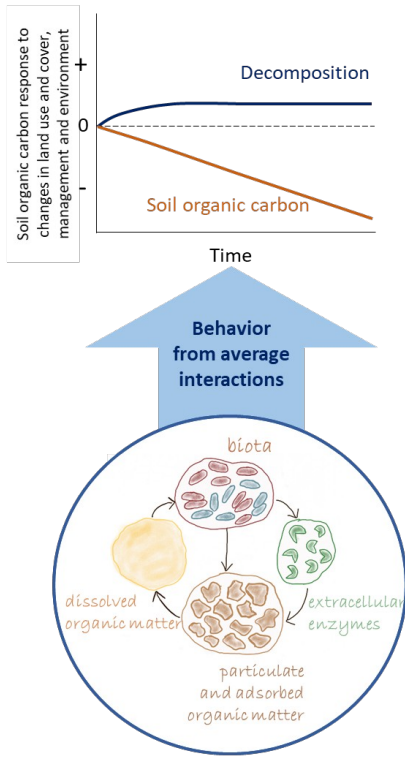
Data availability statement: no applicable.

415



420 **Figure 1 Functional complexity and the persistence of soil organic carbon.** Functional
 425 complexity comprises molecular diversity, spatial heterogeneity, and temporal variability that
 affect the energy, carbon, and nutrient return on investment for the microbial community. **a**,
 lower molecular diversity and concomitant higher concentrations of individual molecules
 facilitate specialization of the decomposer community, whereas higher diversity increases the
 cost-benefit ratio for microorganisms to utilize these molecules. **b**, higher spatial heterogeneity
 decreases the chance that decomposers meet substrate. **c**, greater temporal variability may reduce
 the ability of microbes to adapt to an environment, whereas moisture fluctuations may also
 increase movement of substrate to decomposers; therefore, increased variability may decrease or
 increase persistence.

(a) Traditional “Macroscopic” view: Interactions at the aggregated level



(b) New “Soil as a complex system” view: Nonlinear interactions at different organizational levels

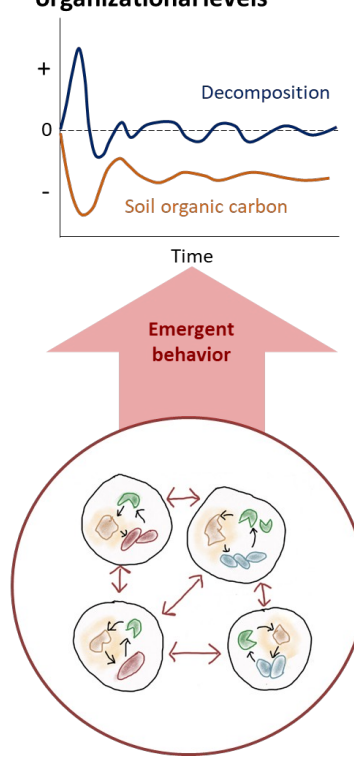
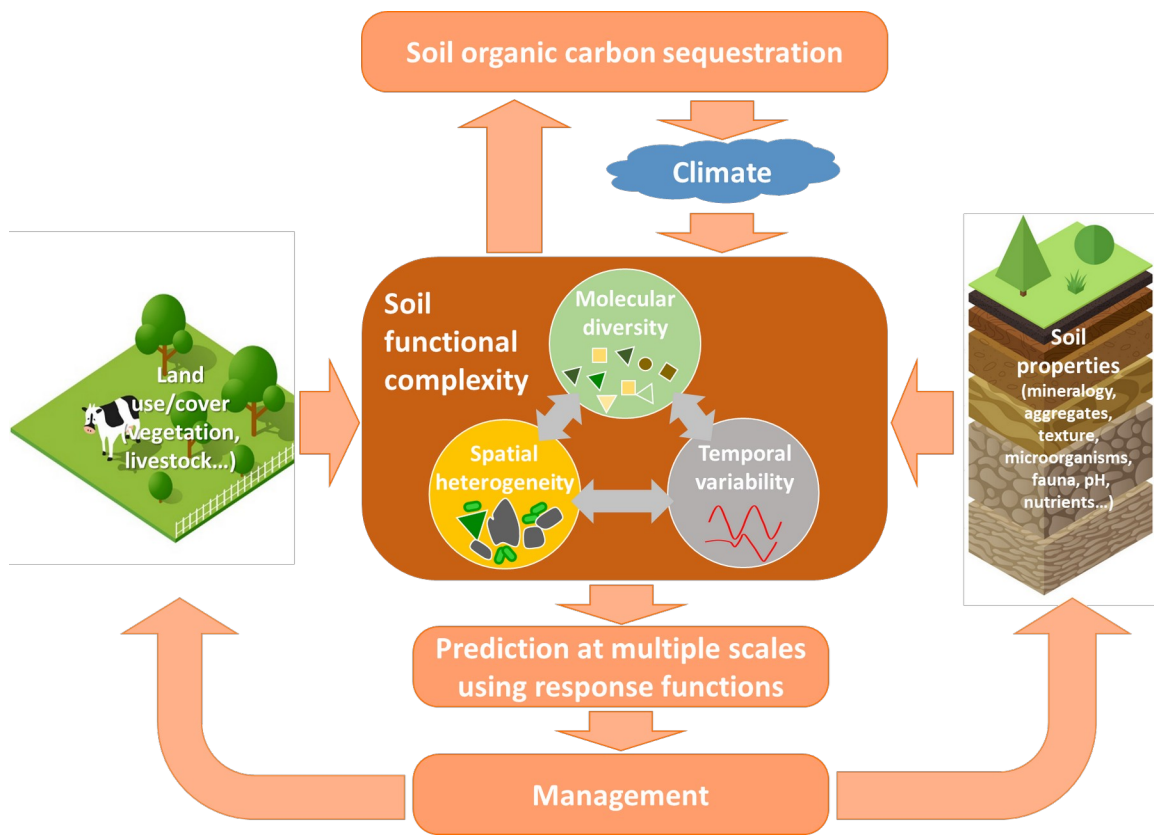


Figure 2 Emergent behavior of soil organic carbon decomposition. **a**, Traditional understanding of soil organic carbon dynamics is based on homogeneously distributed (at the scale of a microorganism) and slowly changing organic matter, microbial biomass, and enzymes (drawings) as a function of environment (soil properties such as texture; environment such as moisture). **b**, by contrast, allowing nonlinear feedbacks that occur at the scale of individual organisms and organic matter generates emergent behavior of the soil system that differs from the sum of the individual interactions. The resulting responses to a change in environmental conditions or management are characteristic of the functional complexity.



445 **Figure 3 Integration of molecular, spatial and temporal complexity with management and prediction of soil carbon sequestration.** The pore-scale functional complexity that modulates the effects of environmental, land use, and management changes on the soil system (including aggregation, mineral interactions, biotic activity and diversity, etc.)^{7,15} may serve as the core concept integrated into prediction at management-relevant scales for soil carbon sequestration.

450 Understanding how soil pore-to-profile scale complexity influences persistence will change how we predict soil organic carbon dynamics and develop more sophisticated management for sequestration.

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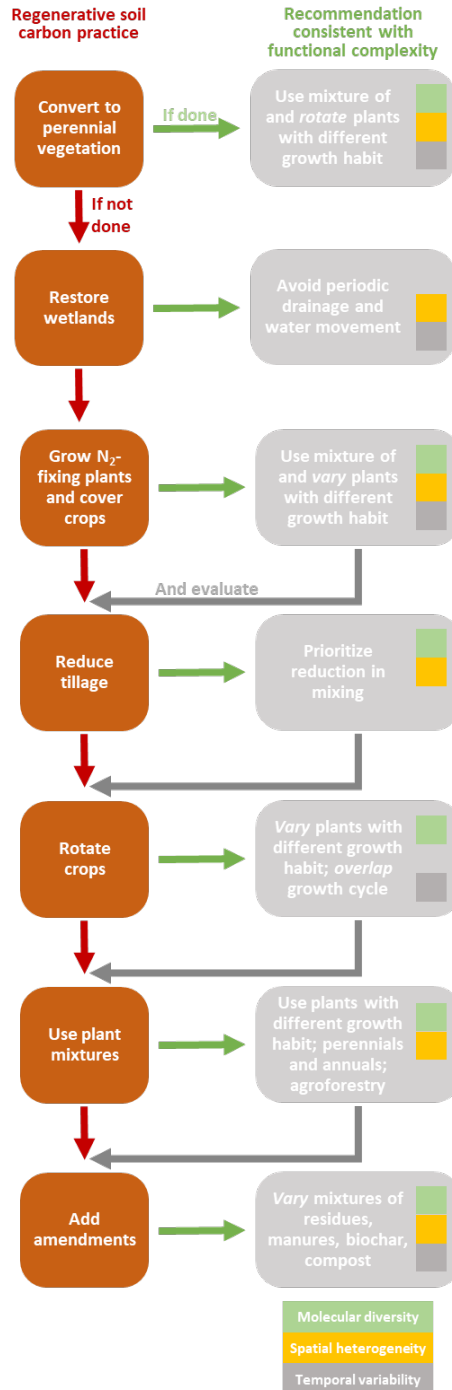


Figure 4 Regenerative soil carbon practice consistent with promotion of functional diversity to increase soil carbon persistence. Soil management designed to increase persistence of soil organic carbon¹ should be investigated for their alignment with functional diversity. The listed management recommendations also increase organic carbon input (e.g., greater plant diversity⁴⁵) or persistence unrelated to functional diversity (e.g., avoiding periodic drainage also reduces aeration in addition to movement of carbon). Inset colors relate to the three aspects of functional diversity (molecular, spatial, temporal) also used in Figs 2 and 3. Interactions of effects over time require specific attention in future research (indicated in italics).

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