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2 **Persistence of soil organic carbon caused by functional complexity**
3

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36 *First paragraph*

37 Soil organic carbon management has the potential to aid climate mitigation through drawdown of
38 atmospheric carbon dioxide. To be effective, such management must account for processes
39 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
41 which processes occur to the scales at which decisions are made. Here, we propose that soil
42 carbon persistence can be understood through the lens of decomposers as a result of functional
43 complexity derived from the interplay between spatial and temporal variation of molecular
44 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
46 constraining the fitness of the microbial community; while greater molecular diversity may
47 increase the metabolic demand of, and thus potentially limit, decomposition. This conceptual
48 shift accounts for emergent behavior of the microbial community and would enable soil carbon
49 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
51 management should be based on constant care rather than one-time action to lock away carbon in
52 soils.

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55 Soils contain the largest active reservoir of terrestrial organic carbon, which has the potential to
56 exacerbate global warming, but is also believed to offer a viable strategy for climate change
57 mitigation. The wide range of soil management and land use change proposed to increase soil
58 carbon sequestration¹ for the long term requires global-scale prediction of soil organic carbon
59 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
61 assessing the global potential and future risk from environmental change. However, we lack the
62 theoretical framework to bridge the gap between the fine scales where carbon accrues and large
63 scales relevant for carbon management policy³. This deficiency in understanding manifests itself
64 in projections of soil carbon dynamics at regional to global scales that diverge greatly from each
65 other and from observations⁴.

66
67 We propose that soil organic carbon persistence can be understood based on functional
68 complexity in the following three aspects: (1) molecular diversity, (2) spatial heterogeneity, and
69 (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
71 complexity may provide the basis for developing models that explain and quantify soil carbon
72 persistence without invoking the existence of organic carbon forms with very long residence
73 times prevalent in current approaches^{5,6}. Rather, the proposed conceptual approach builds on and
74 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
76 experiments and new types of observations. New models should also identify directions to better
77 manage soils to sequester carbon and thereby mitigate climate change. To be successful, these

78 models should borrow advances in scaling and modeling from engineering and material science
79 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
81 policy need for what we propose to call ‘models with intent’ that enable us to raise organic
82 carbon levels in soils where they are currently undersaturated, and to maintain maximal carbon
83 levels in soil systems in ways that contribute to functional ecosystems and a healthy biosphere.

84

85 **Molecular diversity**

86 Until recently, the chemical and physical characteristics of plant litter were perceived as the main
87 control over decomposition in addition to moisture and temperature⁷; hence, predictions of
88 decomposition are typically based upon litter nitrogen or lignin contents^{5,6}. Meanwhile, in
89 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
91 compounds⁸. Here we propose that the molecular diversity of the organic compounds (Fig. 1)
92 rather than the material properties of individual compounds controls decomposition. For large
93 molecules and particulate organic matter requiring extracellular enzymes for microbial uptake
94 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
96 directly, such as root exudates, may require diverse metabolic investments. Different
97 requirements for metabolizing different molecules result not only from large differences in
98 molecular structures (e.g., lignin vs. cellulose) but sometimes for molecules that are structurally
99 similar (e.g., ortho- vs. para-benzoic acid)¹⁰.

100

101 Consequently, beyond a certain point, a greater diversity of molecules increases the cost of
102 metabolism. Investments to use molecules that are rare in the soil solution, because of low
103 production rates or rapid adsorption, are energetically less rewarding¹¹; thus such molecules may
104 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
106 metabolic pathways are^{10,11}. Therefore, the greater the molecular diversity of available substrates,
107 the greater the cost:benefit ratio associated with their assimilation¹². Molecular diversity can
108 increase decomposition rates, however, if one compound provides the energy or nutrients needed
109 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
111 of other molecules is not sufficiently understood. Equally uncertain is which molecular
112 properties best capture the diversity characteristics that are relevant to organic carbon
113 persistence, since elemental composition, oxidation state and molecular diversity do not increase
114 in the same ways during decomposition¹³. In addition, the diversity of organic carbon binding to
115 minerals also increases persistence¹⁴.

116

117 A focus on molecular diversity may reconcile the divide between the scientific communities
118 studying organic and mineral horizons¹⁵. This reconciliation is based on the increasing diversity
119 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
121 dominate the substrate available to decomposers in litter and at the top of the mineral soil. Here,
122 lower molecular diversity coupled to high concentrations of individual compounds facilitates
123 both specialization and more efficient “investment strategies” for soil biota¹⁷, which we argue

124 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
126 remaining organic carbon^{14,19}.

127

128 **Spatial heterogeneity and temporal variability**

129 Large tracts of the soil-pore network are practically devoid of decomposers²⁰, and the
130 distribution and forms of organic matter are equally patchy at this scale²¹. Physical separation
131 has for some time been invoked as an important stabilization mechanism²², emphasizing
132 occlusion within aggregates or encapsulation of easily mineralizable organic matter within large
133 organic molecules rather than the spatial distance between decomposer and substrate *per se*²³.

134 Here we propose that spatial heterogeneity alone can limit decomposition (Fig. 1): for
135 decomposition to proceed, degraders or their enzymes must come into contact with substrate.
136 This aligns with observed carbon turnover times on the order of months²⁴, shorter than the
137 assumed long-term sequestration of carbon within soil aggregates and may therefore not be the
138 sole reason for carbon persistence. Aggregation (as well as adsorption) may also help in
139 promoting spatial heterogeneity²¹, which is consistent with observations that aggregation
140 increases organic carbon persistence²⁴.

141

142 Predicting and managing decomposition is then not only a question of when a compound
143 becomes soluble but rather the likelihood that decomposer and substrate are co-located²⁵.
144 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
146 water, bacteria are energetically limited to move long distances. Fungal growth over short

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

148 Therefore, the likelihood of contact between substrate and decomposer should be examined and
149 to what extent it depends on short-distance transport of organic carbon rather than microbial
150 mobility that is typically invoked.

151
152 In addition to spatial heterogeneity, temporal variations of soil moisture, temperature, nutrients,
153 and organic carbon can cause non-linear decreases or increases in decomposition, even
154 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
156 moisture and temperature fluctuations, and their response is independent of how extreme or
157 frequent environmental fluctuations are^{5,6}. This view is not sufficient for guiding management
158 and predictions of soil organic carbon dynamics, because high temporal variation causes two
159 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;
161 and (ii) adaptation of microbial communities to rapid changes in environmental and substrate
162 conditions contributes to their ability to utilize organic carbon³¹. Mounting evidence suggests
163 that not only current but also historical environmental conditions may significantly alter rates
164 and pathways of carbon transformations³². For example, adaptation to high soil temperatures
165 were shown to decrease the sensitivity of decomposition to changing temperatures³². The
166 responses that allow microbes to tolerate or adapt to environmental stress therefore lead to
167 characteristic life history traits and physiological trade-offs³³ that shape microbial community
168 composition, activity, and function over the long term.

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170

171 **Interactions of molecular, spatial, and temporal complexity**

172 Interaction among molecular diversity, spatial heterogeneity, and temporal variability increases
173 the uncertainty that decomposers must confront and adapt to, compared to facing each of these
174 complexities individually. Spatial heterogeneity and temporal variability may exacerbate the
175 consequences of molecular diversity. The cost of having the capability to decompose diverse
176 organic matter is already high^{11,34} and, in patchy and unreliable resource landscapes, enzyme
177 production may further decline due to low as well as fluctuating concentrations of specific
178 organic molecules or nutrients³⁵. This can even result in the loss of the capacity to use substrates
179 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
181 become available. Adaptation of the biotic community to this pulsed nature of the environment
182 has significant effects on the dynamics of carbon in soil, as a reduced ability of an individual
183 decomposer to utilize a certain type of molecule would diminish the probability of contact
184 between substrate and competent decomposer.

185

186 In turn, molecular diversity may influence spatial heterogeneity when certain molecules adsorb
187 to iron oxides while others adsorb to silicates or accumulate in pores^{8,14}. Therefore, the
188 combination of spatial heterogeneity and molecular diversity likely further reduces organic
189 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
191 diversity and how these complexities interact.

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Emergent behavior of soil organic carbon decomposition

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 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 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 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.

216

217 **Implications for Management and Policy**

218 We propose to integrate soil functional complexity into the development of management and
219 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
221 molecules with individually low concentrations are distributed throughout a heterogeneous
222 landscape of pores interacting with different minerals under variable environmental conditions.
223 Soil management will therefore need to focus on ongoing care to manipulate the intricate balance
224 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
226 plant species^{44,45} (which will stimulate a diverse microbial community⁴⁵ and rhizodeposits¹⁴), and
227 with lower soil mixing (by tillage), should therefore be explored to increase soil carbon
228 persistence and sequestration (Fig. 4). Specifically, it is important to better understand how to
229 sequester carbon in soil by increasing persistence based on functional complexity in comparison
230 to merely increasing organic carbon inputs.

231

232 Using predictive models to explore soil carbon behavior under different scenarios can be the
233 basis for substantial policy and industry investment⁴⁶. We propose to combine soil functional
234 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
236 of invoking stable carbon forms with long⁶ or infinite⁵ turnover times that relay a false policy
237 and extension message of irreversible carbon storage in soil. Such ‘models with intent’ need to
238 operate regionally to globally, at scales large enough to justify policy interventions but local

239 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
241 propose multi-scale modeling approaches that combine ‘microscale’ and ‘macroscale’ models,
242 either concurrently or by extrapolating over time with broad macroscale assumptions. The most
243 complex and highly resolved model (in space, process, and time) should serve as the basis model
244 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
246 rather than static properties (Fig. 2), processes occurring at the finer scales are accounted for.
247 Examples of multi-scale modeling are found in chemical engineering and material science⁴⁷, in
248 atmospheric science to describe cloud physics⁴⁸, in reactive transport in groundwater⁴⁹, and may
249 be combined with artificial intelligence⁴³.

250

251 Quantifying soil functional complexity to parameterize such models will not be easy, particularly
252 for global applications. In the near term, this challenge may be resolved by measuring carbon-
253 relevant responses to a change in land cover or use, soil properties, or climate, because these
254 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
256 increasingly done in soil microbial ecology⁵⁰. Initially, such microbial responses may be used to
257 define soil functional types⁵¹, or rather what we may call “soil functional response types”, to
258 distinguish them from types based on static soil properties. The multi-scale models we envision
259 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’
261 predictive power. The functional response types would ideally be further integrated into dynamic

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

266

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

277

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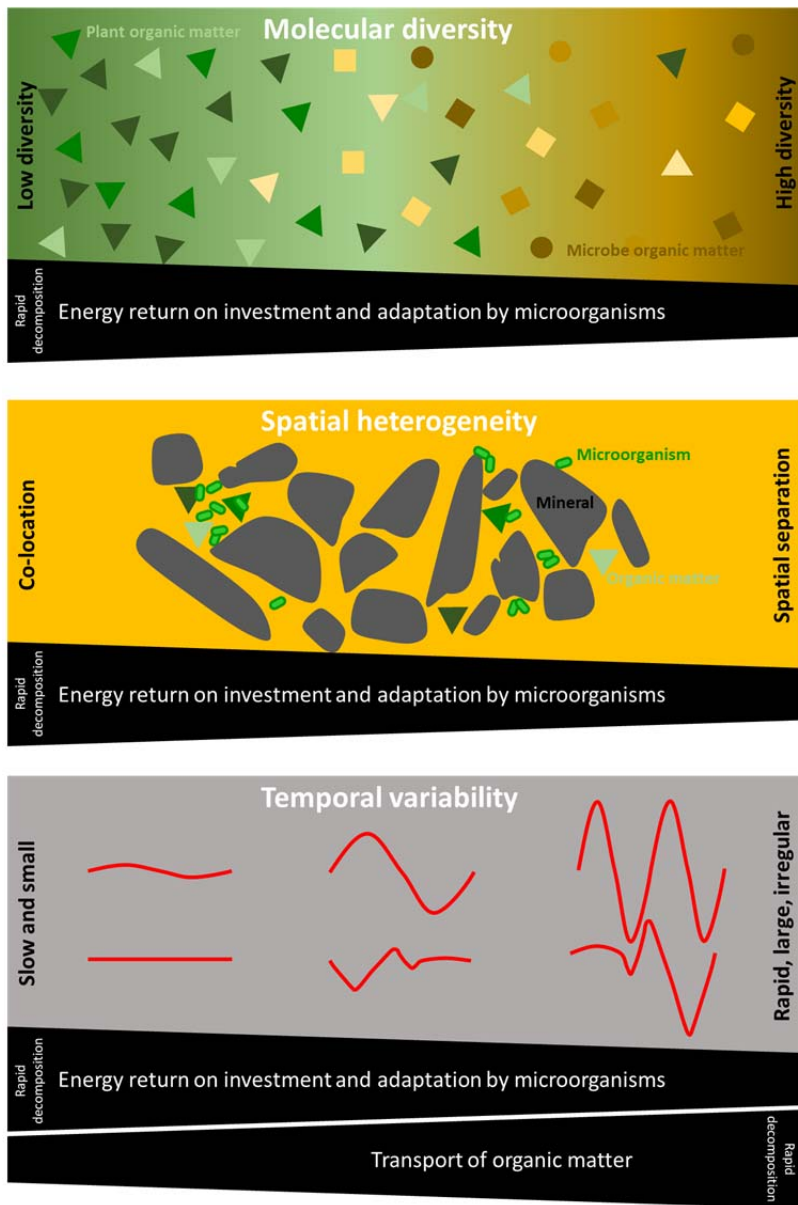
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412 KM drafted first versions of the figures; all authors contributed to writing and editing.

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414 **Data availability statement:** no applicable.

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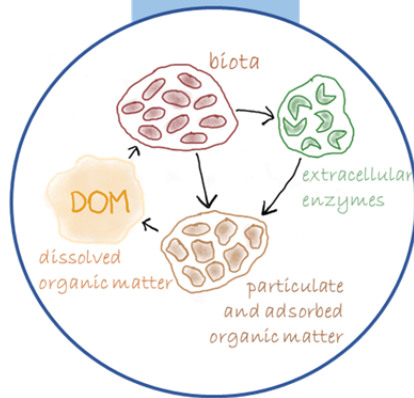
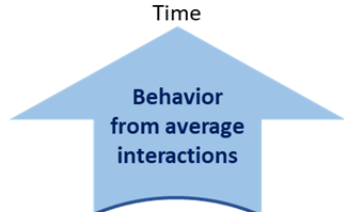
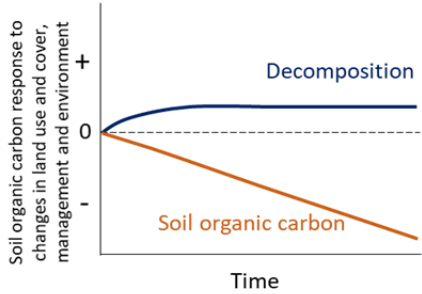
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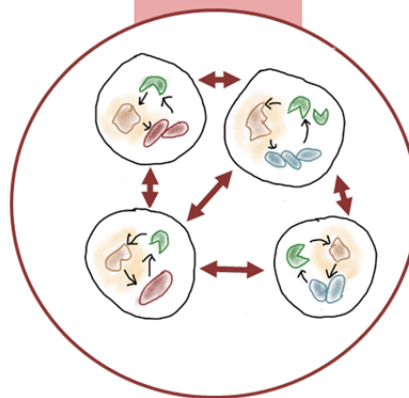
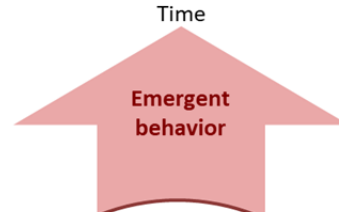
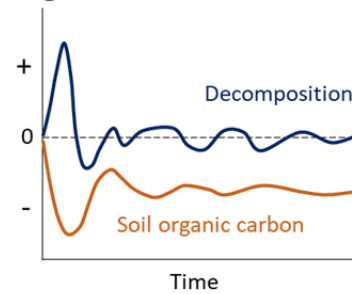
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 419 **Figure 1 Functional complexity and the persistence of soil organic carbon.** Functional
 420 complexity comprises molecular diversity, spatial heterogeneity, and temporal variability that
 421 affect the energy, carbon, and nutrient return on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

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

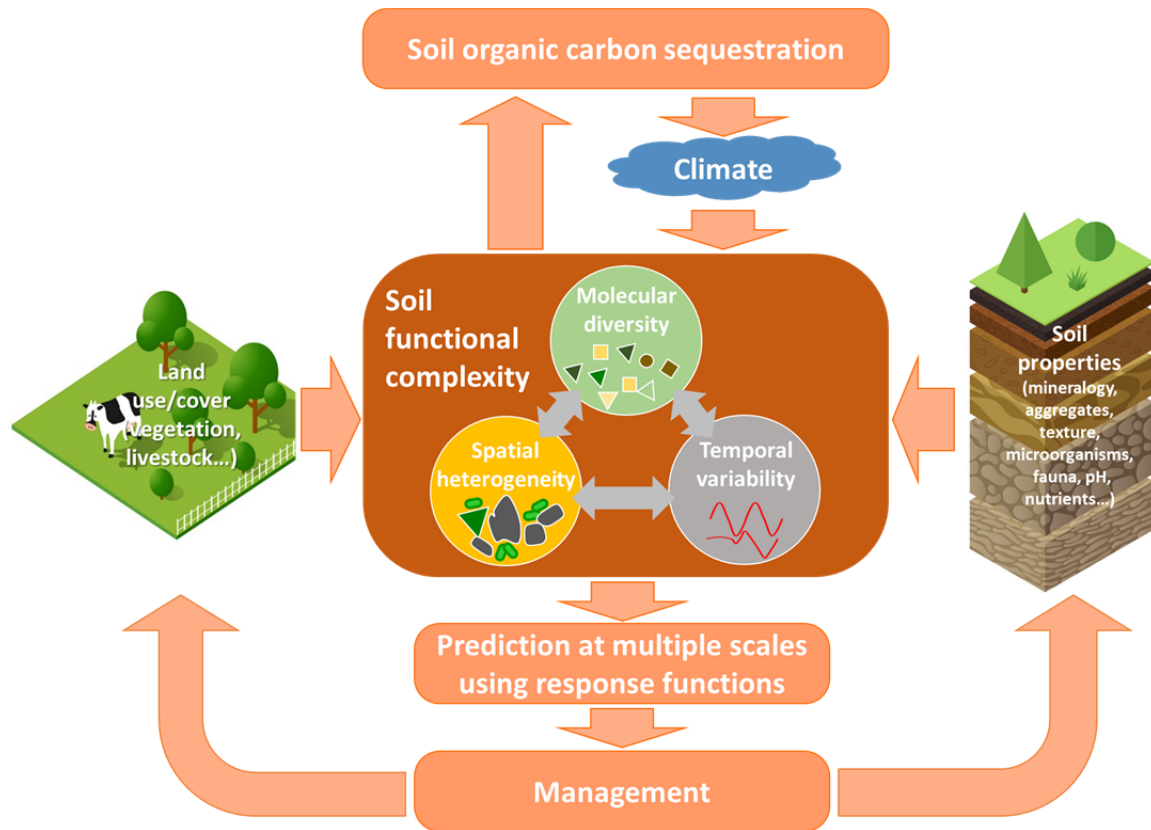


**(b) New “Soil as a complex system” view:
Nonlinear interactions at different
organizational levels**



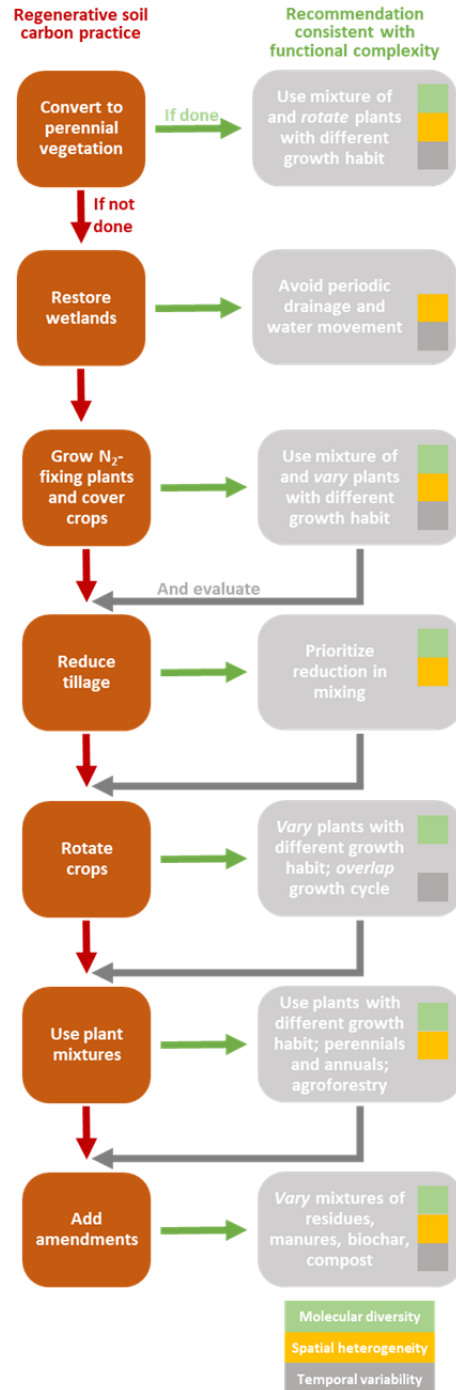
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Figure 2 Emergent behavior of soil organic carbon decomposition. (a) Traditional understanding of soil organic carbon dynamics is based on homogeneously distributed (at the scale of a microorganism) and slowly changing organic matter, microbial biomass, 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.

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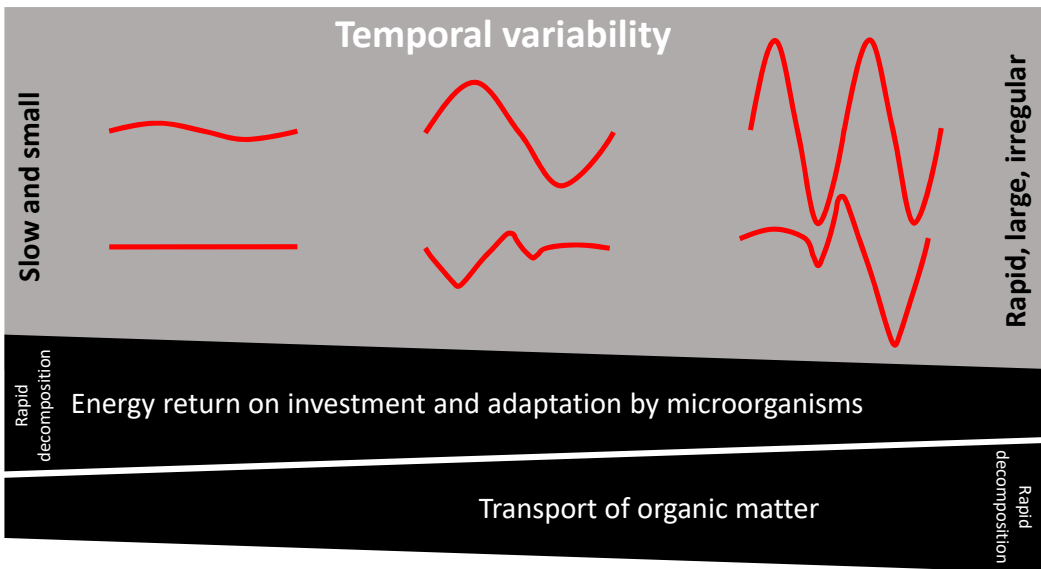
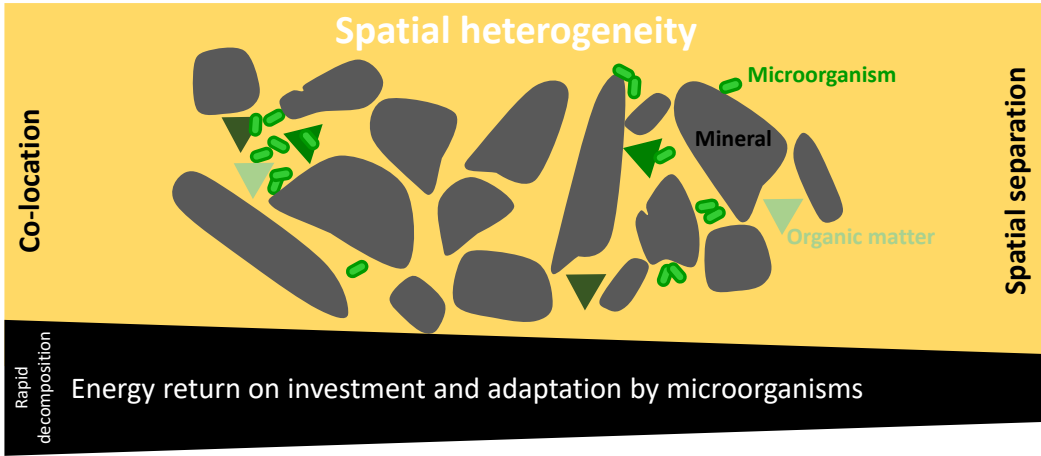
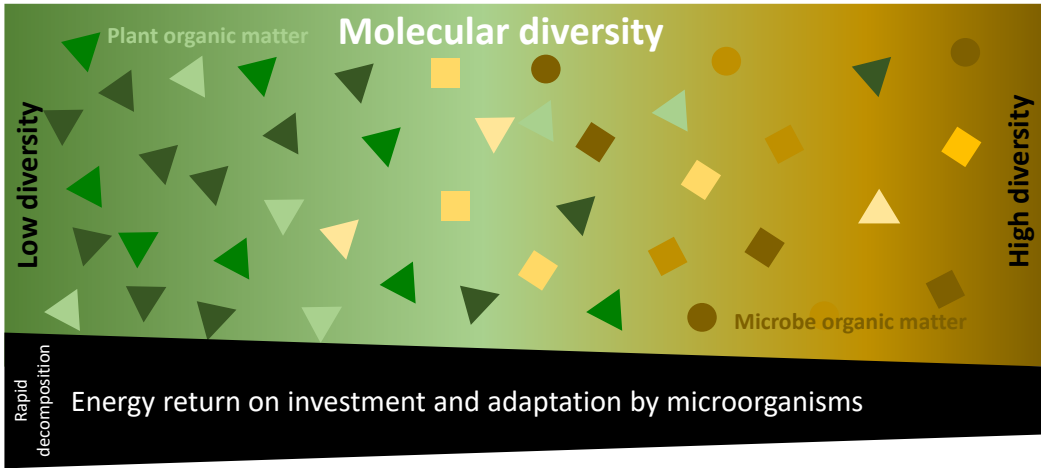
445 **Figure 3 Integration of molecular, spatial and temporal complexity with management and**
 446 **prediction of soil carbon sequestration.** The pore-scale functional complexity that modulates
 447 the effects of environmental, land use, and management changes on the soil system (including
 448 aggregation, mineral interactions, biotic activity and diversity, etc.)^{7,15} may serve as the core
 449 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
 451 we predict soil organic carbon dynamics and develop more sophisticated management for
 452 sequestration.

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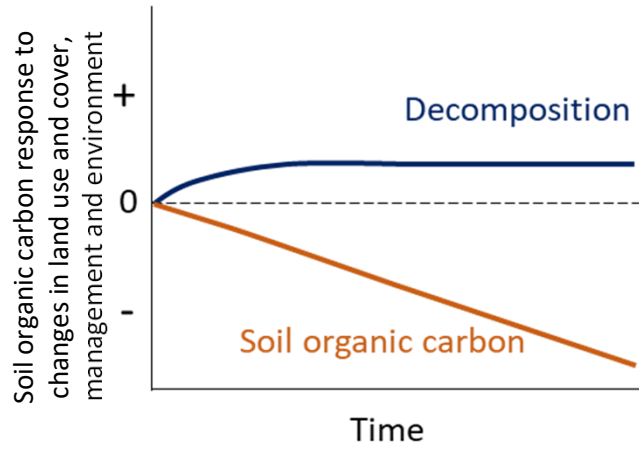


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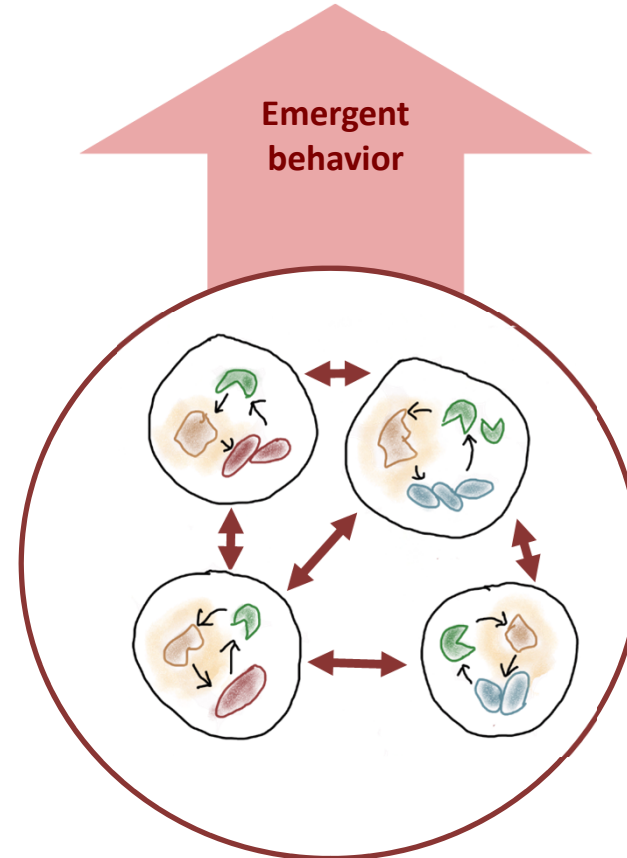
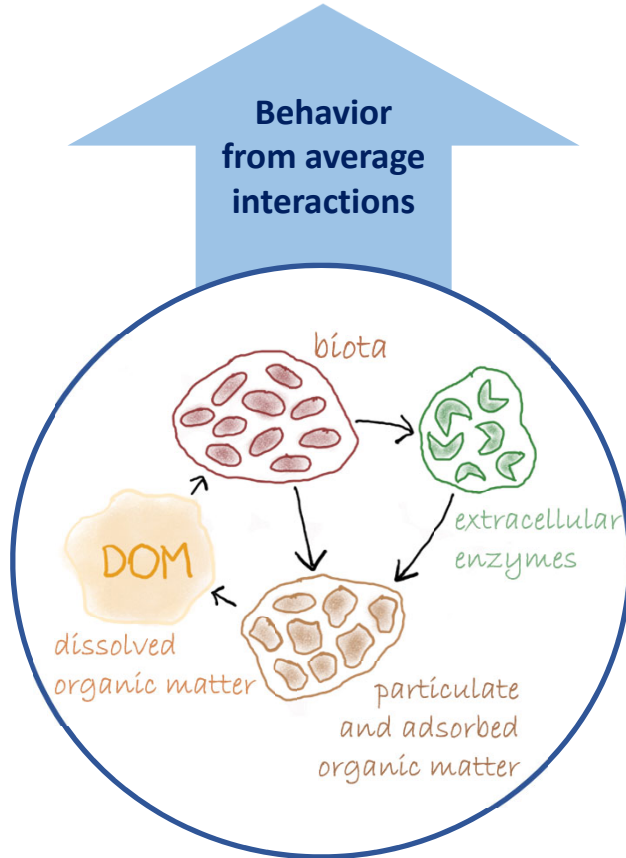
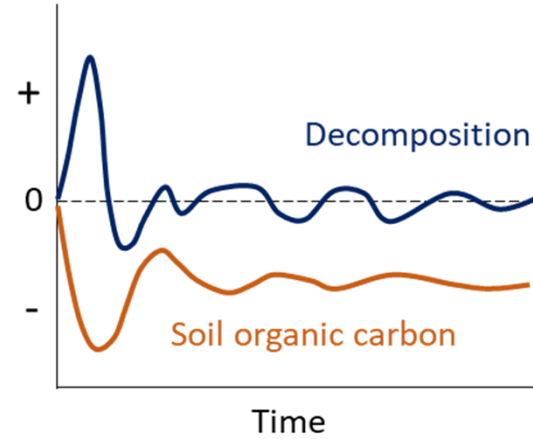
Figure 4 Regenerative soil carbon practice consistent with promotion of functional diversity to increase soil carbon persistence. Soil management designed to increase persistence of soil organic carbon¹ should be investigated for their alignment with functional diversity. The listed management recommendations 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).

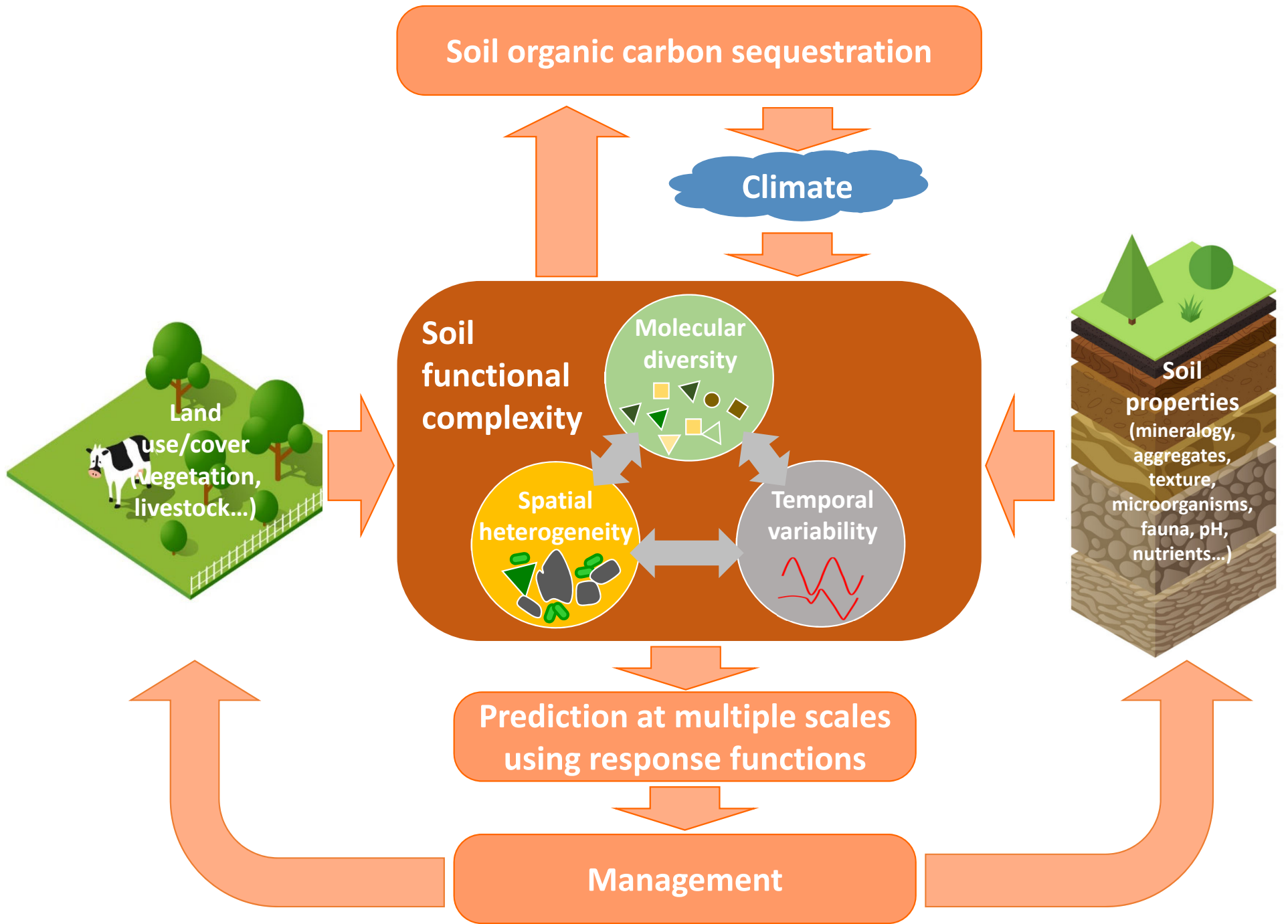


**(a) Traditional “Macroscopic” view:
Interactions at the aggregated level**



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





Regenerative soil carbon practice

Recommendation consistent with functional complexity

