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PERSPECTIVE

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Persistence of soil organic carbon caused by functional complexity

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Soil organic carbon management has the potential to aid climate change 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 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 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 behaviour of the microbial community and would enable soil carbon changes to be predicted without invoking recalcitrant carbon forms that have not been observed 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.

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 changes put forward to increase soil carbon sequestration[1] for the long term requires global-scale prediction of soil organic carbon persistence and vulnerabilities under novel climate conditions[2]. Such a global effort also requires 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 the large scales relevant for carbon-management policy[3]. This deficiency in understanding manifests itself in projections of soil carbon dynamics at regional to global scales that diverge greatly from each other and from observations[4].

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 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 the organic carbon forms with very long residence times that are 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 organic carbon with soil biota, minerals and environment[7]. It can inform the design of field experiments and new types of observations. New models should also identify directions for better management of soils to sequester carbon and thereby mitigate climate change. To be successful, these models should borrow advances in scaling and modelling from engineering and material science in combination with new and growing soil datasets that capture decomposition responses to changes in land use and cover, soil properties or climate. Such an approach would fulfil the policy need for what we suggest calling 'models with intent', which 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.

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 temperature[7]; hence, predictions of decomposition are typically based upon litter nitrogen or lignin contents[5,6]. Meanwhile, in mineral soils, the concept of 'chemical

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recalcitrance' of plant and microbial material causing slow turnover times has been replaced in favour of a continuum model for soil organic carbon compounds[8]. 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 energetically worthwhile[9]. Even metabolizing smaller, 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 (for example, lignin versus cellulose) but also sometimes from molecules that are structurally similar (for example, *ortho*- versus *para*-benzoic acid)[10].

Consequently, beyond a certain point, a greater diversity of molecules increases the cost of metabolism. Investments in using molecules that are rare in the soil solution, because of low production rates or rapid adsorption, are energetically less rewarding[11]; thus, such molecules may remain in soil even if they are potentially easily metabolized. The magnitude of additional cost 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 assimilation[12]. Molecular diversity can increase decomposition rates, however, if one compound provides the energy or nutrients needed to decompose another one, a process often referred to as priming. How to quantify diversity to predict whether changes in the concentrations 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 decomposition[13]. In addition, the diversity of organic carbon binding to minerals also increases persistence[14].

A focus on molecular diversity may reconcile the divide between the scientific communities studying organic and mineral horizons[15]. This reconciliation is based on the increasing diversity of molecular configurations from plants to litter to topsoil to subsoil[16]. Plant material comprises 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 biota[17], which we argue supports faster decomposition (Fig. 1). With increasing decomposition and consumption of the most common molecules, molecular diversity increases[18] 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 decomposers[20], and the distribution and forms of organic matter are equally patchy at this scale[21]. Physical separation has for some time been invoked as an important stabilization mechanism[22], 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 proceed, degraders or their enzymes must come into contact with substrate. This aligns with observed carbon turnover times on the order of months[24], 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 heterogeneity[21], which is consistent with observations that aggregation increases organic carbon persistence[24].

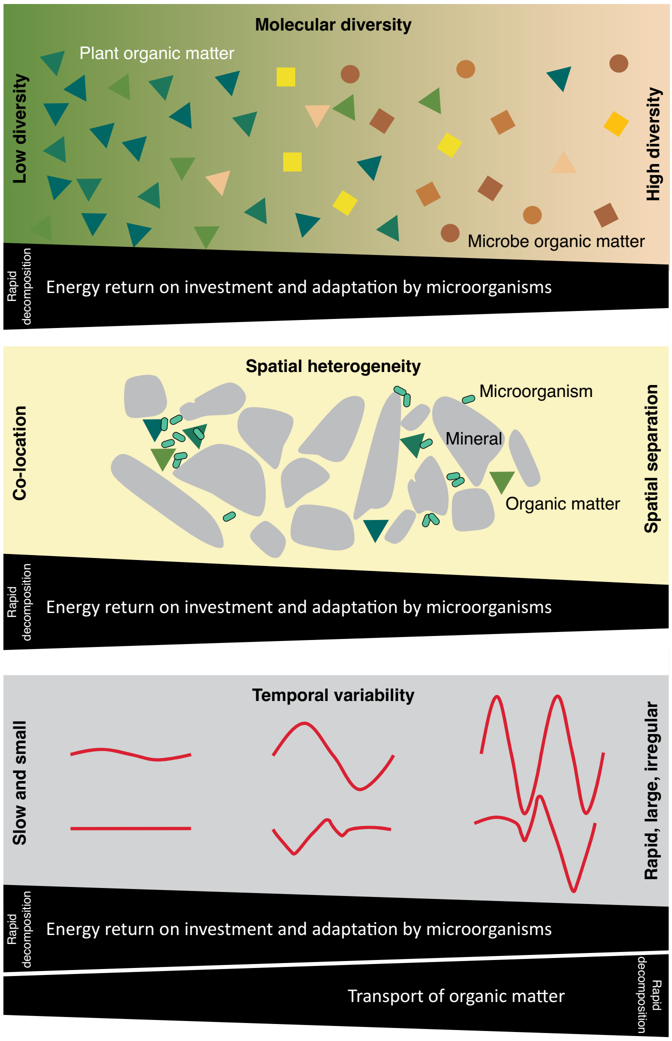

Fig. 1 | Functional complexity and the persistence of soil organic carbon. Functional complexity comprises molecular diversity, spatial heterogeneity and temporal variability that affect the energy, carbon and nutrient return on investment for the microbial community. A lower molecular diversity and 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. Higher spatial heterogeneity decreases the probability that decomposers meet substrate. 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.

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-located[25]. Bacteria are relatively immobile because water films in hydrologically unsaturated soil are not thick enough for the complete immersion of bacterial cells[26], and even with full immersion in water, bacteria are energetically limited from moving 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 the extent to which it depends on the short-distance transport of

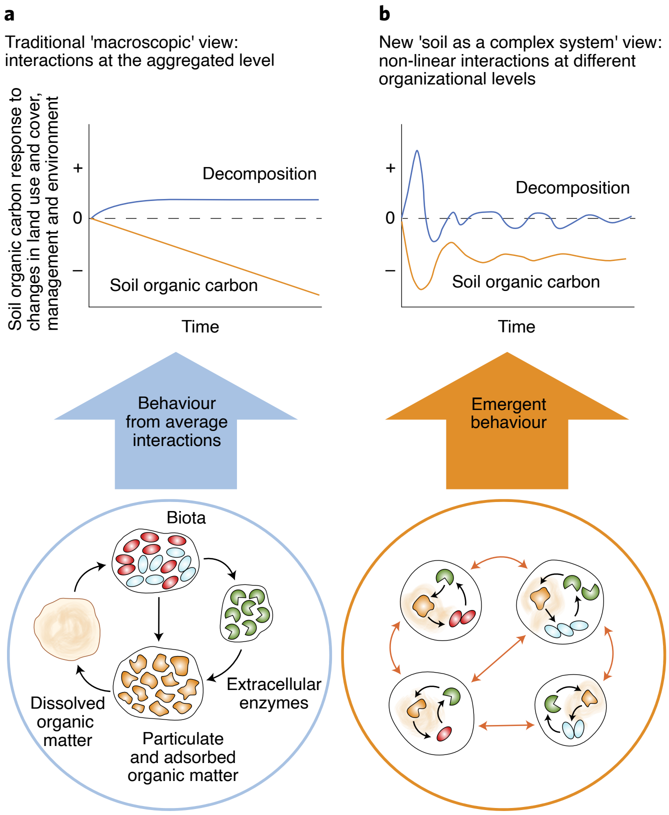

Fig. 2 | Emergent behaviour of soil organic carbon decomposition. a, Traditional understanding of soil organic carbon dynamics is based on homogeneously distributed (at the scale of a microorganism) and slowly changing organic matter, microbial biomass and enzymes (drawings) as a function of environment (soil properties such as texture; environmental properties such as moisture). **b**, In contrast, allowing non-linear feedbacks that occur at the scale of individual organisms and organic matter generates emergent behaviour 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.

organic carbon rather than on the microbial mobility, which is what 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, and even unexpected access to very old carbon[29], reflecting biogeochemical thresholds of ecosystem properties (Fig. 1). It is typically assumed that microbes change their activity in tandem with moisture and temperature fluctuations, and that 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: (1) not only solubility of substrate but also transport within soil pores changes the amount of organic carbon that can be assimilated by microorganisms[30], and (2) adaptation of microbial communities to rapid changes in environmental and substrate conditions contributes to their ability to utilize organic carbon[31]. Mounting evidence suggests that not only current but also historical environmental conditions may substantially alter rates and pathways of carbon transformations[32]. For example, adaptation to high soil temperatures were shown to decrease the sensitivity of decomposition to changing temperatures[32]. The responses that allow microbes to tolerate or adapt to environmental stress therefore lead to characteristic life history traits and physiological trade-offs[33] that shape microbial community composition, activity and function over the long term.

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 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 nutrients[35]. This can even result in the loss of the capacity to use substrates for growth[36] and the development of metabolic flexibility, including dormancy[34]. This loss of 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 notable 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.

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 probably further reduces organic carbon decomposition, as suggested by theory[25]. It remains an interesting question whether spatial heterogeneity poses a more important constraint on decomposition than does molecular diversity, and how these complexities interact.

Emergent behaviour of soil organic carbon decomposition

The described functional complexity is expected to cause 'emergent behaviour', as seen in other complex systems[37], in which fine-scale interactions among individual parts of the system lead to the emergence of a behaviour with a quality that cannot be inferred from the behaviour of these parts[37]. Even though the concept of emergent behaviour and self-organization is well established in theoretical ecology[37], it has only rarely been applied to soil systems[38]. Rather, organic carbon decomposition is traditionally described from a large-scale perspective as the sum of the individual behaviours of microbes and substrate (Fig. 2a).

Recognizing soil as a complex system opens up possibilities to describe persistence as an emergent behaviour arising from non-linear 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 communities[39], studies on microbial self-organization in soil interacting with its environment are limited[20]. Modelling individual microorganisms in soil decomposer communities (individual-based modelling)[40,41] demonstrated the potential importance of emergent behaviour for soil organic carbon turnover. The next steps include (1) obtaining better representation of how emergent behaviour affects soil organic carbon persistence, (2) translating these insights into model structures that capture essential insights at the pore scale as well as further translating these to a global scale[42] that may also include machine-learning approaches[43], and (3) implementing these insights into management-relevant recommendations as part of policy-relevant decision support systems.

Implications for management and policy

We propose integrating soil functional complexity into the development of management and prediction, as this complexity mediates the effects of land use and cover, soil properties and climate

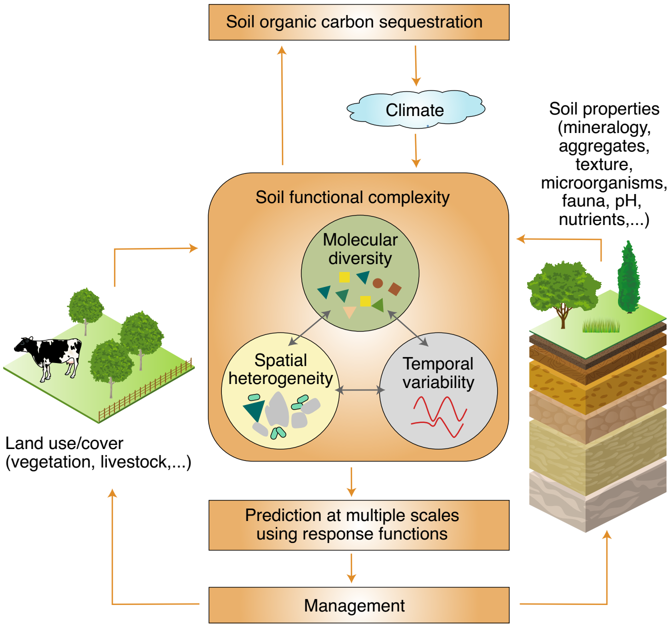

Fig. 3 | Integration of molecular, spatial and temporal complexity with management and prediction of soil carbon sequestration. The pore-scale functional complexity that modulates the effects of environmental, land-use and management changes on the soil system (including aggregation, mineral interactions,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

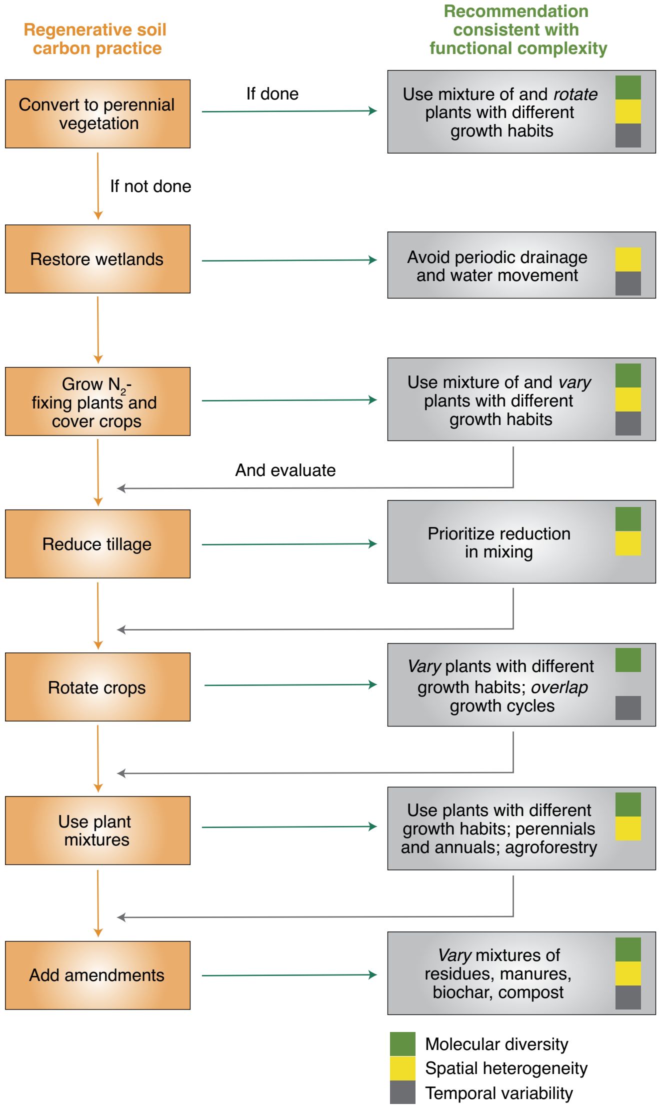

Fig. 4 | Regenerative soil carbon practice consistent with promotion of functional diversity to increase soil carbon persistence. Soil management designed to increase persistence of soil organic carbon[1] should be investigated for its alignment with functional diversity. The listed management recommendations also increase organic carbon input (for example, greater plant diversity[45]) or persistence unrelated to functional diversity (for example, avoiding periodic drainage also reduces aeration in addition to movement of carbon). Inset colours relate to the three aspects of functional diversity (molecular, spatial and temporal) also used in Figs. 2 and 3. Interactions of effects over time require specific attention in future research (indicated by italics).

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 term. Promoting functional complexity consistent with a mixture of inputs and a diversity of plant species[44,45] (which will stimulate a diverse microbial community[45] and rhizodeposits[14]), 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 to merely increasing organic carbon inputs.

Using predictive models to explore soil carbon behaviour under different scenarios can be the basis for substantial policy and industry investment[46]. We propose combining soil functional complexity—molecular, spatial and temporal—with multiscale modelling to optimize such global efforts in soil carbon sequestration[25]. The concept of functional complexity also avoids the pitfall of invoking stable carbon forms with long[6] or infinite[5] 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 contrast to traditionally employed upscaling approaches for such decision-support tools, we propose multiscale modelling 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 macroscale projections. By integrating results from the basis model into the macroscale 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 multiscale modelling are found in chemical engineering and material science[47], atmospheric science to describe cloud physics[48] and reactive transport in groundwater[49], and may be combined with artificial intelligence[43].

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 molecular complexity may motivate a new generation of scientific experiments such as those increasingly conducted in soil microbial ecology[50]. Initially, such microbial responses may be used to define soil functional types[51], or rather what we may call 'soil functional response types', to distinguish them from types based on static soil properties. The multiscale models we envision could then be used to predict functional response types based on fine-scale information; a 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 technology[52] must be intensified to provide the capacity to quantify these responses through laboratory measurements and eventually through real-time and high-resolution field measurements.

The way in which 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 modelling approaches will allow testing of the robustness of scaling 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 testbed[53]. Such an ensemble approach will allow rigorous comparison of their behaviours 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 have the potential to generate the policy-relevant soil management recommendations that are required to underpin international programs needed to address global-change challenges.

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Author contributions

All authors participated in generating the concept. J.L., S.M., N.N., C.K. and K.M. drafted first versions of the figures. All authors contributed to writing and editing.

Competing interests

The authors declare no competing interests.

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