Developing systems theory in soil agroecology: Incorporating heterogeneity and dynamic instability

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Abstract

Ecosystem management is integral to the future of soils, yet anthropogenic drivers represent a key source of uncertainty in ecosystem models. First- and new-generation soil models formulate many soil pools using first-order decomposition, which tends to generate simpler yet numerous parameters. Systems or complexity theory, developed across various scientific and social fields, may help improve robustness of soil models, by offering consistent assumptions about system openness, potential dynamic instability and distance from commonly assumed stable equilibria, as well as new analytical tools for formulating more generalized model structures that reduce parameter space and yield a wider array of possible model outcomes, such as quickly shrinking carbon stocks with pulsing or lagged respiration. This paper builds on recent perspectives of soil modeling to ask how various soil functions can be better understood by applying a complex systems lens. We synthesized previous literature reviews with concepts from non-linear dynamical systems in theoretical ecology and soil sciences more broadly to identify areas for further study that may help improve the robustness of soil models under the uncertainty of human activities and management. Three broad dynamical concepts were highlighted: soil variable memory or state-dependence, oscillations, and tipping points or hysteresis. These themes represent less intuitive yet key dynamics that can emerge after assuming nuanced observations, such as reversibility of organo-mineral associations, dynamic aggregate- and pore hierarchies, persistent wet-dry cycles, higher-order microbial community and predator-prey interactions, cumulative legacy land use history, and social management interactions and/or cooperation. We discuss how these aspects may contribute useful analytical tools, metrics, and frameworks that help integrate the uncertainties in future soil states, ranging from micro- to regional scales, including those indirectly affected by human activities and management decisions. Overall, this study highlights the potential benefits of incorporating spatial heterogeneity and dynamic instabilities into future model representations of whole soil processes. Additionally, it advocates for transdisciplinary collaborations between natural and social scientists, extending research into anthropedology and biogeosociochemistry, to better integrate and understand longer-term anthropogenic drivers of soil processes, potentially from soil structural dynamics to microbial community and food web ecology.

Introduction

Soils represent the basis of recurring civilization *(Montgomery, 2007; Marris, 2022)*, and models depicting their structure and dynamics may help improve generalized understanding of their behavior and ecology. New generation models of soil nutrient cycles *(Sulman et al., 2018; Zhang et al., 2021)* certainly improve on older generation ones *(Coleman and Jenkinson, 1996; Powlson et al., 1996; Berardi et al., 2020)*, adding foci on organic matter stabilization by mineral association that considers the efficiency of microbial degradation *(Cotrufo et al., 2013)*, molecular and pool stochasticity *(Sierra et al., 2018; Waring et al., 2020; Azizi-Rad et al., 2021)*, and increasingly large datasets *(Todd-Brown et al., 2022).* However, both handling large parameter spaces and making predictions across microbial to global scales remain difficult *(Wieder et al., 2015; Vereecken et al., 2016)*, explaining common decisions to make design tradeoffs between model generality, or qualitative diversity of dynamical output and potential case applications, with numerical precision and realism at a particular scale (e.g. global) *(Levins, 1966; Livingtson, 1985).* Additionally, the increasing recognition of soil habitat structure for organic matter storage and stability *(Cotrufo et al., 2013; Kravchenko et al., 2019a; King, 2020)*, as well as for community assembly and biodiversity maintenance *(Erktan et al., 2017; Charlotte et al., 2022; Schweizer, 2022; Vogel et al., 2022)*, highlights the potential utility of re-conceptualizing how the soil environment is modeled and formulated. Given the breadth of services that soils offer, adopting modeling strategies that are transferable across soil ecology sub-disciplines *(Buchkowski et al., 2017)* indeed helps move toward addressing the most general of goals in soil ecology, such as how soil biotic and abiotic spheres or networks interact over time to confer bulk soil properties. Fortunately, an old yet increasingly studied field of complex systems focuses on gaining generalized insights from large multi-component systems, from social and neural networks *(Marder and Calabrese, 1996)* to oscillating chemical reactions *(Epstein et al., 1983; Pacault et al., 1987; Epstein and Showalter, 1996)*, that offer potentially useful analytical perspectives and strategies for generalizing about how heterogeneous soil environments can behave. This synthesis builds on previous efforts to highlight how soil ecology may benefit from integrating tools and concepts from complex systems *(Baveye et al., 2000; Young and Crawford, 2004; Lavelle et al., 2016; Pachepsky and Hill, 2017; Bennett et al., 2019)*, elaborating on how specific modeling principles may help gain insight into a variety of soil processes in more generalized ways.

Systems perspective

Early studies of complex systems tended to include explicitly recognized spatial extent and/or separation among modules *(Turing, 1952; Levins, 1969; Mandelbrot, 1983)*, and others recognized explicit state-dependence or time lags *(Rutherford and Do, 1997)*. Mathematical roots of systems and complexity theory built upon nonlinear dynamics *(Lorenz, 1963; Winfree and Strogatz, 1984)* and chaos theory *(May, 1974; Li and Yorke, 1975; Rogers et al., 2022)*, which was facilitated by computational technologies allowing simulation. In soil science, early reports on fractal dimensions of particle size distributions also represent narratives working toward scale-invariant descriptions of the physical habitat *(Young and Crawford, 1991; Kravchenko et al., 1999)*, though fractal methods can also be useful in describing non-physical domains. Given how large and complicated some systems can be, analytical research questions have tended to switch focus from valuing the precision of model predictive ability to its generality *(Levins, 1966)*, or how consistent a result is across example systems. This strategy of finding intersecting truths across case studies is already somewhat familiar to research in the form of useful reviews, meta-analyses, and model comparison projects *(Sulman et al., 2018)*, but it can also take a more computational form. More useful analysis metrics for complex models with variable outputs tend to shift from distribution centrality (e.g. median, mean) to variance and/or key single exponents in cases of high skewness. Accordingly, research questions about similar complex systems also benefit in switching from precise future values to the probability of certain types of events occurring at any future time or location, depending on input data. Focusing on variance as output also promotes including realistic inherent variation or randomness as input, known as stochasticity, which has been a necessary part of explaining and reproducing natural time series of experimental populations *(Henson et al., 2001)*. Embracing and allowing for variability in time series also offers the potential to predict and observe temporal autocorrelation in anticipation of critical transitions of tipping points *(Scheffer et al., 2012)*, such as during accelerated soil degradation or restoration, or naturally unpredictable chaotic fluctuations with predictable bounds *(Schaffer and Kot, 1985; Hastings et al., 1993)*, such as in response to human drivers *(Berryman and Millstein, 1989)*.

Key examples across fields of study have become increasingly emblematic of complex systems theory. For example, in geophysics, measuring irregular structures in nature using relative units instead of absolute ones *(Mandelbrot, 1983)* has widely uncovered power law frequencies of system components sub-sets, famously used in geophysics to study regional earthquake magnitudes *(Bak et al., 2002; Christensen et al., 2002)*. This tool from the fractal geometry branch of mathematics was later applied to ecology, both implicitly *(Macarthur* *and Wilson, 1963)* and explicitly *(Harte, 1999; Ostling, 2000)*, as well as to soil structure, including aggregation and porosity, with implications for predator-prey (i.e. invertebrate-microbe) interactions *(Baveye et al., 2000).* Although current applications of nonlinear dynamical systems principles to soils remain somewhat siloed in geophysics, potential applications to soil ecology remain. Another exemplary analysis tool is re-framing focal metrics from distribution centrality to variance measures, as mentioned above. This shift has advanced understanding of consistent spatial and temporal fluctuations *(Taylor, 1961)* to focus on sub-module synchronization potential, notably formulated as coupled pendulum dynamics in physics *(Kuramoto, 1984)*, and has recently inspired various applications in ecology, including to predator-prey dynamics on interaction networks *(Vandermeer, 2021)*, dispersal shifts across urban agricultural landscapes *(Ong et al., 2020)*, and to biodiversity collapse broadly. These analytical methods tend to uncover internal consistencies or rules among heterogeneous components that predict relatively new patterns at the whole system level, advancing the specific goal of using theory to advance hypothesis testing, compared to other assumed goals like precision forecasting.

Early complexity in soils

In ecology generally, there appears to be a consensus that micro- and meso-habitats are complex, and indeed natural soil systems are regarded as the most complex habitats we know of. Yet formal modeling frameworks remain relatively simplified, in part due to common statistical limitations and disciplinary influences. For example, Michaelis-Menten kinetics generated a strong biochemical influence on representing soil organic carbon cycling and decomposition, which has over time been modified to be “reversed” to focus on total enzyme production rather than individual catalysis *(Schimel and Bennett, 2004)*, and has maintained wide use as a core model structure for fine-scale carbon and nutrient transformations. This was even applied to population ecology *(Volterra, 1928)*, where population growth equations analogous to enzyme kinetics have been well analyzed to yield technically unstable but noticeably consistent oscillatory dynamics, also observable in soil data empirically *(Reijneveld, 2013; Kuzyakov and Zamanian, 2019)* and modeled *(Wang et al., 2014).* Other modeling approaches can also yield counter-intuitive results, which may contradict existing empirical data, or pre-date supporting data from future long-term studies. One case of this was the incorporation of adaptive or environmentally-responsive (i.e. non-linear) enzyme production, also interpretable as emphasizing a positive biological feedback based on phenotypic plasticity, and formulated as a flux- or interaction modification *(Ludington, 2022).* This early modeling study *(Schimel, 2003)* predicted, in part contrasting contemporary evidence supporting decomposition as primarily nitrogen-limited while aligning with others , that nitrogen additions to soil would suppress rather than stimulate decomposition, a result that preceded future validating evidence of this from longer-term nitrogen fertilization studies . In this case, a key multiplicative (i.e. non-linear) model term associating organic matter decay with both its current pool size (first-order decay) and also a dynamically-responsive enzyme pool, ultimately improved model generality, specifically across time scales from minutes when proteins turnover to multiple years and seasons. More broadly, mathematical ecology has provided very interesting insights based on linear stability analysis tools to focus analyses *(King and Schaffer, 1999)*, but recent pursuits have expanded to include what was otherwise considered unstable outcomes, like transient dynamics *(Hastings, 2004; Hastings et al., 2018)* with implications for introduced species establishment *(Armstrong and McGehee, 1976; McGehee and Armstrong, 1977; Wilson and Abrams, 2005; Xiao and Fussmann, 2013)*. These approaches indeed provided new insight on consistently observable patterns, based on the increasing use and acceptance of graphical analytical methods like cobwebbing following the rise of personal computing and simulation power. Recently, comparable tools and concepts from community ecology have been synthetically presented to potentially help address questions in soil carbon cycling and soil community ecology *(Buchkowski et al., 2017)*.

Accordingly, this perspective now draws from theoretical ecology to further extend recent efforts to integrate complex systems principles into soil sciences *(Baveye et al., 2000; Young and Crawford, 2004; Sierra and Müller, 2015; Lavelle et al., 2016; Buchkowski et al., 2017; Pachepsky and Hill, 2017; Bennett et al., 2019)*, and thereby generalize our understanding of the soil habitat, from micro- to macro- scales, notably embracing persistent variation and heterogeneity as notably critical to fundamental soil processes *(O'Leary et al., 2018)*. Specifically, this paper includes non-exhaustive discussion of various aspects of soil research that may benefit from integrating perspectives from other complex systems research: including memory, oscillations, tipping points and hysteresis. Relevant supporting phenomena observed in soils include reversible organo-mineral associations, aggregate- and pore hierarchy and dynamics, persistent wet-dry cycles, multi-year gas fluxes (e.g. respiration) and nutrient availability, higher-order microbial community and predator-prey interactions, and cumulative legacy land use history. Overall, adopting tools from systems and complexity theory primarily offers ways of reducing model structural uncertainties *(Bradford et al., 2016)*, thereby also potentially facilitating model-data integration efforts, for example by reducing parameter space *(Bennett et al., 2019)*.

Memory

Iteration and hierarchy

The concept of memory represents a form of self-referential dynamics specifically based on an event occurring at least one time step in the past, also referred to as time lags, which in some real systems can result in hierarchical structures. An example from the field of physics is nuclear fusion, in which heavier atoms with more protons are made not by the instant fusion of many lighter atoms, but the simpler merging of few medium atoms previously built, interestingly, also with an apparent critical drop in stability at higher atomic numbers after iron *(Pfützner et al., 2012)*. This shows not only a hierarchical building process resulting from the dependence of the existence of larger nuclei on past states (i.e. previously formed smaller nuclei), but this also shows related consequences, namely a skewed distribution of nuclear stability across the spectrum of existing nucleus sizes, where the nuclei of smaller atoms are more tightly bound together than larger ones.

Highly skewed or long-tailed distributions, like the power law family, based on component or module attributes like cluster size, are increasingly recognized as *(Gillespie, 2015)* properties of complex systems *(Clauset et al., 2009; Locey and Lennon, 2016)*. This contrasts the normal "bell curve" distribution, which is often assumed for classic statistical procedures, from simple averages to within-group variance during linear regression. As a result, observing power laws in data has served as initial support for hypothesizing hierarchical or self-organizing processes, offering a novel path to infer process from pattern. Although various underlying processes can yield similar distributions *(Bashkirov and Vityazev, 2000; Curado et al., 2018)*, observing non-normal distributions may at least help de-emphasize selection-like mechanisms that tend to produce bell curves.

Somewhat surprisingly, the nuclear fusion example parallels soil aggregation almost exactly, where larger aggregates tend to be weaker and less structurally stable than smaller aggregates. In this case soil aggregation is in part affected by the amount of surface area allotted to binding agents, as well as the strengths of the various binding agents themselves, ranging from fine-scale organo-mineral associations to fungal mycelial networks *(Tisdall and Oades, 1982)*. Ultimately, this can be tied back to early discussions of fractal dimension parameters of power law distributions observed in porous media and landscsapes *(Burrough, 1981)*, which simultaneously converged with empirical support for soil aggregation as a hierarchical processes *(Tisdall and Oades, 1982)*, and later exploration *(Nortcliff, 1984; Armstrong, 1986; Tyler and Wheatcraft, 1989; Perrier et al., 1996; Assouline et al., 1998)*. As a result, while perhaps controversial *(Baveye et al., 2000; Pachepsky and Hill, 2017)*, one approach for theoreticians and modelers may be to further attempt the study of simple models *(Vitousek et al., 2022)* to explore ideas and test underlying hypotheses about the implications of hierarchical structural dynamics for soil properties *(Stamati et al., 2013)*. This may be especially important for processes that remain near impossible to measure empirically *(Bennett et al., 2019)*. Some studies seem to align with this process-based modeling focus *(Waring et al., 2020)*, while others tend to prioritize more output precision after long-term simulation *(Coleman and Jenkinson, 1996; Powlson et al., 1996; Cong et al., 2014)*. Additionally, there is also supporting evidence for various hierarchical processes in soils, including those underlying clay flocculation *(Brostow et al., 2007; Cuthbertson et al., 2018)*, aggregation of solids *(Tisdall and Oades, 1982)* (mentioned above) as a result of physical mixing *(Klaminder et al., 2013)* and fungal enmeshment *(Rillig and Mummey, 2006)* amplified by wet-dry cycles *(Denef et al., 2001)*, and for pore cluster networks *(Quigley and Kravchenko, 2022; Vogel et al., 2022)*, all of which represent interesting modules of the soil environment to explore with hypotheses about hierarchical structural dynamics and their implications. Specifically, hierarchical aggregation has been previously analyzed by binning all aggregates into either micro- or macroaggregate functional groups, a fractionation that has served as a basic structure for some models specific to solid aggregation *(Segoli et al., 2013; Stamati et al., 2013)*, though it may also be relevant for other soil models, such as ones specific to greenhouse gas production *(Kravchenko et al., 2019b; Wang et al., 2019)* or microbial diversity.

Overall, these hierarchical patterns emerging from system-wide memory (i.e. past state-dependence) tend to generally reflect natural solutions for coarser level system limitations. Endogenous solutions to system limits can in some cases be formulated and analyzed as an issue of optimizing information flow *(Czaplicka et al., 2013)*. If applied to modeling soil pore dynamics, for example, this general mechanism or principle could help explain empirical soil pore structure data specifically as a single naturally-resulting geometric solution (stable or temporary/unstable) for a set of constraints. Biological constraints might be microbial cross-feeding rates fueled by metabolite-carrying water flowing through pore networks. Physical constraints could be spatial, such as topsoil depth, and/or temporal, such as growing season length, both of which would affect pore-forming processes including microbial secretions and gas exchange (micro-pores) and invertebrate burrowing activity (macro-pores). Importantly, real soils also have historical constraints, which state where pores have been and intuitively predict where new ones can potentially form, which ultimately holistically frames pore network structures as ongoing solutions, with varying robustness, for both past and present ecological activity. Similarly, hierarchical aggregation of solids may also elongate the effects of environmental changes enough to minimize compositional variance of microbial communities living in the smallest habitat pockets *(Rillig et al., 2017; Wilpiszeski et al., 2019)*.

System memory, in the form of iterative structural dynamics, can also be environmentally adaptive, such as when system components are dynamic or continuously dismantled and re-assembled into new yet familiar structures, which range in scope from soil micro-habitats to landscape profiles over months and years. Fine-scale positive feedbacks may help explain the diversity of soil profiles and pedons across and within order-level taxonomic soil classifications *(Jenny, 1961; Phillips, 2017)*. In addition to hierarchies, soil systems' internal or temporal memory can also be a regular source of heterogeneity that increases uncertainty about how soil behaves. In soils, this hypothesis of increasing heterogeneity along hierarchical trajectories could, for example, predict greater variance in diversity or simply beta diversity among microbial communities observed in macro-aggregates compared to those among micro-aggregates. However, there remains little evidence addressing this topic, although technological advances may facilitate future studies *(Bailey et al., 2012)*.

Soil depth and history

Studying subsoils and soil depth also represents an axis that integrates soil profile memory and time lags. Often only topsoils (e.g. to 10 or 20 cm depth) are studied due to high nutrient concentrations there, yet subsoil horizons store more total carbon *(Hicks Pries et al., 2017)* and can influence topsoil microbial activity, ultimately highlighting their relevance to whole profile soil functions. Pedological studies have long recognized that land use history, in addition to the classic five state factors of soils, affects current soil function *(Turley et al., 2020)*, especially tillage and fertilization via changes in soil structure and soil fertility *(Weitzman et al., 2022)*. Additionally, microbes may decompose stable organic matter reserves when new labile organic matter is added, known as soil priming *(Kuzyakov, 2006; Bastida et al., 2019; Liu et al., 2020)*, to which subsoils may be more sensitive *(Li et al., 2022)*, and thus overall priming may offset any expected new carbon storage in topsoils. Similarly, a multi-year whole profile warming experiment recently showed that soil overall lost carbon mostly from subsoil even though topsoil accumulated carbon *(Soong et al., 2021)*, suggesting that opposite patterns in subsoils may require re-shaping fundamental understanding of soil systems at the profile and pedon levels. In contrast, subsoils at over one meter depth in agricultural systems may be better posed to accumulate carbon in the long-term compared to their topsoils, due to existing degradation from deeper tillage and the potential for added fertility from added root inputs by perennial plants with deep roots *(Button et al., 2022)* and other biological subsoiling methods *(Ning et al., 2022)*. Since soil pedogenesis is now understood to follow complex trajectories *(Phillips, 2017)*, future study of subsoils should help develop explanations for underlying processes simultaneously affecting different soil horizons.

Ideas of memory also relate to group-level patterns and processes which are increasingly reported, alongside individual component-level processes *(Kerr and Godfrey-Smith, 2002; Traulsen and Nowak, 2006)*, and can have important implications for overall soil processes. Cooperation often manifests itself as synchrony among individuals, as in early examples of tree seed masting *(Ostfeld et al., 2006; Victor et al., 2016)* as well as disease transmission *(Ostfeld et al., 2005)*, with similar principles extended to apply to forests *(Filotas et al., 2014)* and soil rhizospheres to describe nutrient exchange *(Simard et al., 1997)* along with mycorrhizal symbioses *(van der Heijden and Horton, 2009; Simard et al., 2012)*. Similarly, population quorum sensing by soil bacteria has affected antibiotic production *(Li et al., 2021)* and other benefits at critical population sizes *(Heilmann et al., 2015)* and likely with weak time delays in reciprocity *(Alfaro and Sanjuan, 2022)*, and quorum sensing has also been hypothesized to affect enzyme production with implications for nitrogen cycling *(DeAngelis et al., 2008; Wang et al., 2014)*. Time delays also affecting interactions between partners changing at different rates or temporal scales – like between monthly root turnover and exudation affecting momentary microbial gene expression and predatory grazing below- and aboveground – could affect reciprocity of symbioses in soil. Ultimately, the combinations of spatial and temporal variation generate the fluctuations that make treating dynamic instability as a somewhat unavoidable and thus inherent property of natural soil systems.

Oscillations

Focus on variance

Diel cycles in soil temperature and respiration are commonly observed, yet few studies analyze the implications of natural cycles for modeling soil responses to environmental changes, which in some cases can lead to hysteretic irreversibility *(Phillips et al., 2011)*. Complexity and systems theory offer generalized tools and perspectives to better incorporate variance (i.e. by soil depth) into more generalized models of soil processes. The tendency of a systems perspective to shift analysis toward variance is ultimately more inclusive of a diversity of model outcomes, such as regular oscillations or constrained chaotic fluctuations, and more generally validates informative model outputs that are not precise single point solutions and otherwise considered unstable by linear stability analysis. One method of incorporating variances has been to re-formulate dynamical systems using trigonometric functions, which are unique for producing repeated symmetrical curves, from bounded measures of relative distance from a fixed line segment *(Coolidge, 1952)*. These first principles already reflect modern principles now understood about many complex systems, like relativity and symmetry with modification, which likely increase the generality and applicability of modeled output especially when processes and questions are newly framed and formulated in tractable ways.

Soil cycles

Oscillations have been predicted by novel and widely cited model structures in agroecology *(Vandermeer and Perfecto, 2017)* and soil ecology *(Baveye et al., 2018)*, and supported by empirical data across fine- and coarse scales. At fine scales, soil carbon molecular turnover has been recently proposed to depend on functional group complexity that also hypothesizes spatial modularity or hotspots in activity, which could produce oscillations of broader soil properties over time *(Lehmann et al., 2020)*. Spatial structuring also strengthens positive feedbacks in decomposition between exo-enzyme activity and assembly or production, which has influenced some early soil models toward predicting consistent variance, in the form of limit cycles, in soil nutrient availability *(Schimel, 2003; Wang et al., 2014)*. Wet-dry cycle frequency has also been cited as affecting soil aggregate stability and as a determinant of patterns in microbial activity *(Evans et al., 2022)*. Various types of limit cycles have also been a classic prediction of predator-prey models, but are rarely applied to describe soil faunal grazer food webs *(Baveye et al., 2000; Buchkowski et al., 2017; Erktan et al., 2020; McCary et al., 2021)* especially involving viruses and their traits *(Emerson et al., 2018; Trubl et al., 2018)*. When these low-dimensional ecological models are explicitly extended in space, for example as metacommunities, a wide variety of mosaic landscapes can be generated with some sensitivity to model formulation or structure *(Vandermeer and Yitbarek, 2012; Vandermeer, 2013; Yitbarek and Vandermeer, 2017)*, suggesting that flexible model structures are likely important for robust understanding of causes and consequences of soil heterogeneity. Spatial explicitness also emphasizes studying dispersal processes among soil modular populations more than internal community dynamics shaped by particular parameterizations, which have been increasingly studied *(Chaudhary et al., 2020; Hajian-Forooshani and Vandermeer, 2020)*. Spatial or temporal separation of populations has also inspired other model structures proposing competitive hierarchies resulting in intransitive loops *(Vandermeer, 2013; Vandermeer and Jackson, 2018)*, which is already supported by strong evidence *(Kerr et al., 2002; Lozano et al., 2019)*. Again, this is a case where new and diverse model predictions precede empirical supporting evidence, which ultimately highlights the potential value of general models, with a wide range of output, over precise ones, specifically for more basic than applied research. At coarser scales, soil respiration has also experienced regular variance in magnitude over multiple years, explained by regime shifts among various dominant stages of community-level decomposer activity *(Sihi et al., 2016; Melillo et al., 2017).* Various soil nutrients have also shown regular oscillations over decades *(Reijneveld, 2013)*, although common statistical analyses remain linear which remains an analytical limitation. Some nutrient oscillations are expected from direct harvests, but if nutrient cycles are coupled (i.e. by microbial metabolisms) while oscillating, unintended and unintuitive synergies or conflicts may emerge, as oscillations align either in- or out of phase *(Vandermeer, 2006)*, leading to either robust, or more likely quickly degrading, soil nutrient availabilities. The appearance and prediction of oscillations among a range of soil variables from both advanced first principles and several empirical studies justifies further study of non-linear models of soil behavior and ecology, with example approaches listed in Table 1.

Tipping points and hysteresis

Hysteresis can be framed as a specific kind of non-linear transition and tipping point occurring in soils. Hysteresis is revealed when model stability analyses include outcomes across range of parameters, and underlying component processes also change pace at different speeds *(Ong and Vandermeer, 2018).* In soils, this occurs with overall water content and its matric pressure, or availability; this is because water always moves through wide pores first regardless of whether the process is drying or wetting, and wide pores have a weaker relationship between these two water variables than in narrow pores, which always mediate water movement second. Here the phenomenon is explained by temporal consistency in process across spatial heterogeneity, which can be another cause of dynamical asymmetry more generally. For example, the relationship between soil temperature and total soil respiration is also hysteretic in that soil respiration responds only after considerable changes in temperature, making respiration stay low as soil warms yet stay high while it cools, even across the same middle temperatures *(Riveros-Iregui et al., 2007; Phillips et al., 2011; Zhang et al., 2015)*, which can also be described as state-dependence or short-term memory for a system. A widely recognized implication of hysteresis is the practical and sometimes permanent *(Ong and Vandermeer, 2018)* irreversibility of past ecological states, like permanent wilting points for roots under drought, or more internally regulated predator or pest populations.

Soil carbon saturation is a related concept, which is supported by field experiments and models, and is inspiring useful model structures for describing and understanding non-linear processes in soil. Appropriately, the concept of soil carbon saturation has already been formulated and incorporated into new generation soil models like MEMS *(Zhang et al., 2021).*

Table 1: Example cases where employing modeling strategies based on systems theory could be useful for generalizing about soil ecology and agroecology.

Goal	**Limitation**	**Systems concept**	**Model approach**	**Pro**	**Con**	**Related Refs**
Forecast soil C for general agricultural or climate change management decisions	Reversible organo-mineral associations (priming); Enzyme production plasticity	Oscillatory dynamics; strong positive feedbacks	Simpler implicitly oscillatory pools, with different winding frequencies	Fewer pool-specific parameters; Computational efficiency allows more stochastic simulations for system accuracy	Less precise final SOM pool sizes	Schimel & Weintraum 2003; Wang et al 2014 Biogeosci; Sulman et al 2018; Kuramoto 1975
Estimate soil biodiversity for conservation and sustainable development	Large nested food webs, with trophic cascades	Indirect / higher-order interactions	Collection of coupled oscillator predator-prey pairs and/or synchronous community clusters	Fewer taxon-specific parameters; Computational efficiency allows more taxon pairs	Less precise species population sizes	Potapov 2022; Buchkowski et al 2017; Vandermeer et al 2021
Assess persistent pathogen risk from soil, compost, or municipal sludge	High heterogeneity in microbial pathogen population sizes	Chaos, bifurcations, period-doubling	Metapopulation with chaotic (high) discrete growth and/or dispersal rates	Higher statistical confidence compared to plate colony count estimates	Output states more parameter dependent	Levins 1969; May 1974; Feigenbaum 1978

An early proposed model *(Stewart et al., 2007)* simulated decadal field data by mixing two pools with different local equilibria: a stable mineral-bound carbon pool that saturates, and a labile pool that mostly decomposes but with no growth limit. This mixed structure produced flexible output – slow linear increases in soil carbon at high concentrations, and quicker but saturating increases at low concentrations – making it more widely applicable and representing a more generalized understanding of long-term soil carbon dynamics.

In contrast, older-generation soil models like CENTURY *(Powlson et al., 1996)* and RothC *(Coleman and Jenkinson, 1996)* did not incorporate pool saturation, but instead offered a simpler initial models offering widespread practical use. The relative simplicity of the model structure is broadly observed in the overall linear successive flow from one decomposition pool to the next. Furthermore, each individual pool was formulated to observe first-order decomposition kinetics. While first-order decomposition represents exponential decay, which is curvi-linear over time, the non-linearities and complex dynamics under investigation by systems theory instead stem from multiplicative associations or interactions among dynamic variables. In many cases, multi-pool soil systems tend to be represented with an attempted thoroughness, resulting in a list of coupled equations that influence each other by additive (or subtraction) terms, which usually consist of a key variable multiplied by a corresponding abiotic parameter, which is static relative to carbon or the nutrient of interest *(Zhang et al., 2021)*. This style of formulation acknowledges that soils are complicated habitats, but leaves room to lean into the complexities of the habitat with various nonlinear additions.

Fundamentally, because parameters and dynamic variables in an ordinary differential equation often represent concepts formulated to be operating at relatively distinct time scales, the re-formulation to incorporate multiplicative variable associations can also be interpreted as a change in descriptive timescale. For example, a representative modeling study may test the hypothesis that particulate organic matter and mineral-associated organic matter, even as distinct pools, might each observe transfer rates that could be affected by both its own and the other's size, within a model time step, rather than between them. More specifically, rather than modeling the primed loss of existing organic matter implicitly in the form of a saturating stable pool, soil priming could be formulated as an interaction modification that implicates the more stable pool's size back into its incoming transfer rate from the labile pool. Generally, this style of formulation may offer a new class of hypothesis testing, especially for soil processes that are currently difficult to test empirically *(Bennett et al., 2019)*, representing a wider array of model outcomes with just a few key soil descriptor variables, in line with recent qualitative syntheses *(Phillips, 2017; Kuzyakov and Zamanian, 2019)*. Modeling soil systems using tools from complexity theory appears to offer an antidote to the increasingly-large soil simulations that have become more popular, in part alongside increasing computing power in cloud systems. The approach using complexity theory can improve conceptual efficiency by reformulating soil models into fewer modular components with more inter-linked process rates *(Lehmann et al., 2020)*. In this way, soil modeling studies may emerge as useful analyses not only for understanding soils themselves, but also for aiding other academic disciplines studying complex systems more generally.

Additional recent studies improved generality of understanding by explicitly modeling biological *(Craig et al., 2021)* and microbial *(Wang et al., 2014)* processes underlying transformation rates, including with saturating enzyme activity *(Buchkowski et al., 2017)*. Even more general understanding can be added by expanding similar model structures to describe effects of soil fauna and invertebrates on soil micro-habitats including predatory and dispersive influences on microbial communities *(Grandy et al., 2016; Creamer et al., 2022)*. However, integrating models of short-term microbial processes with long-term carbon dynamics remains incomplete *(Todd-Brown et al., 2013)*, in part because they operate on very different timescales. Each model class improves understanding of soil, but for generalized predictions, integrating or coupling models with the fewest explicit dimensions that yield the most diverse qualitative output *(Levins, 1966; Lane, 2018)* may help at least bound possible outcomes, such as for soil carbon exchange and net storage, or other nutrient cycles *(Manzoni and Porporato, 2009)*. In addition there are many aspects of soil ecology and functioning such as biodiversity maintenance or specific soil pathogen suppression that warrant continued understanding through modeling the soil environment.

Restorative agropedogenesis

Together, several non-linear dynamics or functions among soil variables may then combine to reveal critical transitions (Fig 1). A recent synthesis *(Kuzyakov and Zamanian, 2019)* revealed many non-linear relationships among key soil variables across several decades, such as between soil bulk density and organic carbon. Their analysis showed distinct phases of pedogenesis, or soil development, under human management, which they termed agropedogenesis. Ultimately, they presented a convergence of these processes into an attractor, which they considered to span a narrower range of values for key soil descriptors than would be found under natural pedogenesis. However, underlying non-linearities between the same key soil descriptors, such as bulk density and soil organic carbon, suggest potential future attractor instability and more potential divergence among local pedons, especially under human management. Relatedly, another recent review *(Phillips, 2017)* highlighted how natural pedogenesis can be described with concepts from non-linear dynamics and complexity theory, notably revealing how pedogenesis can show unstable trajectories, or many possible alternative end states. These studies suggest that while globally, recent anthropedogenesis has converged mostly toward degradation, locally, future anthropedogenesis could still diverge depending on regional management strategies. This inference that helps maintain agro-pedogenesis as a potentially regenerative force for soil fertility, rather than inherently degrading, especially when distinguishing by industrial vs. small-scale agricultural land management. Accordingly, a recent global synthesis of soil microbial biomass carbon showed evidence of higher variance in percent change where existing stocks were lower, also showing relative increases in some tropical regions such as the Caribbean (near southeast Ayiti) *(Patoine et al., 2022)*. In this region and others including southern Africa and central Asia, even where soil microbial biomass carbon was lost in sum due to climate changes, land-use change effects on soil microbial biomass carbon were often much closer to positive. This higher variance in soil microbial biomass carbon, in part driven by positive land-use effects, together with global cropland analyses *(Padarian et al., 2022)*, points to a potential for land management to increase soil carbon, rather than necessarily degrade it *(Dynarski et al., 2020)*. These insights highlight that increasing soil carbon globally may still be still feasible especially by sustainable local or regional management coordination.

Accordingly, even social processes that affect regional land management, such as in agriculture, represent a source of uncertainty affecting soil organic matter dynamics. However, for soil ecology, the understanding offered by systems and complexity theory comes less from understanding farmers' individual decision-making processes, which is still relevant *(Mestre et al., 2020)*, but instead comes from how information spread and collective decision-making processes may affect regional agricultural management regimes and related soil processes. Given the modern corporate food regime *(Campbell, 2009; McMichael, 2009)* and reliance on plantation land systems *(Wolford, 2020)*, widespread deficit narratives about the ecology of agroecosystems have been somewhat normalized. However, a liberal interpretation of a systems approach to soil ecology, by virtue of normalizing and aiming to integrate hard-to-anticipate critical transitions *(Scheffer et al., 2012; Scheffer et al., 2015)*, motivates the vision for a counter-narrative – one that focuses on supporting the world's small-scale farmers. This results from future global changes to, for example, soil carbon, emerging from the sum of local and regional cooperative efforts toward ecosystem restoration and regenerative agriculture .

Rather than continuing to degrade, regional soil organic matter levels could potentially increase rapidly, assuming most soils are far from carbon (or other nutrient) saturation. This could be directly supported by local social movements that have formed to protect small-scale

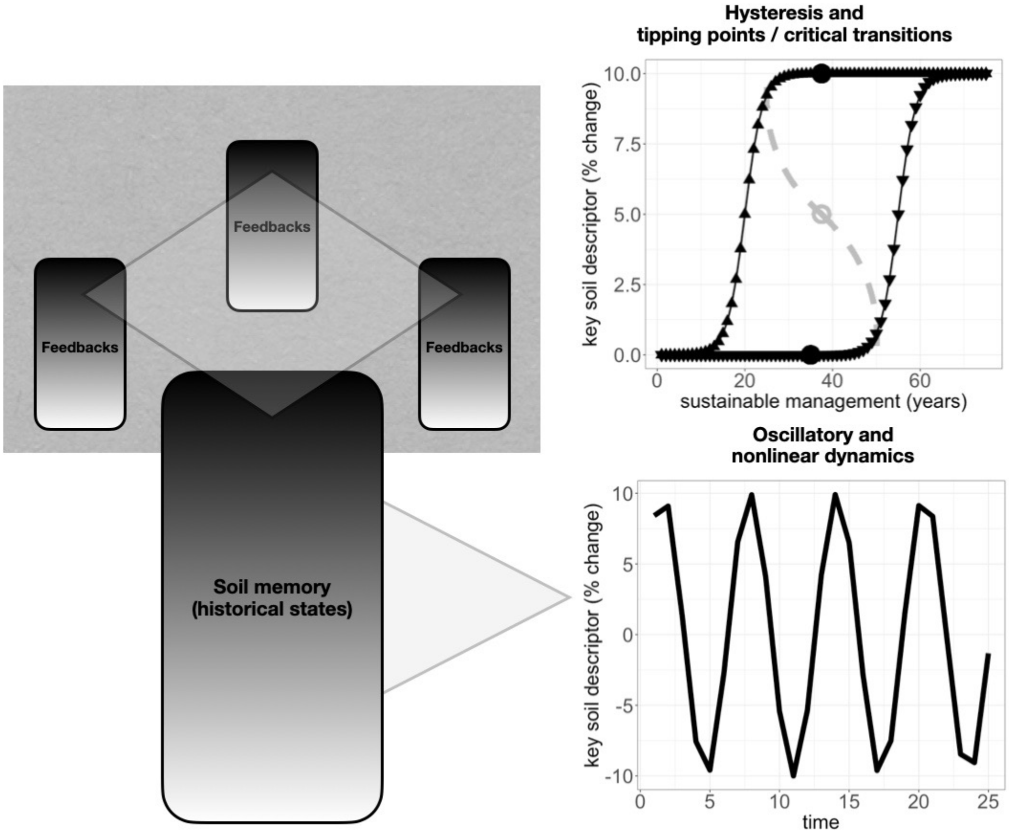

Figure 1: Conceptual diagram highlighting (bottom) that past states incorporated down a soil profile, like buried or subsoil horizons that are plowed, primed and nutrient-poor, or instead deeply fertile (black gradient, bottom-left), may induce oscillatory dynamics (bottom-right) in key soil variables, like moisture and microbial biomass, and that (top) similarly continuous feedbacks across many soil profiles and pedons in a landscape (top-left) may produce nonlinear regional patterns including tipping points (top-right) for key soil variables, like soil organic matter, not only during land degradation, but also during coordinated collective management toward regeneration.

agriculture and land tenure via local neighboring cooperation and collaborative governance. Studies in Brazil near activity of the landless workers movement, or MST, show that soil fertility is positively associated with the recent adoption of and transition to sustainable land management practices *(Stratton et al., 2022)* like cover crop diversity, which could also be promoted by stronger social recognition of benefits *(Williams et al., 2021).* This perspective, together with other studies directly tying soil organic matter to crop yield *(Oldfield et al., 2022)*, ultimately tie soil regeneration to environmental justice issues of land tenure. Integrating socio-ecological processes thus offers an additional means by which key soil variables and anthropedogenesis can show critical non-linear transitions, especially in positive directions, challenging common narratives that depict humans as forces of soil degradation. Some ideas of how social processes affect nutrient cycling have emerged as biogeo-socio-chemistry especially for urban settings *(Pataki et al., 2011; Kaushal et al., 2014)*, and others may help address additional soil ecological dimensions of multi-functionality *(Creamer et al., 2022)* beyond nutrients like spatial patterns of faunal diversity and soil food web network structures. Recent studies of urban ecology already point to interesting patterns that challenge deficit narratives of societal relationships with local soils and agriculture *(Bonilla-Bedoya et al., 2022; Nugent and Allison, 2022; Pindral et al., 2022; Zhang et al., 2022).* Novel insights on soil socio-ecological dynamics may help guide how to tailor sustainable development initiatives by individual countries to achieve international soil governance initiatives *(Farnese, 2022; García et al., 2022)* like through the UN FAO Global Soil Partnership, Global Soil Biodiversity Initiative *(Wall et al., 2015)*, and other working groups generally addressing UN sustainable development goals of combating soil and habitat degradation to enhance ecosystem services via dynamic key soil ecological indicators *(Pradhan et al., 2017; Bennich et al., 2020).*

Conclusion

This synthesis applies a complex systems framework to analyzing key uncertainties about soil processes and habitats, drawing from various analytical tools used across interdisciplinary fields, and presenting how they have and will better address key research questions in the field of soil agroecology. Concepts highlighted include soil memory, or legacy effects of management history and past ecological states; oscillations over time, which are observed in many key soil descriptive variables; and, tipping points and hysteresis, when several correlated variables change at different times and/or rates. Together, these three principles should help decrease uncertainty around soil model structures *(Bradford et al., 2016)* by pointing toward how to improve model generality for key soil processes of interest, such as soil respiration and particulate organic matter storage via occlusion by microbial community byproducts produced during soil aggregation. The complexity perspective on soil agroecology also inspires a positive outlook on the potential feasibility of collective societal solutions to soil degradation crises *(Montgomery, 2007; Richter, 2021)*, by including and better anticipating drastic unexpected changes that often emerge from the combined effects of many interacting processes. Because farms are social-ecological systems, forward steps include collaborating with social sciences, humanities such as history or literature *(Schloss and Handelsman, 2007)*, or non-equilibrium or statistical physics *(Bak et al., 2002)* including geophysics, to expand and improve the set of potentially useful analytical tools and perspectives needed to inclusively and robustly describe the extreme heterogeneity and complexity of soil habitats.

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Declaration of interests

Authors declare no conflicts of interest.

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Data statement

Not applicable; All references to literature data are made in-text.

References

Alfaro, G., and Sanjuan, M. A. F. (2022). Time-dependent effects hinder cooperation on the public goods game. *Chaos, Solitons & Fractals* 160, 112206. doi: 10.1016/j.chaos.2022.112206.

Armstrong, A. C. (1986). On the fractal dimensions of some transient soil properties. *Journal of Soil Science* 37, 641–652. doi: 10.1111/j.1365-2389.1986.tb00393.x.

Armstrong, R. A., and McGehee, R. (1976). Coexistence of species competing for shared resources. *Theoretical Population Biology* 9, 317–328. doi: 10.1016/0040-5809(76)90051-4.

Assouline, S., Tessier, D., and Bruand, A. (1998). A conceptual model of the soil water retention curve. *Water Resour. Res.* 34, 223–231. doi: 10.1029/97WR03039.

Azizi-Rad, M., Chanca, I., Herrera-Ramírez, D., Metzler, H., and Sierra, C. A. (2021). Stochastic and deterministic interpretation of pool models. *Global Change Biology*, 2.

Bailey, V. L., Bilskis, C. L., Fansler, S. J., McCue, L. A., Smith, J. L., and Konopka, A. (2012). Measurements of microbial community activities in individual soil macroaggregates. *Soil Biology and Biochemistry* 48, 192–195. doi: 10.1016/j.soilbio.2012.01.004.

Bak, P., Christensen, K., Danon, L., and Scanlon, T. (2002). Unified Scaling Law for Earthquakes. *Physical Review Letters* 88, 4. doi: 10.1103/PhysRevLett.88.178501.

Bashkirov, A. G., and Vityazev, A. V. (2000). Information entropy and power-law distributions for chaotic systems. *Physica A: Statistical Mechanics and its Applications* 277, 136–145. doi: 10.1016/S0378-4371(99)00449-5.

Bastida, F., García, C., Fierer, N., Eldridge, D. J., Bowker, M. A., Abades, S., et al. (2019). Global ecological predictors of the soil priming effect. *Nat Commun* 10, 3481. doi: 10.1038/s41467-019-11472-7.

Baveye, P. C., Otten, W., Kravchenko, A., Balseiro-Romero, M., Beckers, É., Chalhoub, M., et al. (2018). Emergent Properties of Microbial Activity in Heterogeneous Soil Microenvironments: Different Research Approaches Are Slowly Converging, Yet Major Challenges Remain. *Front. Microbiol.* 9, 1929. doi: 10.3389/fmicb.2018.01929.

Baveye, P., Parlange, J., and Stewart, B. A. (2000). *FRACTALS IN SOIL SCIENCE.*

Bennett, A. E., Preedy, K., Golubski, A., Umbanhowar, J., Borrett, S. R., Byrne, L., et al. (2019). Beyond the black box: Promoting mathematical collaborations for elucidating interactions in soil ecology. *Ecosphere* 10. doi: 10.1002/ecs2.2799.

Bennich, T., Weitz, N., and Carlsen, H. (2020). Deciphering the scientific literature on SDG interactions: A review and reading guide. *Science of The Total Environment* 728, 138405. doi: 10.1016/j.scitotenv.2020.138405.

Berardi, D., Brzostek, E., Blanc-Betes, E., Davison, B., DeLucia, E. H., Hartman, M. D., et al. (2020). 21st-century biogeochemical modeling: Challenges for Century-based models and where do we go from here? *GCB Bioenergy* 12, 774–788. doi: 10.1111/gcbb.12730.

Berryman, A. A., and Millstein, J. A. (1989). Are ecological systems chaotic – and if not, why not? *Trends in Ecology & Evolution.* doi: 10.1016/0169-5347(89)90014-1.

Bonilla-Bedoya, S., Ángel Herrera, M., Vaca, A., Salazar, L., Zalakeviciute, R., Mejía, D., et al. (2022). Urban soil management in the strategies for adaptation to climate change of cities in the Tropical Andes. *Geoderma* 417, 115840. doi: 10.1016/j.geoderma.2022.115840.

Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., and Crowther, T. W. (2016). Managing uncertainty in soil carbon feedbacks to climate change. *Nature Clim Change* 6, 751–758. doi: 10.1038/nclimate3071.

Brostow, W., Pal, S., and Singh, R. P. (2007). A model of flocculation. *Materials Letters* 61, 4381–4384. doi: 10.1016/j.matlet.2007.02.007.

Buchkowski, R. W., Bradford, M. A., Grandy, A. S., Schmitz, O. J., and Wieder, W. R. (2017). Applying population and community ecology theory to advance understanding of belowground biogeochemistry. *Ecol Lett* 20, 231–245. doi: 10.1111/ele.12712.

Burrough, P. A. (1981). Fractal dimensions of landscapes and other environmental data. *Nature* 294, 240–242. doi: 10.1038/294240a0.

Button, E. S., Pett-Ridge, J., Murphy, D. V., Kuzyakov, Y., Chadwick, D. R., and Jones, D. L. (2022). Deep-C storage: Biological, chemical and physical strategies to enhance carbon stocks in agricultural subsoils. *Soil Biology and Biochemistry*, 108697. doi: 10.1016/j.soilbio.2022.108697.

Campbell, H. (2009). Breaking new ground in food regime theory: Corporate environmentalism, ecological feedbacks and the “food from somewhere” regime? *Agric Hum Values* 26, 309–319. doi: 10.1007/s10460-009-9215-8.

Charlotte, V., Laure, V. G., Naoise, N., and Claire, C. (2022). Opportunities and limits in imaging microorganisms and their activities in soil microhabitats. *Soil Biology and Biochemistry*, 108807. doi: 10.1016/j.soilbio.2022.108807.

Chaudhary, V. B., Nolimal, S., Sosa-Hernández, M. A., Egan, C., and Kastens, J. (2020). Trait-based aerial dispersal of arbuscular mycorrhizal fungi. *New Phytol* 228, 238–252. doi: 10.1111/nph.16667.

Christensen, K., Danon, L., Scanlon, T., and Bak, P. (2002). Unified scaling law for earthquakes. *Proceedings of the National Academy of Sciences*, 5.

Clauset, A., Shalizi, C. R., and Newman, M. E. J. (2009). Power-law distributions in empirical data. *SIAM Review* 51, 661–703. doi: 10.1137/070710111.

Coleman, K., and Jenkinson, D. S. (1996). “RothC-26.3 - A Model for the turnover of carbon in soil,” in *Evaluation of Soil Organic Matter Models*, eds. D. S. Powlson, P. Smith, and J. U. Smith (Berlin, Heidelberg: Springer Berlin Heidelberg), 237–246. doi: 10.1007/978-3-642-61094-3_17.

Cong, R., Wang, X., Xu, M., Ogle, S. M., and Parton, W. J. (2014). Evaluation of the CENTURY Model Using Long-Term Fertilization Trials under Corn-Wheat Cropping Systems in the Typical Croplands of China. *PLoS ONE* 9, e95142. doi: 10.1371/journal.pone.0095142.

Coolidge, J. L. (1952). The Origin of Polar Coordinates. 9. doi: 10.1080/00029890.1952.11988074.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology* 19, 988–995. doi: 10.1111/gcb.12113.

Craig, M. E., Mayes, M. A., Sulman, B. N., and Walker, A. P. (2021). Biological mechanisms may contribute to soil carbon saturation patterns. *Glob Change Biol* 27, 2633–2644. doi: 10.1111/gcb.15584.

Creamer, R. E., Barel, J. M., Bongiorno, G., and Zwetsloot, M. J. (2022). The life of soils: Integrating the who and how of multifunctionality. *Soil Biology and Biochemistry* 166, 108561. doi: 10.1016/j.soilbio.2022.108561.

Curado, E., Nobre, F., and Plastino, A. (2018). Associating an Entropy with Power-Law Frequency of Events. *Entropy* 20, 940. doi: 10.3390/e20120940.

Cuthbertson, A. J. S., Samsami, F., and Dong, P. (2018). Model studies for flocculation of sand-clay mixtures. *Coastal Engineering* 132, 13–32. doi: 10.1016/j.coastaleng.2017.11.006.

Czaplicka, A., Holyst, J. A., and Sloot, P. M. A. (2013). Noise enhances information transfer in hierarchical networks. *Sci Rep* 3, 1223. doi: 10.1038/srep01223.

DeAngelis, K. M., Lindow, S. E., and Firestone, M. K. (2008). Bacterial quorum sensing and nitrogen cycling in rhizosphere soil: Bacterial QS and rhizosphere nitrogen cycling. *FEMS Microbiology Ecology* 66, 197–207. doi: 10.1111/j.1574-6941.2008.00550.x.

Denef, K., Six, J., Bossuyt, H., Frey, S. D., Elliott, E. T., Merckx, R., et al. (2001). Influence of dry-wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. *Soil Biology*, 13. doi: 10.1016/S0038-0717(01)00076-1.

Dynarski, K. A., Bossio, D. A., and Scow, K. M. (2020). Dynamic Stability of Soil Carbon: Reassessing the “Permanence” of Soil Carbon Sequestration. *Frontiers in Environmental Science* 8, 514701. doi: 10.3389/fenvs.2020.514701.

Emerson, J. B., Roux, S., Brum, J. R., Bolduc, B., Woodcroft, B. J., Jang, H. B., et al.

(2018). Host-linked soil viral ecology along a permafrost thaw gradient. *Nat Microbiol* 3, 870–880. doi: 10.1038/s41564-018-0190-y.

Epstein, I. R., Kustin, K., De Kepper, P., and Orbán, M. (1983). Oscillating Chemical Reactions. *Sci Am* 248, 112–123. doi: 10.1038/scientificamerican0383-112.

Epstein, I. R., and Showalter, K. (1996). Nonlinear Chemical Dynamics: Oscillations, Patterns, and Chaos. *J. Phys. Chem.* 100, 13132–13147. doi: 10.1021/jp953547m.

Erktan, A., Balmot, J., Merino-Martín, L., Monnier, Y., Pailler, F., Coq, S., et al. (2017). Immediate and long-term effect of tannins on the stabilization of soil aggregates. *Soil Biology and Biochemistry* 105, 197–205. doi: 10.1016/j.soilbio.2016.11.017.

Erktan, A., Rillig, M. C., Carminati, A., Jousset, A., and Scheu, S. (2020). Protists and collembolans alter microbial community composition , C dynamics and soil aggregation in simplified consumer - prey systems. 4961–4980.

Evans, S. E., Allison, S. D., and Hawkes, C. V. (2022). Microbes, memory and moisture: Predicting microbial moisture responses and their impact on carbon cycling. 12.

Farnese, P. L. (2022). Soil governance in a pandemic. *Soil Security* 6, 100033. doi: 10.1016/j.soisec.2021.100033.

Filotas, E., Parrott, L., Burton, P. J., Chazdon, R. L., Coates, K. D., Coll, L., et al. (2014). Viewing forests through the lens of complex systems science. *Ecosphere* 5, art1. doi: 10.1890/ES13-00182.1.

García, S. O., Santillán, V. S., Vivier, V. B., Anglés-Hernánez, M., Pérez, M. E., and Prado, B. (2022). Soil governance and sustainable agriculture in Mexico. *Soil Security*, 100059. doi: 10.1016/j.soisec.2022.100059.

Gillespie, C. S. (2015). Fitting heavy tailed distributions: The powerlaw package. *Journal of Statistical Software* 64, 1–16. doi: 10.18637/jss.v064.i02.

Grandy, A. S., Wieder, W. R., Wickings, K., and Kyker-Snowman, E. (2016). Beyond microbes: Are fauna the next frontier in soil biogeochemical models? *Soil Biology and Biochemistry* 102, 40–44. doi: 10.1016/j.soilbio.2016.08.008.

Hajian-Forooshani, Z., and Vandermeer, J. (2020). Spatial structure and pathogen epidemics: The influence of management and stochasticity in agroecosystems. *bioRxiv*, 100872. doi: 10.1101/2020.06.19.161810.

Harte, J. (1999). Self-Similarity in the Distribution and Abundance of Species. *Science* 284, 334–336. doi: 10.1126/science.284.5412.334.

Hastings, A. (2004). Transients: The key to long-term ecological understanding? *Trends in Ecology and Evolution* 19, 39–45. doi: 10.1016/j.tree.2003.09.007.

Hastings, A., Abbott, K. C., Cuddington, K., Francis, T., Gellner, G., Lai, Y. C., et al. (2018). Transient phenomena in ecology. *Science* 361. doi: 10.1126/science.aat6412.

Hastings, A., Hom, C. L., Ellner, S., Turchin, P., and Godfray, H. C. J. (1993). Chaos in Ecology: Is Mother Nature a Strange Attractor? *Annual Review in Ecology and Sytematics*, 35. doi: 10.1146/annurev.es.24.110193.000245.

Heilmann, S., Krishna, S., and Kerr, B. (2015). Why do bacteria regulate public goods by quorum sensing?–How the shapes of cost and benefit functions determine the form of optimal regulation. *Front. Microbiol.* 6. doi: 10.3389/fmicb.2015.00767.

Henson, S. M., Costantino, R. F., Cushing, J. M., Desharnais, R. A., Dennis, B., and King, A. A. (2001). Lattice Effects Observed in Chaotic Dynamics of Experimental Populations. *Science* 294, 602–605. doi: 10.1126/science.1063358.

Hicks Pries, C. E., Castanha, C., Porras, R. C., and Torn, M. S. (2017). The whole-soil carbon flux in response to warming. *Science* 355, 1420–1423. doi: 10.1126/science.aal1319.

Jenny, H. (1961). Derivation of State Factor Equations of Soils and Ecosystems. *Soil Science Society of America Journal* 25, 385–388. doi: 10.2136/sssaj1961.03615995002500050023x.

Kaushal, S. S., McDowell, W. H., and Wollheim, W. M. (2014). Tracking evolution of urban biogeochemical cycles: Past, present, and future. *Biogeochemistry* 121, 1–21. doi: 10.1007/s10533-014-0014-y.

Kerr, B., and Godfrey-Smith, P. (2002). Individualist and Multi-level Perspectives on Selection in Structured Populations. *Biol Philos* 17, 477–517. doi: 10.1023/A:1020504900646.

Kerr, B., Riley, M. A., Feldman, M. W., and Bohannan, B. J. M. (2002). Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. *Nature* 418, 171–174. doi: 10.1038/nature00823.

King, A. A., and Schaffer, W. M. (1999). The rainbow bridge: Hamiltonian limits and resonance in predator-prey dynamics. *Journal of Mathematical Biology* 39, 439–469. doi: 10.1007/s002850050174.

King, A. E. (2020). Soil Organic Matter as Catalyst of Crop Resource Capture. *Frontiers in Environmental Science* 8, 8.

Klaminder, J., Giesler, R., and Makoto, K. (2013). Physical mixing between humus and mineral matter found in cryoturbated soils increases short-term heterotrophic respiration rates. *Soil Biology and Biochemistry* 57, 922–924. doi: 10.1016/j.soilbio.2012.10.038.

Kravchenko, A. N., Boast, C. W., and Bullock, D. G. (1999). Multifractal Analysis of Soil Spatial Variability. *Agron.j.* 91, 1033–1041. doi: 10.2134/agronj1999.9161033x.

Kravchenko, A. N., Guber, A. K., Razavi, B. S., Koestel, J., Quigley, M. Y., Robertson, G. P., et al. (2019a). Microbial spatial footprint as a driver of soil carbon stabilization. *Nat Commun* 10, 3121. doi: 10.1038/s41467-019-11057-4.

Kravchenko, A., Otten, W., Garnier, P., Pot, V., and Baveye, P. C. (2019b). Soil aggregates as biogeochemical reactors: Not a way forward in the research on soil–atmosphere exchange of greenhouse gases. *Glob Change Biol* 25, 2205–2208. doi: 10.1111/gcb.14640.

Kuramoto, Y. (1984). *Chemical Oscillations, Waves, and Turbulence.*

Kuzyakov, Y. (2006). Sources of CO2 efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry* 38, 425–448. doi: 10.1016/j.soilbio.2005.08.020.

Kuzyakov, Y., and Zamanian, K. (2019). Reviews and syntheses: Agropedogenesis – humankind as the sixth soil-forming factor and attractors of agricultural soil degradation. *Biogeosciences* 16, 4783–4803. doi: 10.5194/bg-16-4783-2019.

Lane, P. A. (2018). The road before us: Have we come to a "fork in the road" in defining complexity? *Ecological Complexity* 35, 1–5. doi: 10.1016/j.ecocom.2017.07.005.

Lavelle, P., Spain, A., Blouin, M., Brown, G., Decaëns, T., Grimaldi, M., et al. (2016). Ecosystem engineers in a self-organized soil: A review of concepts and future research questions. *Soil Science* 181, 91–109. doi: 10.1097/SS.0000000000000155.

Lehmann, J., Hansel, C. M., Kaiser, C., Kleber, M., Maher, K., Manzoni, S., et al. (2020). Persistence of soil organic carbon caused by functional complexity. *Nat. Geosci.* 13, 529–534. doi: 10.1038/s41561-020-0612-3.

Levins, R. (1966). THE STRATEGY OF MODEL BUILDING IN POPULATION BIOLOGY. *AMERICAN SCIENTIST*, 12.

Levins, R. (1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Entomological Society of America* 15, 237–240. doi: 10.1093/besa/15.3.237.

Li, K., Xu, G., Wang, B., Wu, G., Hou, R., and Liu, F. (2021). The predatory soil bacterium Lysobacter reprograms quorum sensing system to regulate antifungal antibiotic production in a cyclic-di-GMP-independent manner. *Commun Biol* 4, 1131. doi: 10.1038/s42003-021-02660-7.

Li, M., Meador, T., Sauheitl, L., Guggenberger, G., and Angst, G. (2022). Substrate quality effects on stabilized soil carbon reverse with depth. *Geoderma* 406, 115511. doi: 10.1016/j.geoderma.2021.115511.

Li, T.-Y., and Yorke, J. A. (1975). Period Three Implies Chaos. *The American Mathematical Monthly*, 9.

Liu, T., Yang, L., Hu, Z., Xue, J., Lu, Y., Chen, X., et al. (2020). Biochar exerts negative effects on soil fauna across multiple trophic levels in a cultivated acidic soil. *Biology and Fertility of Soils* 56, 597–606. doi: 10.1007/s00374-020-01436-1.

Livingtson, K. (1985). The Dialectical Biologist.. Richard Levins and Richard Lewontin. Harvard University Press, Cambridge, Mass., 1985. Xiv, 303 pp. $20. *Science*, 2.

Locey, K. J., and Lennon, J. T. (2016). Scaling laws predict global microbial diversity. *Proc Natl Acad Sci USA* 113, 5970–5975. doi: 10.1073/pnas.1521291113.

Lorenz, E. (1963). Nonlinear Periodic Flow. *Journal of the Atmospheric Sciences* 20.

Lozano, G. L., Bravo, J. I., Diago, M. F. G., Park, H. B., Hurley, A., Peterson, S. B., et al. (2019). Introducing THOR, a model microbiome for genetic dissection of community behavior. *mBio* 10, 1–14. doi: 10.1128/mBio.02846-18.

Ludington, W. B. (2022). Higher-order microbiome interactions and how to find them. *Trends in Microbiology*, S0966842X22000890. doi: 10.1016/j.tim.2022.03.011.

Macarthur, R. H., and Wilson, E. O. (1963). An Equilibrium Theory of Insular Zoogeography. *Evolution*, 16.

Mandelbrot, B. B. (1983). The fractal geometry of nature. 1.

Manzoni, S., and Porporato, A. (2009). Soil carbon and nitrogen mineralization: Theory and models across scales. *Soil Biology and Biochemistry* 41, 1355–1379. doi: 10.1016/j.soilbio.2009.02.031.

Marder, E., and Calabrese, R. L. (1996). Principles of rhythmic motor pattern generation. *Physiological Reviews* 76, 687–717. doi: 10.1152/physrev.1996.76.3.687.

Marris, E. (2022). A call for governments to save soil. *Nature* 601, 503–504. doi: 10.1038/d41586-022-00158-8.

May, R. M. (1974). Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. *Science* 186, 645–647. doi: 10.1126/science.186.4164.645.

McCary, M. A., Phillips, J. S., Ramiadantsoa, T., Nell, L. A., McCormick, A. R., and Botsch, J. C. (2021). Transient top-down and bottom-up effects of resources pulsed to multiple trophic levels. *Ecology* 102. doi: 10.1002/ecy.3197.

McGehee, R., and Armstrong, R. A. (1977). Some mathematical problems concerning the ecological principle of competitive exclusion. *Journal of Differential Equations* 23, 30–52. doi: 10.1016/0022-0396(77)90135-8.

McMichael, P. (2009). A food regime analysis of the “world food crisis.” *Agric Hum Values* 26, 281–295. doi: 10.1007/s10460-009-9218-5.

Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., et al. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* 358, 101–105. doi: 10.1126/science.aan2874.

Mestre, M. C. V., Hoey, L., and Vandermeer, J. (2020). Tree Management and Balancing Process Among Panamanian Farmers. *Small-scale Forestry* 19, 541–563. doi: 10.1007/s11842-020-09453-6.

Montgomery, D. R. (2007). Soil erosion and agricultural sustainability. 104, 13268–13272.

Ning, T., Liu, Z., Hu, H., Li, G., and Kuzyakov, Y. (2022). Physical, chemical and biological subsoiling for sustainable agriculture. *Soil and Tillage Research* 223, 105490. doi: 10.1016/j.still.2022.105490.

Nortcliff, S. (1984). Spatial analysis of soil. *Progress in Physical Geography: Earth and Environment* 8, 261–269. doi: 10.1177/030913338400800205.

Nugent, A., and Allison, S. D. (2022). A framework for soil microbial ecology in urban ecosystems. *Ecosphere* 13. doi: 10.1002/ecs2.3968.

O'Leary, J., Eastwood, D., Müller, C., and Boddy, L. (2018). Emergent properties arising from spatial heterogeneity influence fungal community dynamics. *Fungal Ecology* 33, 32–39. doi: 10.1016/j.funeco.2018.02.001.

Oldfield, E. E., Eagle, A. J., Rubin, R. L., Rudek, J., Sanderman, J., and Gordon, D. R. (2022). Crediting agricultural soil carbon sequestration. *Science* 375, 1222–1225. doi: 10.1126/science.abl7991.

Ong, T. W. Y., and Vandermeer, J. (2018). Multiple hysteretic patterns from elementary population models. *Theor Ecol* 11, 433–439. doi: 10.1007/s12080-018-0376-1.

Ong, T. W., Li, K., Lucatero, A., Pak, D., Hawkes, L., Hunter, M., et al. (2020). Taylor Made Landscapes: Using Taylor's Law to Scale Between Metapopulations and Source-Sinks in Urban Garden Space. *Front. Sustain. Food Syst.* 4, 46. doi: 10.3389/fsufs.2020.00046.

Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J., and Keesing, F. (2006). Climate, Deer, Rodents, and Acorns as Determinants of Variation in Lyme-Disease Risk. *PLoS Biol* 4, e145. doi: 10.1371/journal.pbio.0040145.

Ostfeld, R., Glass, G., and Keesing, F. (2005). Spatial epidemiology: An emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* 20, 328–336. doi: 10.1016/j.tree.2005.03.009.

Ostling, A. (2000). Self-Similarity and Clustering in the Spatial Distribution of Species. *Science* 290, 671a–671. doi: 10.1126/science.290.5492.671a.

Pacault, A., Ouyang, Q., and De Kepper, P. (1987). Bistable and oscillating chemical reactions. *J Stat Phys* 48, 1005–1016. doi: 10.1007/BF01009529.

Pachepsky, Y., and Hill, R. L. (2017). Scale and scaling in soils. *Geoderma* 287, 4–30. doi: 10.1016/j.geoderma.2016.08.017.

Padarian, J., Minasny, B., McBratney, A., and Smith, P. (2022). Soil carbon sequestration potential in global croplands. *PeerJ* 10, e13740. doi: 10.7717/peerj.13740.

Pataki, D. E., Carreiro, M. M., Cherrier, J., Grulke, N. E., Jennings, V., Pincetl, S., et al. (2011). Coupling biogeochemical cycles in urban environments: Ecosystem services, green solutions, and misconceptions. *Frontiers in Ecology and the Environment* 9, 27–36. doi: 10.1890/090220.

Patoine, G., Eisenhauer, N., Cesarz, S., Phillips, H. R. P., Xu, X., Zhang, L., et al. (2022). Drivers and trends of global soil microbial carbon over two decades. *Nat Commun* 13,

4195. doi: 10.1038/s41467-022-31833-z.

Perrier, E., Rieu, M., Sposito, G., and de Marsily, G. (1996). Models of the water retention curve for soils with a fractal pore size distribution. *Water Resour. Res.* 32, 3025–3031. doi: 10.1029/96WR01779.

Pfützner, M., Karny, M., Grigorenko, L. V., and Riisager, K. (2012). Radioactive decays at limits of nuclear stability. *Rev. Mod. Phys.* 84, 567–619. doi: 10.1103/RevModPhys.84.567.

Phillips, C. L., Nickerson, N., Risk, D., and Bond, B. J. (2011). Interpreting diel hysteresis between soil respiration and temperature. *Global Change Biology* 17, 515–527. doi: 10.1111/j.1365-2486.2010.02250.x.

Phillips, J. D. (2017). Soil Complexity and Pedogenesis. *Soil Science* 182, 117–127. doi: 10.1097/SS.0000000000000204.

Pindral, S., Kot, R., and Hulisz, P. (2022). The influence of city development on urban pedodiversity. *Sci Rep* 12, 6009. doi: 10.1038/s41598-022-09903-5.

Powlson, D. S., Smith, P., and Smith, J. U. eds. (1996). *Evaluation of Soil Organic Matter Models: Using Existing Long-Term Datasets.* Berlin, Heidelberg: Springer Berlin Heidelberg doi: 10.1007/978-3-642-61094-3.

Pradhan, P., Costa, L., Rybski, D., Lucht, W., and Kropp, J. P. (2017). A Systematic Study of Sustainable Development Goal (SDG) Interactions: A SYSTEMATIC STUDY OF SDG INTERACTIONS. *Earth's Future* 5, 1169–1179. doi: 10.1002/2017EF000632.

Quigley, M. Y., and Kravchenko, A. N. (2022). Inputs of root-derived carbon into soil and its losses are associated with pore-size distributions. *Geoderma* 410, 115667. doi: 10.1016/j.geoderma.2021.115667.

Reijneveld, J. A. (2013). Unravelling changes in soil fertility of agricultural land in The Netherlands. 240.

Richter, D. D. (2021). Searching for solutions to our soil woes–A World Without Soil: The Past, Present, and Precarious Future of the Earth Beneath Our Feet, Jo Handelsman, Yale University Press, 2021, 272 pp. *Science* 374, 1452–1452. doi: 10.1126/science.abm4765.

Rillig, M. C., Muller, L. A. H., and Lehmann, A. (2017). Soil aggregates as massively concurrent evolutionary incubators. 11, 1943–1948. doi: 10.1038/ismej.2017.56.

Rillig, M. C., and Mummey, D. L. (2006). Mycorrhizas and soil structure. *New Phytologist* 171, 41–53. doi: 10.1111/j.1469-8137.2006.01750.x.

Riveros-Iregui, D. A., Emanuel, R. E., Muth, D. J., McGlynn, B. L., Epstein, H. E., Welsch, D. L., et al. (2007). Diurnal hysteresis between soil CO2 and soil temperature is controlled by soil water content. *Geophysical Research Letters* 34, 1–5. doi:

10.1029/2007GL030938.

Rogers, T. L., Johnson, B. J., and Munch, S. B. (2022). Chaos is not rare in natural ecosystems | Nature Ecology & Evolution. *Nature Ecology & Evolution* 6, 1105–1111. doi: 10.1038/s41559-022-01787-y.

Rutherford, S. W., and Do, D. D. (1997). Review of time lag permeation technique as a method for characterisation of porous media and membranes. *Adsorption* 3, 283–312. doi: 10.1007/BF01653631.

Schaffer, W. M., and Kot, M. (1985). Do Strange Attractors Govern Ecological Systems? *BioScience* 35, 342–350. doi: 10.2307/1309902.

Scheffer, M., Barrett, S., Carpenter, S. R., Folke, C., Green, a. J., Holmgren, M., et al. (2015). Ecosystem collapsed. *Science*, 8–10. doi: 10.1126/science.aaa9484.

Scheffer, M., Carpenter, S. R., Lenton, T. M., Bascompte, J., Brock, W., Dakos, V., et al. (2012). Anticipating Critical Transitions. *Science* 338.

Schimel, J. (2003). The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: A theoretical model. *Soil Biology and Biochemistry* 35, 549–563. doi: 10.1016/S0038-0717(03)00015-4.

Schimel, J. P., and Bennett, J. (2004). NITROGEN MINERALIZATION: CHALLENGES OF A CHANGING PARADIGM. *Ecology* 85, 591–602. doi: 10.1890/03-8002.

Schloss, P. D., and Handelsman, J. (2007). The last word: Books as a statistical metaphor for microbial communities. *Annual review of microbiology* 61, 23–34. doi: 10.1146/annurev.micro.61.011507.151712.

Schweizer, S. A. (2022). Perspectives from the Fritz-Scheffer Awardee 2021: Soil organic matter storage and functions determined by patchy and piled-up arrangements at the microscale. *J. Plant Nutr. Soil Sci.*, jpln.202200217. doi: 10.1002/jpln.202200217.

Segoli, M., De Gryze, S., Dou, F., Lee, J., Post, W. M., Denef, K., et al. (2013). AggModel: A soil organic matter model with measurable pools for use in incubation studies. *Ecological Modelling* 263, 1–9. doi: 10.1016/j.ecolmodel.2013.04.010.

Sierra, C. A., Hoyt, A. M., He, Y., and Trumbore, S. E. (2018). Soil Organic Matter Persistence as a Stochastic Process: Age and Transit Time Distributions of Carbon in Soils. *Global Biogeochem. Cycles* 32, 1574–1588. doi: 10.1029/2018GB005950.

Sierra, C. A., and Müller, M. (2015). A general mathematical framework for representing soil organic matter dynamics. *Ecological Monographs* 85, 505–524. doi: 10.1890/15-0361.1.

Sihi, D., Gerber, S., Inglett, P. W., and Inglett, K. S. (2016). Comparing models of microbial–substrate interactions and their response to warming. *Biogeosciences* 13, 1733–1752. doi: 10.5194/bg-13-1733-2016.

Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., and Teste, F.

P. (2012). Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews* 26, 39–60. doi: 10.1016/j.fbr.2012.01.001.

Simard, S. W., Perry, D. A., Jones, M. D., Myrold, D. D., Durall, D. M., and Molina, R. (1997). Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388, 579–582. doi: 10.1038/41557.

Soong, J. L., Castanha, C., Hicks Pries, C. E., Ofiti, N., Porras, R. C., Riley, W. J., et al. (2021). Five years of whole-soil warming led to loss of subsoil carbon stocks and increased CO $_2$ efflux. *Sci. Adv.* 7, eabd1343. doi: 10.1126/sciadv.abd1343.

Stamati, F. E., Nikolaidis, N. P., Banwart, S., and Blum, W. E. H. (2013). A coupled carbon, aggregation, and structure turnover (CAST) model for topsoils. *Geoderma* 211–212, 51–64. doi: 10.1016/j.geoderma.2013.06.014.

Stewart, C. E., Paustian, K., Conant, R. T., Plante, A. F., and Six, J. (2007). Soil carbon saturation: Concept, evidence and evaluation. *Biogeochemistry* 86, 19–31. doi: 10.1007/s10533-007-9140-0.

Stratton, A. E., Comin, J. J., Siddique, I., Zak, D. R., Dambroz Filipini, L., Rodrigues Lucas, R., et al. (2022). Assessing cover crop and intercrop performance along a farm management gradient. *Agriculture, Ecosystems & Environment* 332, 107925. doi: 10.1016/j.agee.2022.107925.

Sulman, B. N., Moore, J. A. M., Abramoff, R., Averill, C., Kivlin, S., Georgiou, K., et al. (2018). Multiple models and experiments underscore large uncertainty in soil carbon dynamics. *Biogeochemistry* 141, 109–123. doi: 10.1007/s10533-018-0509-z.

Taylor, L. R. (1961). Aggregation, Variance and the Mean. *Nature* 189, 732–735. doi: 10.1038/189732a0.

Tisdall, J. M., and Oades, J. M. (1982). Organic matter and water-stable aggregates in soils. *Journal of Soil Science* 33, 141–163. doi: 10.1111/j.1365-2389.1982.tb01755.x.

Todd-Brown, K. E. O., Abramoff, R. Z., Beem-Miller, J., Blair, H. K., Earl, S., Frederick, K. J., et al. (2022). Reviews and syntheses: The promise of big diverse soil data, moving current practices towards future potential. *Biogeosciences* 19, 3505–3522. doi: 10.5194/bg-19-3505-2022.

Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. A. G., et al. (2013). Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences* 10, 1717–1736. doi: 10.5194/bg-10-1717-2013.

Traulsen, A., and Nowak, M. A. (2006). Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. U.S.A.* 103, 10952–10955. doi: 10.1073/pnas.0602530103.

Trubl, G., Jang, H. B., Roux, S., Emerson, J. B., Solonenko, N., Vik, D. R., et al. (2018).

Soil Viruses Are Underexplored Players in Ecosystem Carbon Processing. 3, 21.

Turing, A. M. (1952). The Chemical Basis of Morphogenesis. *Proceedings of the Royal Society B*.

Turley, N. E., Bell-Dereske, L., Evans, S. E., and Brudvig, L. A. (2020). Agricultural land-use history and restoration impact soil microbial biodiversity. *J Appl Ecol* 57, 852–863. doi: 10.1111/1365-2664.13591.

Tyler, S. W., and Wheatcraft, S. W. (1989). Application of Fractal Mathematics to Soil Water Retention Estimation. *SOIL SCIENCE SOCIETY OF AMERICA*, 987–996. doi: 10.2136/sssaj1989.03615995005300040001x.

van der Heijden, M. G. A., and Horton, T. R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*, 12.

Vandermeer, J. (2006). Oscillating Populations and Biodiversity Maintenance. 56, 967–975.

Vandermeer, J. (2013). Forcing by rare species and intransitive loops creates distinct bouts of extinction events conditioned by spatial pattern in competition communities. *Theoretical Ecology* 6, 395–404. doi: 10.1007/s12080-012-0175-z.

Vandermeer, J. (2021). The meta-Allee effect: A generalization from intermittent metapopulations. *Ecological Complexity* 46. doi: 10.1016/j.ecocom.2021.100912.

Vandermeer, J., and Jackson, D. (2018). Stabilizing intransitive loops: Self-organized spatial structure and disjoint time frames in the coffee agroecosystem. *Ecosphere* 9, 17. doi: 10.1002/ecs2.2489.

Vandermeer, J., and Perfecto, I. (2017). Ecological complexity and agroecosystems : Seven themes from theory. *Agroecology and Sustainable Food Systems* 41, 697–722. doi: 10.1080/21683565.2017.1322166.

Vandermeer, J., and Yitbarek, S. (2012). Self-organized spatial pattern determines biodiversity in spatial competition. *Journal of Theoretical Biology* 300, 48–56. doi: 10.1016/j.jtbi.2012.01.005.

Vereecken, H., Schnepf, A., Hopmans, J. W., Javaux, M., Or, D., Roose, T., et al. (2016). Modeling Soil Processes: Review, Key Challenges, and New Perspectives. *Vadose Zone Journal*, 57.

Victor, J. M., Goulet, L. M., Schmidt, K., Linds, W., Episkenew, J.-A., and Goulet, K. (2016). Like Braiding Sweetgrass: Nurturing Relationships and Alliances in Indigenous Community-based Research. *International Review of Qualitative Research*, 23.

Vitousek, P. M., Treseder, K. K., Howarth, R. W., and Menge, D. N. L. (2022). A “toy model” analysis of causes of nitrogen limitation in terrestrial ecosystems. *Biogeochemistry*. doi: 10.1007/s10533-022-00959-z.

Vogel, H., Balseiro-Romero, M., Kravchenko, A., Otten, W., Pot, V., Schlüter, S., et al. (2022). A holistic perspective on soil architecture is needed as a key to soil functions. *European J Soil Science* 73. doi: 10.1111/ejss.13152.

Volterra, V. (1928). Variations and Fluctuations of the Number of Individuals in Animal Species living together. *ICES Journal of Marine Science* 3, 3–51. doi: 10.1093/icesjms/3.1.3.

Wall, D. H., Nielsen, U. N., and Six, J. (2015). Soil biodiversity and human health. *Nature* 528, 69–76. doi: 10.1038/nature15744.

Wang, J., Yi, X., Cui, J., Chang, Y., Yao, D., Zhou, D., et al. (2019). Nonlinear effects of increasing nitrogen deposition on rice growth and heavy metal uptake in a red soil ecosystem of southeastern China. *Science of the Total Environment* 670, 1060–1067. doi: 10.1016/j.scitotenv.2019.03.245.

Wang, Y. P., Chen, B. C., Wieder, W. R., Leite, M., Medlyn, B. E., Rasmussen, M., et al. (2014). Oscillatory behavior of two nonlinear microbial models of soil carbon decomposition. *Biogeosciences* 11, 1817–1831. doi: 10.5194/bg-11-1817-2014.

Waring, B. G., Sulman, B. N., Reed, S., Smith, A. P., Averill, C., Creamer, C. A., et al. (2020). From pools to flow: The PROMISE framework for new insights on soil carbon cycling in a changing world. *Global Change Biology*, 6631–6643. doi: 10.1111/gcb.15365.

Weitzman, J. N., Brooks, J. R., Compton, J. E., Faulkner, B. R., Mayer, P. M., Peachey, R. E., et al. (2022). Deep soil nitrogen storage slows nitrate leaching through the vadose zone. *Agriculture, Ecosystems & Environment* 332, 107949. doi: 10.1016/j.agee.2022.107949.

Wieder, W. R., Allison, S. D., Davidson, E. A., Georgiou, K., Hararuk, O., He, Y., et al. (2015). Explicitly representing soil microbial processes in Earth system models: Soil microbes in earth system models. *Global Biogeochem. Cycles* 29, 1782–1800. doi: 10.1002/2015GB005188.

Williams, T. G., Dressler, G., Stratton, A. E., and Müller, B. (2021). Ecological and financial strategies provide complementary benefits for smallholder climate resilience: Insights from a simulation model. *E&S* 26, art14. doi: 10.5751/ES-12207-260214.

Wilpiszeski, R. L., Aufrecht, J. A., Retterer, S. T., Sullivan, M. B., Graham, D. E., Pierce, E. M., et al. (2019). Soil Aggregate Microbial Communities: Towards Understanding Microbiome Interactions at Biologically Relevant Scales. *Applied and environmental microbiology* 85, 1–18. doi: 10.1128/AEM.00324-19.

Wilson, W. G., and Abrams, P. A. (2005). Coexistence of cycling and dispersing consumer species: Armstrong and McGehee in space. *American Naturalist* 165, 193–205. doi: 10.1086/427733.

Winfree, A. T., and Strogatz, S. H. (1984). Organizing centres for three-dimensional chemical waves. *Nature* 311, 611–615. doi: 10.1038/311611a0.

Wolford, W. (2020). The Plantationocene: A Lusotropical Contribution to the Theory. *Annals of the American Association of Geographers*. doi: 10.1080/24694452.2020.1850231.

Xiao, X., and Fussmann, G. F. (2013). Armstrong – McGehee mechanism revisited : Competitive exclusion and coexistence of nonlinear consumers. *Journal of Theoretical Biology* 339, 26–35. doi: 10.1016/j.jtbi.2013.05.025.

Yitbarek, S., and Vandermeer, J. H. (2017). Reduction of species coexistence through mixing in a spatial competition model. *Theoretical Ecology* 10, 443–450. doi: 10.1007/s12080-017-0341-4.

Young, I. M., and Crawford, J. W. (1991). The fractal structure of soil aggregates: Its measurement and interpretation. *Journal of Soil Science* 42, 187–192. doi: 10.1111/j.1365-2389.1991.tb00400.x.

Young, I. M., and Crawford, J. W. (2004). Interactions and Self-Organization in the Soil-Microbe Complex. *Science* 304, 1634–1638. doi: 10.1126/science.1097394.

Zhang, Q., Katul, G. G., Oren, R., Daly, E., Manzoni, S., and Yang, D. (2015). The hysteresis response of soil CO2 concentration and soil respiration to soil temperature. *J. Geophys. Res. Biogeosci.* 120, 1605–1618. doi: 10.1002/2015JG003047.

Zhang, Y., Lavallee, J. M., Robertson, A. D., Even, R., Ogle, S. M., Paustian, K., et al. (2021). Simulating measurable ecosystem carbon and nitrogen dynamics with the mechanistically defined MEMS 2.0 model. *Biogeosciences* 18, 3147–3171. doi: 10.5194/bg-18-3147-2021.

Zhang, Z., Gao, X., Zhang, S., Gao, H., Huang, J., Sun, S., et al. (2022). Urban development enhances soil organic carbon storage through increasing urban vegetation. *Journal of Environmental Management* 312, 114922. doi: 10.1016/j.jenvman.2022.114922.