

*Annual Review of Ecology, Evolution, and Systematics*

The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls

Robert B. Jackson,<sup>1,2,3</sup> Kate Lajtha,<sup>4</sup> Susan E. Crow,<sup>5</sup> Gustaf Hugelius,<sup>1,6</sup> Marc G. Kramer,<sup>7</sup> and Gervasio Piñeiro<sup>8,9</sup>

<sup>1</sup>Department of Earth System Science, Stanford University, Stanford, California 94305; email: rob.jackson@stanford.edu

<sup>2</sup>Woods Institute for the Environment, Stanford University, Stanford, California 94305

<sup>3</sup>Precourt Institute for Energy, Stanford University, Stanford, California 94305

<sup>4</sup>Department of Crop and Soil Sciences, Oregon State University, Corvallis, Oregon 97331; email: lajthak@science.oregonstate.edu

<sup>5</sup>Department of Natural Resources and Environmental Management, University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822; email: crows@hawaii.edu

<sup>6</sup>Department of Physical Geography, Stockholm University, Stockholm SE-10691, Sweden; email: gustaf.hugelius@natgeo.su.se

<sup>7</sup>School of the Environment, Washington State University Vancouver, Vancouver, Washington 98686; email: marc.kramer@wsu.edu

<sup>8</sup>IFEVA/CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires C1417DSE, Argentina; email: pineiro@agro.uba.ar

<sup>9</sup>Facultad de Agronomía, Universidad de la República, Montevideo 12900, Uruguay



**ANNUAL REVIEWS Further**

Click here to view this article's online features:

- Download figures as PPT slides
- Navigate linked references
- Download citations
- Explore related articles
- Search keywords

Annu. Rev. Ecol. Evol. Syst. 2017. 48:419–45

First published online as a Review in Advance on September 6, 2017

The *Annual Review of Ecology, Evolution, and Systematics* is online at [ecolsys.annualreviews.org](http://ecolsys.annualreviews.org)

<https://doi.org/10.1146/annurev-ecolsys-112414-054234>

Copyright © 2017 by Annual Reviews.  
All rights reserved

**Keywords**

global carbon stocks, litter and root inputs, soil carbon mitigation and vulnerabilities, soil fauna and food web ecology, soil organic carbon, soil organic nitrogen, soil organic matter

**Abstract**

Soil organic matter (SOM) anchors global terrestrial productivity and food and fiber supply. SOM retains water and soil nutrients and stores more global carbon than do plants and the atmosphere combined. SOM is also decomposed by microbes, returning CO<sub>2</sub>, a greenhouse gas, to the atmosphere. Unfortunately, soil carbon stocks have been widely lost or degraded through land use changes and unsustainable forest and agricultural practices.

To understand its structure and function and to maintain and restore SOM, we need a better appreciation of soil organic carbon (SOC) saturation capacity and the retention of above- and belowground inputs in SOM. Our analysis suggests root inputs are approximately five times more likely than an equivalent mass of aboveground litter to be stabilized as SOM. Microbes, particularly fungi and bacteria, and soil faunal food webs strongly influence SOM decomposition at shallower depths, whereas mineral associations drive stabilization at depths greater than  $\sim 30$  cm. Global uncertainties in the amounts and locations of SOM include the extent of wetland, peatland, and permafrost systems and factors that constrain soil depths, such as shallow bedrock. In consideration of these uncertainties, we estimate global SOC stocks at depths of 2 and 3 m to be between 2,270 and 2,770 Pg, respectively, but could be as much as 700 Pg smaller. Sedimentary deposits deeper than 3 m likely contain  $> 500$  Pg of additional SOC. Soils hold the largest biogeochemically active terrestrial carbon pool on Earth and are critical for stabilizing atmospheric  $\text{CO}_2$  concentrations. Nonetheless, global pressures on soils continue from changes in land management, including the need for increasing bioenergy and food production.

to the bacteria, tumblebugs, scavengers,  
wordsmiths—the transfigurers, restorers

—A.R. Ammons, *Garbage*

## 1. INTRODUCTION

Soils and soil organic matter (SOM) are the foundation of terrestrial life. The dynamic accumulation and distribution of SOM arise from stabilization and destabilization processes that in turn are influenced by biotic, abiotic, and anthropogenic factors (**Figure 1**). Biotic factors such as the amount, chemical composition, and relative allocation of plant inputs are critical regulators of SOM, as is the soil food web arising from the diverse community of soil organisms. Important abiotic factors include climate, mineralogy, landscape position (e.g., slope and aspect), and the abundance of fires. Increasingly, anthropogenic factors control and change SOM distributions. Such factors include fire, nitrogen deposition, climate change, land use, and tillage and other management practices that alter soil biota and aggregates. Examining the roles of these factors and how they interact to control the balance of terrestrial SOM is a primary focus of this review.

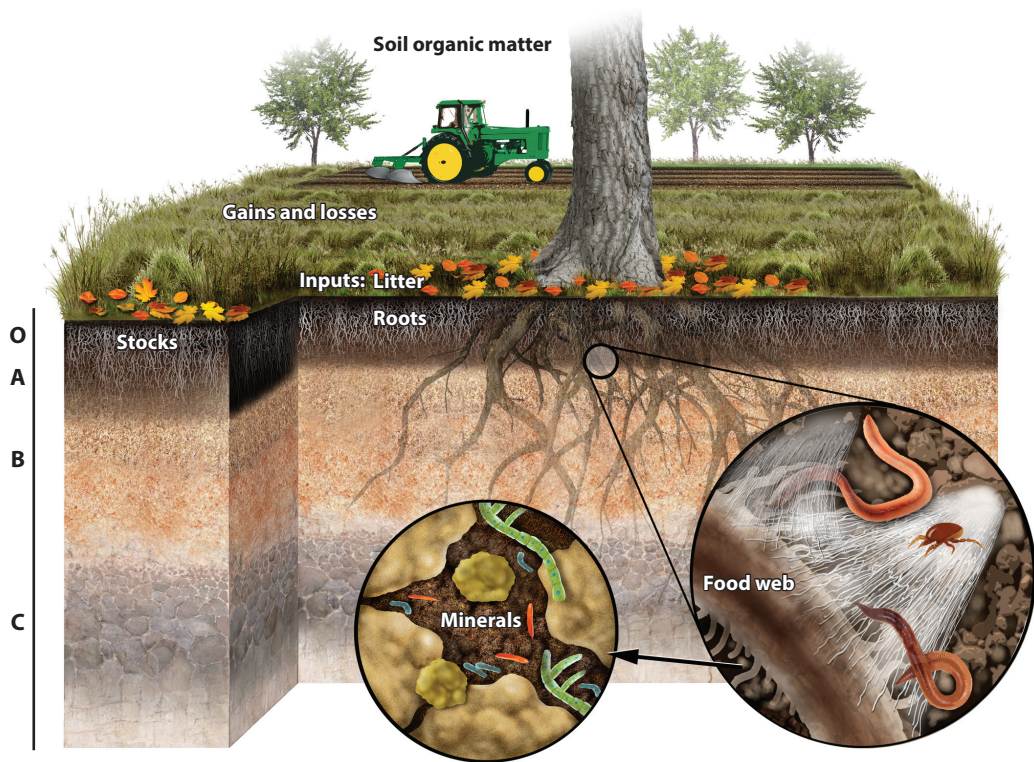
Our understanding of how SOM is formed and stabilized is changing rapidly. New technologies and studies are highlighting key interactions among plant carbon allocation, soil biota, and microaggregates and soil structure. For example, the ecological and evolutionary relationships found in food webs help determine the balance between carbon lost through respiration and the amount of plant carbon inputs stabilized in soils, as influenced by free-living soil microbes, mycorrhizae, and plant roots. New evidence suggests that thermal acclimation and adaptation by microbes, local evolution of microbial community assemblages, mycorrhizal status, and the presence or absence of native and invasive earthworms can play key roles in determining soil carbon content and its response to environmental changes. A deeper understanding of the ecological controls on soil carbon is needed if we are to create models of carbon balance under changing patterns of climate, land use, and other factors.

Empirical studies generally focus on single-parameter controls of carbon turnover, including mineralogical control of SOM chemistry and accumulation (e.g., Torn et al. 1997, Kaiser &

---

**SOM:** soil organic matter

---



**Figure 1**

Some of the many factors important for the formation and retention of soil organic matter (SOM). The factors shown here provide the outline for the topics covered in this review, including plant inputs (Section 2), belowground food webs and other biotic factors (Section 3), minerals and abiotic factors (Section 4), global stocks and distributions of SOM (Section 5), and vulnerabilities and opportunities for restoring SOM (Section 6). Soil horizons marked are O (the surface organic horizon), A (the topmost mineral horizon that contains higher concentrations of partially decomposed organic matter than in lower horizons), B (subsoil, a zone of weathering products and material leached from the A horizon), and C (primarily weathered bedrock).

Guggenberger 2000, Parfitt et al. 2002, Plante et al. 2006, Kramer et al. 2012), climate/temperature control of SOM stability (e.g., Townsend et al. 1997, Leifeld & Fuhrer 2005, Giardina et al. 2014, Lefèvre et al. 2014), and detrital quantity and chemistry effects on SOM formation and stability (Hobbie 2000; Sayer 2006; Fekete et al. 2014; Lajtha et al. 2014a,b; Huang & Spohn 2015). These studies have yielded surprising results and nonlinearities; for example, the relationship between litter inputs and carbon sequestration in soil can be positive, negative, or neutral, possibly because of carbon saturation (Stewart et al. 2009, Chung et al. 2010, Mayzelle et al. 2014), priming (Sulzman et al. 2005, Kuzyakov 2010), or both. Nitrogen addition through atmospheric deposition or fertilization might accelerate initial litter decomposition but nevertheless promotes soil carbon stabilization. Most existing carbon models, on the other hand, assume static linear relationships between carbon inputs and transformation of carbon pools to more stable forms (Jackson et al. 2000, Liski et al. 2002, Gottschalk et al. 2012, Wieder et al. 2013).

SOM is also a major component of the global carbon cycle; it contains more carbon than do plant biomass and the atmosphere combined (Schlesinger 1990, Field & Raupach 2004). Despite the key role of SOM in Earth's operating systems, interactions among the biological, chemical,

**SOC:** soil organic carbon

**NPP:** net primary productivity

and physical processes regulating SOM turnover are not well understood or well represented in ecosystem-scale models or Earth system models (Amundson 2001, Todd-Brown et al. 2013, Wieder et al. 2013, Xu et al. 2014). These interactions are critically important for understanding and predicting carbon cycle responses to environmental change at ecosystem, continental, and global scales. For example, increases in carbon uptake by plants under rising atmospheric CO<sub>2</sub> may be partially offset by the accelerated loss of soil carbon due to plant-induced stimulation of microbial decomposition (Drake et al. 2011, Phillips et al. 2012).

Understanding the ecological and physical controls over SOM is critical for maintaining a balanced carbon cycle, increasing food and fiber production, and safeguarding species and ecosystem services. Despite our recognition of its importance, soil carbon stocks have been widely lost or degraded through land use changes and unsustainable forest and agricultural management practices. Management practices for restoring soil organic carbon (SOC) are therefore important tools to slow the rise in atmospheric CO<sub>2</sub>.

The goal of this review is to examine the state of knowledge for the stocks of, inputs to, and outputs from SOM around the world. Section 2 examines carbon inputs to SOM from plants, including the critical importance of above- and belowground allocation for SOM formation. Section 3 discusses a second biotic factor, belowground food webs and their diversity, for effects on net carbon sequestration. Section 4 reviews critical abiotic interactions with biotic factors, including fire and temperature, and mixing processes such as those by earthworms and plowing. Section 5 evaluates global SOM stocks and depth distributions, acknowledging some uncertainties concerning bedrock depths, double counting of carbon stocks in mineral soils and peat, and other factors.

In each section, we recommend areas for future research and highlight some of the greatest uncertainties in the science of SOM today. In Section 6 we also prioritize some opportunities for enhancing SOM through management and briefly discuss vulnerabilities for SOM, processes that oxidize it and release CO<sub>2</sub> to the atmosphere. As in any brief review, we lack the space to cover many important topics, including advances in molecular ecology relevant to decomposition and mineralization (González-Chang et al. 2016) and detailed discussions of how to more explicitly incorporate SOM distributions and dynamics into global models (Luo et al. 2016).

## 2. PLANT PRODUCTION AND ALLOCATION EFFECTS ON SOM

Climate, soils, topography, and land use interact to determine vegetation types and thus the amount, location, timing, and composition of carbon inputs to soil. Because both the amount and the vertical distribution of SOM are strongly influenced by vegetation (Jobbágy & Jackson 2000), land use often alters SOM formation and respiration through changes in net primary productivity (NPP), the dominant species in plant assemblages, and plant allocation. Harvesting and grazing in human-dominated landscapes change not only productivity but also the proportion of above- and belowground inputs. Managing carbon inputs and relative allocation, for instance, through selection for deep roots or for greater belowground allocation in crops (Kell 2011), has been suggested as a way to increase SOM formation and stabilization in such systems (Bolinder et al. 2007, Ecclesia et al. 2016). However, plant breeding has traditionally selected for aboveground yields alone; therefore, potential trade-offs between yield and root production must be carefully evaluated (DeHaan et al. 2005). New tools for monitoring root systems and in situ SOM in the field are needed (Molon et al. 2017).

Increasing aboveground biomass sequesters carbon from the atmosphere, but increases in biomass do not necessarily lead to immediate or long-term increases in SOC storage. Models of ecosystem carbon balance, such as the Rothamsted carbon model, generally assume a strong, direct

## CARBON ALLOCATION

Greater plant productivity often increases SOM stocks, but rarely linearly. Better understanding is needed to predict the carbon saturation capacity of soils and to quantify the higher percentage of carbon inputs retained in SOM derived from belowground inputs compared with those from aboveground inputs.

relationship between NPP, litter inputs, and SOC accumulation (Liski et al. 2002, Gottschalk et al. 2012), yet there is little direct evidence for such a simple relationship. Accounting for ecosystem differences in carbon allocation of gross primary productivity (GPP) and its partitioning between above- and belowground plant tissues improved simulations of global woody carbon fluxes and storage in multiple ecosystem models (Ise et al. 2010). Many forests, for instance, show little or no change in total soil carbon content through time following harvesting (Nave et al. 2010), even though the forest stand and ecosystem first lose carbon and then regain it through regrowth (Lajtha et al. 2014b).

Soils have a finite capacity to sequester carbon and can saturate, decoupling litter inputs and carbon sequestration (Stewart et al. 2009, Chung et al. 2010, Mayzelle et al. 2014). The saturation level depends in part on climate and soil mineralogy. Biochemical composition and the quantity of carbon inputs matter as well, however (see Section 4). Adding both simple and complex organic substrates to soil frequently increases turnover of native SOM, termed priming (Kuzyakov et al. 2000, Knicker 2011). As a result, the stoichiometry of plant inputs can alter microbial growth and carbon retention on clay and silt soil particles, thus determining long-term SOC storage (Manzoni et al. 2012b). Increased SOM losses due to priming may similarly open space on clay and silt particles that can be refilled by microbial detritus, maintaining SOC stocks but increasing turnover (Mazzilli et al. 2014).

The lack of a linear relationship between NPP and SOM accumulation may also be related to changes in carbon allocation between above- and belowground biomass and the differential retention or stabilization of inputs to SOM (see the sidebar titled Carbon Allocation). Globally, allocation patterns combined with vertical root distributions strongly affect SOC depth distributions (Jobbágy & Jackson 2000). Partitioning of GPP to belowground components changes with plant species and ecosystems, ranging from less than 10% in croplands to ~60% in native grasslands; in forests, ~20% of total NPP was allocated to roots (Jackson et al. 1997, Parton et al. 1998, Poorter et al. 2012). Because shrublands and grasslands have greater carbon allocation to root systems than forests or croplands have, they usually show higher SOM stocks, even when accounting for climate, soil texture, and other factors (Jobbágy & Jackson 2000). Therefore, some changes in SOM stocks after land use change have been attributed to altered carbon allocation of the new vegetation (Guo & Gifford 2002, Ecclesia et al. 2016).

The proportion of plant tissue carbon incorporated into SOM is greater for belowground biomass than for aboveground litter inputs, although this relationship is poorly captured in most simulation models (Rasse et al. 2005, Bird et al. 2008, Mazzilli et al. 2015). The importance of root inputs for SOM formation is likely attributable to both their chemical composition and, almost certainly, their presence in the soil; upon death, they immediately interact with soil minerals, microbes, and aggregates. Roots tend to be characterized more by aliphatic compounds that are readily sorbed to mineral surfaces, and their composition (and that of root exudates) can increase microbial carbon use efficiency (CUE), defined as the ratio of microbial growth to carbon uptake, more than litter can. High CUE promotes microbial growth and carbon stabilization in mineral-associated soil pools, and low CUE favors biomass respiration (Manzoni et al. 2012a). Both

---

**GPP:** gross primary productivity

**CUE:** carbon use efficiency

---

**Table 1** Proportion of aboveground and belowground biomass contributing to SOM formation in agricultural field studies performed in situ using primarily isotopic approaches

| Vegetation type or treatment                             | Belowground carbon inputs retained in SOM (%) | Aboveground carbon inputs retained in SOM (%) | Ratio    | Reference                 |
|--|---|---|----------|---------------------------|
| Conventional agriculture                                 | 35%   | 4.8%  | 7.4      | Kong & Six 2010           |
| Low-input agriculture                                    | 65%   | 4.9%  | 13.2     | Kong & Six 2010           |
| Organic agriculture                                      | 91%   | 3.6%  | 25.6     | Kong & Six 2010           |
| Mixed C <sub>3</sub> and C <sub>4</sub> crops            | 36%   | 4.0%  | 9.0      | Ghafoor et al. 2017       |
| Mixed C <sub>3</sub> and C <sub>4</sub> fertilized crops | 18%   | 10%   | 1.8      | Ghafoor et al. 2017       |
| Maize  | 61%   | 5.0%  | 12.2     | Mazzilli et al. 2015      |
| Soybean  | 80%   | 3.0%  | 26.7     | Mazzilli et al. 2015      |
| Rye cover crop, 5 months                                 | 26%   | 5.2%  | 5.0      | Austin et al. 2017        |
| Rye cover crop, 12 months                                | 27%   | 3.5%  | 7.7      | Austin et al. 2017        |
| Rye cover crop   | 24%   | 5.9%  | 4.1      | Austin et al. 2017        |
| Maize  | 21%   | 12%   | 1.7      | Bolinder et al. 1999      |
| Maize  | 38%   | 11%   | 3.5      | Balesdent & Balabane 1996 |
| Maize  | 73%   | 14%   | 5.1      | Clapp et al. 2000         |
| Maize, fertilized  | 58%   | 16%   | 3.6      | Clapp et al. 2000         |
| Vetch  | 49%   | 13%   | 3.7      | Puget & Drinkwater 2001   |
| Maize  | 34%   | 8.0%  | 4.3      | Barber 1979               |
| Mix C <sub>3</sub> and C <sub>4</sub> crops              | 39%   | 17%   | 2.3      | Kätterer et al. 2011      |
| <b>Average, median</b>                                   | 46%, 39%                                      | 8.3%, 6.6%                                    | 8.1, 5.0 |                           |

chemical composition and soil proximity may operate simultaneously to increase the microbial CUE of roots, but experiments performed with undisturbed roots systems grown in soil show higher root carbon retention rates in the soil than do litterbag or incubation experiments where the soil is disturbed. This result suggests that soil proximity plays an important role, but root exudation of labile carbon compounds may also be important (Rasse et al. 2005).

Stable isotopes and fallow experiments allow researchers to estimate the proportion of roots and litter stabilized in the soil in undisturbed conditions. An analysis of 10 primarily stable isotope experiments from the field with roots grown in situ (i.e., excluding litterbag, incubation, or disturbed-soil experiments) suggests that 45% of belowground inputs on average are stabilized as SOM compared with only 8% for aboveground carbon inputs through litter, a fivefold difference (Table 1). All these experiments, however, were conducted in agricultural systems, highlighting the need to understand differences between above- and belowground inputs for SOM formation in more natural conditions. The overall effect of roots and exudates on SOM formation is complex (Lajtha et al. 2014a). Priming effects, variable aggregate formation, and root associations with mycorrhizae can change the quantity and quality of belowground carbon inputs and SOM formation (Shahbaz et al. 2016).

### 2.1. Emerging Research Questions for Plant Production, Allocation, and SOM

The relationship between plant inputs to soil and SOM formation is often represented (and modeled) as being linear, although evidence suggests otherwise. SOM formation and stabilization

## SOIL FOOD WEBS

Fungi and bacteria are the primary organisms controlling plant litter decomposition and the products that form SOM. The soil fauna has complex interactions with the soil microbial community, but their effects on net soil carbon sequestration are not well understood. The efficiency of the incorporation of plant litter into SOM may depend heavily on soil mineralogy and the interactions among soil minerals and the soil food web.

are complex and affected particularly by the type of plant residues and by plant allocation. Future research should focus on the following questions:

1. What is the relative contribution of roots compared with that of litter inputs to the accumulation of SOM under different vegetation types, soil conditions, land uses, and climates?
2. Is the higher CUE of root litter compared with that of aboveground litter explained by differences in chemical composition or root-soil interactions?
3. What is the fate of nutrients such as nitrogen and phosphorus from aboveground and belowground organic matter respired during decomposition, and what is their role in SOM formation?
4. In consideration of trade-offs with production, how feasible is it to manage plant allocation patterns in managed landscapes to sequester SOM but maintain growth and yield?

### 3. BELOWGROUND FOOD WEB ECOLOGY

Soil fauna communities are often diverse, and these organisms form complex food webs in the soil (**Figure 1**) that include termites, mites, nematodes, arthropods, rotifers, collembolans, isopods, ants, spiders, and earthworms (Wolters 2000). These organisms can be herbivores that feed on plant roots, saprotrophs that process dead or decaying organic matter, and consumers that feed on other soil organisms (Wagg et al. 2014). Whereas much attention has been given to the role of aboveground plant and animal species on ecosystem functioning and carbon dynamics, the functional role of soil food web composition in net carbon sequestration is less well known (see the sidebar titled Soil Food Webs). Anthropogenic influences affect the structure (e.g., composition and diversity) and function (e.g., productivity) of both terrestrial and aquatic biota and the belowground soil food web. Many observational and experimental studies have shown that elevated CO<sub>2</sub>, elevated nitrogen deposition, and agricultural management affect the species composition and diversity of soil organisms (Wardle et al. 1995, Moore et al. 1996, Osler & Sommerkorn 2007, de Vries et al. 2013). Agricultural activity, for example, including tilling, strongly reduces the biomass of most feeding groups in the soil food web (Eisenhauer et al. 2012). As SOM turnover is the result of the ecological interactions among soil organisms that feed on plant litter inputs, it is logical to assume that both biotic and abiotic factors will also affect processes that determine both the turnover and the stabilization of SOM.

Microbes, soil fauna, and their interactions exert strong controls on the rates, pathways, and fates of plant litter decay (Beare et al. 1992, Cárcamo et al. 2000, David 2014), both through direct consumption and transformation of plant detritus and through shredding and fragmentation, which provide increased surface area for microbial activity (Moore et al. 2004). Soil animals also directly affect the population sizes and composition of microbes that colonize and degrade plant litter, and this effect can be either positive or negative, as these organisms both consume microbes and provide substrates, including bodies and fecal pellets, for microbial colonization. However, these controls and interactions differ substantially in the soil mineral matrix owing to interactions

with soil aggregates, soil pores, and mineral surfaces, as well as to activities such as bioturbation (Vetter et al. 2004). Whereas the activity of soil fauna has been shown to increase nutrient turnover and litter decomposition (e.g., Wagg et al. 2014), the direct effects of soil fauna on net SOM stabilization or destabilization are less well studied; thus, soil animals are generally excluded from most global models of SOM processes (Wall et al. 2008). In a litter labeling experiment, Soong et al. (2016) found that suppression of microarthropods slowed plant litter mass loss during the first 18 months of decomposition but did not alter the total amount of carbon and nitrogen incorporated into the soil after complete litter mass loss. Grandy et al. (2016) similarly concluded that the direct effects of soil fauna are stronger on litter decomposition than on SOM stabilization.

In contrast to these studies, other reports suggest that specific soil taxa may significantly modify soil carbon dynamics and pools. For example, dung beetles in particular increase plant productivity and soil nutrient content by burying surface-deposited manure (Bang et al. 2005). Presumably, this increase in plant productivity, especially in grasslands, is associated with greater soil carbon pools. In pastured livestock operations, particularly in the tropics, dung beetles help mitigate greenhouse gas emissions and aid carbon sequestration in part by increasing grass growth, aerating soil, and delivering manure carbon to mineral surfaces (Slade et al. 2016). Thus, it is not surprising that fragmentation of intact tropical forest ecosystems, which strongly decreases population sizes of forest-dwelling dung beetles, decreases soil nutrient availability and tree productivity (Nichols et al. 2008).

As large, abundant, structure-forming ecosystem engineers, earthworms have profound direct influence on litter decay and soil carbon stability and, further, deterministic effects on other organisms (Lavelle et al. 1997). Earthworm feeding, digestion, transportation, and casting in aggregates move aboveground inputs belowground (Bossuyt et al. 2006), which may in turn move litter residues more quickly into more stable mineral-associated carbon pools. Earthworm functional groups are defined largely by eating strategies that differ in the amount and form of organic matter ingested and the degree of mixing with mineral soil as it passes through the gut and is excreted as casts throughout the soil profile (Curry & Schmidt 2007). Detritivores feed at or near the soil surface on plant detritus, and include epigeic earthworms, which restrict feeding to the organic-rich surface horizons, and anecic earthworms, which preferentially feed at the surface on litter but reside in burrows in deeper horizons (Lavelle 1988). Geophages, also termed endogeics, eat SOM and dead roots deep in the soil while also consuming mineral soil (Bouché 1977). Earthworm burrows provide aeration, preferential flow paths for water, and surface area for the development of microbial hot spots, which are small soil volumes with greater process rates than the surrounding sites associated with earthworm activity and casts (Kuzyakov & Blagodatskaya 2015). Groffman et al. (2015) noted that earthworms in a northern hardwood forest increased the microbial biomass carrying capacity of soils and the flow of nitrogen into stabilized SOM.

The earthworm dilemma, akin to the soil carbon dilemma, whereby one must simultaneously accumulate and decompose SOM to derive the potential benefits (Janzen 2006, Lubbers et al. 2013), is an apparent paradox in the functioning of earthworms in soil ecosystems. Earthworms may improve soil fertility, increase soil structure development, and improve infiltration, especially in agricultural systems (Zhang et al. 2013, Bertrand et al. 2015). Although it is only through accelerated decomposition and increased aggregation that earthworms increase net carbon sequestration in the soil (Six et al. 2004, Lubbers et al. 2013), the introduction and spread of invasive earthworms can be detrimental to soil carbon sequestration, particularly in regions where no native earthworms were present (Hendrix et al. 2008). Invasive species can decrease detrital inputs to soil and fundamentally change SOM chemistry (Filley et al. 2008, Crow et al. 2009, Szlavecz et al. 2011). Thus, studies of the effects of earthworms on soil carbon dynamics are mixed and have not yet shown conclusive effects of earthworms on soil carbon pools.



The direct effects of the microbial community on the balance between carbon stabilization and destabilization are clearer. In particular, mycorrhizae, and the nature of the mycorrhizal association, play a large role in soil carbon stabilization. Plant carbon allocation to mycorrhizal symbionts can be large, especially in nutrient-poor or boreal ecosystems (Clemmensen et al. 2013), and turnover of the mycorrhizal external mycelium can be the dominant pathway by which carbon enters the SOM pool (Godbold et al. 2006). Orwin et al. (2011) used a model to demonstrate that organic nutrient uptake by mycorrhizae can significantly increase soil carbon storage, especially under nutrient-limited conditions. They suggested that the increased carbon storage was due both to an increase in plant carbon fixation and to subsequent increased carbon inputs to soil through mycorrhizal fungi, as well as reduced decomposition from the increased nutrient limitation of saprotrophs. Gadgil & Gadgil (1971) hypothesized that competition between saprotrophic and mycorrhizal fungi for limiting resources in SOM would suppress saprotrophic decomposition rates, resulting in greater sequestration of soil carbon, a phenomenon known as the Gadgil effect. Recent research (Averill et al. 2014, Averill & Hawkes 2016) demonstrated that ecosystems dominated by plants with symbiotic ectomycorrhizal fungi store more carbon in soils than ecosystems dominated by arbuscular mycorrhizal (AM)-associated plants. These researchers hypothesized that ectomycorrhizal fungi produce enzymes to degrade and sequester organic nitrogen from plant litter, which limits soil nitrogen available for microbial communities to decompose SOM and release carbon to the atmosphere.

At the same time, mycorrhizae may also stimulate the decomposition of soil carbon to mine nutrients and thus paradoxically destabilize soil carbon pools. Even AM fungi that do not have saprotrophic capabilities appear able to degrade organic patches, possibly by exuding labile carbon substrates to enhance saprotrophic microbes (Hodge & Fitter 2010). The effects of mycorrhizae on soil carbon balance are thus complicated by the interplay between carbon stabilization effects and soil carbon priming effects (Brzostek et al. 2015).

Controversy surrounds the differing roles bacteria and fungi have in net SOM accumulation. Fungi-dominated communities may accumulate more soil carbon than bacteria-dominated systems because fungi produce more recalcitrant compounds and because they have higher CUE than bacteria do, although some recent analyses question this conclusion (Six et al. 2006). Soil fungi have a dominant role in the formation of soil macroaggregates (soil particles >2,000  $\mu\text{m}$ ), which sequester carbon from microbial decomposition (Peng et al. 2013).

Microbial CUE is often expressed as the ratio of growth to carbon uptake (Geyer et al. 2016); thus, systems with high CUE have lower respiratory losses of substrate than do systems with low CUE and therefore, presumably, store more soil carbon. Microbial growth efficiencies, along with mineral-matrix interactions with specific carbon compounds, are now thought to be dominant forces controlling soil carbon stabilization (Schmidt et al. 2011, Bradford et al. 2016). Expanding on this paradigm, Cotrufo et al. (2013) postulated the microbial efficiency-matrix stabilization (MEMS) framework. This framework hypothesizes that although interactions of organic materials with the soil mineral matrix are the ultimate controllers of SOM stabilization over long timescales, a microbial filter that either delivers organic products to this matrix or respire plant-derived carbon to the atmosphere is the critical link between plant litter and products available for stabilization. As such, microbial substrate use efficiency and the potential ability of the products of microbial decay to stabilize on soil minerals are critical controls determining SOM formation. Cotrufo et al. (2013) also suggest that recalcitrant organic matter inputs reduce microbial CUE; therefore, relatively labile substrates, which are used more efficiently by microbes, are responsible for a greater proportion of mineral-stabilized soil carbon. A study by Manzoni et al. (2012a) showed that CUE decreases with increased temperature, suggesting that CUE, and SOM formation, might decrease with global warming. Other studies, however, have demonstrated

thermal adaptation of microbes to long-term warming (Bradford et al. 2008), implying that global temperature rise may not significantly increase soil respiration rates or decrease CUE.

### 3.1. Emerging Research Questions for Belowground Food Webs and Soil Ecology

Although it is well established that microbes and soil fauna exert strong controls on the rates and pathways of plant litter decay, their role in soil carbon stabilization is less clear. Mycorrhizae have a strong role in carbon stabilization in many ecosystems, but the relative role of fungi in soil carbon stabilization, compared with that of bacteria, is not well characterized. Several questions deserve particular attention:

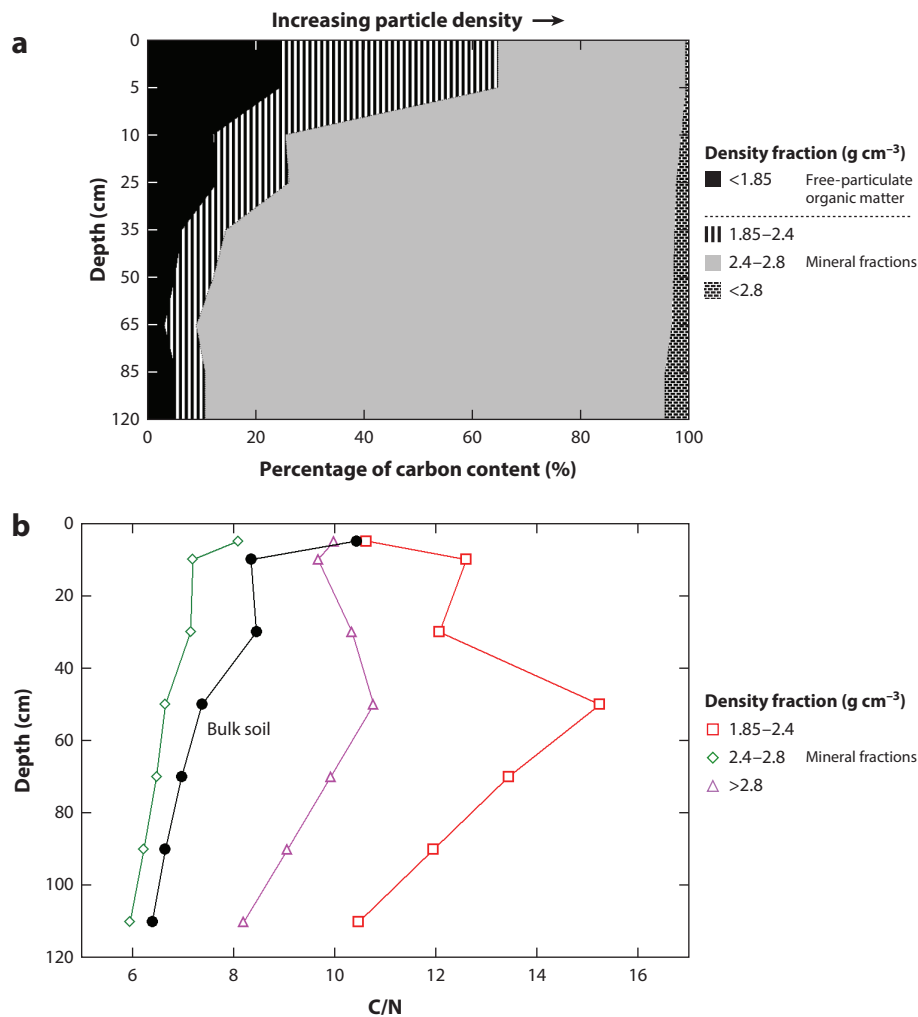
1. How critical is understanding microbial physiology to predicting future changes in soil carbon stocks with climate change?
2. Will microbial CUE be altered by global warming, will thermal adaptation occur, or will broad changes in the microbial community lead to unexpected changes in soil carbon stabilization patterns?
3. How will changes in future vegetation patterns affect detrital inputs to soil and the stabilization of these inputs?
4. Do soil fauna need to be added to models of SOM that include microbes?

## 4. MINERAL INTERACTIONS WITH THE BIOTIC WORLD

Biological activity is most intense near the soil surface (Taylor et al. 2002). In this shallow zone of the soil, litter and root plant inputs continually replenish and sustain a fresh carbohydrate source for biological activity (**Figure 1**) (Oades 1967, Cheshire 1979, Hu et al. 1997). Micro-aggregation, physical protection, interaction with carbon compounds, and bacteria and fungi help retain SOM (**Figures 1 and 2**) (Oades 1984). This shallow zone of the soil is also highly vulnerable to many disturbance processes that mix the soil, such as windstorms, earthworm activity (bioturbation), and plowing (Bohlen et al. 2004, Kramer et al. 2004, Hupy & Schaetzl 2006). Other factors that influence surface SOM include fire, fluctuating rainfall, soil saturation, and temperature effects. As a result, surface soil carbon pools are constantly being rejuvenated through inputs and respired away as CO<sub>2</sub> (Trumbore et al. 1996). Soil minerals play a relatively limited role in stabilizing carbon in shallower soils compared with deeper soils in part because lighter, free-particulate organic matter is more prevalent and because new litter and root inputs provide a steady supply of nonmineral-associated (free) particulate organic matter (**Figure 1; Table 1**). Priming effects of rapidly respiring light-fraction SOM also result in mineral-associated carbon loss in this region (Lajtha et al. 2014b). Most studies to date indicate rapid turnover associated with the active layer of the soil zone (Trumbore et al. 1996, van der Voort et al. 2016).

Many studies of litter decomposition demonstrate that litter biochemistry can determine the decomposition rate and fate of residual products (Bonanomi et al. 2013). However, at greater depths in the soil (>30 cm), minerals such as clays and silts increasingly stabilize most of the organic matter and determine accessibility to microbes; organic matter biochemistry appears to play a less important role in SOM stability at these depths. Temperature and soil moisture regimes become increasingly stable at depth (Hall et al. 2016) as well; thus, variability in environmental conditions is greatly reduced and the impact of soil mineral chemistry becomes more pronounced.

A significant (>50%) component of the global soil carbon pool can be found at these greater depths (Jobbágy & Jackson 2000) (**Table 2**). Most (>90%) organic matter deeper than 30 cm



**Figure 2**

Role of minerals in the subsoil in driving patterns of soil organic matter accumulation and biochemistry, and the resultant carbon-to-nitrogen (C/N) ratio of the soil depth profile, for an Oxisol soil. (a) Proportion of mineral-associated carbon content across density fractions and with depth. (b) Bulk soil patterns of C/N ratio relative to those of mineral-associated density fractions with depth. All data are from Kramer et al. (2017).

is associated with (i.e., sorbed to) minerals (**Figure 2**). Biological activity is severely reduced, and, increasingly, abiotic factors such as soil mineral chemistry drive organic matter dynamics (Schrumpf et al. 2013). Secondary minerals (1:1 and 2:1 clays, amorphous and crystalline) interact with organic matter via hydrogen bonding, van der Waals interactions, and inner-sphere complexation (Kleber et al. 2015). Mineral surface area is also an important control on the amount of SOM retained (Mayer 1994). Less reactive mineral particles with low surface area preferentially accumulate microbially derived nitrogen-rich proteins (Sollins et al. 2009, Kramer et al. 2017). In contrast, more reactive mineral particles (Fe and Al oxyhydroxides) preferentially sorb to aromatic acids, compounds with an abundance of carboxyl/carbonyl functional groups (Kaiser &

## MINERAL INTERACTIONS

Mineral interactions more than biochemical composition determine the stability of deeper SOM. The importance of this abiotic factor in regulating organic matter chemistry and quantity with depth highlights the need to address both biotic and abiotic factors and their interactions in soil.

Guggenberger 2000, Kramer et al. 2012). In either case, the accumulation of secondary minerals in the subsoil horizon results in significant accumulation of carbon in this portion of the soil zone.

Once associated with minerals, there are numerous factors that may affect the long-term persistence of organic matter. These factors include the ease of desorption (Mikutta et al. 2007, Bachmann et al. 2008); microbial accessibility (Ekschmitt et al. 2008), especially to organic matter held in micropores (van Loosdrecht et al. 1990, Zimmerman et al. 2004); and conformational changes upon binding that render enzymes ineffective (van Loosdrecht et al. 1990). Retention mechanisms that bind strongly and mostly irreversibly (e.g., ligand exchange) likely confer the longest-term stability to organic matter (Kramer et al. 2012), whereas organic matter retained by weak electrostatic attractions and noncoulombic (i.e., van der Waals forces) interactions may be easier for microbes to access and thus have shorter residence times in soils.

Soil temperature and pH in the soil profile are influenced by rainfall amount, aboveground biomass, and air temperature (Slessarev et al. 2016). In wet climates, soil pH declines and soils can remain waterlogged for at least some portion of the year, retarding microbial decomposition of soil carbon (Keiluweit et al. 2016). In very cold climates, soil at depth is frozen year-round (permafrost), which may also limit soil drainage. These additional environmental controls act in concert with soil mineralogy in the subsoil. Although less prevalent at the global scale, waterlogged soils result in mineral-free organic matter accumulation and can produce vast areas of peat or Histosols.

At even greater depth, such as in the C horizon or in highly weathered parent material (saprolite), SOM concentration and mineral associations decline appreciably, owing mostly to the prevalence of primary minerals. Such minerals have a low specific surface area and are unreactive. However, even in this portion of the soil zone, total organic matter accumulation can be appreciable because of the extent of this zone, as occurs, for instance, in a deep saprolite, a deeply weathered bedrock zone common in the tropics.

To date, most studies have concluded that SOM at depths greater than 30 cm is composed more of microbially derived materials than of plant-derived materials and is associated primarily with soil minerals (see the sidebar titled Mineral Interactions) (Schmidt et al. 2011, Schrumpf et al. 2013). Recent radiocarbon studies indicate that most of the deeper soil carbon is older, and turnover is slower, indicating it is unlikely to respond rapidly to warming global temperatures (He et al. 2016, van der Voort et al. 2016). The low rates of carbon accumulation observed across chronosequence sites also indicate that SOM pools are unlikely to accumulate carbon or rapidly increase carbon sequestration with warming temperatures (Schlesinger 1990).

Other abiotic factors such as disturbance events, including land use change, soil erosion from landslides, hurricanes, and earthquakes, can impact both surficial and subsoil carbon. The principal effects are redistribution of mineral-associated SOM either across the land surface or with depth and accelerated decomposition due to increased aeration of the soil. Eventually, these disturbance processes, combined with effects of topography, result in a net export of mineral-associated SOM to ocean environments through fluvial processes, although the role of mass export of SOM via riverine loss is not well understood (Syvitski et al. 2003, Galy et al. 2015).

**Table 2 Summary of global soil organic carbon (SOC) stocks subdivided using the biome descriptions of Olson et al. (2001)**

| Biome                            | Soil area (M km <sup>2</sup> ) | Global SOC (Pg C) <sup>a,b</sup> |       |       |                         |       |       |                    |       |       |                          |       |       |    |    |     |
|----------------------------------|--------------------------------|----------------------------------|-------|-------|-------------------------|-------|-------|--------------------|-------|-------|--------------------------|-------|-------|----|----|-----|
|                                  |                                | Total                            |       |       | Mineral (no permafrost) |       |       | Permafrost mineral |       |       | Peatland (no permafrost) |       |       |    |    |     |
|                                  |                                | 0–0.3 m                          | 0–1 m | 0–2 m | 0–0.3 m                 | 0–1 m | 0–2 m | 0–0.3 m            | 0–1 m | 0–2 m | 0–0.3 m                  | 0–1 m | 0–2 m |    |    |     |
| <i>Forests</i>                   |                                |                                  |       |       |                         |       |       |                    |       |       |                          |       |       |    |    |     |
| (Sub-)Tropical moist broadleaf   | 33                             | 177                              | 350   | 502   | 157                     | 292   | 399   | 0                  | 0     | 0     | 20                       | 58    | 103   | 0  | 0  | 0   |
| (Sub-)Tropical dry broadleaf     | 3                              | 9                                | 18    | 26    | 9                       | 17    | 24    | 0                  | 0     | 0     | 0                        | 1     | 1     | 0  | 0  | 0   |
| (Sub-)Tropical dry conifer       | 1                              | 4                                | 7     | 9     | 4                       | 7     | 9     | 0                  | 0     | 0     | 0                        | 0     | 0     | 0  | 0  | 0   |
| Temperate broadleaf and mixed    | 24                             | 161                              | 303   | 434   | 142                     | 240   | 301   | 0                  | 0     | 1     | 19                       | 63    | 132   | 0  | 0  | 0   |
| Temperate conifer                | 6                              | 35                               | 70    | 105   | 27                      | 50    | 67    | 3                  | 6     | 9     | 4                        | 14    | 28    | 0  | 0  | 1   |
| Boreal forest                    | 13                             | 165                              | 354   | 623   | 45                      | 78    | 126   | 82                 | 157   | 263   | 23                       | 75    | 153   | 15 | 45 | 82  |
| <i>Grasslands and shrublands</i> |                                |                                  |       |       |                         |       |       |                    |       |       |                          |       |       |    |    |     |
| (Sub-)Tropical                   | 18                             | 56                               | 110   | 154   | 55                      | 107   | 147   | 0                  | 0     | 0     | 1                        | 3     | 6     | 0  | 0  | 0   |
| Temperate                        | 8                              | 37                               | 70    | 95    | 36                      | 67    | 91    | 1                  | 2     | 3     | 0                        | 1     | 2     | 0  | 0  | 0   |
| Flooded                          | 2                              | 4                                | 7     | 11    | 3                       | 7     | 10    | 0                  | 0     | 0     | 0                        | 0     | 0     | 0  | 0  | 0   |
| Montane                          | 2                              | 10                               | 19    | 25    | 4                       | 10    | 13    | 5                  | 9     | 12    | 0                        | 0     | 0     | 0  | 0  | 0   |
| <i>Other</i>                     |                                |                                  |       |       |                         |       |       |                    |       |       |                          |       |       |    |    |     |
| Tundra                           | 4                              | 59                               | 132   | 223   | 3                       | 5     | 10    | 49                 | 109   | 180   | 0                        | 0     | 1     | 7  | 17 | 33  |
| Mediterranean climates           | 3                              | 8                                | 15    | 21    | 8                       | 15    | 20    | 0                  | 0     | 0     | 0                        | 0     | 0     | 0  | 0  | 0   |
| Deserts and xeric shrublands     | 8                              | 15                               | 31    | 44    | 15                      | 31    | 44    | 0                  | 0     | 0     | 0                        | 0     | 0     | 0  | 0  | 0   |
| Sum                              | 126                            | 738                              | 1,486 | 2,273 | 509                     | 926   | 1,263 | 140                | 283   | 466   | 67                       | 215   | 427   | 22 | 62 | 116 |

<sup>a</sup>Global SOC stocks are calculated using the WISE30sec database (Batjes 2016) for all regions except the northern permafrost, where we incorporated the NCSCDy2 database (Hugelius et al. 2014) and used geographic information systems software (ArcGIS 10; ESRI, Redlands, CA) overall in relevant equal-area projections. A new aspect of the data presented here is that global SOC stocks are separated into peatlands without permafrost, peatlands with permafrost, and mineral permafrost soils. Note that stocks for the permafrost-affected soils also include SOC in the seasonally thawed active layer above the permafrost layer.

<sup>b</sup>The WISE30sec database does not report 0–30 cm SOC stocks. This interval was interpolated by fitting a regression of log(depth) to log(SOC) through the reported SOC stocks of the 0–20, 20–40, 40–60, 60–80, and 80–100 cm for each map polygon. The interpolation for 0–30 cm was used if  $R^2 > 0.9$  and  $P < 0.05$ ; otherwise, the 0–20 cm stock was used.

**Pg:** petagram ( $10^{15}$  g)

**HWSD:** Harmonized World Soil Database

**WISE30sec:**  
ISRIC-WISE  
Harmonized Global  
Soil Profile Data  
(version 3.1)

#### 4.1. Emerging Research Questions for Biotic–Abiotic Interactions and SOM

Soil minerals exert strong controls on the rates and pathways of SOM accumulation, but the relationship between biotic processes and soil mineral interactions remains less clear. Soil minerals have a strong role in carbon stabilization in many ecosystems. However, the relative roles of different types of organic matter–mineral interactions are not well characterized globally.

1. How will interactions between biotic processes (e.g., NPP, detrital inputs, and microbial activity) and carbon retention on mineral surfaces be altered by climate change?
2. Do soil minerals and their interactions with biotic processes need to be included in future SOM models?
3. How can abiotic and biotic factors be incorporated into land surface and Earth system models to reduce future uncertainty?

### 5. SOM STOCKS

#### 5.1. Estimates of Total Soil Carbon Stocks Globally and at Specific Depths

Soils hold the largest biogeochemically active terrestrial carbon pool on Earth (**Figure 3**). Estimates of its size were first made in the 1950s. Later updates have ranged by a factor of at least six, from 500 to 3,000 Pg SOC (Scharlemann et al. 2014). Most estimates converged to 1,100 to 1,500 Pg SOC for the top meter of soil but remain more variable for deeper soils (Schlesinger 1977, Post et al. 1982, Batjes 1996, Jobbágy & Jackson 2000).

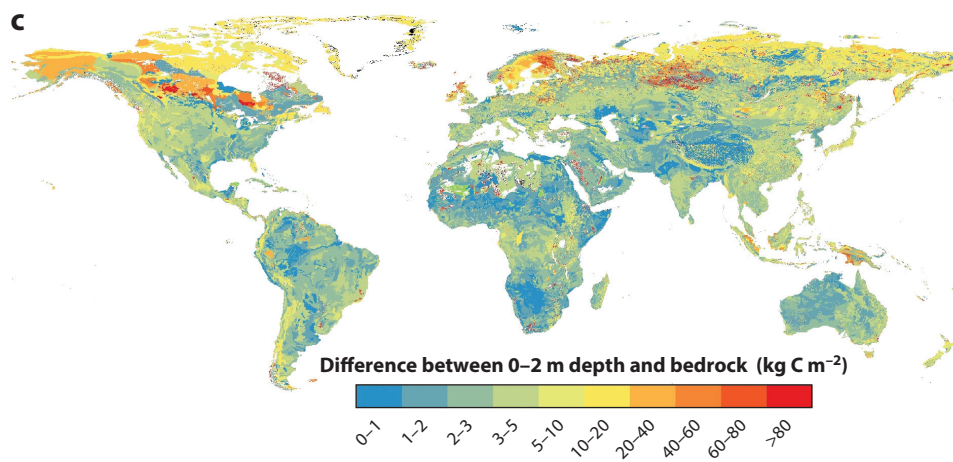
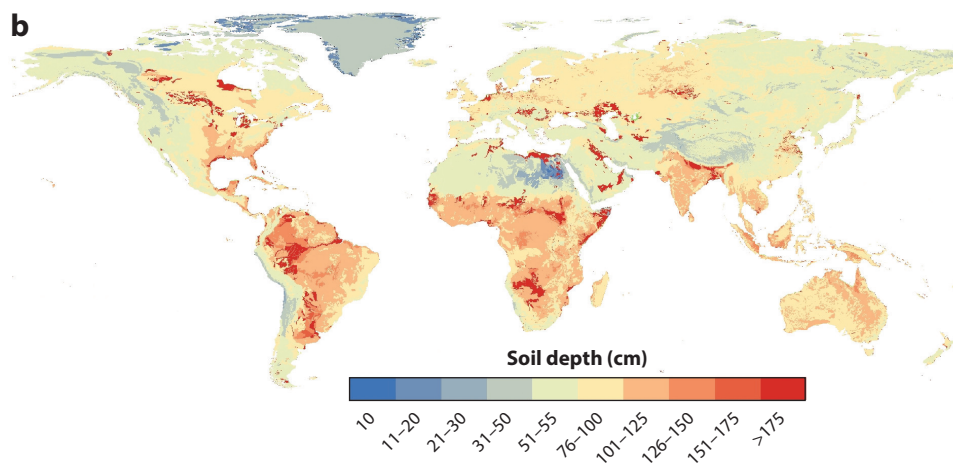
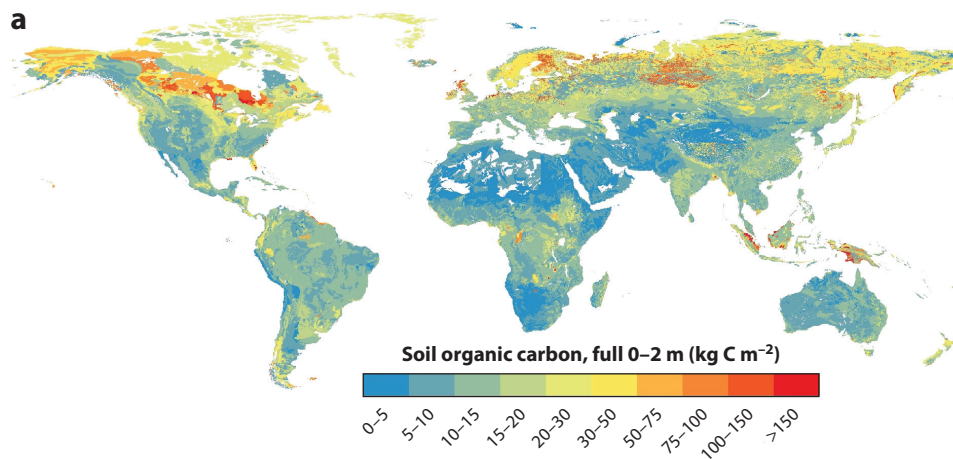
Geospatial products to map SOC typically rely on digitized soil maps combined with soil profile databases (e.g., Reich 2006, Batjes 2016). The Harmonized World Soil Database (HWSD; FAO 2012) has been widely used in global carbon cycle applications (Todd-Brown et al. 2013, Köchy et al. 2015). The recent WISE30sec database (Batjes 2016) updates the HWSD to include information from Köppen–Geiger climate maps and a soil profile dataset with improved representation at northern high latitudes.

At local and regional scales, most modern soil inventories are based on digital soil mapping techniques. Soil properties in a given location are predicted on the basis of soil profile reference data combined with remotely sensed data, climate, terrain, and other variables (McBratney et al. 2003). Using machine-learning techniques, Hengl et al. (2017) modeled soil properties for the world at a resolution as fine as 250 m. Such high-resolution gridded datasets of SOC and other soil variables are increasingly important for global modeling and validation.

---

#### Figure 3

(a) The estimated soil organic carbon (SOC) stocks to a depth of 2 m based on data in the WISE30sec dataset (Batjes 2016). (b) The estimated depth to bedrock in a dataset (Pelletier et al. 2016) that partitions bedrock into three depth categories for upland hillslopes, upland valley bottoms, and lowlands. (c) The amount of SOC in panel *a* that would be decreased if SOC accumulation were constrained by the bedrock depths shown in panel *b*. The estimates of depth-constrained SOC stocks in panel *c* were interpolated from observations in the WISE30sec dataset by fitting a regression of  $\log(\text{depth})$  to  $\log(\text{SOC})$  through the reported SOC stocks of the different depths reported for each map polygon. For each polygon, one regression was fitted for interpolations shallower than 100 cm and another regression was fitted for interpolations between 100 and 200 cm. The interpolation was used if  $R^2 > 0.9$  and  $P < 0.05$ ; otherwise, the closest reported SOC stock in that polygon was used. All analyses were performed using geographic information systems software (ArcGIS 10; ESRI, Redlands, CA) in relevant equal-area projections.



## GLOBAL DATASETS

Estimates of amounts and controls for SOM distributions are improving rapidly, owing in part to analyses of >100,000 soil profiles in global databases. High-resolution gridded datasets of soil properties are also becoming available and will be important for broad-scale modeling and validation. Global uncertainties concerning the amounts and locations of SOM include the extent of wetland, peatland, and permafrost systems and the extent to which factors such as shallow bedrock constrain soil depths.

Estimates of SOC and SON (soil organic nitrogen) that incorporated depth distributions provided new insight into the amounts, biotic and abiotic controls, and vulnerabilities of SOC. Batjes (1996) provided the first global estimate of SOC to a depth of 2 m, adding 911 Pg C to the previous estimate for the top meter of soil. Jobbágy & Jackson (2000) provided the first estimate of SOC to a depth of 3 m (2,344 Pg SOC, or 56% more than the 1,502 Pg in the top meter) and included depth functions by plant functional type and biome. They found that the relative distribution of SOC with depth had a stronger association with vegetation type than with climate, through factors such as belowground allocation, but the opposite was true for absolute SOC amounts. Permafrost and peatland regions typically have deeper SOC profiles than temperate and tropical systems do, as determined primarily through soil coring and sampling (e.g., Harden et al. 2012, Hugelius et al. 2014, Loisel et al. 2017).

Previous global estimates for SOC have not included regional permafrost data or SOC stocks separated by biome or by peatland/permafrost categories (e.g., peatlands without permafrost, peatlands with permafrost, and mineral permafrost soils). We present a new estimate for global SOC content by overlaying a global soil database with regional permafrost data, reconciling regional estimates, and providing biome-based totals (**Table 2**). The global SOC stock in the upper 2 m of soil is 2,273 Pg C, with the boreal forest biome containing 623 Pg, or 27% of the global total (**Table 2**). Peatlands contain 543 Pg SOC, most of it in boreal, temperate broadleaf and tropical, moist broadleaf forest biomes; permafrost regions contain 582 Pg SOC, or 26% of the global total (**Table 2**).

Global soil databases have no data for soil deeper than 2 m (see the sidebar titled Global Datasets). If we extrapolate the data in **Table 2** to include soil depths of 2–3 m using the biome depth distributions in Jobbágy & Jackson (2000), we find an additional 199 Pg SOC for nonpermafrost mineral soils. For the permafrost region, the third meter of soil is estimated to hold  $207 \pm 42$  Pg C (Hugelius et al. 2014); for peatlands outside permafrost areas, we estimate  $\sim 92$  Pg OC (organic carbon) for the global 2–3 m depth (assuming an OC concentration multiplier of 0.5 to calculate the 2–3-m depth carbon content from the 1–2-m depth increment, and assuming a mean peat depth of 2.3 m). Thus, the global total soil carbon pool to a depth of 3 m is estimated as 2,800 Pg C. Deeper (>3 m) deposits include an additional  $\sim 300$ –500 Pg OC in the permafrost region (Schuur et al. 2015),  $\sim 30$ –50 Pg C in tropical peatlands, and an unknown quantity of OC in other environments with deep sediments such as deltas, floodplains, and loess deposits.

**SON:** soil organic nitrogen

**OC:** organic carbon

### 5.2. Uncertainties and Opportunities for Improving Estimates of SOC

Despite recent advances, estimates of global SOC stocks and distributions remain limited by insufficient data for many regions. Boreal and arctic regions are relatively remote and under-sampled, even though they contain more OC than the atmosphere does (Tarnocai et al. 2009).



Estimates of peatland carbon are also strongly limited by a lack of peat bulk density data (Köchy et al. 2015).

Another concern with estimates of SOC content is that wetlands, peatlands, and permafrost soils are defined differently across countries and scientific disciplines. Wetland and shallow freshwater lakes are difficult to distinguish using remote sensing approaches and are sometimes classified differently. Most soil classification systems distinguish peatlands (organic soils) from mineral soils on the basis of whether surface peat accumulates to a depth of at least 40 cm. However, inventory estimates usually define peatlands as having at least 30 cm of near-surface peat and typically include the full depth of peat rather than only 1 or 2 m (Joosten & Clarke 2002). Based on inventories and different ways of scaling peat area to OC stocks, an estimated 3.8–4.4 M km<sup>2</sup> of global peatlands store 450–650 Pg OC in the top 2 m (Joosten & Clarke 2002, Yu et al. 2010, Loisel et al. 2017). Our estimate in **Table 2** is 543 Pg OC. Tropical peatlands cover only 0.38–0.66 M km<sup>2</sup> but are typically deeper and store as much as 82–92 Pg OC (Page et al. 2011). An additional ~15 Pg OC is stored in southern hemisphere peatlands (Yu et al. 2010).

Permafrost soils have their own uncertainties. Permafrost cover is locally irregular and includes an upper active layer, ranging from a few decimeters to several meters in depth, that thaws seasonally. As a consequence, the estimated soil carbon is roughly equally divided between permanently and seasonally frozen soils. An additional complication is that ~300 Pg of the permafrost region soil carbon is stored in peatlands, which must not be counted twice when summing separate peatland estimates (Loisel et al. 2017).

In light of the large potential of soil carbon stocks at depth, another global source of uncertainty is the extent to which shallow bedrock restricts the depth of SOM pools and biological activity (**Figure 3b**). Functions for extrapolating SOC and SON contents overestimate the amount of organic matter if bedrock is shallower than the extrapolated depth. Although estimates of the depths of soil and other surficial material (e.g., regolith) are available at coarse scales and for some regions (Soller et al. 2009), particularly using geophysical approaches (Miller et al. 1999, Jayawickreme et al. 2014), global datasets have been sparse. Pelletier et al. (2016) recently published a modeled dataset gridded at 30 arcsec (~1 km) based on input data for topography, climate, and geology.

We applied the Pelletier et al. (2016) dataset of bedrock depth to global soil carbon from the WISE30sec database (**Figures 3b,c**). This reduces our current global estimate of SOC stocks by nearly one-third, from 2,047 to 1,354 Pg C for the top 2 m of soil (**Figure 3**). The main differences in mapped soil depth distributions occur in boreal and arctic regions, where bedrock potentially constrains peat and permafrost soils. The reduction for 1-m SOC stocks is more modest, ~10%, from 1,425 to 1,277 Pg C, because the WISE30sec database partly accounts for shallower soils. We do not yet know the appropriateness of applying such a bedrock depth dataset to estimates of SOM; it has been validated primarily with data from lower latitudes rather than global data. Generating the strongest possible dataset of soil and bedrock depths will improve estimates of SOM pools as well as other variables important for biogeochemistry and global primary production, including soil nutrient availability and water holding capacity.

### 5.3. Emerging Research Questions for Global SOM Stocks, Distributions, and Controls

Soils hold more than twice as much carbon as the atmosphere and play a crucial role in carbon cycling, food production, and water and nutrient retention. Estimates of where SOM is found and how deep it lies have improved considerably, but the science is still data limited. New global datasets coming online will help fill part of the data gap; additional sampling beyond temperate

systems in North America and Europe is especially needed. Answers to the following important research questions could help close the data gap:

---

**Mg:** megagram  
( $10^6$  g)

---

1. How can we better constrain the distributions of peatland and permafrost systems, the amount of SOC and SON they contain, and their vulnerability to a warming climate?
2. How can computational approaches enhance our understanding of depth distributions for SOM and their biotic and abiotic controls?
3. How can we best improve and verify estimates of bedrock depth and its influence on the global content of SOC and SON?

## 6. SOM VULNERABILITY, OPPORTUNITIES, AND MITIGATION

Soil carbon is vulnerable to oxidation and release to the atmosphere through a variety of human activities (**Figure 1**), including land use disturbance and the effects of climate change. The greatest human-induced loss of SOC has come from the conversion of native forests and grasslands to annual crops (Paustian et al. 1997, Lal 2004). Understanding the role of agricultural management on SOC stocks is therefore critical both for predicting future carbon fluxes and for devising best-management strategies to mitigate and reverse soil loss. Globally, native soils lost on average  $43.1 \pm 1.1\%$  of their original topsoil carbon after conversion to agriculture (Wei et al. 2014).

The effects of forest management on SOC are less consistent. A meta-analysis by Nave et al. (2010) suggested that whereas forest floor litter carbon was lost with forest harvest and management, losses of mineral soil carbon were not significant, and that losses were neither permanent nor unavoidable. However, some studies have suggested that Spodosols in particular might be susceptible to carbon loss from harvest and that deep mineral pools change more rapidly after harvest than previously thought (e.g., Diochon et al. 2009, Lacroix et al. 2016, although see Hoover & Heath 2015), especially over many decades or centuries (e.g., Dean et al. 2017).

Mitigating and even reversing these land use effects, however, are both possible and desirable (Minansy et al. 2017). A meta-analysis of afforestation effects on SOC storage in US states and Canadian border provinces found that land conversion to forest increased SOC by 21% (Nave et al. 2013). However, a global analysis at 153 sites to depths of 30 cm showed that the effects of afforestation on SOC and SON were insignificant except for pine plantations, where SOC and SON decreased by 15% and 20%, respectively (Berthrong et al. 2009). The initial status of the land is critical to the interpretation of afforestation studies. A degraded system often gains SOM with afforestation or other management; a healthy, native ecosystem may sometimes lose it. The depth at which the comparison is made is also important, as less is known about the long-term effects in deeper soils (Richter & Markewitz 1995).

The adoption of soil conservation practices such as reduced tillage, improved residue management, reduced bare fallow, and conservation reserve plantings has stabilized, and partially reversed, SOC loss in North American agricultural soils (Paustian et al. 2016). Using results from 142 soil studies, Piñeiro et al. (2009) showed that setting aside former agricultural land through the Conservation Reserve Program and similar programs generated greater greenhouse gas benefits than did planting corn for ethanol on the same land for 40 years, at similar cost. Improved grazing management, fertilization, sowing legumes, and improved grass species are additional ways to increase soil carbon by as much as  $1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (Conant et al. 2017).

Over the next century, most projected land use change is expected to arise from repurposing existing agricultural land rather than clearing native forests (Watson et al. 2014). Emerging land use activities that combine carbon sequestration with crop production offer great promise to increase global SOM while sustainably meeting food and fiber production for an increasing human population (Francis et al. 2016). Machmuller et al. (2015) demonstrated the potential of

emerging land use activities to result in economically profitable, more sustainable farming practices that significantly increase soil carbon stocks in degraded lands of the southeastern United States. During the two- to six-year period after conversion of row crop farming to management-intensive dairy grazing, the authors found that soil carbon stocks increased rapidly and attained pre-European native carbon stock levels. Other changes included year-round forage, reduced chemical fertilizer inputs through increased manure use, and increased water-holding capacity and cation exchange capacity of soil. Better global data on land management practices and land cover types will improve estimates of global SOM cycling and stocks. The Food and Agriculture Organization, for example, maintains a global database of conservation agriculture by land area and country (<http://www.fao.org/ag/Ca/6c.html>). However, to our knowledge there is no spatially explicit or gridded dataset of tillage or crop rotations at the global level; such data are readily available only for relatively wealthy countries. These types of data would improve our estimates of not only SOM stocks and potential for losses and mitigation, but also the emissions of trace gases such as methane and nitrous oxide.

Soil carbon stocks are widely predicted to change with climate warming, but the magnitude and, in some cases, even the sign of the change are unclear. A recent meta-analysis showed that topsoil carbon loss with one degree of warming depended strongly on the size of the standing soil carbon stocks (Crowther et al. 2016). Because arctic regions have the largest standing soil carbon stocks and are predicted to warm at rates greater than those at mid-latitudes (Cohen et al. 2014), most warming-induced soil carbon losses are likely to occur at northern latitudes. Crowther et al. (2016) calculate that a business-as-usual climate scenario could drive the loss of  $55 \pm 50$  Pg C from upper soil horizons by 2050, which is  $\sim 12$ – $17\%$  of expected anthropogenic emissions. However, their meta-analysis did not include warming effects on the deeper soils that store the bulk of SOC in northern soils, which could increase SOC oxidation, and did not account for many ecosystem responses that could enhance SOC stocks, such as increased NPP. Studies on the effect of climate warming on SOC in permafrost, including deeper deposits, project permafrost soil carbon losses of 12.2–33.4 (medium warming) to 27.9–112.6 Pg C (high warming) by the end of this century (Koven et al. 2015). Carbon stocks in northern peatlands are potentially vulnerable to local or regional disturbances, including lowered water tables or greater fire frequencies, but most studies suggest that peatlands will remain a weak carbon sink rather than a net source into at least the near future (Loisel et al. 2017).

Ecosystem and Earth system models can improve their representations of SOM by adding modifiers and microbial attributes that influence SOM formation and stabilization across scales. Simple bacteria-to-fungi ratios can be useful for estimating rates of decomposition, particularly for older, highly weathered systems with relatively high inputs and stocks, which are vulnerable to losses in the absence of mineral protection mechanisms (Doetterl et al. 2015). Several recently updated models, for example, derive heterotroph respiration rates on the basis of microbial biomass pools (e.g., Todd-Brown et al. 2012). These models rely on modifiers for this known oversimplification, but a lack of global data for aggregate turnover, as it contributes to substrate accessibility for microbes, is one of several factors limiting this approach. Whether using older or newer models, a central question remains: How many soil factors are needed to adequately capture soil dynamics, particularly across scales? Bioinformatics and molecular genetic tools provide a growing opportunity to link soil functions by using trait-based metagenomics, and community-level microbial functional traits may be one link from local-scale processes to large-scale global models (Wieder et al. 2015). However, the potential benefits of these approaches, and the use of microbially explicit models in general, to improve global estimates of SOM dynamics must be weighed against the costs of increased model complexity and the lack of global microbial datasets needed to parameterize the models.

Finally, anthropogenic greenhouse gas emissions have altered the planet's climate, including temperatures, precipitation, and vapor pressure deficit, and will continue to do so. Additional changes are apparent in the patterns and extremes of weather and in the frequency, intensity, and severity of disturbances. All the factors, knowledge, and skill illustrated through the examples in this review will be needed to project the effects of climate change on SOM. Global pressures on soils are coming from continuing changes in land management, such as the need for increasing bioenergy and food production. For these reasons and more, furthering progress in experiments, synthesis, and modeling of SOM will remain a research priority for decades.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

The authors wish to acknowledge the work of countless scientists who have sampled soil profiles and support from the US Department of Agriculture (USDA) National Institute of Food and Agriculture 2012-68002-19795 (R.B.J.); the Gordon and Betty Moore Foundation (R.B.J. and G.H.); the National Science Foundation DEB-1257032 (K.L.); the USDA HAW01130-H (S.E.C.); the Swedish Research Council E0641701 (G.H.); and the Inter-American Institute Collaborative Research Network 3005 and 3095, the Comisión Sectorial de Investigación Científica, and the Proyecto Plurianuales de Investigación 2015-0709 (G.P.). This paper is a contribution to the Global Carbon Project ([www.globalcarbonproject.org](http://www.globalcarbonproject.org)).

## LITERATURE CITED

- Amundson R. 2001. The carbon budget in soils. *Annu. Rev. Earth Planet. Sci.* 29:535–62
- Austin EE, Wickings K, McDaniel MD, Robertson GP, Grandy AS. 2017. Cover crop root contributions to soil carbon in a no-till corn bioenergy cropping system. *GCB Bioenergy* <https://doi.org/10.1111/gcbb.12428>
- Averill C, Hawkes CV. 2016. Ectomycorrhizal fungi slow soil carbon cycling. *Ecol. Lett.* 19(8):937–47
- Averill C, Turner BL, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505(7484):543–45
- Bachmann J, Guggenberger G, Baumgartl T, Ellerbrock RH, Urbanek E, et al. 2008. Physical carbon-sequestration mechanisms under special consideration of soil wettability. *J. Plant Nutr. Soil Sci.* 171:14–26
- Balesdent J, Balabane M. 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biol. Biochem.* 28:1261–63
- Bang HS, Lee J-H, Kwon OS, Na YE, Jang YS, Kim WH. 2005. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. *Appl. Soil Ecol.* 29(2):165–71
- Barber SA. 1979. Corn residue management and soil organic matter. *Agron. J.* 71(4):625–27
- Batjes NH. 1996. Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* 47(2):151–63
- Batjes NH. 2016. Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* 269:61–68
- Beare MH, Parmelee RW, Hendrix PF, Cheng W, Coleman DC, Crossley D. 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62(4):569–91
- Berthrong ST, Jobbágy EG, Jackson RB. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecol. Appl.* 19(8):2228–41
- Bertrand M, Barot S, Blouin M, Whalen J, De Oliveira T, Roger-Estrade J. 2015. Earthworm services for cropping systems. A review. *Agron. Sustain. Dev.* 35(2):553–67

- Bird JA, Kleber M, Torn MS. 2008.  $^{13}\text{C}$  and  $^{15}\text{N}$  stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Organ. Geochem.* 39:465–77
- Bohlen PJ, Pelletier DM, Groffman PM, Fahey TJ, Fisk MC. 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. *Ecosystems* 7:13–27
- Bolinder MA, Angers DA, Giroux M, Laverdière MR. 1999. Estimating C inputs retained as soil organic matter from corn (*Zea mays* L.). *Plant Soil* 215:85–91
- Bolinder MA, Janzen HH, Gregorich EG, Angers DA, Vandenbygaart AJ. 2007. An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Environment* 118:29–42
- Bonanomi G, Incerti G, Giannino F, Mingo A, Lanzotti V, Mazzoleni S. 2013. Litter quality assessed by solid state  $^{13}\text{C}$  NMR spectroscopy predicts decay rate better than C/N and lignin/N ratios. *Soil Biol. Biochem.* 56:40–48
- Bossuyt H, Six J, Hendrix PF. 2006. Interactive effects of functionally different earthworm species on aggregation and incorporation and decomposition of newly added residue carbon. *Geoderma* 130:14–25
- Bouché M. 1977. Stratégies lombriciennes. *Ecol. Bull.* 25:122–32
- Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, et al. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol. Lett.* 11(12):1316–27
- Bradford MA, Wieder WR, Bonan GB, Fierer N, Raymond PA, Crowther TW. 2016. Managing uncertainty in soil carbon feedbacks to climate change. *Nat. Clim. Change* 6(8):751–58
- Brzostek ER, Dragoni D, Brown ZA, Phillips RP. 2015. Mycorrhizal type determines the magnitude and direction of root-induced changes in decomposition in a temperate forest. *New Phytol.* 206(4):1274–82
- Cárcamo H, Abe T, Prescott C, Holl F, Chanway C. 2000. Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. *Can. J. Forest Res.* 30(5):817–26
- Cheshire M. 1979. *Nature and Origin of Carbohydrates in Soils*. London: Academic
- Chung H, Ngo KJ, Plante A, Six J. 2010. Evidence for carbon saturation in a highly structured and organic-matter-rich soil. *Soil Sci. Soc. Am. J.* 74:130–38
- Clapp CE, Allmaras RR, Layese MF, Linden DR, Dowdy RH. 2000. Soil organic carbon and  $^{13}\text{C}$  abundance as related to tillage, crop residue, and nitrogen fertilization under continuous corn management in Minnesota. *Soil Tillage Res.* 55(3):127–42
- Clemmensen K, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, et al. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339(6127):1615–18
- Cohen J, Screen JA, Furtado JC, Barlow M, Whittleston D, et al. 2014. Recent Arctic amplification and extreme mid-latitude weather. *Nat. Geosci.* 7:627–37
- Conant RT, Cerri CEP, Osborne BB, Paustian K. 2017. Grassland management impacts on soil carbon stocks: a new synthesis. *Ecol. Appl.* 27:662–68
- Cotrufo MF, Wallenstein MD, Boot CM, Denef K, 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? *Glob. Change Biol.* 19(4):988–95
- Crow SE, Filley TR, McCormick M, Szlávecz K, Stott DE, et al. 2009. Earthworms, stand age, and species composition interact to influence particulate organic matter chemistry during forest succession. *Biogeochemistry* 92(1–2):61–82
- Crowther TW, Todd-Brown KEO, Rowe CW, Wieder WR, Carey JC, et al. 2016. Quantifying global soil carbon losses in response to warming. *Nature* 540:104–8
- Curry JP, Schmidt O. 2007. The feeding ecology of earthworms—a review. *Pedobiologia* 50(6):463–77
- David J. 2014. The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biol. Biochem.* 76:109–18
- de Vries FT, Thébaud E, Liiri M, Birkhofer K, Tsiafouli MA, et al. 2013. Soil food web properties explain ecosystem services across European land use systems. *PNAS* 110(35):14296–301
- Dean C, Kirkpatrick JB, Friedland AJ. 2017. Conventional intensive logging promotes loss of organic carbon from the mineral soil. *Glob. Change Biol.* 23:1–11
- DeHaan LR, Van Tassel DL, Cox TS. 2005. Perennial grain crops: a synthesis of ecology and plant breeding. *Renew. Agric. Food Syst.* 20(01):5–14

- Diochon A, Kellman L, Beltrami H. 2009. Looking deeper: an investigation of soil carbon losses following harvesting from a managed northeastern red spruce (*Picea rubens* Sarg.) forest chronosequence. *Forest Ecol. Manag.* 257:413–20
- Doetterl S, Stevens A, Six J, Merckx R, Van Oost K, et al. 2015. Soil carbon storage controlled by interactions between geochemistry and climate. *Nat. Geosci.* 8(10):780–83
- Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, et al. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO<sub>2</sub>. *Ecol. Lett.* 14(4):349–57
- Eclesia RP, Jobbágy EG, Jackson RB, Rizzotto M, Piñeiro G. 2016. Stabilization of new carbon inputs rather than old carbon decomposition determines soil organic carbon shifts following woody or herbaceous vegetation transitions. *Plant Soil* 409:99–116
- Eisenhauer N, Cesarz S, Koller R, Worm K, Reich PB. 2012. Global change belowground: impacts of elevated CO<sub>2</sub>, nitrogen, and summer drought on soil food webs and biodiversity. *Glob. Change Biol.* 18(2):435–47
- Ekschmitt K, Kandeler E, Poll C, Brune A, Buscot F, et al. 2008. Soil-carbon preservation through habitat constraints and biological limitations on decomposer activity. *J. Plant Nutr. Soil Sci.* 171:27–35
- FAO. 2012. *Harmonized World Soil Database (version 1.2)*. Rome: FAO. <http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>
- Fekete I, Kotroczo Z, Varga C, Nagy PT, Várbíró G, et al. 2014. Alterations in forest detritus inputs influence soil carbon concentration and soil respiration in a Central-European deciduous forest. *Soil Biol. Biochem.* 74:106–14
- Field CB, Raupach MR, eds. 2004. *The Global Carbon Cycle: Integrating Humans, Climate, and the Natural World*. Washington, DC: Island Press
- Filley TR, McCormick MK, Crow SE, Szlavecz K, Whigham DF, et al. 2008. Comparison of the chemical alteration trajectory of *Liriodendron tulipifera* L. leaf litter among forests with different earthworm abundance. *J. Geophys. Res. Biogeosci.* 113(G1):1–14
- Francis F, Artru S, Brédart D, Lassois L, Francis F. 2016. Towards sustainable food systems: the concept of agroecology and how it questions current research practices. A review. *Biotechnol. Agron. Soc. Environ.* 20(S1):215–24
- Gadgil RL, Gadgil PD. 1971. Mycorrhiza and litter decomposition. *Nature* 233:133
- Galy V, Peucker-Ehrenbrink B, Eglinton T. 2015. Global carbon export from the terrestrial biosphere controlled by erosion. *Nature* 521(7551):204–7
- Geyer KM, Kyker-Snowman E, Grandy AS, Frey SD. 2016. Microbial carbon use efficiency: accounting for population, community, and ecosystem-scale controls over the fate of metabolized organic matter. *Biogeochemistry* 127(2–3):173–88
- Ghafoor A, Poeplau C, Kätterer T. 2017. Fate of straw- and root-derived carbon in a Swedish agricultural soil. *Biol. Fertil. Soils* 53:257–67
- Giardina CP, Litton CM, Crow SE, Asner GP. 2014. Warming-related increases in soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nat. Clim. Change* 4(9):822–27
- Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, et al. 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant Soil* 281(1–2):15–24
- González-Chang M, Wratten SD, Lefort M-C, Boyer S. 2016. Food webs and biological control: a review of molecular tools used to reveal trophic interactions in agricultural systems. *Food Webs* 9:4–11
- Gottschalk P, Smith JU, Wattenbach M, Bellarby J, Stehfest E, et al. 2012. How will organic carbon stocks in mineral soils evolve under future climate? Global projections using RothC for a range of climate change scenarios. *Biogeosciences* 9:3151–71
- Grandy AS, Wieder WR, Wickings K, Kyker-Snowman E. 2016. Beyond microbes: Are fauna the next frontier in soil biogeochemical models? *Soil Biol. Biochem.* 102:40–44
- Groffman PM, Fahey TJ, Fisk MC, Yavitt JB, Sherman RE, et al. 2015. Earthworms increase soil microbial biomass carrying capacity and nitrogen retention in northern hardwood forests. *Soil Biol. Biochem.* 87:51–58
- Guo LB, Gifford RM. 2002. Soil carbon stocks and land use change: a meta analysis. *Glob. Chang. Biol.* 8:345–60
- Hall SJ, Liptzin D, Buss HL, DeAngelis K, Silver WL. 2016. Drivers and patterns of iron redox cycling from surface to bedrock in a deep tropical forest soil: a new conceptual model. *Biogeochemistry* 130(1–2):177–90

- Harden JW, Koven CD, Ping CL, Hugelius G, McGuire AD, et al. 2012. Field information links permafrost carbon to physical vulnerabilities of thawing. *Geophys. Res. Lett.* 39:L15704
- He Y, Trumbore SE, Torn MS, Harden JW, Vaughn LJ, et al. 2016. Radiocarbon constraints imply reduced carbon uptake by soils during the 21st century. *Science* 353(6306):1419–24
- Hendrix PF, Callahan MA Jr., Drake JM, Huang C-Y, James SW, et al. 2008. Pandora's box contained bait: the global problem of introduced earthworms. *Annu. Rev. Ecol. Evol. Syst.* 39:593–613
- Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, et al. 2017. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* 12(2):e0169748
- Hobbie SE. 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems* 3(5):484–94
- Hodge A, Fitter AH. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *PNAS* 107(31):13754–59
- Hoover CM, Heath LS. 2015. A commentary on 'Mineral soil carbon fluxes in forests and implications for carbon balance assessments': a deeper look at the data. *GCB Bioenergy* 7:362–65
- Hu S, Coleman D, Carroll C, Hendrix P, Beare M. 1997. Labile soil carbon pools in subtropical forest and agricultural ecosystems as influenced by management practices and vegetation types. *Agric. Ecosyst. Environ.* 65:69–78
- Huang W, Spohn M. 2015. Effects of long-term litter manipulation on soil carbon, nitrogen, and phosphorus in a temperate deciduous forest. *Soil Biol. Biochem.* 83:12–18
- Hugelius G, Strauss J, Zubrzycki S, Harden JW, Schuur E, et al. 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences* 11(23):6573–93
- Hupy JP, Schaeztl RJ. 2006. Introducing “bombturbation,” a singular type of soil disturbance and mixing. *Soil Sci.* 171(11):823–36
- Ise T, Litton CM, Giardina CP, Ito A. 2010. Comparison of modeling approaches for carbon partitioning: impact on estimates of global net primary production and equilibrium biomass of woody vegetation from MODIS GPP. *J. Geophys. Res. Biogeosci.* 115(G4):1–11
- Jackson RB, Mooney HA, Schulze E-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *PNAS* 94:7362–66
- Jackson RB, Schenk HJ, Jobbágy EG, Canadell J, Colello GD, et al. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecol. Appl.* 10:470–83
- Janzen H. 2006. The soil carbon dilemma: Shall we hoard it or use it? *Soil Biol. Biochem.* 38(3):419–24
- Jayawickreme DH, Jobbágy EG, Jackson RB. 2014. Geophysical subsurface imaging for ecological applications. *New Phytol.* 201:1170–75
- Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10(2):423–36
- Joosten H, Clarke D. 2002. *Wise Use of Mires and Peatlands: Background and Principles Including a Framework for Decision-Making*. Devon, UK: Int. Mire Conserv. Group/Int. Peatl. Soc.
- Kaiser K, Guggenberger G. 2000. The role of DOM sorption to mineral surfaces in the preservation of organic matter in soils. *Organ. Geochem.* 31(7):711–25
- Kätterer T, Bolinder MA, Andrén O, Kirchmann H, Menichetti L. 2011. Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agric. Ecosyst. Environ.* 141:184–92
- Keiluweit M, Nico PS, Kleber M, Fendorf S. 2016. Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? *Biogeochemistry* 127(2–3):157–71
- Kell DB. 2011. Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. *Ann. Bot.* 108:407–18
- Kleber M, Eusterhues K, Keiluweit M, Mikutta C, Mikutta R, Nico PS. 2015. Mineral–organic associations: formation, properties, and relevance in soil environments. *Adv. Agron.* 130:1–140
- Knicker H. 2011. Soil organic N: an under-rated player for C sequestration in soils? *Soil Biol. Biochem.* 43:1118–29

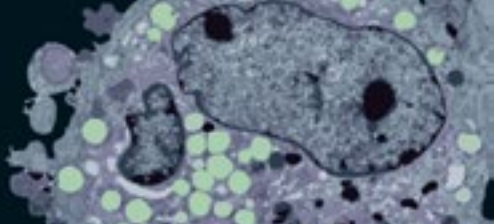
- Köchy M, Hiederer R, Freibauer A. 2015. Global distribution of soil organic carbon—Part 1: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *Soil* 1:351–65
- Kong AYY, Six J. 2010. Tracing root versus residue carbon into soils from conventional and alternative cropping systems. *Soil Sci. Soc. Am. J.* 74:1201
- Koven CD, Schuur EAG, Schädel C, Bohn TJ, Burke EJ, et al. 2015. A simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. *Philos. Trans. R. Soc. A* 373:20140423
- Kramer MG, Lajtha K, Aufdenkampe A. 2017. Natural abundance  $^{15}\text{N}$  and C/N soil depth trends controlled more by association with minerals than by microbial decay. *Biogeochem. Lett.* In press
- Kramer MG, Sanderman J, Chadwick OA, Chorover J, Vitousek PM. 2012. Long-term carbon storage through retention of dissolved aromatic acids by reactive particles in soil. *Glob. Change Biol.* 18(8):2594–605
- Kramer MG, Sollins P, Sletten RS. 2004. Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology* 85(8):2230–44
- Kuzyakov Y. 2010. Priming effects: interactions between living and dead organic matter. *Soil Biol. Biochem.* 42:1363–71
- Kuzyakov Y, Blagodatskaya E. 2015. Microbial hotspots and hot moments in soil: concept and review. *Soil Biol. Biochem.* 83:184–99
- Kuzyakov Y, Friedel J, Stahr K. 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32(11):1485–98
- Lacroix EM, Petrenko CL, Friedland AJ. 2016. Evidence for losses from strongly bound SOM pools after clear cutting in a northern hardwood forest. *Soil Sci.* 181:202–7
- Lajtha K, Bowden RD, Nadelhoffer K. 2014a. Litter and root manipulations provide insights into soil organic matter dynamics and stability. *Soil Sci. Soc. Am. J.* 78:S261
- Lajtha K, Townsend KL, Kramer MG, Swanston C, Bowden RD, Nadelhoffer K. 2014b. Changes to particulate versus mineral-associated soil carbon after 50 years of litter manipulation in forest and prairie experimental ecosystems. *Biogeochemistry* 119(1–3):341–60
- Lal R. 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304:1623–27
- Lavelle P. 1988. Earthworm activities and the soil system. *Biol. Fertil. Soils* 6:237–51
- Lavelle P, Bignell D, Lepage M, Wolters W, Roger P, et al. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* 33(4):159–93
- Lefèvre R, Barré P, Moyano FE, Christensen BT, Bardoux G, et al. 2014. Higher temperature sensitivity for stable than for labile soil organic carbon—evidence from incubations of long-term bare fallow soils. *Glob. Change Biol.* 20(2):633–40
- Leifeld J, Fuhrer J. 2005. The temperature response of  $\text{CO}_2$  production from bulk soils and soil fractions is related to soil organic matter quality. *Biogeochemistry* 75(3):433–53
- Liski J, Perruchoud D, Karjalainen T. 2002. Increasing carbon stocks in the forest soils of western Europe. *Forest Ecol. Manag.* 169:159–75
- Loisel J, van Bellen S, Pelletier L, Talbot J, Hugelius G, et al. 2017. Insights and issues with estimating northern peatland carbon stocks and fluxes since the Last Glacial Maximum. *Earth-Sci. Rev.* 165:59–80
- Lubbers IM, Van Groenigen KJ, Fonte SJ, Six J, Brussaard L, Van Groenigen JW. 2013. Greenhouse-gas emissions from soils increased by earthworms. *Nat. Clim. Change* 3(3):187–94
- Luo Y, Ahlström A, Allison SD, Batjes NH, Brovkin V, et al. 2016. Toward more realistic projections of soil carbon dynamics by Earth system models. *Glob. Biogeochem. Cycles* 30:40–56
- Machmuller MB, Kramer MG, Cyle TK, Hill N, Hancock D, Thompson A. 2015. Emerging land use practices rapidly increase soil organic matter. *Nat. Commun.* 6:6995
- Manzoni S, Piñeiro G, Jackson RB, Jobbágy EG, Kim JH, Porporato A. 2012a. Analytical models of soil and litter decomposition: solutions for mass loss and time-dependent decay rates. *Soil Biol. Biochem.* 50:66–76
- Manzoni S, Taylor P, Richter A, Porporato A, Ågren GI. 2012b. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytol.* 196:79–91
- Mayer LM. 1994. Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chem. Geol.* 114(3–4):347–63
- Mayzelle MM, Krusor ML, Lajtha K, Bowden RD, Six J. 2014. Effects of detrital inputs and roots on carbon saturation deficit of a temperate forest soil. *Soil Sci. Soc. Am. J.* 78(S1):S76–83



- Mazzilli SR, Kemanian AR, Ernst OR, Jackson RB, Piñeiro G. 2014. Priming of soil organic carbon decomposition induced by corn compared to soybean crops. *Soil Biol. Biochem.* 75:273–81
- Mazzilli SR, Kemanian AR, Ernst OR, Jackson RB, Piñeiro G. 2015. Greater humification of belowground than aboveground biomass carbon into particulate soil organic matter in no-till corn and soybean crops. *Soil Biol. Biochem.* 85:22–30
- McBratney AB, Santos MM, Minasny B. 2003. On digital soil mapping. *Geoderma* 117:3–52
- Mikutta R, Mikutta C, Kalbitz K, Scheel T, Kaiser K, Jahn R. 2007. Biodegradation of forest floor organic matter bound to minerals via different binding mechanisms. *Geochim. Cosmochim. Acta* 71(10):2569–90
- Miller RD, Xia J, Park CB, Ivanov JM. 1999. Multichannel analysis of surface waves to map bedrock. *Leading Edge* 18(12):1392–96
- Minasny B, Malone BP, McBratney AB, Angers DA, Arrouays D, et al. 2017. Soil carbon 4 per mille. *Geoderma* 292:59–86
- Molon M, Boyce JI, Arain MA. 2017. Quantitative, nondestructive estimates of coarse root biomass in a temperate pine forest using 3-D ground-penetrating radar (GPR). *J. Geophys. Res. Biogeosci.* 122:80–102
- Moore JC, Berlow EL, Coleman DC, Ruitter PC, Dong Q, et al. 2004. Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* 7(7):584–600
- Moore JC, de Ruitter PC, Hunt HW, Coleman DC, Freckman DW. 1996. Microcosms and soil ecology: critical linkages between field studies and modelling food webs. *Ecology* 77(3):694–705
- Nave LE, Swanston CW, Mishra U, Nadelhoffer KJ. 2013. Afforestation effects on soil carbon storage in the United States: a synthesis. *Soil Sci. Soc. Am. J.* 77:1037–45
- Nave LE, Vance ED, Swanston CW, Curtis PS. 2010. Harvest impacts on soil carbon storage in temperate forests. *Forest Ecol. Manag.* 259(5):857–66
- Nichols E, Spector S, Louzada J, Larsen T, Amezcua S, et al. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141(6):1461–74
- Oades JM. 1967. Carbohydrates in some Australian soils. *Soil Res.* 5:103–15
- Oades JM. 1984. Soil organic matter and structural stability: mechanisms and implications for management. *Plant Soil* 76:319–37
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51:933–38
- Orwin KH, Kirschbaum MUF, St. John MG, Dickie IA. 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecol. Lett.* 14:493–502
- Osler GH, Sommerkorn M. 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. *Ecology* 88(7):1611–21
- Page SE, Rieley JO, Banks CJ. 2011. Global and regional importance of the tropical peatland carbon pool. *Glob. Change Biol.* 17(2):798–818
- Parfitt R, Parshotam A, Salt G. 2002. Carbon turnover in two soils with contrasting mineralogy under long-term maize and pasture. *Soil Res.* 40:127–36
- Parton WJ, Hartman M, Ojima D, Schimel D. 1998. DAYCENT and its land surface submodel: description and testing. *Glob. Planet. Change* 19:35–48
- Paustian K, Andr en O, Janzen HH, Lal R, Smith P, et al. 1997. Agricultural soils as a sink to mitigate CO<sub>2</sub> emissions. *Soil Use Manag.* 13:230–44
- Paustian K, Lehmann J, Ogle S, Reay D, Robertson GP, Smith P. 2016. Climate-smart soils. *Nature* 532:49–57
- Pelletier JD, Broxton PD, Hazenberg P, Zeng X, Troch PA, et al. 2016. A gridded global data set of soil, immobile regolith, and sedimentary deposit thicknesses for regional and global land surface modeling. *J. Adv. Model. Earth Syst.* 8:41–65
- Peng S, Guo T, Liu G. 2013. The effects of arbuscular mycorrhizal hyphal networks on soil aggregations of purple soil in southwest China. *Soil Biol. Biochem.* 57:411–17
- Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO<sub>2</sub>. *Ecol. Lett.* 15(9):1042–49
- Piñeiro G, Jobb agy EG, Baker J, Murray BC, Jackson RB. 2009. Set-asides can be better climate investment than corn ethanol. *Ecol. Appl.* 19(2):277–82
- Plante AF, Conant RT, Stewart CE, Paustian K, Six J. 2006. Impact of soil texture on the distribution of soil organic matter in physical and chemical fractions. *Soil Sci. Soc. Am. J.* 70:287–96

- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193:30–50
- Post WM, Emanuel WR, Zinke PJ, Stangenberger AG. 1982. Soil carbon pools and world life zones. *Nature* 298(5870):156–59
- Puget P, Drinkwater LE. 2001. Short-term dynamics of root- and shoot-derived carbon from a leguminous green manure. *Soil Sci. Soc. Am. J.* 65(3):771–79
- Rasse DP, Rumpel C, Dignac M-F. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269:341–56
- Reich P. 2006. *Soil organic carbon map*. Washington, DC: USDA-NRCS. [https://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/soils/?cid=nrcs142p2\\_054018](https://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/soils/?cid=nrcs142p2_054018)
- Richter DD, Markewitz D. 1995. How deep is soil? *BioScience* 45:600–9
- Sayer EJ. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol. Rev.* 81:1–31
- Scharlemann JP, Tanner EV, Hiederer R, Kapos V. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* 5:81–91
- Schlesinger WH. 1977. Carbon balance in terrestrial detritus. *Annu. Rev. Ecol. Syst.* 8:51–81
- Schlesinger WH. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348(6298):232–34
- Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, et al. 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478(7367):49–56
- Schrumpf M, Kaiser K, Guggenberger G, Persson T, Kögel-Knabner I, Schulze E-D. 2013. Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. *Biogeosciences* 10:1675–91
- Schuur EAG, McGuire AD, Schädel C, Grosse G, Harden JW, et al. 2015. Climate change and the permafrost carbon feedback. *Nature* 520:171–79
- Shahbaz M, Kuzyakov Y, Heitkamp F. 2016. Decrease of soil organic matter stabilization with increasing inputs: mechanisms and controls. *Geoderma* 304:76–82
- Six J, Bossuyt H, Degryze S, Denef K. 2004. A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. *Soil Tillage Res.* 79:7–31
- Six J, Frey S, Thiet R, Batten K. 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.* 70(2):555–69
- Slade EM, Riuatta T, Roslin T, Tuomisto HL. 2016. The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Sci. Rep.* 6:18140–40
- Slessarev E, Lin Y, Bingham N, Johnson J, Dai Y, et al. 2016. Water balance creates a threshold in soil pH at the global scale. *Nature* 540(7634):567–69
- Soller DR, Reheis MC, Garrity CP, Van Sistine DR. 2009. *Map database for surficial materials in the conterminous United States*. US Geol. Surv. Data Ser. 425. <https://pubs.usgs.gov/ds/425/>
- Sollins P, Kramer MG, Swanston C, Lajtha K, Filley T, et al. 2009. Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial- and mineral-controlled soil organic matter stabilization. *Biogeochemistry* 96(1–3):209–31
- Soong JL, Vandegehuchte ML, Horton AJ, Nielsen UN, Denef K, et al. 2016. Soil microarthropods support ecosystem productivity and soil C accrual: evidence from a litter decomposition study in the tallgrass prairie. *Soil Biol. Biochem.* 92:230–38
- Stewart CE, Paustian K, Conant RT, Plante AF, Six J. 2009. Soil carbon saturation: implications for measurable carbon pool dynamics in long-term incubations. *Soil Biol. Biochem.* 41(2):357–66
- Sulzman EW, Brant JB, Bowden RD, Lajtha K. 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO<sub>2</sub> efflux in an old growth coniferous forest. *Biogeochemistry* 73:231–256
- Syvitski JPM, Peckham SD, Hilberman R, Mulder T. 2003. Predicting the terrestrial flux of sediment to the global ocean: a planetary perspective. *Sediment. Geol.* 162:5–24
- Szłavec K, McCormick M, Xia L, Saunders J, Morcol T, et al. 2011. Ecosystem effects of non-native earthworms in Mid-Atlantic deciduous forests. *Biol. Invasions* 13(5):1165–82

- Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem. Cycles* 23(2):GB2023. <https://doi.org/10.1029/2008GB003327>
- Taylor J, Wilson B, Mills MS, Burns RG. 2002. Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. *Soil Biol. Biochem.* 34(3):387–401
- Todd-Brown KEO, Hopkins FM, Kivlin SN, Talbot JM, Allison SD. 2012. A framework for representing microbial decomposition in coupled climate models. *Biogeochemistry* 109(1–3):19–33
- Todd-Brown KEO, Randerson J, Post W, Hoffman F, Tarnocai C, et al. 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences* 10(3):1717–36
- Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, Hendricks DM. 1997. Mineral control of soil organic carbon storage and turnover. *Nature* 389(6647):170–73
- Townsend AR, Vitousek PM, Desmarais DJ, Tharpe A. 1997. Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38:1–17
- Trumbore SE, Chadwick OA, Amundson R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272(5260):393–96
- van Loosdrecht MC, Lyklema J, Norde W, Zehnder A. 1990. Influence of interfaces on microbial activity. *Microbiol. Rev.* 54:75–87
- van der Voort TS, Hagedorn F, McIntyre C, Zell C, Walthert L, et al. 2016. Variability in <sup>14</sup>C contents of soil organic matter at the plot and regional scale across climatic and geologic gradients. *Biogeosciences* 13(11):3427–39
- Vetter S, Fox O, Ekschmitt K, Wolters V. 2004. Limitations of faunal effects on soil carbon flow: density dependence, biotic regulation and mutual inhibition. *Soil Biol. Biochem.* 36(3):387–97
- Wagg C, Bender SF, Widmer F, van der Heijden MG. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *PNAS* 111(14):5266–70
- Wall DH, Bradford MA, St. John MG, Trofymow JA, Behan-Pelletier V, et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob. Change Biol.* 14(11):2661–77
- Wardle DA, Yeates GW, Watson RN, Nicholson KS. 1995. The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. *Plant Soil* 170:35–43
- Watson SJ, Luck GW, Spooner PG, Watson DM. 2014. Land-use change: incorporating the frequency, sequence, time span, and magnitude of changes into ecological research. *Front. Ecol. Environ.* 12(4):241–49
- Wei X, Shao M, Gale W, Li L. 2014. Global pattern of soil carbon losses due to the conversion of forests to agricultural land. *Sci. Rep.* 4:4062
- Wieder WR, Bonan GB, Allison SD. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nat. Clim. Change* 3(10):909–12
- Wieder WR, Grandy AS, Kallenbach CM, Taylor PG, Bonan GB. 2015. Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geosci. Model Dev.* 8(6):1789–808
- Wolters V. 2000. Invertebrate control of soil organic matter stability. *Biol. Fert. Soils* 31:1–19
- Xu X, Schimel JP, Thornton PE, Song X, Yuan F, Goswami S. 2014. Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. *Ecol. Lett.* 17(5):547–55
- Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ. 2010. Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* 37:L13402
- Zhang W, Hendrix PF, Dame LE, Burke RA, Wu J, et al. 2013. Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nat. Commun.* 4:2576
- Zimmerman AR, Chorover J, Goyne KW, Brantley SL. 2004. Protection of mesopore-adsorbed organic matter from enzymatic degradation. *Environ. Sci. Technol.* 38(17):4542–48



## New From Annual Reviews:

### ***Annual Review of Cancer Biology***

cancerbio.annualreviews.org • Volume 1 • March 2017

**ONLINE NOW!**

Co-Editors: **Tyler Jacks**, *Massachusetts Institute of Technology*

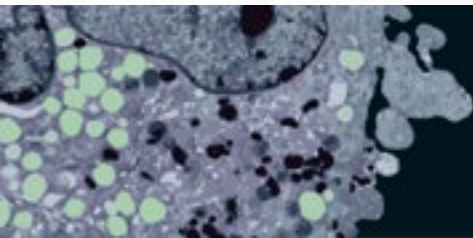
**Charles L. Sawyers**, *Memorial Sloan Kettering Cancer Center*

The *Annual Review of Cancer Biology* reviews a range of subjects representing important and emerging areas in the field of cancer research. The *Annual Review of Cancer Biology* includes three broad themes: Cancer Cell Biology, Tumorigenesis and Cancer Progression, and Translational Cancer Science.

#### TABLE OF CONTENTS FOR VOLUME 1:

- *How Tumor Virology Evolved into Cancer Biology and Transformed Oncology*, Harold Varmus 
- *The Role of Autophagy in Cancer*, Naiara Santana-Codina, Joseph D. Mancias, Alec C. Kimmelman
- *Cell Cycle-Targeted Cancer Therapies*, Charles J. Sherr, Jiri Bartek
- *Ubiquitin in Cell-Cycle Regulation and Dysregulation in Cancer*, Natalie A. Borg, Vishva M. Dixit
- *The Two Faces of Reactive Oxygen Species in Cancer*, Colleen R. Reczek, Navdeep S. Chandel
- *Analyzing Tumor Metabolism In Vivo*, Brandon Faubert, Ralph J. DeBerardinis
- *Stress-Induced Mutagenesis: Implications in Cancer and Drug Resistance*, Devon M. Fitzgerald, P.J. Hastings, Susan M. Rosenberg
- *Synthetic Lethality in Cancer Therapeutics*, Roderick L. Beijersbergen, Lodewyk F.A. Wessels, René Bernards
- *Noncoding RNAs in Cancer Development*, Chao-Po Lin, Lin He
- *p53: Multiple Facets of a Rubik's Cube*, Yun Zhang, Guillermina Lozano
- *Resisting Resistance*, Ivana Bozic, Martin A. Nowak
- *Deciphering Genetic Intratumor Heterogeneity and Its Impact on Cancer Evolution*, Rachel Rosenthal, Nicholas McGranahan, Javier Herrero, Charles Swanton
- *Immune-Suppressing Cellular Elements of the Tumor Microenvironment*, Douglas T. Fearon
- *Overcoming On-Target Resistance to Tyrosine Kinase Inhibitors in Lung Cancer*, Ibiayi Dagogo-Jack, Jeffrey A. Engelman, Alice T. Shaw
- *Apoptosis and Cancer*, Anthony Letai
- *Chemical Carcinogenesis Models of Cancer: Back to the Future*, Melissa Q. McCreery, Allan Balmain
- *Extracellular Matrix Remodeling and Stiffening Modulate Tumor Phenotype and Treatment Response*, Jennifer L. Leight, Allison P. Drain, Valerie M. Weaver
- *Aneuploidy in Cancer: Seq-ing Answers to Old Questions*, Kristin A. Knouse, Teresa Davoli, Stephen J. Elledge, Angelika Amon
- *The Role of Chromatin-Associated Proteins in Cancer*, Kristian Helin, Saverio Minucci
- *Targeted Differentiation Therapy with Mutant IDH Inhibitors: Early Experiences and Parallels with Other Differentiation Agents*, Eytan Stein, Katharine Yen
- *Determinants of Organotropic Metastasis*, Heath A. Smith, Yibin Kang
- *Multiple Roles for the MLL/COMPASS Family in the Epigenetic Regulation of Gene Expression and in Cancer*, Joshua J. Meeks, Ali Shilatifard
- *Chimeric Antigen Receptors: A Paradigm Shift in Immunotherapy*, Michel Sadelain

Annu. Rev. Ecol. Syst. 2017.48:419-445. Downloaded from www.annualreviews.org. Access provided by 86.139.252.155 on 11/08/17. For personal use only.





# Contents

|  |     |
|--|-----|
| Ecological Responses to Habitat Fragmentation Per Se<br><i>Lenore Fabrig</i> .....   | 1   |
| Ecological Networks Across Environmental Gradients<br><i>Jason M. Tylianakis and Rebecca J. Morris</i> .....   | 25  |
| Impacts of Artificial Light at Night on Biological Timings<br><i>Kevin J. Gaston, Thomas W. Davies, Sophie L. Nedelec, and Lauren A. Holt</i> .....  | 49  |
| The Utility of Single Nucleotide Polymorphism (SNP) Data in<br>Phylogenetics<br><i>Adam D. Leaché and Jamie R. Oaks</i> .....  | 69  |
| The Role of Sexual Selection in Local Adaptation and Speciation<br><i>Maria R. Servedio and Janette W. Boughman</i> .....  | 85  |
| The Potential Impacts of Climate Change on Biodiversity in Flowing<br>Freshwater Systems<br><i>Jason H. Knouft and Darren L. Ficklin</i> .....   | 111 |
| The Ecology of Mating and Its Evolutionary Consequences in Seed Plants<br><i>Spencer C.H. Barrett and Lawrence D. Harder</i> .....   | 135 |
| Process-Based Models of Phenology for Plants and Animals<br><i>Isabelle Chuine and Jacques Régnière</i> .....  | 159 |
| Evolution of Ecological Niche Breadth<br><i>Jason P. Sexton, Jorge Montiel, Jackie E. Shay, Molly R. Stephens,<br/>and Rachel A. Slatyer</i> .....   | 183 |
| Analysis of Population Genomic Data from Hybrid Zones<br><i>Zachariah Gompert, Elizabeth G. Mandeville, and C. Alex Buerkle</i> .....  | 207 |
| Biogeography and Biotic Assembly of Indo-Pacific Corvid Passerine Birds<br><i>Knud Andreas Jønsson, Michael Krabbe Borregaard, Daniel Wisbech Carstensen,<br/>Louis A. Hansen, Jonathan D. Kennedy, Antonin Machac,<br/>Petter Zabl Marki, Jon Fjeldså, and Carsten Rabbek</i> ..... | 231 |
| Attached Algae: The Cryptic Base of Inverted Trophic Pyramids in<br>Freshwaters<br><i>Yvonne Vadeboncoeur and Mary E. Power</i> .....  | 255 |

|  |     |
|--|-----|
| Temporal Variation in Trophic Cascades<br><i>Jonah Piovia-Scott, Louie H. Yang, and Amber N. Wright</i> .....  | 281 |
| Anthropogenic Extinction Dominates Holocene Declines<br>of West Indian Mammals<br><i>Siobhán B. Cooke, Liliana M. Dávalos, Alexis M. Mychajliw,<br/>Samuel T. Turvey, and Nathan S. Upham</i> .....  | 301 |
| Spatially Explicit Metrics of Species Diversity, Functional Diversity,<br>and Phylogenetic Diversity: Insights into Plant Community<br>Assembly Processes<br><i>Thorsten Wiegand, María Uriarte, Nathan J.B. Kraft, Guochun Shen,<br/>Xugao Wang, and Fangliang He</i> ..... | 329 |
| Pollinator Diversity: Distribution, Ecological Function, and Conservation<br><i>Jeff Ollerton</i> .....  | 353 |
| Evolution of Animal Neural Systems<br><i>Benjamin J. Liebeskind, Hans A. Hofmann, David M. Hillis,<br/>and Harold H. Zakon</i> .....   | 377 |
| Variability in Fitness Effects Can Preclude Selection of the Fittest<br><i>Christopher J. Graves and Daniel M. Weinreich</i> .....   | 399 |
| The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic<br>Controls<br><i>Robert B. Jackson, Kate Lajtha, Susan E. Crow, Gustaf Hugelius,<br/>Marc G. Kramer, and Gervasio Piñeiro</i> .....  | 419 |
| Apparent Competition<br><i>Robert D. Holt and Michael B. Bonsall</i> .....   | 447 |
| Marine Infectious Disease Ecology<br><i>Kevin D. Lafferty</i> .....  | 473 |
| Ecosystem Processes and Biogeochemical Cycles in Secondary Tropical<br>Forest Succession<br><i>Jennifer S. Powers and Erika Marín-Spiotta</i> .....  | 497 |
| Interactions Among Invasive Plants: Lessons from Hawai'i<br><i>Carla M. D'Antonio, Rebecca Ostertag, Susan Cordell, and Stephanie Yelenik</i> .....  | 521 |
| Phylogenetics of Allopolyploids<br><i>Bengt Oxelman, Anne Krag Brysting, Graham R. Jones,<br/>Thomas Marcussen, Christoph Oberprieler, and Bernard E. Pfeil</i> .....  | 543 |
| Identifying Causes of Patterns in Ecological Networks: Opportunities and<br>Limitations<br><i>Carsten F. Dormann, Jochen Fründ, and H. Martin Schaefer</i> .....   | 559 |

|   |     |
|---|-----|
| Innate Receiver Bias: Its Role in the Ecology and Evolution<br>of Plant–Animal Interactions<br><i>Florian P. Schiestl</i> ..... | 585 |
| Evolutionary Rescue<br><i>Graham Bell</i> .....   | 605 |

**Indexes**

|   |     |
|---|-----|
| Cumulative Index of Contributing Authors, Volumes 44–48 ..... | 629 |
| Cumulative Index of Article Titles, Volumes 44–48 .....       | 633 |

**Errata**

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://www.annualreviews.org/errata/ecolsys>