

Review

Lifting the Profile of Deep Forest Soil Carbon

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Abstract: Forests are the reservoir for a vast amount of terrestrial soil organic carbon (SOC) globally. With increasing soil depth, the age of SOC reportedly increases, implying resistance to change. However, we know little about the processes that underpin deep SOC persistence and what deep SOC is vulnerable to climate change. This review summarizes the current knowledge of deep forest SOC, the processes regulating its cycling, and the impacts of climate change on the fate of deep forest SOC. Our understanding of the processes that influence deep SOC cycling and the extent of SOC stores is limited by available data. Accordingly, there is a large degree of uncertainty surrounding how much deep SOC there is, our understanding of the influencing factors of deep SOC cycling, and how these may be distinct from upper soil layers. To improve our ability to predict deep SOC change, we need to more accurately quantify the deep SOC pool and deepen our knowledge of how factors related to the tree root–soil–microbiome control deep SOC storage and cycling. Thereby, addressing the uncertainty of deep SOC contribution in the global C exchange with climate change and concomitant impacts on forest ecosystem function and resilience.

Keywords: deep soil carbon; C sources; SOC protection; microbiome; climate change



Citation: Garrett, L.G.; Byers, A.K.; Wigley, K.; Heckman, K.A.; Hatten, J.A.; Wakelin, S.A. Lifting the Profile of Deep Forest Soil Carbon. *Soil Syst.* **2024**, *8*, 105. <https://doi.org/10.3390/soilsystems8040105>

Academic Editor: Nick B. Comerford

Received: 23 July 2024

Revised: 2 October 2024

Accepted: 4 October 2024

Published: 7 October 2024



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1. Introduction

Forests are carbon (C)-rich ecosystems. Forest plant biomass alone comprises over 80% of the world's terrestrial biomass C, with an estimated 363 Pg C in the live biomass [1,2]. Forest soils also hold massive reservoirs of C. It is estimated that 70% of the world's soil organic carbon (SOC) is held by the 30% of earth's land surface that is forested [3,4]. These SOC pools contribute significantly to forest ecosystem total OC stocks, with estimates ranging from 32 to 39% in tropical forests, 52 to 53% in temperate forests, and 60 to 85% in boreal forests globally [1,5]. This is significant, as net gain or loss in forest SOC has a disproportionately large influence on atmospheric C concentrations, thereby affecting climate change mitigation and adaptation efforts [6,7].

Recent data have revealed extensive deposits of OC deep in soils [8,9]. These have not previously been quantified but likely have a significant role in global C budgets [1]. Whilst 'deep soil' has no formal definition, soil-sampling efforts rarely extend below 30 cm, and hence, these OC stocks have been overlooked [10]. Similarly, national-level SOC-reporting guidelines have a default minimum depth of 30 cm [11,12]. However, while we know many soils extend far deeper than 30 cm [13], predicting soil thickness globally is challenging [14]. In some ways, it is not surprising that soil is typically collected to <30 cm depth; collecting soils down to 1 m depth or more often comes with considerable sampling and handling challenges, particularly in stony or compacted soils, incurring large time and financial

costs [13,15]. Whilst there are significant obstacles to the measurement of deep soils in general, and particularly understanding the ecology of OC within these systems, these are challenges we must urgently address.

Forest SOC supports a suite of ecosystem benefits. SOC is a key driver of soil fertility and nutrient provision to trees and other plants [5]. SOC is directly linked to total forest-ecosystem productivity (net primary productivity) supporting the delivery of wood, fibre, and food products [16]. The amount and cycling of SOC also impacts hydraulic regulation, water quality, biodiversity, and interacts with the environmental, biological, chemical, and physical properties and processes that determine forest functionality [17]. The above- and below-ground forest OC pools are in a dynamic and interconnected system that forms a virtuous cycle between OC pools and flows with forest function, productivity, and resilience. Our understanding of the aboveground OC stocks residing in forest vegetation is more advanced than those in soils (e.g., [1,18]). Our knowledge of forest SOC abundance, distribution, dynamics, ecology, and the impact of forest management on SOC declines rapidly with soil depth (e.g., [19,20]).

Current models of the terrestrial OC cycle show large discrepancies between predicted and observed C balances and fluxes (e.g., [21,22]). The predictive capacity of OC-cycling models is expected to reduce further under climate change. Many models are based on quasi-semi-state conditions, which do not necessarily represent ecosystem processes in general or the increasing extent of instability—from across a multitude of abiotic and biotic sources—that extend from climate change [23,24]. Current SOC models are also primarily focused on processes occurring within the upper soil. For example, the dynamic interactions between ecosystem inputs (i.e., litter fall and root exudates which are tied to net primary productivity) and SOC mineralization processes that are driven by moisture, temperature, and the chemistry of the OC inputs. What is lacking is consideration for how factors affect SOC change with depth [25,26]. Addressing uncertainty in deep SOC with empirically collected data is critical for the prediction of global C exchange and pool balance between soil, biomass, and atmospheric pools in the future [1,27–29] and concomitant impacts on forest ecosystem function and resilience.

Our ability to accurately model the global C budget is important to help navigate our trajectory through the volatility in conditions that climate change brings. Globally, for example, many forest ecosystems are approaching thermodynamic thresholds in which rates of biological C fixation (SOC inputs) will plateau and decline, whilst SOC mineralization (C returned to the atmosphere pool) will continue to increase exponentially [30]. The consequence is a tipping point whereby forests transition from net C sinks to net C sources until they reach a dynamic equilibrium with the new climate. In short, the fate and security of forest SOC affects not only the sustainability and resilience of our forests but the global climate and biomes more widely. It will influence our own trajectory towards either a safe or dangerous future for humankind. In many ways, the security and fate of forest SOC and our own fate are intertwined, where the health of the soil and land are inter-connected to that of the people and communities they support.

Our paper provides a review of the current understanding of deep SOC processes and impacts from climate change specific to mineral soils in forest ecosystems. Forest ecosystems are unique from other land uses, in particular through the depth of their rooting systems, which can be many metres deep, contributing to deep OC inputs [31,32]. We give an overview of how much deep forest SOC there is and review the evidence available for forest ecosystems on deep-SOC dynamics and processes and how climate change may impact these deep forest SOC pools. We discuss and summarize what is needed to improve our understanding of deep forest SOC for climate security.

2. How Much Deep Soil Carbon Is There?

It is estimated that large pools of OC are present deep in soil, i.e., billions of tonnes at the regional-scale, reported by Gonzalez, Bacon [8] and Ross, Grunwald [9]. In forest systems, an average of 50% of SOC stocks can be present in the soil below 20 cm to 1 m

depth, with an additional 56% estimated in the 100–300 cm depth [33]. A wide range of 27–77% is also reported for forest SOC stocks below a 20 cm to at least 80 cm depth [13]. The deeper soil is measured, the more SOC can be found, capturing that soil can be deep [34] and tree roots can supply OC deep into the soil profile [31,35]. For example, an additional 36% of SOC was found in the 100–200 cm layer in tropical forests [36]. Moreover, SOC has been found in 10 m deep soil pits in the Amazon forests, with 16% of all SOC found below 3 m depth [15]. However, deep soil layers are rarely explored compared to upper soil layers [10]. Moreover, the soil coarse fraction (>2 mm size) is rarely included in SOC reporting but can contribute significantly to total SOC stocks, particularly in deeper soils [13,19,37,38]. This fundamental lack of information leaves us with high quantitative uncertainties related to the extent of deep SOC missing in forest OC biome reporting (Figure 1).

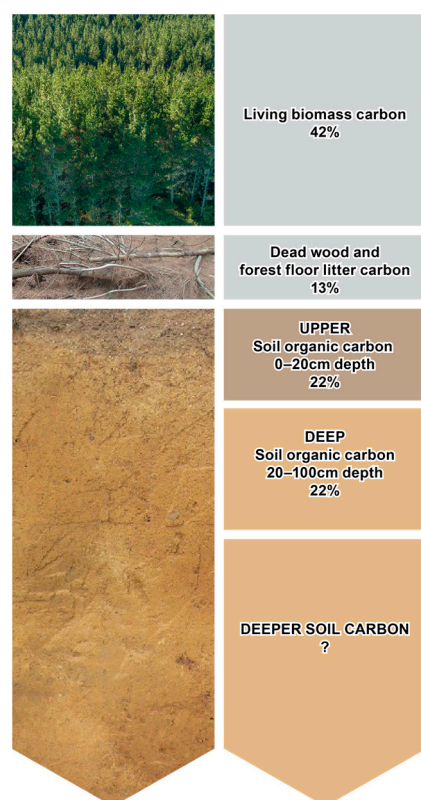


Figure 1. What deep SOC has not been measured within the forest? Global forest OC pool percent by forest component (living biomass, dead wood and forest floor, and soil to 1 m depth) from Pan, Birdsey [1]. SOC in the 20–100 cm soil layer is 50% of the total SOC to 1 m depth from Jobbágy and Jackson [33].

Deep SOC has been reported as soil below 20 cm depth (e.g., [13]) or below 30 cm (e.g., [35]) as below these depths soil is typically not sampled [10]. We know little about the distribution of deep SOC pools vertically, including what exists below the rooting zone, the extent of spatial variation, or changes over time. We do know that, in general, with increasing soil depth, there is typically a decrease in total SOC, an increase in older SOC, a decrease in root biomass and microbial biomass, and an increasing influence of soil mineralogy as a driver of SOC cycling [19,39]. Also, with increasing depth, the direct connectivity to the atmosphere decreases, and upper soil layers are more dynamic in temperature change, moisture availability, freeze–thaw cycles, and have greater oxygen concentrations which impact SOC cycling [40–42] (Figure 2). The maximum extent of deep soil is where bedrock is found or where the soil vadose zone ends and transitions into the saturated zone where there is little or no plant root interaction with the soil (Figure 2).

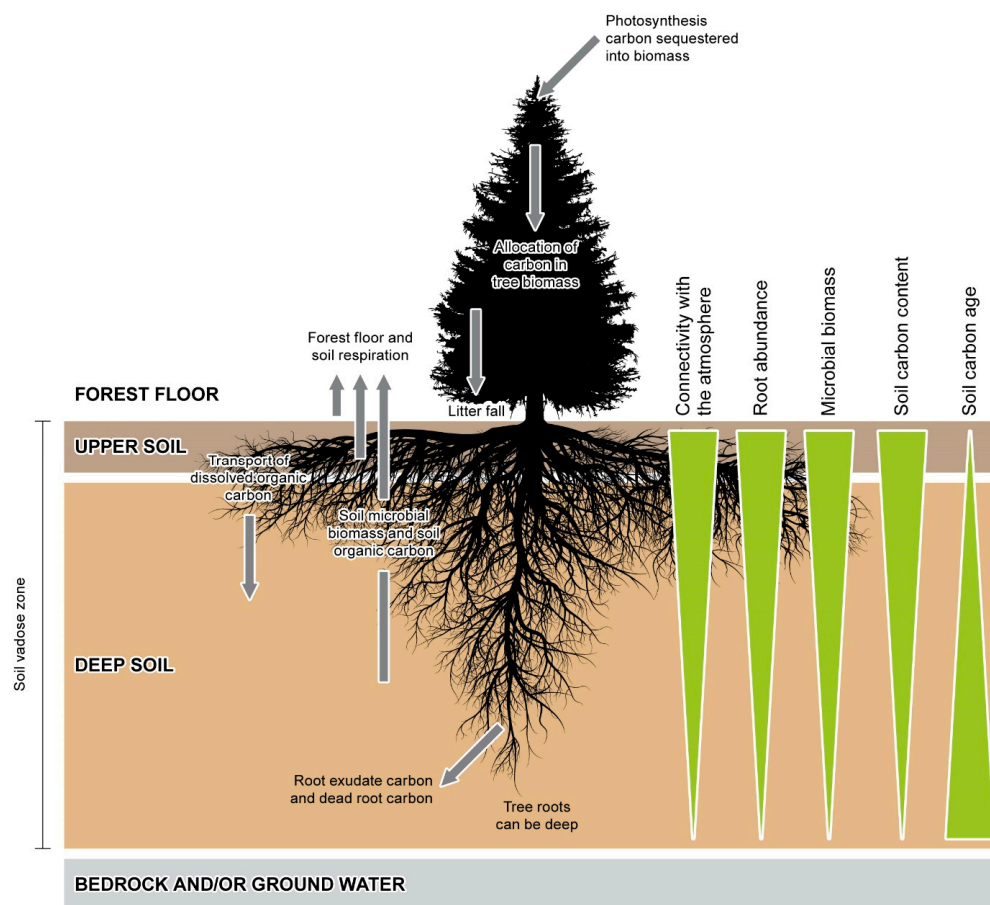


Figure 2. Conceptual representation of upper soil and deep soil in a forest system and the key differences between the distinct but connected soil layers related to SOC cycling.

Considering how heterogeneous soil environments are both within and between ecosystems for any one soil, the depth at which SOC-cycling processes change and deep soil begins will be different and more linked to soil-pedologic characteristics, the depth of the soil vadose zone, and the ecological context. Therefore, deep soil could be defined as ‘soil that is sufficiently different from the upper soil layers in biological, physical, or chemical components, such that it comprises a distinct ecosystem that is connected on a vertical gradient but influence by different factors, and in which processes and constituents cannot be readily or accurately estimated from observation or measurement of upper soil layer properties’. This is compared to generalized sampling depth cut-offs defining the upper limit of deep soil (i.e., 30 cm), which appear arbitrary when considering the wide variability in soil structure and formation, especially for soils that are many metres deep [43].

Currently, the lack of data to define deep soil is limiting our understanding of forest ecosystems and the ability to predict and manage deep-SOC dynamics going into an uncertain climate future. As the ability to predict deep SOC pools and its sensitivity in response to ecological change is critical to successfully manage deep SOC, we undertook a brief analysis of forest SOC in managed systems from a meta-analysis on harvesting effects on SOC by James and Harrison [44] (see Appendix A for methods). The findings are important. In particular, data collected from the topsoil layer poorly predict deeper SOC stocks (Figure A1). Moreover, the response of the topsoil layer to harvesting effects was essentially uncorrelated with the effect of harvesting on deeper soil layers (Figure A2). Therefore, an understanding of deep-SOC dynamics and processes are needed to support our ability to predict and manage deep-SOC dynamics going into an uncertain climate future.

3. Deep-Soil-Carbon Dynamics and Processes

3.1. Deep-Soil Organic Carbon Source

Forests store much OC as live biomass, above and below ground, and in the forest floor [1], which is the primary source of OC for forest soil. Deep soil is highly influenced by OC from tree root systems, including root biomass itself and exudates [19,35,45], compared to the upper soil layer where the forest floor also has an important role in supplying OC [46] (Figure 3). Tree roots comprise 18 to 32% of the total tree biomass and can reach substantial depths in soil [32,47,48]. Key tree root traits can strongly vary in the root system and with soil depth [31,49]. These include key characteristics such as lifespan, activity, respiration, exudation, chemistry, decomposition rates, root-hair density, and mycorrhizal colonization [31,50], all of which are directly connected to OC cycling. Fine roots in particular can represent >20% of net primary production [50]. While this fraction is proportionately small in terms of total root biomass per se, a massive investment in OC entering the forest soil is allocated to this relatively short-lived, but highly active, component of the root system [50]. With increasing soil depth, fine root decomposition has been reported to change, with slower decomposition rates at depth (95 cm) compared to upper soil layers (15 cm) as the pool of labile OC and nitrogen are depleted and the microbial capacity at depth becomes limited [51]. Thus, they have a disproportionate impact on SOC pools and cycling in deeper soils. Furthermore, 10–44% of root-allocated OC may flow to mycorrhizal fungi [52–54], portions of which will be directly respired, or converted to microbial–organic matter (living cellular material), and move into the soil food web and be subsequently modified and transported. Soil depth can also impact root-exudate chemistry with, for example, deeper roots allocating low-C organic acids to acquire mineral bound phosphorus compared to shallower roots that are accessing organic-bound nutrients [55].

While the initial sources of SOC are forms of plant-C, a large fraction of SOC in deep soils can be dead microbial cells (microbial necromass) (Figure 3). In forest soils, microbial necromass can comprise 44% of the SOC below 20 cm depth [56] and 62% of total SOC below depths of 50 cm (Figure 3) [57]. This compares to ~30% of the total SOC in upper soil layers [56–58]. Microbial transformations are central to the conversion and cycling of OC compounds, shaping the composition and stability of SOC in soil ecosystems and are an important component of total SOC in deep soils.

Deep SOC deposits can also occur from the downward movement of dissolved OC (DOC) and small particulate SOC through preferential flow pathways (Figure 3) [59–62]. In some soils, this results in the formation of C-rich subsoil horizons, where SOC is immobilized with or by reactive metals (i.e., podzolization [63]). Subsoil podzol horizons can hold significant deep SOC stocks [8]. Buried soils (paleosols) and SOC buried by alluvial and colluvial deposits can also result in deep-soil layers rich in OC [64]. Volcanic deposits from explosive eruptions can additionally result in deep SOC in the form of pyrogenic SOC [65]. Moreover, deeper SOC inputs can occur through disturbance events such as the wind throw of trees or forest management activities, which can mix upper soil into deeper layers (e.g., [66]), or fire events, which can result in deep pyrogenic SOC [67].

What emerges is a complexity of processes involved in the source of deep SOC, including the interaction of factors related to total root biomass, age, turnover, activity, the extent of microbial interactions, particularly mycorrhization, and allochthonous SOC inputs during soil formation. These factors are expressed against a background of plant genetic influences, plant health, site variation, environment, soil formation, management (in production forests), and ecosystem complexity (e.g., plants present, herbivory, and other interactions) to be collectively expressed as variation in deep forest SOC. The overall parameter space for interactions and variation in outcomes related to OC flow and storage is considerable. In light of this complexity, it is not unreasonable that when modelling roots and their influence on deep SOC, they are typically based on gross estimates extrapolated from a few well-characterized systems, leading to uncertainties regarding roots and their influence on deep-SOC supply (e.g., [31,49]).

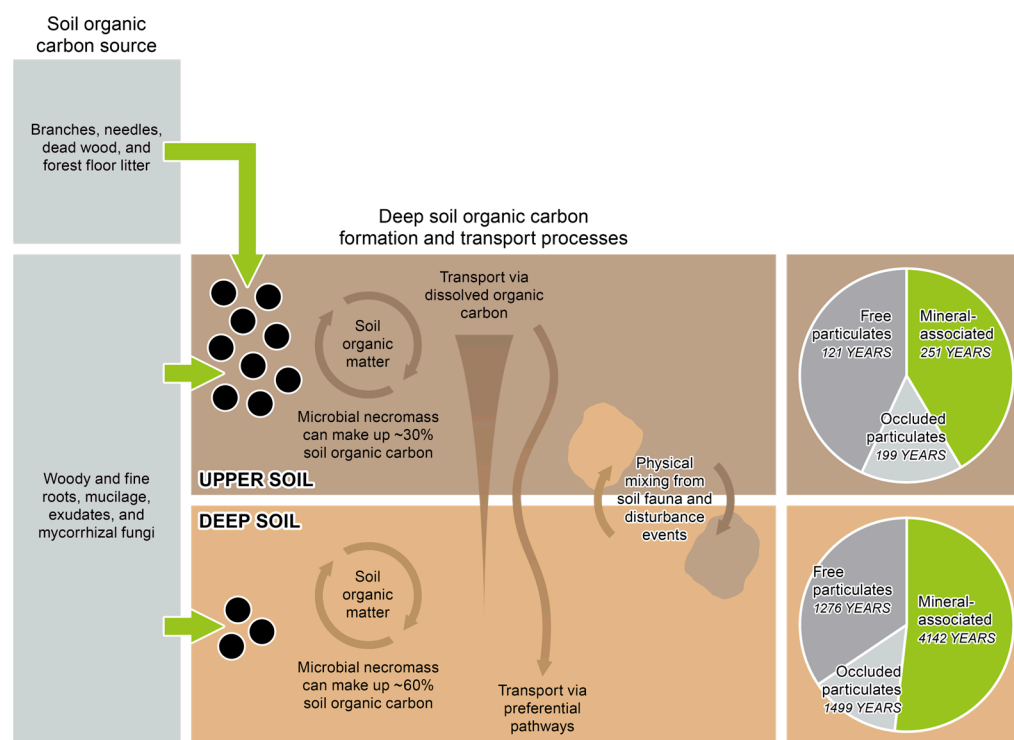


Figure 3. Generalization of forest systems deep-SOC source, SOC formation and transport processes, and resulting SOC fraction pools, their dominance, and turnover time compared to upper soil. The soil fraction proportion and turnover time in years data are from Heckman, Hicks Pries [68], selected for forest landcover less than 50 degrees north and comparing ≤ 0.1 m soil depth with ≥ 0.5 –2 m soil depth.

3.2. How Old Is Deep-Soil Carbon and What Keeps It There?

With increasing soil depth, SOC age increases, and even at just 1 m depth, the average age of SOC often exceeds several thousands of years [69–71]. This considerable age is an outcome of complex and poorly understood processes. These include large variability in the chemical diversity and decay rates of OC substrates, physical protection of SOC via aggregates, mineral stabilization, physical disconnection between microbial decomposers and SOC, and variability in ecosystem conditions such as soil redox states, oxygen concentrations, and temperature [42,69,72]. As several of these key attributes typically all change with depth, ‘depth’ itself often captures the largest proportion of variation associated with SOC abundance and age [68,73]. However, this disguises which components are key to controlling the age of OC in soils.

With increasing depth, the chemical/molecular structure of SOC can vary due to soil pedological processes. Typically, with increasing depth, SOC becomes more highly modified, with a decline in molecular complexity and diversity when compared to SOC in upper soil layers, moving from labile to more recalcitrant forms [74–76]. Despite this, experimental evidence shows that the molecular structure of SOC is rarely a key protective mechanism per se. [77]. When microbes within soil can access these molecules, mineralization typically proceeds [72]. Rather, the emerging view is that environmental and biological factors, including microbial community composition, organo-mineral associations, and temperature and moisture, exert stronger control over SOC persistence than the molecular structure of the OC itself [72,77]. Furthermore, low ratios of other key nutrients (nitrogen, phosphorus, and sulphur stoichiometry withing soil organic matter) necessitates additional effort to scavenge these from the environment, metabolic adaptations for redistribution and reutilization of OC, or restructuring cellular processes to minimize requirements [78,79].

At the micro-environment scale, soil properties related to SOC protection include the extent and nature of reactive mineral surfaces, moisture, soil age, mineral protection, and depth [80]. For example, substantial amounts of old SOC can be protected through mineral-associated organic carbon (MAOC) and protected as occluded particulate organic carbon (POC). Approximately, 60% and 14% of SOC are held in these fractions, respectively [68]. With increasing soil depth, the relative proportion and age of the MAOC fraction generally increases (Figure 3), highlighting the important role of MAOC protection for deep SOC pools [68,81]. Minerals that are most typically found to be associated with OC include phyllosilicates, oxides, hydroxides, and short-range-order minerals like ferrihydrite, allophane, and imogolite [81]. Thus, changes in the concentration of iron (Fe), aluminium (Al) (hydro)oxides, and the qualitative and quantitative amount of clay with soil depth [82] influences SOC protection [57]. In addition, tree roots have an increasingly important role in deep SOC protection at the microaggregate scale through the physical protection of the SOC, which is positively influenced by high root suberin concentration, symbiosis with mycorrhizae, and increased rhizodeposition [45].

Free POC (Figure 3) is typically younger than both the MAOC and occluded POC fractions and can be an important contributor to forest SOC [68]. POC is typically of plant origin, not bound to minerals or occluded in aggregates and can be protected through its inherent biochemical (chemical/molecular structure) recalcitrance [83]. The division of MAOC and free POC has been useful in describing SOC persistence and vulnerability to disturbances, and, in general, free POC is more vulnerable to disturbance and cycling faster than MAOC [83,84].

Soil DOC (Figure 3) is an active, mobile, and typically younger SOC pool that generally decreases in amount and becomes progressively more chemically recalcitrant with increasing depth, undergoing microbial decay and change through soil surface exchange mechanisms [85,86]. Soils that have little adsorption capacity, for example, sandy soils, would be the exception. In these soils, DOC can comprise a large component of deep SOC, retain chemical similarity to fresh plant leachates and, therefore, be more susceptible to microbial degradation [85].

We have outlined several known processes that contribute to the persistence of deep SOC stocks. The key questions, however, are ‘does older SOC stay protected when changes to the wider SOC cycle occur’ and ‘at what soil depth do these changes remain relevant?’ The examples given related to land use change and management demonstrate some of the current uncertainties related to SOC protection that need addressing, for example, uncertainties as to why deep SOC can be protected for hundreds to several thousands of years even under major shifts in land cover and management [87–89]. There are unanswered questions linked to the response of protected deep SOC to management changes as mediated by soil type (degree of weathering, abundance of reactive mineral surfaces). For example, highly weathered and young soils are affected by forest harvest practices differently compared to soils with significant secondary mineral accumulations [90]. A meta-analysis by James and Harrison [44] showed a substantial variation in the response of different soil depths to harvesting impacts, with soils 60–100 cm and deeper exhibiting greater SOC losses compared to surficial layers. As the soil environment changes with depth, the strength and influence of these different influencing factors in controlling SOC protection are likely to shift. However, the knowledge that is required to develop a fundamental understanding of these interacting factors for deep soil is limited.

3.3. Deep-Soil Microbiota: What Is Going on Down There?

The soil microbiome comprises only a small percent of the total soil organic matter and with increasing soil depth, the richness and biomass of both bacterial and fungal communities typically decrease (Figure 4) [91–94]. Although small, this living and dynamic component constitutes a key driver of SOC transformation and storage [95]. Factors influencing the soil microbiome can, therefore, influence the rate and types of SOC transformations. Towards this, soil pH, moisture, temperature, plant community composition,

nutrient availability (e.g., N and phosphorus), OC inputs (amount and type), and oxygen concentration are all important [96–100]. All these factors exhibit a large spatial heterogeneity [101], especially down-soil profiles [102]. As a consequence, the deep-soil climatic conditions are less dynamic than the surface soil's (Figure 4); microbial access to SOC in deep soil becomes increasingly limited, mostly due to protection from biodegradation as MAOC and occluded POC [39,103–106]; and increasing nutrient and oxygen limitation alters microbial activity or metabolic strategies [42,98,107]. This, coupled with reduced microbial biomass, results in a decline in microbial respiration with depth [108–110].

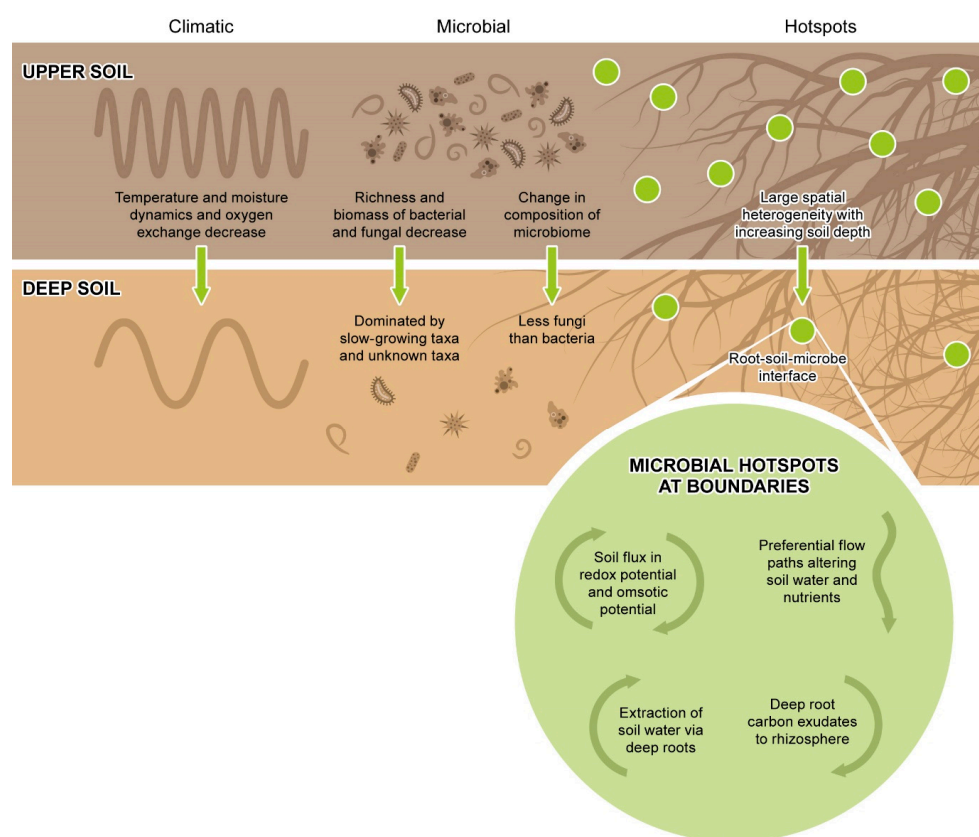


Figure 4. Generalization of the main trends in soil-microbial changes and the influencing factors with increasing soil depth.

With increasing soil depth, microbial activity becomes increasingly restricted to small microhabitats, or ‘hotspots’ comprising less than 1% of total soil volume (Figure 4) [111,112] (Figure 4). In deep soil, microbial hotspots can arise from the input of fresh substrates and nutrients from rhizodeposition [113,114]. Additionally, hotspots can arise in preferential flow paths and biopores that enable the transport of dissolved and particulate OC down soil. These flow paths are more exposed to drying and wetting and, coupled with their enhanced nutrient/substrate supply, provide conditions favourable for microbial activity [62].

The hydrological alteration of soil is important for supporting microbial hotspots. This occurs, for example, through significant rainfall and flood events, extraction of soil water via deep roots, preferential flow paths, or rising/fluctuating ground water, and results in fluctuations in soil redox state and osmotic potential (Figure 4) [42]. Migrating soil redox boundaries provides conditions conducive to electron flow across different geochemical moieties, enabling energy generation for microbial respiration and growth [115]. In addition, soil redox potential can impact microbial community assemblage due to species shifts in relation to soil redox adaptation [116]. Furthermore, the microbial communities themselves can influence soil redox by catalyzing redox reactions and altering local soil redox states [42,117]. Yet, despite being tightly coupled, our understanding of how the

interplay between the soil microbiota and changes in redox state changes with soil depth is poor.

With increasing soil depth the composition of the soil microbiome changes, the relative abundances of archaea, Gram-positive bacteria (including Actinobacteria) increase, whilst Gram-negative bacteria, protozoa, fungi, and the fungi/bacteria ratio typically decline (Figure 4) [56,118]. Changes in soil conditions such as oxygen concentration and soil moisture with depth are associated with many of these compositional shifts. For example, an increased abundance of archaea and sulphate-reducing bacteria is indicative of increasingly anaerobic soil conditions with depth [119]. Furthermore, changes in the amount and accessibility (molecular composition and soil protection mechanisms) of SOC influence microbial distribution in soils, and taxonomic differences in substrate utilization patterns may explain the compositional shifts in microbial communities with depth [120]. For example, members of the Proteobacteria and Bacteroidetes have been found in greater abundance in upper soils due to their preference for utilizing easily degradable, labile OC [102]. The abundances of these bacterial groups are positively correlated to increased SOC mineralization rates [121]. In contrast, deeper soils have a greater abundance of oligotrophic bacteria, such as Firmicutes, Chloroflexi, Nitrospirae, Verrucomicrobia, and Dormibacteriaota, of which some members show adaptation to utilizing recalcitrant OC and inorganic nutrients [119,122,123].

Fungi are an important contributor to deep-soil SOC stability, as the fungal cell compounds are decomposed more slowly than bacteria and therefore able to persist longer in the soil; moreover, the fungal hyphae can extend into the soil mineral matrix and transport OC within the soil and to mineral soil particles to form MAOC [56]. Although fungal communities are reported to exhibit distinct compositional shifts with depth [124], their fundamental relationships with deep-soil ecosystems are under-studied compared to bacteria. Furthermore, previous research has predominantly focused on mycorrhizal fungi and, as such, is largely confined to the rooting depth of the plant system under study [125,126]. The abundance of saprophytic fungi is known to sharply drop with soil depth as the importance of OC resources derived from the litter layer decreases [127,128]. In contrast, ectomycorrhizal fungi generally increase with soil depth [124,129], as they are supplied with OC inputs directly provided by plant roots. More recent research by Frey, Walthert [119] identified several poorly known fungal taxa, of both ectomycorrhizal and saprophytic guilds, that increased in abundance in forest soils down to 2 m deep. This was the first time several of these fungal taxa were reported to be associated with such soil layers. These findings highlight how the under-representation of studies focused on exploring the deeper soil microbiome forms a major barrier in our understanding of the forest soil microbiome and SOC cycling.

Research to date has shown that depth has a strong impact on microbial community structure and processes [102], but the collective impact of the factors involved (discussed above) are largely unknown. Plus, other critical knowledge gaps remain in how structural soil properties such as mineralogy, bulk density, aggregation, and porosity directly and indirectly affect microbial communities and processes [130]. A fundamental understanding of the relative importance of these soil properties and how they are collectively expressed to influence soil microbiome and OC cycling in deep soils is needed for the effective modelling of long-term SOC changes.

4. Climate Change Impacts on Deep Soil Carbon

4.1. Deep-Soil Connectivity with the Changing Atmosphere

Global climate change and the resulting increases in atmospheric carbon dioxide (CO₂) and temperature, shifts in precipitation, and increased frequency of extreme weather events will inextricably change the amount of OC entering into, moving through, and exiting forest ecosystems [30]. Climate change is also expected to increase the frequency and severity of forest disturbance events, abiotic and biotic, which can have direct and indirect impacts on forest ecosystems [131–133]. The simultaneous effects of an increasing number of global

change stressors together, be they atmospheric changes or disturbance events, are expected to have a more negative impact on SOC cycling than a single event on its own [134]. The C security in deep forest soils will ultimately comprise the expression of the tree root–soil–microbiome interaction under changing climatic conditions (Figure 5). The altered distribution of OC among pools will impact and destabilize the delivery of forest ecosystem benefits [7]. Although deeper soils are less directly connected with the atmosphere than upper soils (Figure 2) and benefit from increased buffering to climatic fluxes, they will nevertheless be impacted by temperature and soil moisture shifts. For example, in deeper soils (*sensu* below 1 m depth), it is predicted that the rate of soil warming will occur in step with soil at 10 cm [135]. Shifts in soil moisture and extreme drought will also reach deep within the soil profile [136,137].

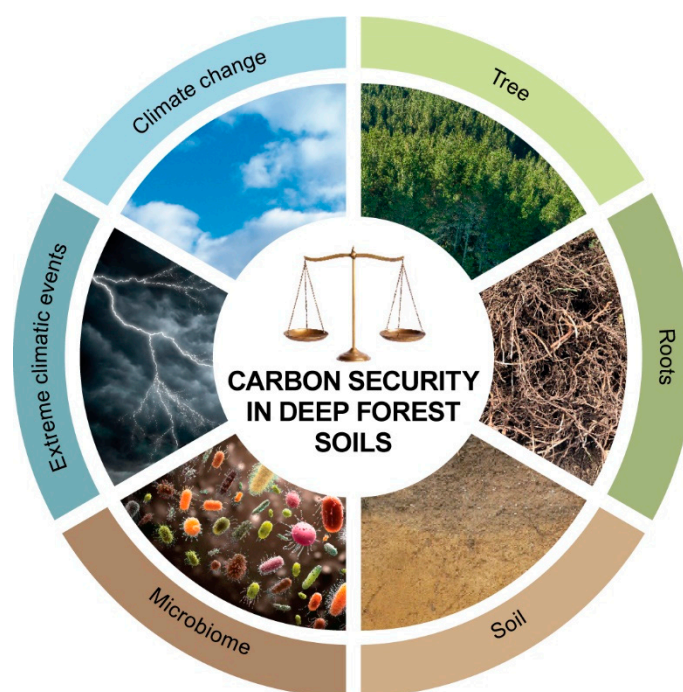


Figure 5. Carbon security in deep forest soils is the balance of the tree root–soil–microbiome under changing climatic conditions.

OC in deep soil is, however, directly connected with processes associated with tree roots. Indeed, roots are a key connection conduit between deep soils and alteration in above-ground atmosphere; these are expressed through changes in tree ecophysiology. Under environmental change, deep fine roots will be sensitive to changing soil moisture, nutrients, and soil atmosphere compositions due to their plasticity to adapt to heterogeneous soil conditions [31]. For example, under elevated CO₂, fine root proliferation is expected to increase, including deeper extension into the soil profile [138], and the amount and forms of root exudates they release will be modified [139]. Similarly, elevated CO₂ levels indirectly impact the soil microbiota by altering plant diversity, growth, outputs of litter, and release of plant root exudates [140].

4.2. Vulnerability of Deep-Soil Carbon

4.2.1. Change in Temperature and Moisture

Climate change will impact microbial processes critical in regulating the flux of CO₂ from the soil to the atmosphere. This will occur via shifts in the structure, diversity, physiology, and activity of the soil microbiome [140–142]. Direct impacts of climate change on the soil microbiota are primarily expressed through changes in temperature and soil moisture regimes [140]. In particular, microbial enzyme activity is highly sensitive to temperature optima [29]; as temperature increases, this will be expressed as faster SOC

decomposition and release of CO₂ to the atmosphere [143]. Overall, the resulting climate-change-driven shifts in the source and turnover of deep forest SOC are intertwined with complex interactions and feedback that occur between microorganisms and other biotic and abiotic factors. We urgently need to improve our mechanistic understanding of forest ecosystem OC cycling [84,140,144].

Changes in the soil moisture, which controls nutrient and oxygen supply to microorganisms, may alter the depth, distribution, and activity in soil hotspots, such as soil redox states and osmotic potential. This will have flow-on effects for SOC cycling. As deep SOC is typically dominated by older SOC that is bound to mineral surfaces and has low bioavailability [68] (Figure 3), it could be assumed that deep SOC would be more resistant to microbial degradation compared to upper SOC. However, the different SOC fraction pools (Figure 3) behave in unique ways that cannot be readily determined from bulk SOC responses [84]. Previous research in forest systems has identified losses of deeper SOC may be more vulnerable to increasing temperatures than upper SOC, particularly where deep soils have greater free POC, linking SOC protection mechanisms to deep-soil temperature sensitivity [26,145]. For example, following whole-soil warming, consistent increases in soil respiration rates and net losses of deeper SOC were identified (deficit of 33% SOC stored between 20 and 90 cm) [146,147]. This was mainly due to the decomposition of free POC, including pyrogenic SOC, which made up 36% of SOC in deeper soil layers [147,148]. In the same experiment, the loss of free POC due to warming resulted in a more degraded and possibly more stable pool of SOC at depth, raising uncertainty on the impacts of future soil function [149].

As the MAOC fraction has longer turnover rates, its sensitivity to increasing temperatures and changes in moisture has been difficult to accurately determine [84]. However, observations from natural climatic gradients [68] have found that increasing mean annual temperature results in decreased persistence (overall age) of all SOC fraction pools. Furthermore, increasing mean annual temperature resulted in increased occluded POC and MAOC fractions at all depths. These findings indicate that increasing temperatures are less likely to destabilize older protected SOC and could add new SOC to these pools [68]. In the same study, wetter deep soils had increased occluded POC with no change in other SOC pools [68].

In a laboratory study, SOC was shown to be sensitive to changes in temperature and moisture with the degree of change linked to SOC protection mechanisms influenced by the mineral properties of the sub-soil [150]. Moreover, it could be expected that elevated precipitation would transport more DOC to deep soils, increasing opportunities for DOC to interact with mineral soil surfaces and adding to the MAOC fraction [84]. Moreover, mineral weathering is expected to be impacted by both temperature and moisture shifts. For example, higher soil moisture may have negative consequences over the short term on the development of mineral–organic complexes but positive consequences over the longer term through soil depth development and therefore greater soil volume for SOC storage [68].

4.2.2. Priming Effect

The soil-priming effect occurs when either fresh OC is added to the soil or liberated from existing SOC pools as conditions change. This promotes microbial SOC respiration/mineralization and net SOC loss [139,151]. In response to climate change, fresh OC inputs to deep soil are predicted to occur via plants allocating increased resources to rhizosphere extension/growth and exudation; both will likely result in priming via the addition of fresh OC to deep soil [138,139]. Moreover, priming may increase with rainfall, where liable SOC is transported from upper to deeper soil layers through preferential flow paths. Understanding how the priming effect impacts deep SOC is important, especially considering trees can be deep rooting, and there can be a large pool of accumulated OC at depth in forest soils.

The impact of the priming effect may be stronger on MAOC rather than POC [19]. This is significant as old, MAOC comprises a large portion of SOC in deeper soil layers (Figure 3). Under laboratory conditions, for example, increased input of root exudates into boreal forest soil resulted in an enhanced turnover of MAOC, and this priming effect increased with depth [152]. Likewise, in a sub-tropical forest the OC in the sub-soil had approximately twice the sensitivity to priming compared to topsoil OC [153]. Importantly, both priming and SOC sequestration should be considered as complementary, not opposing, processes. For example, in a temperate forest upper soil layer (0–8 cm depth), mineral-associated SOC can accumulate due to strong positive effects on the microbial biomass [154]. Overall, however, we currently have large uncertainties regarding deep fine root dynamics and even greater uncertainties for tree root–soil–microbiome interactions and any impacts of climate change on the priming effect.

4.2.3. Impact of Extreme Climatic Events

Extreme climatic events can severely impact forest ecosystem OC cycling. In particular extreme drought, heavy rainfall, storms, and heat are all linked to a disruption of terrestrial OC cycling [137,155] or even forest die-off (e.g., [156]). Extreme climatic events can also increase the frequency and severity of forest-damaging abiotic factors such as fire, wind throw, and erosion, which can cause high disturbance to forest ecosystems [131,132], including likely impacts on deep SOC cycling. However, knowledge of the specific impacts of extreme climatic events on deep SOC is lacking. Nevertheless, it is evident that extreme climatic events will directly alter the environmental conditions under which SOC is both formed and cycled within soil. Similarly, it is reasonable to expect that there will be flow-on impacts on SOC transformation; changes in environmental conditions are directly connected to impacts on microbial activity composition and activity/respiration, and thereby influence rates of SOC recycling and flow through soil food webs.

During extreme drought, drying of the upper soil layers will drive plants to explore deeper soil layers for water and nutrients. Accordingly, more plant biomass allocation and activity (roots) will be allocated to deep soil which may stimulate a priming effect [31,138,139]. Moreover, when soils are dry, they are particularly susceptible to the impacts of heavy rainfall events as water rapidly infiltrates cracks, preferential flow paths and biopores, directing SOC to deeper soil layers. This includes DOC and small particulate SOC, both of which may stimulate the priming of resident deep-soil SOC [19].

Altered precipitation patterns that change cycling between wet and dry soil states are important. An increase in the frequency or magnitude of extreme moisture cycles exposes soils to more events of rewetting dry soils and a burst of CO₂ from microbial activity in the soil—known as the ‘Birch effect for CO₂’ [157]. The importance of the Birch effect in a deep-soil system is largely unknown. A single study conducted within planted forests reported that drying–wetting cycles alone (i.e., no new OC inputs) did not influence respiration in deep soil (3 m max depth) [137]. With climate change altering both moisture relationships in deep soil systems and also feedback with the live forest biomass, there is a potential risk to the security of deep forest SOC. Thus, understanding soil microbiota response to altered environmental conditions is important for us to identify how they may amplify or reduce the rate of climate change.

4.2.4. Change in Microbial Composition

As well as impacting the activities of the soil microbiota, the effects of climate change can alter the composition of soil microbial communities and/or the biogeochemical processes they mediate. These impacts may cascade to impacts on SOC [155]. For example, Dove, Torn [158] found that microorganisms in deep forest soils were more resistant to compositional changes following soil warming compared to upper soils. This was suggested to be due to their slower growth rates providing a lag-time for the expression of changes. Although these taxa may exhibit delayed response, the response of fast-growing

oligotrophic bacteria is evident [123]. As such, proportional shifts in microbial groups associated with different rates of SOC cycling occur [121].

Under elevated CO₂ levels and across multiple land uses, Sun, Wang [159] reported overall declines in the ratio of fungi/bacteria, Gram-positive/Gram-negative bacteria, and Acidobacteria/Proteobacteria (but findings varied). These results highlight the difficulty in predicting how climate change will impact the activity and composition of the soil microbiota, an issue that is further heightened in knowledge-poor deep-soil environments. To better understand how climate change will impact the composition and functional properties of the deep soil microbiome and regulation of SOC, focused and ecosystem-specific research is required.

5. Discussion

The relationship between soil depth, C security, and environmental conditions is complex. However, understanding these is important as deep forest SOC is integral to the functioning and resilience of forest ecosystems and significantly contributes to Earth's C budget. In this section, we summarize key steps needed to improve our understanding of deep SOC to inform future action.

Our knowledge of deep SOC, from stocks to biogeochemical processes to sensitivity to climate change is drastically poor across ecosystems, including forests. There are only a few locations where soil has been sampled at depth and/or with scientific rigour, but forests and the biomes in which they reside are extensive and diverse. There is an urgent need to sample deep soils in forests more frequently and with a concerted and systematic approach. Priority initially needs to be given to better utilization of existing long-term experimental trial infrastructure and targeting an integrated forest ecosystem-level understanding of OC cycling to determine the connectivity among deep and upper soil layers, forest biomass, the atmosphere, and climate change (e.g., [160]). The consequences of this are two-fold. Firstly, there is a relatively poor data set on which to parameterize models and, concomitant with this, a large degree of uncertainty and error in our current assessments of deep SOC pools. Secondly, our understanding of deep SOC is driven by a small set of samples. The view out of this window may not be realistic to much of the world's soils yet is driving our perspectives (including in this paper).

Deep soil comprises a distinct ecosystem that is connected to upper soil on a vertical gradient but influenced by different factors. The physicochemical conditions, biological entities, and biogeochemical process are all different and often operate at different rates/kinetics. With increasing soil depth, there are changes in the connectivity to the atmosphere, the amount and age of SOC present, the dominance of different SOC protection mechanisms, and microbiomes (Figures 1–4), and these are under different influences from changing climatic conditions. We cannot continue to rely on sampling upper soil alone to infer deeper-soil characteristics. We know there is high uncertainty in correlations among top and deep SOC stocks (Figures A1 and A2). Yet, despite this, we still often consider soil as a singular entity. This view is also limiting our progress in understanding the size and types of SOC pools, residency, climate and biological sensitivity, and rates of change in deeper forest soils. A fundamental change in perspective needs to occur so that 'upper' and 'deep' soil layers are recognized as fundamentally distinct ecosystems that are connected on a vertical gradient. This will enable better consideration for approaches to modelling these systems.

In order to understand fundamental processes underpinning deep SOC cycling, there is a pressing need for ongoing measurement of targeted soil properties in conjunction with total SOC. These need to be assessed using standardized approaches. The use of tools such soil fractionation and radiocarbon abundance are important in understanding deep-SOC dynamics (turnover and storage), enabling the exploration of risk under a changing climate [69,70], and furthering our understanding of the ecosystem benefits linked with SOC-fraction pools. A more nuanced understanding of the controlling factors shaping SOC cycling is also needed, including the influence of the soil microbiome on SOC within the

deep soil environment, their interaction with SOC and access to protected SOC, and nutrient flow and transport [72,77]. A fuller understanding of the processes that explain how closely soil properties are mapped together with SOC, how they control each other, and if there are any threshold responses for the tree root–soil–microbiome interactions that will impact SOC is required. Repeated sampling over time will allow for a temporal understanding of SOC and deep soil processes and is required to develop and parameterize models.

While sampling SOC at depth can be challenging, particularly in forests due to the presence of woody roots [13], it is possible, and soil auger technologies are making such sampling easier (e.g., [88]). Any difficulty in recovering deep SOC is compensated by the wealth of information these samples provide. Once the material is out of the ground, samples should be securely archived for future use and be openly available. This will extend the value of collecting the sample. For example, archived soil and associated data for tens of thousands of sample points in the United States Department of Agriculture (USDA) National Soil Survey Center—Kellogg Soil Survey Laboratory (NSSC-KSSL) have demonstrated how valuable it is to archive soil and share data (e.g., [161]).

The response of deep SOC to climate change remains uncertain. It is unclear, but highly unlikely, that deep SOC will respond in the same way to the myriad of climate change impacts expressed in forests as SOC held in upper layers. There are many challenges in modelling SOC pools for both surface and deep soil [72]. The limited data currently available for deep SOC restrict any ability to effectively model deep SOC changes under a changing climate. There are modelling advances in considering microbial physiology and SOC fractions, protection mechanisms, which behave in unique ways that cannot be determined from bulk SOC response (e.g., [162]). However, the inclusion of deep-soil processes in forest-OC-cycling modelling is limited to a single example, exploring to 1.5 m depth [163]. There is a need to include deep soil in forest-OC-cycling models, including, for example, the rapid flux of OC supplied deep into the soil to mycorrhizal fungi by plant roots (e.g., [52]), an understanding of deep-fine-root function and contribution to the pool of SOC [31], and the impact of climate change on these. There is a need for models on a continuum of flux and change and how OC moves through soil that includes the processes driving SOC cycling [72,77] and a better understanding of how to incorporate deep SOC uncertainty into modelling in a forest system. The functional prediction of deep SOC within the forest system to enable decision-making will support the continued delivery of ecosystem benefits from forests under a changing climate.

6. Conclusions

Urgent action is needed if we are to address uncertainty and understand the scale of risk associated with the impact of our changing climate on deep SOC in forest ecosystems. The limited information we have is restricted to a small number of sites. Estimates of deep SOC stocks have been made; however, they are not robust due to a lack of empirical data underpinning estimates. As a result, considerable uncertainty exists regarding the fate of OC in forest soils. Accurate characterization of SOC stocks and flows is complicated due to the interactive dynamics in the soil environment, including between the soil microbiome, mineralogy, and forest management. These factors and interrelationships currently confound any predictions of trends in SOC stocks, particularly as our climate and forestry practices change. Yet, understanding responses is critical to identify potential impacts on the ecosystem benefits that forest SOC supports. The scale of impact of temperature or soil moisture change on C budgets and subsequent risks to the provision of ecosystem benefits are dependent on spatial changes in climate drivers over the next few decades. Through a deeper understanding of the spatio-temporal variation in OC stocks, resolving links with changes in deep OC inputs, and microbiological factors of deep SOC transformation and storage, we can greatly reduce levels of uncertainty in terrestrial C models, thus supporting more sustainable land management decisions. Deliberate effort is required to gather more empirical evidence of how much deep SOC there is and to understand the processes driving deep-SOC cycling. This knowledge is urgently needed if policymakers, foresters,

communities, and other stakeholders are to make informed forest management decisions aimed at addressing C security and in sustaining and enhancing forest ecosystems.

Author Contributions: Conceptualization, L.G.G. and S.A.W.; methodology, L.G.G., A.K.B., K.A.H., J.A.H., and S.A.W.; investigation, L.G.G., A.K.B., and J.A.H.; visualization, L.G.G., A.K.B., K.A.H., J.A.H., and S.A.W.; writing—original draft, L.G.G., A.K.B., K.W., and S.A.W.; writing—review and editing, L.G.G., A.K.B., K.W., K.A.H., J.A.H., and S.A.W.; supervision, L.G.G.; project administration, L.G.G. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this research came from New Zealand Ministry of Business, Innovation and Employment (MBIE) Strategic Science Investment Fund held by Scion (C04X1703).

Acknowledgments: The authors thank the following people from Scion Peter Clinton and Tim Barnard for their review and Dale Corbett for support with imagery. We also thank the anonymous reviewers for suggested improvements to the manuscript.

Conflicts of Interest: All authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. The authors declare that this study received funding from the New Zealand Ministry of Business, Innovation and Employment. The funder was not involved in the study design, collection, analysis, interpretation of data, the writing of this article, or the decision to submit it for publication.

Appendix A. Predicting the Response of Deep Soil Using the Topsoil

Method aim: Using existing data, demonstrate (1) the relationship between surface and deep-soil horizons' soil carbon pools and (2) the relationship of the effect of harvesting on the soil carbon pools between surface and deep soil horizons.

Method data and analysis: Soil carbon pool (Mg ha^{-1}) meta-data published in James and Harrison [44] were grouped into sampling depths Top (0–15 cm), Mid (15–30 cm), Deep (30–60 cm), and Very Deep (60–100+ cm). Using Spearman correlations for (1) forest soil carbon pool comparison between sampling grouping depth to address the question ‘how successful might we be predicting deep soil carbon if we only looked at the topsoil?’; and (2) effect of management on forest soil carbon pool size using difference between the control (un-harvested or pre-harvest) and treatment (harvested) (i.e., in(control/treatment)) to address the question, ‘how successful might we be at predicting the response of deep soil to management if we only looked at the topsoil?’. Significance was reported for each Spearman correlation.

Results:

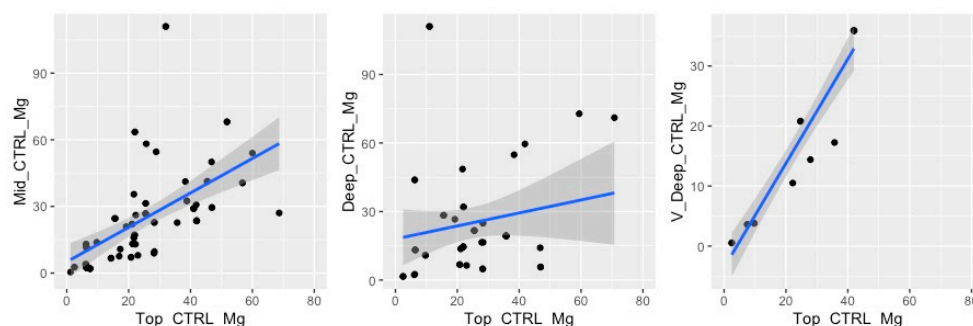


Figure A1. Forest soil carbon pool (Mg ha^{-1}) comparison between sampling grouping depth: Top (0–15 cm), Mid (15–30 cm), Deep (30–60 cm), and Very Deep (60–100+ cm) using meta-data from James and Harrison [44]. The Spearman correlations were 0.77 **, 0.27 *, and 0.98 ** (* sig at $p = 0.1$, ** sig at $p < 0.01$) for Top to Mid, Deep, V_Deep, respectively. Shown is the best-fitting regression line (blue) and 95% confidence interval (grey shaded area).

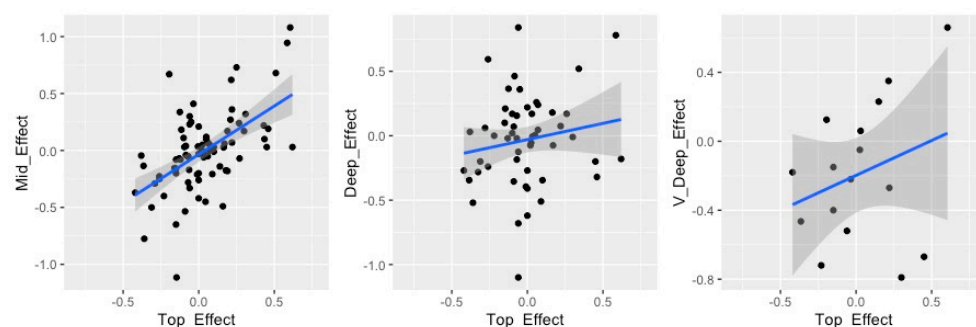


Figure A2. Effect of management on forest soil carbon pool (Mg ha^{-1}) size using difference between the control (un-harvested or pre-harvest) and treatment (harvested) (i.e., in(control/treatment)) using meta-data from James and Harrison [44]. The Spearman correlations were 0.52 **, 0.10, and 0.18 (** sig at $p < 0.01$) for Top to Mid, Deep, V_Deep, respectively. Shown is the best-fitting regression line (blue) and 95% confidence interval (grey shaded area).

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