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Perspective

Innovating carbon-capture biotechnologies through ecosystem-inspired solutions

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SUMMARY

Rising atmospheric carbon concentrations affect global health, the economy, and overall quality of life. We are fast approaching climate tipping points that must be addressed, not only by reducing emissions but also through new innovation and action toward carbon capture for sequestration and utilization (CCSU). In this perspective, we delineate next-generation biotechnologies for CCSU supported by engineering design principles derived from ecological processes inspired by three major biomes (plant-soil, deep biosphere, and marine). These are to interface with existing industrial infrastructure and, in some cases, tap into the carbon sink potential of nature. To develop ecosystem-inspired biotechnology, it is important to identify accessible control points of CO_2 and CH_4 within a given system as well as value-chain opportunities that drive innovation. In essence, we must supplement natural biogeochemical carbon sinks with new bioengineering solutions.

INTRODUCTION

The concentrations of climate-forcing gases—CO_2 and CH_4—have spiked and continue to set new historic benchmarks.[1] Even with an increase in climate crisis mitigation policies around the globe, warming is still occurring at approximately 0.2°C per decade and is currently near 1°C above preindustrial levels.[1] It appears likely that emission reductions themselves will not be sufficient for limiting global warming to 1.5°C, a threshold for which major ecological tipping points are predicted.[1,2] Therefore, in combination with reducing emissions, the climate crisis must also be addressed by active carbon capture, sequestration, and utilization (CCSU) via cooperation between nations and industries in order to reach our net-zero sustainability goal by 2050.

New innovation and technology has enabled the possibility of carbon capture and sequestration (CCS), yet it comes with high investment costs and is akin to waste management.[3,4] Hence, more interest has been focused on CCSU biotechnology in order to create value chains that offset costs.[3,5] Yet, the current state-of-the-art for CCSU is insufficient and limited by economics, human capacity, and constraints imposed by the need to retrofit large-scale industrial equipment with new installations.[3,5] With the current rate of CO_2 emission, the CCSU capacity in place will not be adequate to address the climate crisis.[3,4] Current models suggest that in order to reach the 2050 goal, global CCSU technologies will need to be increased by a factor of 2–4.[3]

So how will we get from the current state of inaction to rapid deployment of new CCSU technologies? We argue that an important part of the solution will be realized by innovative biotechnologies that recapitulate and, in some cases, even tap into the large-scale ecosystems that underpin major global carbon cycles. In other words, the innovation process will be expedited by translating fundamental knowledge we already possess into technology that stores carbon within the earth's large biomes and/or delivers new value chains by harnessing unique biological functions. These will not provide a singular solution for averting the climate crisis, but instead represent an underexplored area of innovation to complement major reduction of emissions. Managing a biotechnological revolution of this

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magnitude will require a large portfolio of innovative strategies that utilize and interface with different ecosystem components, including microbiomes from marine and deep-subsurface environments as well as plant and rhizosphere biomes.

How will this be done? In this perspective we combine contemporary ideas from ecology and biotechnology associated with three major biospheres: plant-soil systems, the deep subsurface, and marine microbial ecosystems (Figure 1). Our ultimate goal is to reduce the accumulation of CO_2 and CH_4 in the atmosphere. We believe ecosystem-inspired biotechnologies have inevitable roles in providing a complementary means toward this goal. We thus culminate this perspective with a proposed three-step process to guide cooperation between ecologists and biotechnologists. The first step is to identify accessible control points for CO_2 and/or CH_4 cycling, which are the junctions between engineered processes and ecosystem components. The next step requires both fundamental and applied scientists to jointly recognize what is understood and which knowledge gaps need to be filled to effectively render ecological insight into new or enhanced engineering design principles. Scientific knowledge of carbon cycling and engineering solutions for CCSU are not in themselves enough to spur action. Hence the third step, and perhaps the most important step toward the solution, is to foster awareness of the problem and close the gap between fundamental research and industrial action.

WHY SHOULD WE LINK BIOMES TO BIOTECHNOLOGIES?

There is much to be gained by reconciling new engineering design principles needed for CCSU with the ecological processes that have shaped plants, animals, and microorganisms in nature. Essentially all life (as we know it) has evolved to exploit ecological interactions associated with transformations of C1 compounds (CO_2 and/or CH_4), giving us opportunities from almost all major ecosystems to harness unique biological functions that drive innovation. As we collectively identify connectivity between genome-encoded functions and carbon cycling for natural ecosystems, we often reveal new biotechnological insights.[6] We encourage ecologists to help engineers identify where accessible ecological/biological control points of CO_2 and/or CH_4 cycling occur within major biospheres. We use the term “accessible control point” to define the existence of current or future opportunities for technology to interface with these biomes. An anthropogenic interface is the point of either emission or capture, maintaining that these will be continually amended as demand to remediate atmospheric carbon emissions becomes more severe. Integrating applied science with the newest fundamental knowledge, obtained from observing nature, is essential to effectively render ecological insight into new or enhanced engineering design principles. We believe that nature’s blueprints provide unsurpassed inspiration for bioengineering and biodesign. Opportunities uncovered here are not limited just to building new biotechnologies, but also open paths for maintaining and promoting ecosystem services that facilitate C sequestration in natural ecosystems. Hence, translating fundamental biological and ecological knowledge into CCSU technology is an opportunity for society and an important complement to current sustainable development goals on our path to combating the climate crisis.

Here, we assert a basic engineering goal to guide future CCSU biotechnologies, which is as follows: *controlled biological uptake of CO_2 and/or CH_4 must be coupled with economically valuable and/or longer-lived carbon bioproducts.* This simple principle has already been realized in several examples that harness plant-soil biomes, the deep subsurface, and marine microbiomes. These have been implemented at various technology readiness levels, as discussed in the sections below. These innovations are driven by strong momentum in fundamental science and the process of asking targeted questions that can guide discovery of accessible control points alongside bioprospecting of organisms, interactive communities, and genetic parts to support CCSU technologies. Some of these questions include the following:

- Where is carbon located within an ecosystem and which biological activities facilitate transport between pools?
- Which biological activities are most influential in controlling the uptake or emission of atmospheric carbon within their respective biomes?
- What is happening to the carbon after biological assimilation and dissimilation and how can it be (re)directed to storage or controlled synthesis of bioproducts?

Identifying and quantifying the major “sinks” of carbon and main “fluxes” is a key area of investigation, related to the first question posed above. Sinks are defined by both the mass of carbon and the time scale at which it remains in a specific form.[7–9] More recalcitrant carbon species have better sink potential, meaning they resist biotic and/or abiotic degradation for longer periods of time. Carbon flux is defined by transport phenomena and reactions that interconvert sources and sinks. Some biologically controlled, natural sinks are soil organic matter (SOM), “raw” fossil fuels, persistent dissolved organic matter (DOM) in oceans, and carbonate minerals stored in both marine and deep subsurface environments.

Current anthropogenic emissions of CO_2 and CH_4 are estimated at 37.5 and 9.7 Gt CO_2 equivalents per year, respectively.[10,11] A gigaton of CO_2 (Gt CO_2) is 1 billion metric tons or 10^{12} kg. Although it is clear that CCSU technology must be designed to offset emissions at this scale, it is less clear how future technologies will work in combination with natural terrestrial and marine ecosystems, which represent our largest biogeological sinks by collectively taking up roughly 21 Gt CO_2 per year from the atmosphere at present.[10] The functional capacity (Box 1) for carbon uptake and storage within plant-soil, deep biosphere, and marine ecosystems is difficult to quantify because these are complex adaptable systems,[12] meaning that emergent behaviors arise from unique interactions or perturbations between ecosystem components. Yet we, as innovators of the next generation of solutions, are ready to harness simplified elements from these ecosystems, such as methane-oxidizing bacteria and photosynthetic microalgae,[13] to be deployed in scalable CCSU bioprocess engineering.

ENGINEERING PRINCIPLES FROM ECOLOGICAL PROCESSES

We believe a part of our path toward sustainability is through innovation in diverse portfolios of CCSU biotechnologies. Given the mandate, we assert that the best possible approach is to

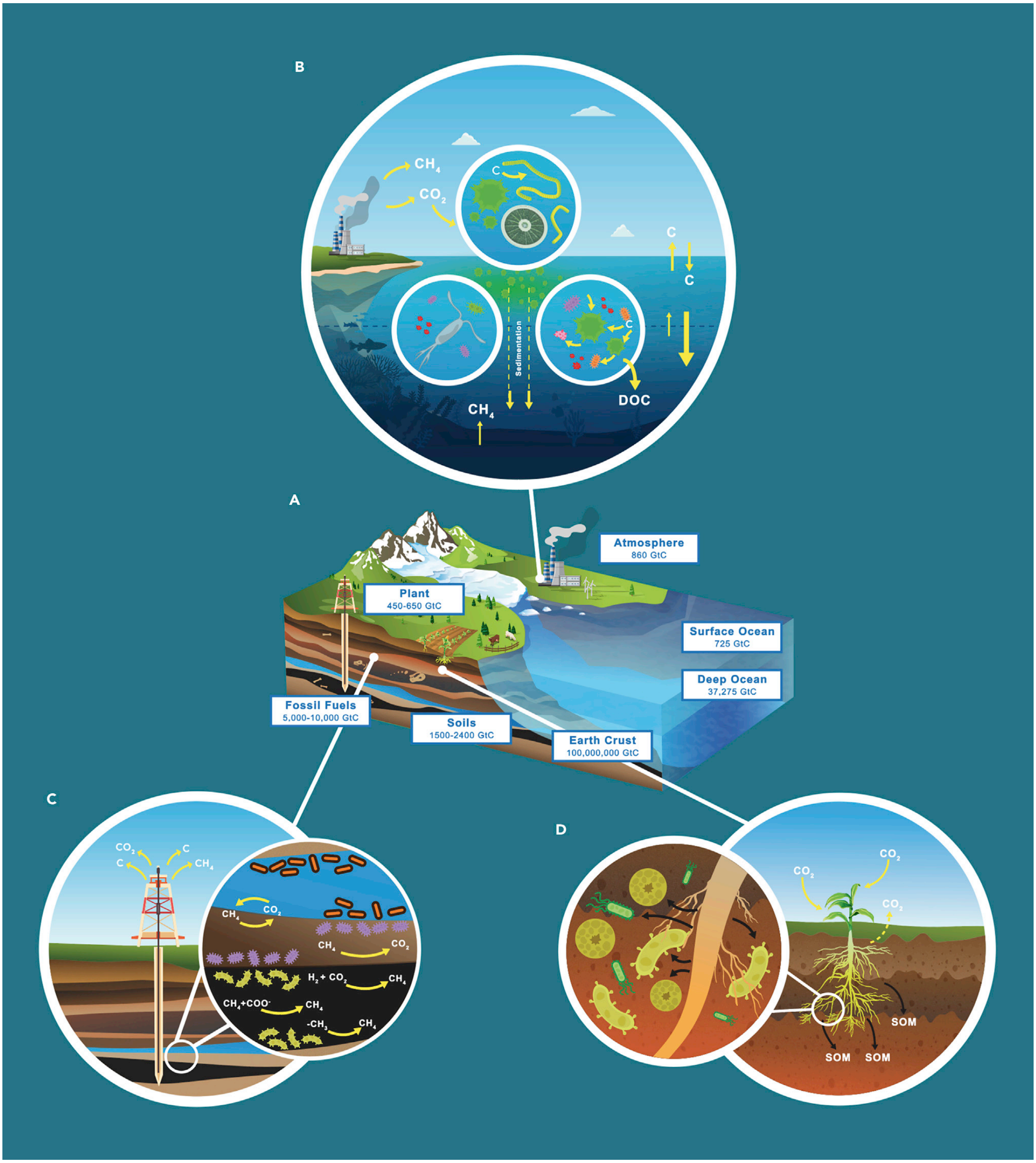

Figure 1. Seven main sinks within the global carbon cycle as given in gigatons of carbon (GtC)
One goal of ecosystem-inspired CCSU biotechnologies is to find accessible control points for both natural and human-influenced fluxes (yellow arrows) that pull more carbon from the atmosphere to one of the other six sinks (A). The focus of this perspective is on the three biospheres: marine (B), the deep subsurface (C), and the plant-soil ecosystem (D). In the ocean (B), CO$_2$ is pulled from the atmosphere by primary producing phytoplankton and cycled between heterotrophic bacteria that can undergo sedimentation into the deep ocean where carbon is stored for long periods of time. The deep subsurface (C) is one of the largest human-caused releases of carbon into the atmosphere due to the extraction of fossil fuels, although the microbial functional capacity for the turnover of deep carbon is still unknown and has great potential for influencing geologic storage. The plant-soil (D) ecosystem, or rhizosphere, consists of primary producer plants that are able to pump CO$_2$ from the atmosphere into the soil. Carbon can then be stored in soils depending on the root system and how it interacts with the rhizosphere and soil microbiome that can convert soil organic matter (black arrows) back into atmospheric carbon.

Box 1. Functional capacity

Functional capacity is defined here as the collective ability of an ecosystem or sub-biome to perform biological actions. In the context of the plant and/or microbial systems that we are discussing for applications in C-cycling and CCSU biotechnology, this pertains to genome-encoded abilities to utilize CO_2/CH_4, produce metabolites, grow, and interact with other organisms and/or abiotic elements in the environment. Although individual organisms have their own functional capacities, community-level functions can emerge from context-specific interactions between organisms and within the environment.[14,15] Much of this has been revealed by the modern "multi-omics" era, which is leading to an explosion of knowledge about plant and microbe diversity, interactions, and emergent properties within both marine and terrestrial habitats.[16] We now have a clear understanding that microbial diversity is vast. Current estimates of microbial diversity are 10^{12} species,[17] with less than 1% characterized via conclusive microscopy or cultivation.[18] This level of diversity also comes with unexplored functional capacity.

Although the field of microbiomics is early on its path to translating knowledge over diversity to functional capacity, lessons from soil ecology have taught us that higher levels of species-diversity lead to greater capacities for C storage.[19] Hence, both functional and species-level diversity should be an important consideration when developing functional capacities for CCSU biotechnologies. The marine microbiome is of interest because in the deep ocean, sequestration of carbon and other substrates is high. In fact, once carbon enters the deep ocean (Figure 1) through the biological pump,[20] the majority of this carbon will remain in the deep ocean for thousands of years.[21] A similar function is facilitated by interacting plants and microbes in the rhizosphere biome, where organic carbon deposition and decomposition are essential for soil and plant health.[22] Microbial communities and fungi are responsible for this decay, creating favorable growth conditions for plants and other organisms. With greater plant and soil health there is an increase in primary productivity and root health to help maintain soil structure and carbon capture.[23] Soil could conversely be a large source of carbon emissions if improperly managed.[24] For example, since the beginning of the industrial revolution, with an increase in cropland cultivation and agricultural methods, there has been an estimated release of 214 ± 67 petagrams of carbon (Pg C) into the atmosphere.[24] Yet, if managed correctly, the soil and specifically the agricultural sector could sequester up to 1.85 Pg C/year.[25] This carbon may get further buried into the deep subsurface, which, like soil, has a high degree of undiscovered functional capacity. The deep subsurface biomass is estimated to exceed that of the earth's surface by ca. 45%, and the bacterial and archaeal biomass may contain up to 31 Pg C.[26,27] The microbial communities of the deep subsurface rely on metabolic approaches using varying chemical redox reactions and are able to utilize carbon in diverse ways. The microbial environment is also able to quickly respond to biotic and abiotic environmental changes.[28]

The three biomes discussed here—plant-microbe, marine, and deep subsurface—are characteristically distinct from one another in that they harbor different species selected by a demand for different genome-encoded functions. Yet, the collective actions of organisms inhabiting each biome can result in an emergent carbon sink capacity under a given set of conditions.[29] A deeper understanding of nature's resilience and different strategies for transporting and storing carbon away from the atmosphere will undoubtedly lead to new opportunities for CCSU innovation.

implement multiple diverse strategies rather than relying on a singular solution. Natural ecosystems have already provided the diversity needed to inspire multiple solutions that can be implemented now or in the near future. There are tremendous biological differences between plant-microbe, deep subsurface, and marine ecosystems, although they can each perform the same basic sink function in contemporary biogeochemical carbon cycles (Box 1). There is also a large diversity between similar biomes. For example, aquatic ecosystems in the Northern and Southern Hemispheres can have essentially matched environments and ecological functions, yet the biology—resident species and genome-encoded functions—can be very different.[30] It is our challenge, as contributors and observers of nature, to untangle the biological complexity of these ecosystems by understanding which localized niches can provide biological parts and/or inspiration for novel operating conditions tailored toward CCSU.

Biotechnological solutions for CCSU will require a joint effort from multiple disciplines, including chemical engineers, microbiologists, geologists, ecologists, plant scientists, and economists. The "Green Shift" toward technology built for sustainability has the potential to be the next big economic boom, and many political-business agendas that support research and implementation of this plan stand to benefit by being early players in the movement.[31] Ecosystem-inspired engineering principles have great promise in this regard because of the potential to overcome barriers in energy demand and carbon conversion efficiencies that set the limits for current state-of-the-art industrial approaches, such as direct air capture of CO_2 using amine-based absorption.[32] Hence, we should maintain an open mind about where solutions can be found and where innovation will come from next. In the remainder of this perspective, we will present a few of the promising examples and considerations that can help drive this type of innovation, but we recognize that there are many other solutions as well as other ecosystems that may lend themselves to this process.

CCSU solutions: plants and soils

Soils are the foundation for almost all biological processes on the Earth's land surface. From a geological perspective, carbon storage in soils is controlled by weathering and erosion, regulated by climatic and tectonic impacts. In the shorter term, and at local scales, anthropogenic activities are regarded as the main drivers of soil erosion. Soils provide numerous critical ecosystem services beyond their roles in carbon cycling, which include the support of plant growth in agriculture and forestry to moderation of flood risks, water purification, and maintenance of terrestrial biodiversity. They store vast reservoirs of carbon

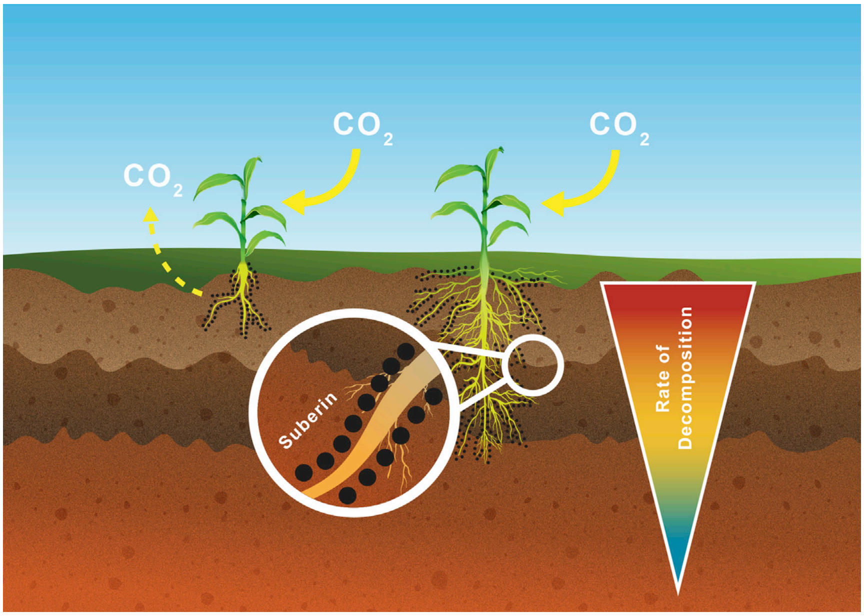

Figure 2. Atmospheric carbon drawdown from an engineered plant-soil ecosystem

The yellow arrows represent the transfer of carbon. Plants can be selected or designed to have deeper root systems, which creates better carbon sink potential in the localized soil. This is because the rate of soil organic matter decomposition decreases with depth. Plants can also be selected or designed to produce biopolymers that resist decomposition. One example is suberin (black dots), which is a major component of cork and able to resist decomposition, thereby presenting an opportunity for crop-based CCS.

estimated at near 3,400 Pg (1 petagram = 1 trillion kg), which includes soil organic carbon (SOC) stored in permafrost.[29,33] This major carbon sink is approximately five times the current atmospheric pool of CO$_2$.[34]

Root-soil or rhizosphere biomes function as a carbon pump by pulling atmospheric CO$_2$ captured by plants below ground to be stored by the rhizosphere. This is where plants interact with soil bacteria and fungi via exchanges of SOC that can be stored or respired back into the atmosphere. The balance for this is governed by tight ecological interactions and localized geochemical factors. Engineering of crop root systems for enhanced carbon sequestration promises to be feasible and to encompass mostly known risks. This is because one of the largest and most successful genetic engineering efforts over the past 10,000 years has been the domestication and breeding of crops. This has led to an enormous portion of the Earth's land masses being covered by only a small number of crop species that generate the majority of human nutrition. These crop plant species provide a profound opportunity to use breeding and genetic engineering to increase the deposition of SOC on enormous swaths of land. As the agricultural system is already concerned with planting and cultivating crops each year, there exists a clear global distribution, production, and value chain of agriculture-based CCSU products.

Root-related traits are the primary targets when it comes to increasing plant carbon sequestration, as they constitute the major input for SOC. It is estimated that a given mass of root inputs contributes approximately five times more SOM than the equivalent mass of aboveground litter.[35] Importantly, more than half of the global soil carbon pool is found in deeper soil layers.[36] This finding is consistent with studies that have found increased soil depth to be associated with a lower root decomposability.[37,38] Such evidence has led to the suggestion that root depth distribution is the most important trait to control carbon sequestration in the soil (Figure 2),[39,40] meaning that SOM derived from roots deeper in the soil is subjected to lower rates of decomposition and therefore less labile. It has been shown that single genes and genetic variants can alter root depth,[41–43] strongly suggesting that achieving deeper rooting is a surmountable challenge for new CCSU biotechnology efforts.

Degradation of SOC is regulated by microorganisms that transform plant debris and SOM into available nutrients that can be taken back up by plants. During this process some of the carbon remains in soil, which creates a CO$_2$ sink. The potential to store carbon depends on the soil structure, which affects binding and stabilization of organic material, in addition to fluxes of gases and water. Labile carbon mainly consists of microbial biomass, DOM, and organic matter that can be easily oxidized, whereas recalcitrant carbon usually refers to the component of SOM that is resistant to microbial decomposition or protected by mineral-soil particles.

Interactions between soil geochemistry, soil microbiomes, and root biochemistry determine the sink capacity of rhizosphere biomes. This provides another opportunity to harness plant genetics for carbon sequestration by engineering roots to contain more carbon compounds that contribute to longer-lived carbon pools in soil. A prime candidate is the natural product suberin (Figure 2). Suberin is a lipophilic complex polyester biopolymer that is composed of long-chain fatty acids and polyaromatics. It is significantly preserved in soil.[40,44] Suberin has been proposed to be very recalcitrant due to its own intrinsic biochemical stability,[44] and due to its interaction with soil minerals and occlusion in topsoil microaggregates.[40] Increased suberin production appears to be a feasible goal for plant-based CCSU. In fact, there are efforts on the way to select or genetically modify crop plants that will both produce deeper root systems and carbon compounds that contribute to longer-lived carbon pools (e.g., suberin) and jointly have the possibility of increasing carbon storage.[45] Whereas it is clear that there is tremendous potential for plant-based carbon sequestration (the top 30 cm of global cropland soils alone has been estimated to have a capacity to sequester up to 1.85 Pg C/year[25]), much research needs to be done beyond plant and soil biology. Carbon accumulation and recalcitrance are also dependent on soil type, climate parameters, and agricultural practices such as the application of cover crops and no-till farming.[46] The latter will require increased cooperation and interdisciplinary research of soil scientists, plant biologists, and other disciplines.

The deep biosphere

The deep subsurface is largely unexplored and remains a mysterious environment. Here, "deep" subsurface refers to the biomes below the soil and ocean floor sediments where community composition and/or function is distinct from those inhabiting the overlaying organic soil layers or sediments interfacing with water columns.[47–49] Complex microbial communities dominate these environments and have a high functional capacity (Box 1) for the turnover of CO_2 and CH_4.[26,27,47–50] The deep subsurface is spatially heterogeneous, and microbial functions change depending on location, which also affects long-term geological storage of carbon. This has implications for engineering efforts aiming to control the geological storage of CO_2, which is the major direction for contemporary CCS. The most common concepts target CO_2 that would otherwise be emitted from point sources, such as power or cement plants. Typical processes involve using compression to temporarily store and/or transport gas via wells into deep geological formations such as oil reservoirs, aquifers, and deep un-minable coal seams.[51,52]

Geological storage is attractive because the technology for injection already exists, and it has already been applied for enhanced oil recovery and deep disposal of hazardous wastes.[53–55] Although geologic CO_2 storage has a key role to play in managing atmospheric carbon,[56] many current technologies are viable only for temporary storage, meaning that more innovation is required to fully sequester CO_2. Leakage is a major concern, and effective sealing of CO_2 injections is a significant hurdle.[28,57–59] Hence, while the deep subsurface represents a major sink for CO_2, more knowledge is needed to understand how resident microbiomes can enhance or limit long-term storage, as well as providing opportunities for carbon capture and utilization (CCU) biotechnology.

Microbial biotechnologies have been developed to prevent CO_2 leakage from wells and adjacent geological formations in the deep subsurface. These innovations harness naturally occurring microbial processes associated with the attachment, biomineralization, and formation of biofilms. The naturally occurring processes will precipitate CO_2 into a carbonated sediment over very long time periods (tens of thousands of years), demonstrating deep subsurface sequestration potential. Innovations in microbial biotechnologies have shown that it is possible to enhance the carbonate precipitation (calcium carbonate) and biomineralization process using several microbial biofilm-forming species. These microbial biofilms have been shown to be effective at plugging pore channels or creating reactive biofilm barriers, which can reduce flow or mass transport through porous geologic formations, thereby helping prevent well leakage.[60–68] More recently, a biofilm barrier technology was applied by harnessing microbially induced calcite precipitation[68], which can be applied to a range of geoscience and engineering applications (CCS biotechnology), including sealing leaky wells, amending or improving construction materials, cementing porous media, environmental remediation, and containment of nuclear waste.

Biofilm barrier technology involves the injection of nutrients to stimulate the growth of microbes attached to the surface and within the pores of geologic formations. This biotechnology can also be coupled with bacterial-induced precipitation of carbonate minerals acting as biocement and will be essential for the overall success of deep subsurface CCS (Figure 3).[61,68,69] Depending on the native subsurface microbiomes, this can require direct injection of specific bacteria to encourage production of extracellular polymer substances (EPSs). If EPS production can be stimulated along with cell growth, the resulting biomass will plug cracks and pores in aquifers, thereby reducing hydraulic conductivity.[68,70–72] This interesting biotechnology application for CCS is already at a relatively high technology readiness level. Engineered biofilm barriers have been evaluated at the field scale[66] and have demonstrated 99% reduction of average hydraulic conductivity across the barrier. They can also act as biofilters, applied to plug leaky wells and even utilize CO_2 or CH_4 that is being transported in or leaking from the subsurface to produce valuable biomass and bioproducts (Figure 3).

The biology and ecology of the deep subsurface have an unknown potential that needs to be further researched for CCSU biotechnology. This understanding spurs an important and self-critical question that must be asked about ecosystem-inspired CCSU biotechnology: is it worth investing in more fundamental knowledge if the functional capacity (Box 1) is still so poorly understood? We believe the answer is yes, for two reasons. First, the time to act is now, and it is important, but difficult, to develop new CCSU technology at low cost, regardless of which discipline the fundamental science is aimed at. The second reason is that we already know these ecosystems naturally exist in tight spatial assemblages with long-lived carbon deposits. Hence, the likelihood that bioprospecting efforts will uncover new properties that can be used to create and stabilize carbon sinks is high.

Marine microbiomes and microalgal biotechnology

Photosynthetic marine microbes—specifically algae and cyanobacteria—have tremendous potential for CCSU biotechnology. Marine phytoplankton, benthic microalgae, and associated members of the microbiome underpin many global food webs and are major biological contributors to marine carbon cycling. Diatoms are a major group of microalgae that contribute roughly 20% of global net primary productivity[73,74] and are amenable to industrial-scale cultivation for CO_2 capture.[75,76] In their natural environment diatoms and other phytoplankton bloom near the ocean surface, and subsequently sink to the deep ocean, thereby sequestering carbon into sediments for centuries or even longer.[76] The productivity of photosynthetic marine microbes can be very high in comparison to terrestrial plants. Some marine cyanobacteria have been characterized to have "ultra-fast" growth rates (2.5 h doubling times) under ideal growth conditions, which directly translates to high rates of CO_2 uptake.[77] Harnessing ultra-fast biomass productivities may be a key development in overcoming major limitations in contemporary algal CCU by enabling continuous feedback control over biomass density to avoid self-shading and/or high operating expenses accrued from artificial illumination.

Despite favorable biomass productivities (more typically observed near one doubling per day), it is still widely understood that economic feasibility limits the application of industrial-scale algal CCSU. Yet, new value chains and socioeconomic drivers for these technologies are emerging, which include food, feed, and sustainable bioproducts. Value-chain

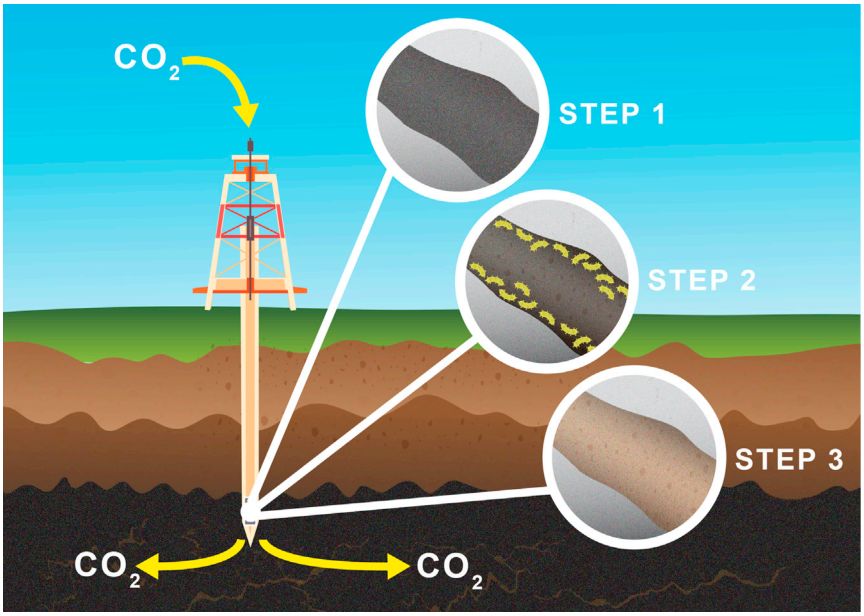

Figure 3. CCS biofilm technology using existing well infrastructure to inject CO_2 into the deep subsurface

The deep subsurface contains high microbial functional capacity for cycling of C compounds. Biotechnologies that seal the wellbore to reduce leaking of CO_2 or CH_4 are being developed for managing carbon storage after injection. The three steps on the right depict the use of biocement to seal cracks, leaks, or channels in the deep subsurface, specifically of a wellbore. Step 1 represents the crack in the wellbore to seal. Step 2 represents the injection or stimulation of microbial communities that form biofilms and produce an extracellular polymeric substance, which will attach and stimulate growth along cracks within geologic formations. Step 3 represents bacterially induced biomineralization, specifically calcium carbonate precipitates that can act as a biocement sealant.

development in these areas meet multiple United Nations Sustainable Development Goals, including zero hunger, clean water, and climate action.[1,78] Nitrogen-fixing marine cyanobacteria also present unique opportunities for CCSU-linked fertilizers and related value chains that support sustainability in both agriculture and aquaculture sectors. Engineered communities of marine microalgae and cyanobacteria are also promising biotechnology platforms because they can be built to recapitulate natural ecological interactions that promote nutrient recycling[79] and simultaneous uptake of CO_2 and CH_4.[13] Multiple industrial- and pilot-scale efforts are in operation, including examples in Europe (Monzon Biotech, Spain; Swedish Algae Factory, Sweden; Finnfjord AS, Norway), North America (MicroTerra, Mexico; Symbiotic Envirotek, Canada), and Asia (Shaivaa Algaetech, India; Alvita Corp., Japan).

Marine microbial ecology offers multiple roadmaps for new CCSU technologies. Our oceans play a critical role in global carbon sequestration by exerting control over atmospheric carbon concentrations.[80] Marine microbiomes help facilitate this through photosynthetic primary productivity, resulting in large amounts of dissolved organic matter (DOM) being stored in our oceans. Heterotrophic community members live in tight association with algae/cyanobacteria and consume much of the DOM at or near the surface. The remaining fractions of this DOM accumulate and can persist for several thousands of years.[81] The molecular properties of plankton-derived DOM dictate heterotrophic utilization and turnover rates.[82] This is a major global carbon sink and an ecological process that can be explicitly designed and engineered into algal mass cultivation efforts to integrate CCU (biomass harvesting) to CCS (marine storage of DOM) (Figure 4). The deep ocean has high functional capacity potential (Box 1), and in the last glaciation (70 thousand years ago), the Atlantic Ocean alone sequestered an equivalent amount of carbon that was lost from the atmosphere.[83] The sequestration potential of the deep ocean is unknown, but carbon that is currently being sequestered is estimated to be stored for thousands of years.[21] Previous research has focused on the possibility of enhancing ocean primary production, leading to carbon sequestration, using ocean macronutrient and/or iron fertilization where it is limited.[84] Although initial sequestration capacity will be up to 3.6 Pg C, the sequestration capacity over time will decrease, and the environmental risks have either not fully been evaluated or are estimated to outweigh the advantages.[84,85]

Marine microbes can also be harnessed for their ability to produce recalcitrant, inorganic carbon. For example, cyanobacteria can be used as agents for biomineralization of CO_2 through calcium carbonate precipitation,[86] and even heterotrophic microorganisms are able to fix CO_2 through anaplerotic metabolic strategies mediated by carbonic anhydrase[87], pyruvate carboxylase, and phosphoenolpyruvate carboxylase.[88] Microbial production of both DOM and inorganic carbonates is an integral component of natural marine carbon cycles that can be elevated to a viable CCSU technology with more research and innovation on economic sustainability and industrial scale-up. We believe that part of this path for these nascent CCS biotechnologies will be to combine them with utilization and value-chain efforts to create CCSU biotechnology. For example, a deeper understanding of how to direct the metabolic flux of CO_2 toward production of recalcitrant DOM and/or carbonate minerals can lead to new carbon drawdown technologies that may be deployed in tandem with industrial-scale algal biomass factories designed for production of food, feed, fuels, and other bioproducts.

SOCIOECONOMIC DRIVERS OF INNOVATION

Despite the growing excitement and implementation of CCS infrastructure, the actual installed capacity to date (ca. 0.04 Gt CO_2 annually)[89] is so small that it raises concerns that we cannot meet the International Energy Agency's estimated requirement of 2.3 Gt CO_2 annually.[1,90] However, we believe that by realizing the full potential of biotechnology for CCSU we can increase global capacity to not only remove a portion of the accumulating atmospheric carbon but also drive new economic growth. The advantage of a value-chain approach associated with CCSU is

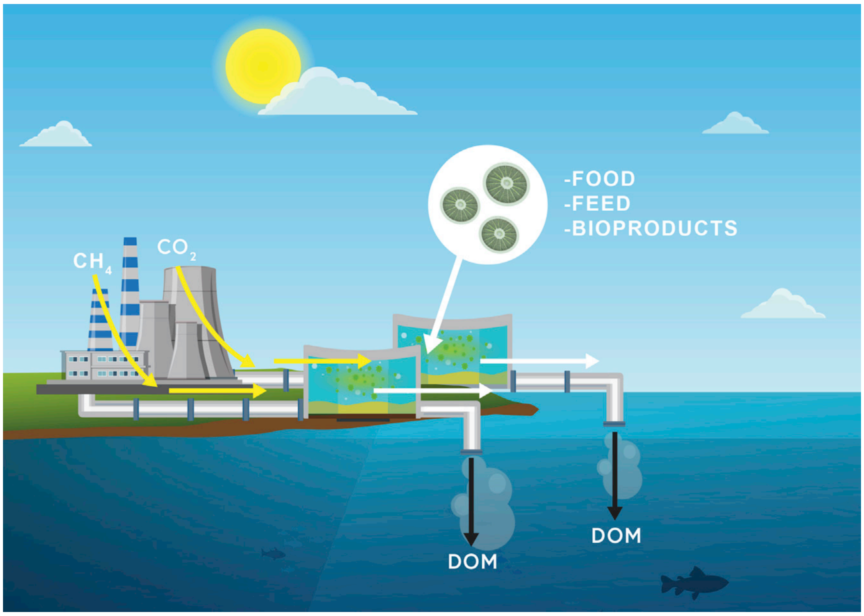

Figure 4. Industrial carbon capture, utilization, and storage via marine microorganisms

Algae and/or controlled microbial communities containing methane oxidizers can be mass cultivated using photobioreactors to capture industrial emissions. This is primarily conceptualized as CCU, where the algal and other microbial biomass is harvested to be used as food, feed, fuels, and value-added bioproducts. Systems that operate within or near marine ecosystems are of specific interest because they can utilize seawater and avoid competition for freshwater resources. This presents another relatively new concept of combining CCS with the algae-based value chains by sending dissolved organic carbon from the spent media to the ocean with the returning seawater. Certain fractions of phytoplankton-derived dissolved organic matter (DOM) are resistant to microbial degradation and represent a major, natural carbon sink that can persist in the ocean for millennia.

that carbon management translates into economic opportunities and builds upon the growing Green Shift, compared with traditional CCS that is often perceived by investors as a cost burden akin to waste management. Controlling the accumulation of atmospheric carbon will require massive investment, yet a common misinterpretation is that these will only incur costs and not add economic or social value in themselves. We argue that part of the final solution to achieve and protect sustainability will involve implementing a large suite of industrial-scale biotechnologies that integrate each unique biome with emission points across the globe. Innovation is required not only to reduce atmospheric carbon but also to develop economic sustainability, technical communication, and cultural/social drivers that offset major costs.

Each biome offers unique inspiration and opportunities for providing both economic value and reduction of atmospheric carbon. Ecologists and biotechnologists are encouraged to increase multidisciplinary cooperation to expand possible solutions. We advise those beginning on this path to look toward nature's blueprints and to consider a three-step process that we outline to guide translation of ecosystem science into actionable CCSU.

Step 1 requires us to identify accessible control points. We define these as junctions between engineered processes and ecosystem components. This can be a whole biome, such as the rhizosphere associated with bioenergy crops, or biological elements extracted from nature, such as marine microalgae strains with unique tolerance to industrial off-gas effluent. Long-term C storage in soil, marine, and deep subsurface environments is part of the solution and amenable to CCS biotechnologies. However, high complexity and major knowledge gaps make it difficult to predict responses and consequences of increasing or even maintaining carbon sink potentials. Harnessing natural biological functions into closed industrial installations—such as CH_4 utilization or algal scrubbing of CO_2—is more feasible for CCU efforts at point sources of emission, but difficult to conceptualize at the scale needed to offset contemporary emissions. We believe the contribution of biotechnology in managing greenhouse gases will require efforts on all fronts.

Step 2 is to address knowledge gaps that bridge basic science and innovation. Fundamental ecology and biology can stimulate the innovation process, yet major knowledge gaps remain significant barriers. For example, we do not know how far life extends into the deep subsurface and we are not certain how much carbon can remain locked inside temperate and Arctic soils after prolonged warming trends. Any CCS technologies seeking to use natural biomes as long-term sinks must account for high levels of uncertainty and unpredictable behavior. There is also much to be gained from new discovery and filling of knowledge gaps. For example, synthetic biologists and material scientists are keen to make discoveries to enable the redesign of algal and plant photosynthesis to drive new innovation for CCU and sustainable food production.[91] Future advances in CCU capability will require enhanced fundamental understanding and leveraging of relevant natural processes.

Step 3 is to foster awareness and communication. We argue that investments into the fundamental knowledge of our ecosystems and the life that inhabits them are also investments into sustainable development. When done properly, new observations of nature can underpin innovation in CCSU, which not only is required for maintaining stable functioning of our ecosystems and associated biogeochemical cycles, but also will have a direct impact on our societies and economies. This is clearly laid out by the United Nations Sustainable Development Goals, with the understanding that policies and social expectations must frame an appropriate economic playing field for dual investments into knowledge and innovation to thrive.[78] Increased public acceptance and awareness for the inevitability of our reliance on CCSU is essential. Fundamental scientists and industrial stakeholders can and should lead this effort by taking the first steps to exchange more knowledge and align their goals. Some of the obvious tools for this are multi-institutional and multidisciplinary centers and events that engage not only technical personnel from industry and academia but also policy makers, funding agencies, society as a whole, and the media.

The examples presented in this perspective demonstrate the use of the three-step process to create biotechnology focused on increasing the amount of carbon being captured, utilized, and/or stored and are provided to encourage application of the process toward the reader's own research on new fusions between biotechnology and ecosystem functions. These three steps, and the examples given here, are meant to guide ecologists and biotechnologists to cooperate and discover opportunities. This type of innovation does not come without the need to consider risks and ethical boundaries. Large-scale ecological and geological engineering are frightening concepts with unknown and unpredictable risks.[92] Many early ideas, such as ocean fertilization, have already been deemed infeasible and/or dangerous.[85] Current CCSU biotechnologies have already embraced both synthetic biology and the use of genetically modified organisms in nature. This is also not without controversy and the need to evaluate ethical practices. However, major disruption and displacement of climate change-impacted societies could likely spur extreme action. We argue that it is our responsibility, as both innovators and scientists, to think now about risk-benefit trade-offs linked to different climate change scenarios and the inevitable role of biotechnology in CCSU.

Conclusion

This perspective introduces biotechnology and innovation efforts that are inspired and/or connected directly to three major biomes (plant-soil, deep biosphere, and marine). Although our message is aimed at ecologists and biotechnologists, we encourage those of you dedicated to other areas of investigation to think about the first step in our proposed three-step process, which is to identify accessible control points of CO_2 and/or CH_4 cycling within your system of study. Biotechnologists and engineers seeking to build ecosystem-inspired solutions will depend on fundamental expertise for a given ecosystem to understand which processes, species, and genetic parts can be rendered into controllable modules or, perhaps more importantly, those that cannot. The other message we have for fundamental scientists is to help identify value-chain opportunities. Innovation requires capital investment from the public and/or industry, and both are often motivated by clear value-chain perspectives such as CCSU aiming to convert factory emissions of CO_2 and/or CH_4 into food, feed, and sustainable bioproducts from algae (Figure 4). Although economic feasibility will clearly help motivate more investment into biotechnology for CCU, we should not omit the role of CCS in combating the climate crisis through ecosystem-inspired innovation. This will not turn a profit in the new Green Shift economy, yet it still requires investment and public support. Hence, we make a final plea to the biotechnologists to gain a deeper understanding of biologically mediated carbon cycling to guide innovation for industrial design. We hope that better communication and cross-disciplinary innovation will motivate future investments into science and industrial action to consider the benefits of ecosystem-inspired CCSU, not as a technology of the future but rather as today's opportunity and mandate.

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AUTHOR CONTRIBUTIONS

All authors contributed to conceptualization and the first-draft outline equally. Writing – Original Draft, H.S., W.B., M.C., R.G., L.Ø., A.W., and H.C.B.; Development of Figure Concepts and Text Box, H.S., R.G., W.B., and H.C.B.; Major Editing, H.S. and H.C.B.; with contributions from all authors.

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