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Review

Ecoevolutionary Dynamics of Carbon Cycling in the Anthropocene

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Climate change is altering natural selection globally, which could shift the evolutionary trajectories of traits central to the carbon (C) cycle. Here, we examine the components necessary for the evolution of C cycling traits to substantially drive changes in global C cycling and integrate these components into a framework of ecoevolutionary dynamics. Recent evidence points to the evolution of C cycling traits during the Anthropocene and the potential to significantly affect atmospheric CO_2. We identify directions for further collaboration between evolutionary, ecosystem, and climate scientists to study these ecoevolutionary feedback dynamics and determine whether this evolution will ultimately accelerate or decelerate the current trend in rising atmospheric CO_2.

Evolution and C Cycling on a Changing Planet

The Earth has entered a new geological epoch, the Anthropocene, marked by rapidly increasing atmospheric CO_2 concentrations and changing environments [1,2]. For many species, these changes will impose strong selection pressures and persistence will require adaptation, directly or indirectly affecting the evolution of functional traits, that is, those that characterize the ecological role and effect of an organism on its environment [3–5]. Understanding these evolutionary trajectories is critical, given the accumulating evidence that trait evolution in response to climate change could alter key ecosystem processes, including the C cycle [6–9]. Describing how the C cycle is affected by trait evolution is particularly important because organism traits influence whether C is stored or released into the atmosphere. In addition to asking whether species will persist via evolutionary adaptation to changing environments, it is also imperative to ask how organism C cycling traits will evolve as species adapt and what the consequences of C cycling trait evolution on the environment will be.

Here, we examine the potential for contemporary evolution to impact global C cycling and storage through shifts in C cycling traits. We first examine how C cycling is mediated by organism traits and evolution. We then discuss natural selection pressures resulting from climate change and the extent of genetic variation for C cycling traits on which this selection can act. Next, we review the potential for rapid adaptive evolution of these traits to occur during the Anthropocene. Finally, we review evidence and approaches to study the direction and magnitude of contemporary evolution on C cycling traits and resulting impacts on the global C cycle. The body of work presented here reveals progress toward a synthesis between ecosystem science and evolutionary biology and suggests valuable directions for further research. We propose that the evolution of C cycling traits in response to climate change exhibits important ecoevolutionary feedback dynamics that provide a useful framework to study global C cycling and storage.

Highlights

Global climate change is altering natural selection and shifting the evolutionary trajectories of organism traits.

C cycling and other ecosystem functions are mediated by organism traits, which are subject to evolutionary processes; however, evolution is not yet explicitly included in current global C cycling models.

Rapid evolution of C cycling traits has been recently observed in several organisms, indicating that evolutionary responses to climate change could alter the C cycle and ultimately impact atmospheric CO_2.

The evolution of C cycling traits could generate particularly important ecoevolutionary feedbacks, the understanding of which will require greater integration of evolutionary, ecosystem, and climate science.

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The Organism-Mediated C Cycle

The C cycle on Earth is dominated by organism-mediated processes [10–12] (Figure 1). Photosynthesis and respiration are the largest fluxes in the global C cycle [2,13], with photosynthesis moving 20 times more C than all anthropogenic sources combined (Figure 2D). If all other fluxes were held constant, an increase or decrease in global photosynthesis by just 2% would either completely offset or double the current rate of increasing atmospheric CO_2 [2]. Therefore, the global C cycle would be significantly affected by changes in photosynthesis and/or respiration, which are influenced by traits such as C use efficiency [14,15], C fixation efficiency [16], growth rate [17], nutrient stoichiometry [18,19], and metabolism [20].

The concentration of atmospheric CO_2 is the net result of simultaneous C cycling processes. If photosynthesis and respiration evolve commensurately, the cumulative effect on atmospheric CO_2 could be zero, but if photosynthesis and respiration evolve at different rates, the effects could be substantial. Recently, these evolutionary rates were quantified experimentally in *Chlamydomonas reinhardtii*, a member of the group of aquatic autotrophic organisms responsible for almost half of global photosynthesis (i.e., phytoplankton) [21,22]. During a decade-long outdoor mesocosm experiment under increased temperatures, *C. reinhardtii* evolved a 3.5-fold

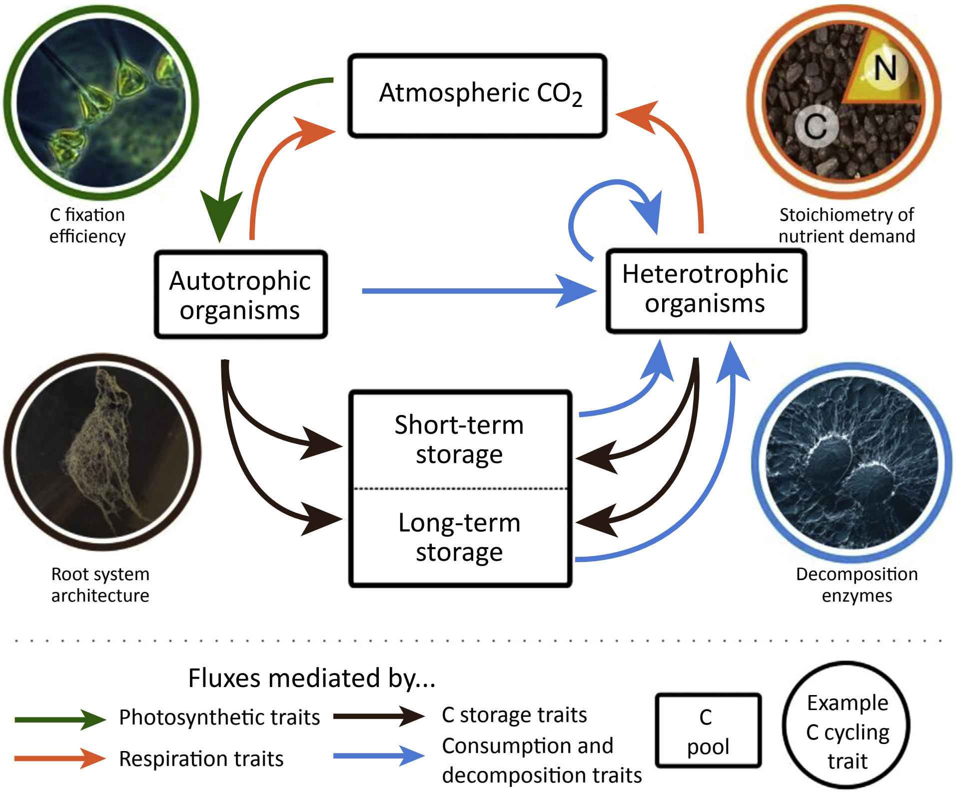

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Figure 1. Trait-Mediated Processes in the Carbon (C) Cycle. Organisms are responsible for the largest fluxes (arrows) of C between biotic and abiotic pools (boxes) in the global C cycle [2]. These fluxes are trait mediated and can be influenced by photosynthesis, respiration, C storage or consumption, and decomposition traits (arrows). Trait-based ecosystem perspectives have revealed the integral relationship between specific organism traits (circles) and the fluxes of C. By studying how these C cycling traits will evolve in response to climate change, we can consider how adaptation might affect C cycling and future atmospheric CO_2 concentrations. Images reproduced courtesy of NOAA and USDA.

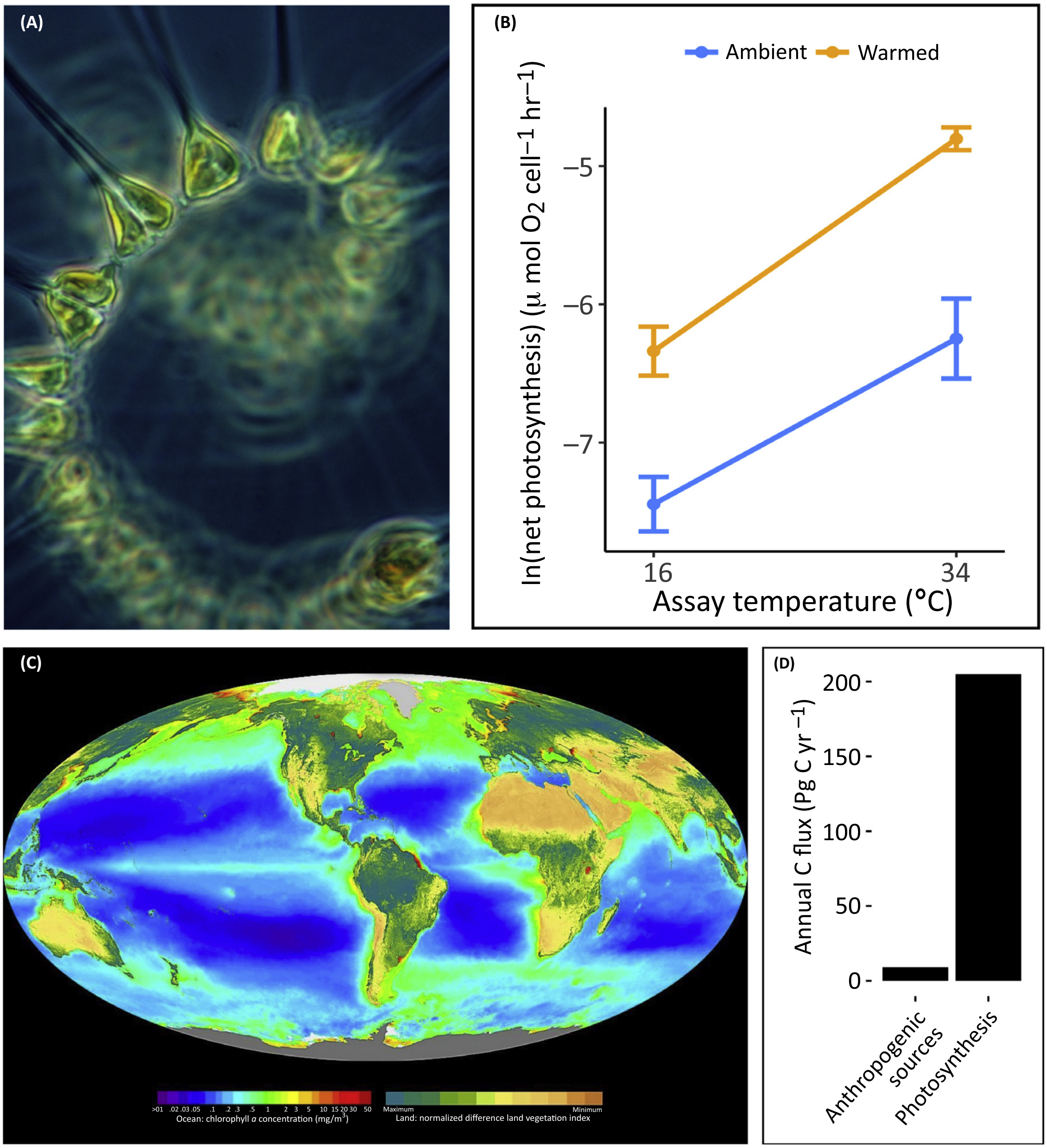

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Figure 2. Contribution of Photosynthesis to Global C Cycle and Potential for Evolution. (A) Algae and other phytoplankton contribute to approximately 40% of global photosynthesis [21] and provide useful models for studying experimentally the evolution of carbon (C) cycling traits in response to climate change-related selection pressures. (B) A decade-long mesocosm experiment found that, under increased temperatures, populations of the algae *Chlamydomonas reinhardtii* evolved 3.5-fold greater net photosynthesis compared with populations evolved under ambient temperatures (data from [22]). (C) Abundances of aquatic and terrestrial photosynthetic organisms as observed from space. (D) Photosynthesis is the largest flux in the global C cycle, moving more than 20 times the C released by anthropogenic sources (data from [2,21]). The potential impact of even minor changes in photosynthesis or other organism-mediated C cycling fluxes is substantial. Earth system models that parameterize genotypic differentiation in C cycling traits could improve predictions of changing atmospheric CO_2 concentrations. Reproduced courtesy of NOAA (A) and NASA (C).

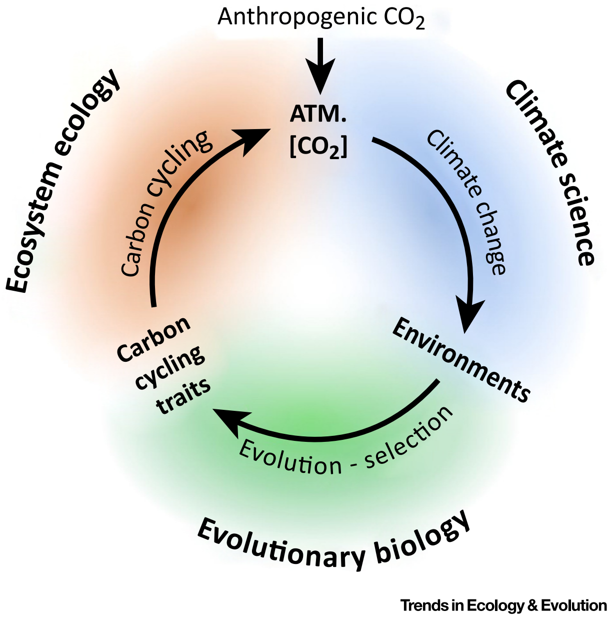

Figure 3. An Ecoevolutionary Feedback Loop Perpetuated by the Evolution of Carbon (C) Cycling Traits in Response to Climate Change. Climate change caused by anthropogenic CO_2 increases has changed biotic and abiotic environments and, thus, altered natural selection experienced by many organisms at a global scale, potentially shifting the evolutionary trajectories of C cycling traits. Evolution of these C cycling traits might in turn lead to changes in atmospheric CO_2 concentrations, which would impact climate change and alter natural selection pressures. Thus, positive feedbacks will arise when trait evolution exacerbates the current trend toward increased atmospheric (ATM) CO_2 concentrations, whereas negative feedbacks would occur when trait evolution leads to increased C storage. Understanding the ecoevolutionary dynamics of C cycling will require the integration of climate science, evolutionary biology, and ecosystem ecology.

increase in net photosynthesis, the difference between photosynthesis and respiration (Figure 2) [22]. The results of this experiment suggest that autotrophic trait evolution resulting from adaptation to warming climates can increase photosynthesis relative to respiration, potentially leading to a reduction in the rate of increase of atmospheric CO_2 toward a negative feedback (Figure 3).

In addition to directly moving C to and from the atmosphere, organism traits affect the accumulation of C in short (months–decades) and long-term (decades–millennia) storage. Soils hold approximately two–three times more C than the atmosphere, and C stocks in many soils are thought to be unsaturated [2,23]. Plant root traits, such as depth, also influence the deposition of C in deep soils [23–25] and it was recently estimated that a 1-m increase in plant root depth across just 3.9% of arable land would completely offset all CO_2 produced by annual fossil fuel emissions [24], indicating the potential for the evolution of root traits to impact atmospheric CO_2.

Similarly, deposition of biomass to the deep ocean can result in long-term C storage. A recent survey of C fluxes to subsurface ocean layers observed an average flux of 47.6 mg particulate organic (POC) and inorganic (PIC) C m^{-2} d^{-1} [26]. If roughly extrapolated across the ocean surface area on Earth (~360 million km^2) this rate equals approximately 6.3 Pg y^{-1}, which is comparable to annual fossil fuel emissions (7.8 Pg y^{-1}) [2]. Traits impacting fecal material in zooplankton and the mineral composition of phytoplankton modify the flux of C to the deep ocean [26–28]. Several studies have reported the evolution of traits (e.g., 26% increase in calcification rate [29] and 30% increase in PIC:POC [30]) that could increase the flux of biomass to deep oceans in phytoplankton adapted to increased temperature or acidification [29–31]. Such a shift could increase deep-sea C storage. Other examples of C cycling traits affecting the storage of C include those influencing the flammability of land plants [32], and the temperature sensitivity of microbial decomposition enzymes [33]. These traits contribute to the storage or release of C from biotic and abiotic storage pools, and further investigation of the direction of their evolution will be valuable toward predicting potential effects on the global C cycle.

There is little doubt that trait evolution has impacted the global C cycle throughout the history of Earth [34]. The evolution of photosynthetic traits likely drove historic fluctuations in atmospheric CO_2 [35–37]; the evolution of cellulose-decomposing enzymes in fungi increased the flux from major terrestrial C pools to the atmosphere [38,39]; and the evolution of angiosperms and deep-rooted trees has been linked to historic 10–20-fold reductions in atmospheric CO_2 [40,41]. Thus, it is critical to recognize that changes in atmospheric CO_2 on Earth are not simply the product of geological or other abiotic processes, but rather can be largely driven by global evolutionary trends. To understand the effect of evolution on C cycling in the Anthropocene, it is important to consider this phenomenon in the context of global selection pressures resulting from climate change.

Natural Selection during the Anthropocene

Increasing atmospheric CO_2 is changing environments and selection pressures globally [2,4]. In addition to the direct effects of increased CO_2, organisms are faced with ocean acidification [42], increased temperatures [43], precipitation changes [44,45], and shifts in ecological communities. Although there are notable challenges in conclusively showing that natural populations adaptively evolve in response to climate change [46], recent studies provide experimental evidence for the evolution of C cycling traits in response to such selection. For example, traits experiencing selection under increasing CO_2 (atmospheric or oceanic) include C fixation rates in phytoplankton [47], nitrogen fixation and growth rates in cyanobacteria [48,49], and stomatal conductance in plants [50]. Adaptation to changes in temperature has also been shown for microbial heterotrophs [51]. The evidence for evolution under experimentally manipulated conditions is compelling, but not sufficient to conclude that adaptation of C cycling traits will be realized under natural conditions [46].

Evidence of local adaptation to climate regimens, such as temperature in land plants [52–54], phytoplankton [55], heterotrophic microbes [56], and other consumers [57], provides additional evidence that global climate change will alter natural selection. Additionally, drought-induced selection as a result of climate change might affect the evolution of plant root traits, which are important to C storage in soils [23]. For example, altered drought regimes might select for genotypes with greater allocation to root biomass for increased water acquisition or may select for genotypes exhibiting a drought escape strategy wherein plants reproduce quickly and produce less belowground biomass.

Predicting the direction of selection for C cycling traits is complicated by the interaction between environmental drivers of selection. Although the effect of CO_2, temperature, and precipitation on organisms is often nonadditive [58], it is difficult to simultaneously manipulate multiple drivers. However, this is important, given recent evidence that selection in *C. reinhardtii* populations can be stronger when responding to multiple drivers than when drivers are isolated [59].

Genetic Variation of C Cycling Traits

Adaptive evolution of C cycling traits requires standing genetic variation on which selection pressures can act [60]. This variation can be in the form of mean differences between genotypes or heritable variation in plastic responses to environmental conditions [61]. For example, the model grass *Brachypodium distachyon* exhibits significant heritable variation in C cycling traits, including root biomass ($0.20 < H^2 < 0.36$), as well as genetic variation in plastic responses (genotype × environment interaction) to drought in the nutrient stoichiometry of leaves [62]. Indeed, there appears to be heritable variation across many plant species in traits such as root structure and leaf lability [63,64]. A review of leaf lability traits indicates that they tend to exhibit significant estimates of heritability (h^2 as high as 0.9), although, in some cases, heritability for C cycling traits has not been detected (reported median h^2 estimates range from 0.1 to 0.3) [65]. Laboratory studies also have revealed that, for C cycling traits such as growth rate, phytoplankton populations generally have high genetic and clonal diversity [66], and there are significant strain-specific responses to elevated CO_2 and temperature [67–70]. This indicates there is significant genetic variation in natural plant and phytoplankton populations and, thus, the capacity to respond to selection of C cycling traits in response to climate change.

We know relatively less about the genetic variation of C cycling traits in nonprimary producers. For example, heritable variation in microbial C cycling traits is rarely measured, because most studies report interspecific rather than intraspecific variation [71]. However, recent reports confirm the presence of genetic variation among soil microbes in the temperature sensitivity and activity of decomposition enzymes [33,72]. Heritable variation in such C cycling traits might be common, but quantification of this variation via traditional quantitative genetics, genomic prediction, or comparison of microbial isolates is still lacking (Box 1). Quantifying this variation and avoiding publication bias to report positive results is important for predicting the capacity for organisms to respond to selection. Additionally, describing genetic correlations between C cycling and other traits can provide insight into constraints on adaptive evolution [73].

Evolution on Ecological Timescales

There is growing appreciation for the prevalence of rapid evolution occurring on timescales comparable with ecological processes (e.g., [74]). However, organism-environment feedbacks with atmospheric CO_2 are often studied with respect to plastic (i.e., physiological) and ecological (i.e., species composition) responses to climate change (e.g., [75]). Although these are certainly important drivers of ongoing C cycling dynamics, they will occur in tandem with contemporary and now apparent rapid evolution of populations. Adaptation to increased temperature in the keystone species zooplankton *Daphnia magna* occurred in as little as 2 years, resulting in an increase in thermal tolerance of 3.5°C [76] and the evolution of metabolism-related genes [77]. Similar rapid adaptation to increased temperature involving metabolic genes or traits has been documented in the phytoplankton *Chlorella vulgaris* in as little as 100 generations [78]. Adaptation to drought has also been observed in less than a decade in a population of the annual plant *Brassica rapa* [79]. In response to several years of late-season droughts, these populations evolved earlier flowering time (up to 8 days earlier) [79], which is genetically correlated with lower root biomass in the close relative *Brassica napus* [80]. Such rapid evolutionary shifts in annual plant species could result in lower soil C storage in environments predicted to experience more-frequent summer droughts as a result of climate change, contributing to positive feedback interactions with atmospheric CO_2.

These examples illustrate the potential for evolution at speeds comparable to plastic and ecological responses to climate change. Interestingly, adaptive evolution can occur in the opposite direction of plastic responses [81]. For example, under ocean acidification, phytoplankton often decrease rates of photosynthesis plastically, but evolution across multiple generations leads to phenotypic shifts in the opposite direction to increase photosynthetic rates and, potentially, the likelihood of C sequestration from the atmosphere [66]. Accordingly, predictions of future trait values should not be based on plastic responses alone. However, not all seemingly strong selection pressures will engender rapid evolutionary responses. For example, *Arabidopsis thaliana* plant populations grown under elevated CO_2 in a field setting showed increased growth and fruit production but no evolutionary effect, suggesting a plastic rather than evolutionary response [82].

Box 1. Progress and Future Objectives

Recent research has led to significant progress in understanding the potential for ecoevolutionary feedbacks involving C cycling. Here, we outline the important criteria that make such feedbacks possible. For each, we highlight a statement that has received emerging empirical support (bolded) and a challenge where future research is needed.

Organism Traits Mediate C Fluxes

Challenge: it is critical that the relationships between specific traits, ecosystem C fluxes, and ultimately atmospheric CO_2 be described quantitatively.

Climate Change Will Impact Selection Pressures

Challenge: more research is needed to predict how different components of climate change (e.g., drought and temperature) will interact to alter evolutionary trajectories of C cycling traits.

Organisms Harbor Significant Genetic Variation for C Cycling Traits

Challenge: genetic variation in C cycling traits has not been explicitly quantified in many organisms, leaving a gap in our ability to predict evolutionary responses.

Evolution Can Occur at Rapid Timescales

Challenge: more studies are needed to understand the limits of this evolution (e.g., in organisms with long generation times or small populations). Studies that go beyond demonstrating that rapid evolution can occur toward determining whether rapid evolution most often does occur will strengthen our ability to consider ecoevolutionary feedbacks in the Anthropocene global C cycle.

Ongoing Environmental Changes Can Lead to Rapid Evolution of C Cycling Traits

Challenge: more research is needed to draw generalizable conclusions about the direction of this evolution across species and environments, and how evolution within native populations and communities can scale to impacts on ecosystem-level carbon cycling. Disparate evidence suggests that the first four criteria described above exist in nature, yet studies that integrate these components are rare. Additionally, determining the sign and magnitude of evolution on global C cycling and atmospheric CO_2 remain pressing research objectives at the intersection of evolutionary biology and ecosystem science.

Direction of Selection on C Cycling Traits

The evolution of C cycling traits could increase, decrease, or stabilize atmospheric CO_2 concentrations, depending on the direction of natural selection on C cycling traits. Assessing experimental evolution in microcosms and mesocosms provides one approach to study the direction of this evolution. By allowing populations to adapt to environments simulating future conditions, the response to selection in C cycling traits can be measured empirically. This approach has proven especially insightful for studying the evolution of phytoplankton. These experiments have observed evolutionary responses to increased CO_2 (and associated ocean acidification) [17,31,47–49,66,83,84], temperature [22,78], or combinations thereof [29,30] and have provided valuable information toward resolving the direction of selection on C cycling traits. *C. reinhardtii* adapted to a decade of elevated temperature in outdoor mesocosms evolved increased net photosynthesis (Figure 2B) [22] and, in a separate experiment, *C. vulgaris* down-regulated respiration relative to photosynthesis [78]. Additionally, populations of the calcifying phytoplankton *Emiliania huxleyi* adapted to elevated temperature, exhibiting shifts in ballasting traits, such as PIC:POC, in directions predicted to increase sinking speed and, thus, the flux of C to deep oceans [30]. Such studies suggest that selection caused by increased temperature acts in directions that increase the net flux of C from the atmosphere to biotic and abiotic storage pools and produce a negative feedback loop with atmospheric CO_2.

However, studies examining phytoplankton evolution in response to acidification highlight that further work is needed to draw generalizable conclusions about the direction of selection caused by ocean acidification. For example, under experimentally increased CO_2 and acidification, *Gephyrocapsa oceanica* evolved higher photosynthetic C fixation and growth rates [47], whereas *Phaeodactylum tricornutum* evolved reduced photosynthesis, respiration, and growth rates [84]. To what extent such discrepancies are caused by differences between the evolutionary responses of species or experimental conditions remain unclear. As a result, a valuable direction for future research would be to compare the evolutionary trajectories of C cycling traits in multiple species (including heterotrophs, such as *Daphnia*), ideally in factorial designs with multiple selection pressures.

Studying evolution under ecologically realistic conditions is also important. For example, recent (<50 years) woody encroachment into grasslands has altered community composition and C balances within these systems [85]. Such shifts in community composition can influence evolution by altering interactions within and across trophic levels (Figure 1). Yet, because mesocosm approaches will not capture the more-complex influences of community-level change, manipulative and observational studies to assess climate-change driven evolutionary dynamics in real communities will be valuable.

There are several alternatives to mesocosm experiments to study the direction of evolution of C cycling traits in natural populations. The strength of selection on C cycling traits could be measured with a quantitative genetic approach in a pedigreed population grown in a common environment reflecting future conditions [86]. Long-term monitoring of populations in experimentally modified native habitats can also be useful. For example, a 10-year precipitation manipulation experiment within native grassland communities found that increased intra-annual precipitation variability selected for genotypes of a dominant grass with greater relative allocation to root biomass [87]. Although such a trait shift might lead to more belowground C storage, selection on this population was variable. As a consequence, how population evolution in this particular case ultimately scaled to ecosystem-level C cycling and atmospheric feedbacks is uncertain.

Naturally occurring CO_2, pH, temperature, or precipitation clines are natural ecological experiments that substitute space for time, representing a chronosequence of environmental change. Genetic differentiation along these clines can be studied to infer the direction of selection in response to climate change. Populations adapted to terrestrial [88] and aquatic CO_2-emitting vents [89] have evolved in environments with higher ambient CO_2 and/or lower pH. A recent study of *Plantago lanceolata* plants adapted to such elevated CO_2 habitats found genetic evidence of an evolved increase in photosynthetic capacity and respiration rate, although the effect on net photosynthesis is unresolved [88]. Similarly, the direction of selection on C cycling traits in response to increased temperature and aridity can be inferred from populations diverged along natural temperature and precipitation clines. Populations of a keystone snail herbivore, *Radix balthica*, adapted to warmer springs have evolved higher metabolic, respiration, and consumption rates (Schaum *et al*. 2017, unpublished data). This is consistent with theoretical predictions that increased temperature leads to shifts in the stoichiometry of the nutrient needs (increased C:nitrogen ratio), increased metabolic demand, and higher respiration rates of consumers [19]. These results indicate the potential for heterotrophic evolution in response to increasing temperatures to perpetuate a positive feedback on atmospheric CO_2. Indeed, an exciting direction for future work will be to assess whether such evolution will counter negative feedbacks occurring at lower trophic levels.

It is also possible to measure the recent direction of evolution in C cycling traits *in situ*. 'Resurrection' studies use seed banks or other sources of dormant organisms to measure recent evolution in plants [90], zooplankton [76], and microbes [91]. Resurrection studies have provided convincing evidence that rapid evolution can occur across different organisms [92] and present a promising opportunity to reconstruct the direction of recent C cycling trait evolution. Past, ongoing, and future evolution of C cycling traits could also be studied using genomic sequence data to predict C cycling phenotypes in preserved specimens [93] or recent collections of natural populations [94].

Evolution of C Cycling Traits as an Ecoevolutionary Feedback

The idea that organisms alter their selective environment originated with Darwin [95] and can be conceptualized under the framework of ecoevolutionary dynamics [96]. Ecoevolutionary feedbacks occur when trait evolution modifies environmental conditions in response to natural selection. This environmental modification then feeds back to influence the trajectory of future selection pressures and, thus, evolutionary change. For example, a positive feedback pressure would arise if evolutionary change results in an even-greater rate of atmospheric CO_2 increase. By contrast, negative feedback pressure results from evolutionary change that reduces the rate of atmospheric CO_2 increase. Here, we have discussed why organisms are expected to experience strong natural selection as a result of climate change. We have also seen the potential for this selection to lead to the evolution of C cycling traits. Yet, to date, few if any studies have integrated these criteria into a complete ecoevolutionary feedback cycle. Given the primary fluxes that interact with atmospheric CO_2 are those mediated by organisms [2], evolutionary changes in C cycling traits are expected to influence the balance between atmospheric C and other pools in the C cycle. Thus, the evolution of C cycling traits might either accelerate or decelerate the current trend toward increasing atmospheric CO_2 and climate change, altering the trajectory of future selection regimes and contributing to an ecoevolutionary feedback loop. Therefore, the model of ecoevolutionary feedback dynamics provides a useful framework to conceptualize the components underlying the evolutionary dynamics of global C cycling (Figure 3). Integrating all of the steps of such feedbacks to characterize the contemporary ecoevolutionary dynamics of C cycling will require an unprecedented yet achievable synthesis among multiple disciplines and across multiple taxa (Box 2).

Concluding Remarks

Here, we have discussed recent evidence for the components of ecoevolutionary dynamics involving C cycling traits (Box 1, Figure 3). There are also a growing number of studies that have begun to integrate these components. For example, recent work generally suggests that C cycling traits in phytoplankton will evolve in response to elevated temperatures in directions predicted to have a stabilizing effect on atmospheric CO_2, contributing toward negative feedback dynamics. By contrast, theory and recent empirical work indicates that metabolism and nutrient stoichiometry in heterotrophs will evolve in directions that establish positive feedback dynamics with atmospheric CO_2. Such complexities speak to the need for greater understanding of the potential tradeoffs among different organisms and traits (as well as across ecosystems and communities) as they evolve in response to climate change. Improved prediction of the evolutionary trajectories of C cycling traits within individual ecosystems is needed because the net effect of evolution at a global scale will be impacted by both positive and negative feedback pressures.

A critical question is whether the magnitude of evolutionary changes in C cycling traits will be large enough to significantly affect atmospheric CO_2 concentrations. It is important to consider that evolution has demonstrated the capacity to affect global C cycling throughout the history of

Outstanding Questions

How can we best quantify relationships between trait values and C fluxes to promote inclusion of traits as parameters in Earth system models of global C cycling?

How will different components of climate change (e.g., drought and temperature) interact to alter evolutionary trajectories of C cycling traits?

What are the limits (genetic variation, population size, and trade-offs between traits) of the rapid evolution of C cycling traits and do these limits vary across taxa?

Are the results of recent empirical work assessing the direction of C cycling trait evolution representative across different species and environments?

What is the expected direction and magnitude of the effect of C cycling trait evolution on atmospheric CO_2?

How can we apply our knowledge of the evolution of C cycling traits to management practices aimed at preparing for, or mitigating, climate change?

How can we create opportunities at the institutional level that facilitate the collaboration necessary to best understand ecoevolutionary feedbacks of C cycling?

How can the ecoevolutionary dynamics of C cycling be extended to understand ecoevolutionary dynamics more broadly?

Box 2. Tools toward a Synthesis

Understanding the ecoevolutionary dynamics of C cycling will require the integration of evolutionary biology, ecosystem ecology, and climate science (see Figure 3 in the main text). Fortunately, each of these disciplines is largely prepared with the tools needed to achieve such a synthesis.

Evolutionary Biology

Evolutionary biology is equipped with the tools to quantify the capacity for evolutionary change and direction of selection on C cycling traits. Quantitative genetics delivers a robust statistical framework to accomplish this, wherein measures of genetic variation (i.e., V_a, and h^2) and the strength (S) and response (R) to selection on C cycling traits can be estimated [90]. Evolutionary responses of C cycling traits can also be directly observed through experiments or by comparison of populations diverged through time or along chronosequences. Tools, such as landscape genomics and genomic prediction [98] of C cycling traits, might also prove useful in predicting evolutionary responses of C cycling traits [99]. Estimating the direction and magnitude of rapid evolutionary responses in these traits and consequences for ecosystem processes remains an important challenge to parameterize C cycling models.

Ecosystem Ecology

Ecosystem ecology provides models that describe the relationships between organisms and environments through processes such as the cycling of nutrients between pools and fluxes, and is well-suited for trait-based approaches. Key predictions of C cycling models include processes such as net ecosystem productivity (NEP), which is fundamentally defined as the difference between total photosynthesis (GPP) and ecosystem respiration (ER) [99], two processes that are driven by a suite of traits. Progress in trait-based ecosystem ecology has led to large-scale community and ecosystem models of the C cycle that include more-specific, typically static, trait values. Yet, as trait-based approaches continue to develop, movement away from static trait values to those that can change as a result of evolutionary processes can add realism, and even constrain model predictions with more-realistic trait values. Additional community and ecosystem models including experimentally derived expected trait value shifts could help inform large-scale Earth system models, allowing better tracking of the magnitude and direction of C ecoevolutionary feedback loops on atmospheric CO_2.

Climate Science

Climate science, while not the focus of this paper, has seen considerable advances in recent years in our ability to model how environmental conditions will change as a function of atmospheric CO_2. These models have moved well beyond predicted increases in mean temperatures, and are able to model changes in climatic variability and extreme events (e.g., [44]), providing improved accuracy and important dimensions in terms of which future selective environments can be characterized.

Earth and that climate change is altering selection on organisms globally. It is also clear that even small changes to the global C cycle can have large impacts, given that anthropogenic CO_2 sources (burning fossil fuels, land-use change, etc.) account for less than 1.5% of global C fluxes, yet are driving major environmental changes across the planet [2]. It is too early to conclude that evolution will dramatically alter contemporary atmospheric CO_2 but there is mounting evidence that the potential exists.

Identifying the feedback potential of different taxa will be useful for management. The evolution of traits that increase C storage represents a particularly valuable ‘evosystem service’ [8] and organisms predicted to do so may be prioritized for conservation and agricultural use. For example, *C. reinhardtii* shows evidence of evolving greater net photosynthesis in response to increased temperature (Figure 2) and lakes it inhabits might be targeted for protection. While the C storage potential of organisms will never be the only factor influencing management, understanding the roles of organisms in the ecoevolutionary dynamics of C cycling could lead to more-purposeful and informed decision-making.

Studying the evolution of C cycling traits also presents a meaningful research objective at a more-fundamental level, because it addresses a universal challenge in biology and ecology:

integrating across different levels of organization [97]. Progress will not only provide insight into important evolutionary processes, but also help to better understand the relative importance of ecoevolutionary dynamics in natural ecosystems (see Outstanding Questions). Evolutionary biologists, ecosystem ecologists, and climate scientists should work together toward the common research goal of quantifying the impact of organism evolution in natural ecosystems on global C cycling.

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