

Annual Review of Environment and Resources The Terrestrial Carbon Sink

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Annu. Rev. Environ. Resour. 2018. 43:219–43

First published as a Review in Advance on
September 26, 2018

The *Annual Review of Environment and Resources* is
online at environ.annualreviews.org

<https://doi.org/10.1146/annurev-environ-102017-030204>

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Keywords

biogeochemical, carbon, cycle, ecosystem, land surface, model, nutrients, plant, terrestrial biosphere, vegetation, water

Abstract

Life on Earth comes in many forms, but all life-forms share a common element in carbon. It is the basic building block of biology, and by trapping radiation it also plays an important role in maintaining the Earth's atmosphere at a temperature hospitable to life. Like all matter, carbon can neither be created nor destroyed, but instead is continuously exchanged between ecosystems and the environment through a complex combination of physics and biology. In recent decades, these exchanges have led to an increased accumulation of carbon on the land surface: the terrestrial carbon sink. Over the past 10 years (2007–2016) the sink has removed an estimated 3.61 Pg C year⁻¹ from the atmosphere, which amounts to 33.7% of total anthropogenic emissions from industrial activity and land-use change. This sink constitutes a valuable ecosystem service, which has significantly slowed the rate of climate change. Here, we review current understanding of the underlying biological processes that govern the terrestrial carbon sink and their dependence on climate, atmospheric composition, and human interventions.

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1. INTRODUCTION TO THE TERRESTRIAL CARBON CYCLE

Each year, plants remove approximately one-fifth of the carbon present in the atmosphere, a vast amount considering the miniscule scale of plants compared to the volume of air above them (1). Carbon enters the leaves in gaseous form as carbon dioxide (CO_2), where it is converted through photosynthesis into sugars and starches (2). The total flux of carbon removed is more than ten times greater than what is emitted into the atmosphere through burning fossil fuels (3) and is the source of sustenance for the majority of life on Earth.

As with many things in the natural world, this process of carbon uptake is balanced by a counteracting force (4). Respiration, the mechanism by which plants, animals, and microbes convert sugars into energy, breaks the complex carbohydrate bonds formed through photosynthesis and releases CO_2 back into the atmosphere. Combined with other processes, such as recurrent fires and dissolved organic carbon transfer to aquatic systems (**Figure 1**), these flows of carbon out of ecosystems largely offset the flows in Reference 3.

The exchange of carbon absorbed by photosynthesis, and released through respiration, waxes and wanes from day to night, through the seasons, and has natural cycles from decades to millennia. Over the past century, this breathing of the biosphere has resulted in a large and persistent net removal of carbon from the atmosphere by global terrestrial ecosystems (5, 6). Termed the terrestrial carbon sink, this has served to slow the rate of accumulation of CO_2 in the atmosphere (7, 8), and thus the rate of climate change (9).

It is critical to understand the reasons for the current sink, and that requires an in-depth understanding of the spatial and temporal changes in the varied responsible processes. Our understanding of the underlying processes and their dependence on the key drivers of climate, atmospheric composition, and human land management has developed rapidly over the past decade, as have the questions we are capable of answering. Here, we review recent developments and the current state of knowledge on the terrestrial carbon sink. We start by giving an overview of the terminology used to refer to different aspects of the terrestrial carbon cycle and present the fundamental principles that characterize carbon cycling in terrestrial ecosystems. We then examine recent developments in our knowledge of how carbon cycles through different ecosystems, and the tools used. Finally, we conclude with discussion of the policy implications of a terrestrial carbon sink.

2. TERMINOLOGY

The terrestrial carbon cycle is the manifestation of multiple different processes operating on varied temporal and spatial scales (**Figure 1**). The diversity of processes is matched by a wealth of terminology (10) (**Table 1**). Here we discuss the key terms and their relationship to one another.

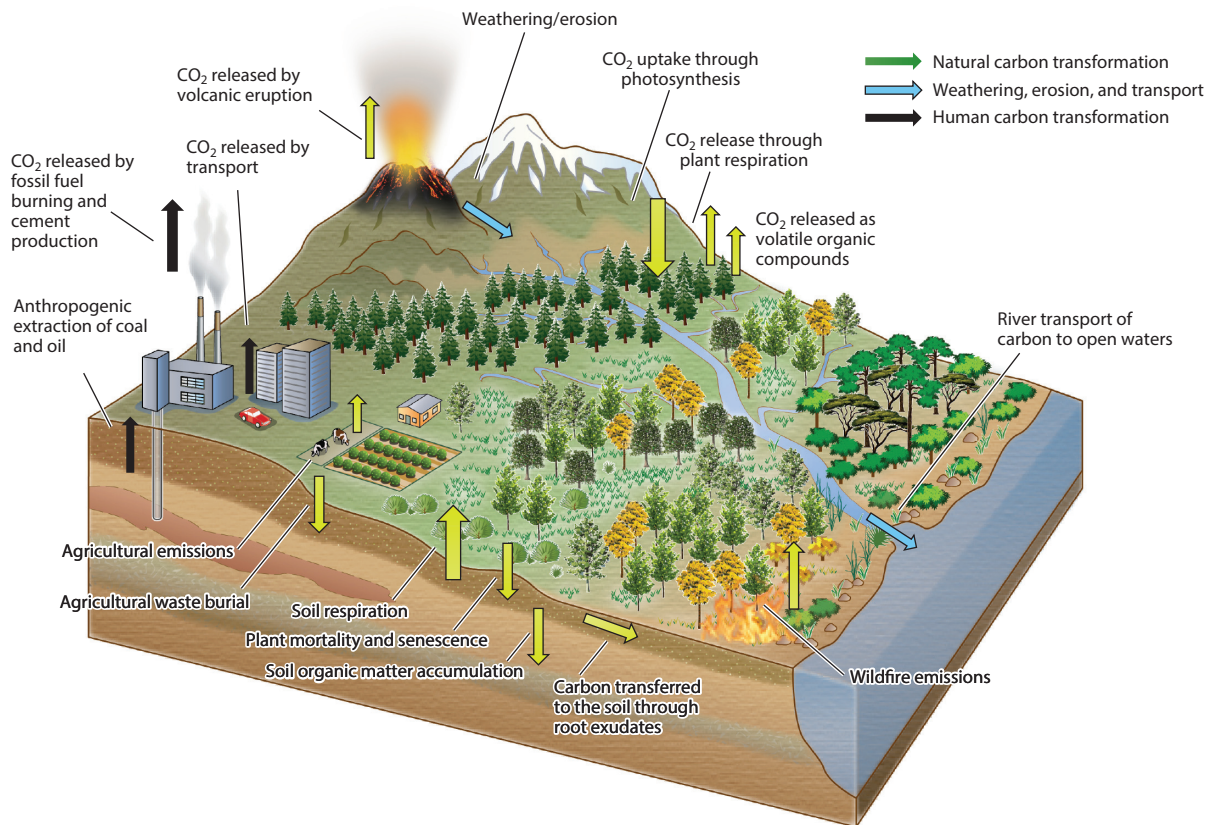


Figure 1

The primary flows and exchanges that constitute the terrestrial carbon cycle, including uptake through photosynthesis, release to the atmosphere through both anthropogenic (fossil fuel emissions, biomass burning, land use) and natural emissions (autotrophic and heterotrophic respiration, wildfires, volcanic eruptions), and weathering, erosion, and transport. Figure modified with permission from Diana Swantek, Lawrence Berkeley National Lab.

Carbon sequestration is the term used to describe the capture and long-term storage of CO₂ from the atmosphere. A forest, ocean, or other natural environment has the ability to sequester carbon, through the movement of carbon from short-lived labile pools such as leaves and hummus, to long-lived pools with slow turnover times such as standing biomass or recalcitrant organic matter in soils. The ability to sequester carbon is determined by the balance of time an ecosystem spends being either a sink or a source of carbon, which is defined based on an ecosystems ability to absorb CO₂ from the atmosphere. An ecosystem can be a sink for carbon in one year, and a source in another, but must be a sink over long timescales to sequester more carbon.

Although ecosystems are often classified as sinks or sources based on observed fluxes of carbon between an ecosystem and the atmosphere, a true quantification of sink strength must take into account all the pathways of carbon transport, many of which are not represented in observations of exchanges with the atmosphere. Such quantification is termed the net ecosystem carbon balance (NECB; 10) and accounts for all vectors of carbon exchange between an ecosystem and its environment. NECB is best conceptualized by considering an ecosystem as a volume (11), where the top

Table 1 Common terms and definitions associated with photosynthesis, respiration, and the natural carbon cycle

Term	Definition
Photosynthesis	The mechanism by which plants synthesize complex carbohydrates from light and carbon dioxide (CO₂)
Gross photosynthesis	The sum of carbon fixed through carboxylation within the leaf chloroplasts (also referred to as true photosynthesis)
Apparent photosynthesis	Carbon assimilated though carboxylation minus photorespiration
Net photosynthesis	Gross photosynthesis, minus photorespiration and dark respiration
Gross primary productivity	Ecosystem-scale apparent photosynthesis
Net primary productivity	Ecosystem-scale apparent photosynthesis minus autotrophic respiration
Gross/net primary production	Ecosystem-scale gross/net primary productivity when considered over longer time periods
Respiration	The mechanism by which plants, animals, and microbes convert sugars into energy
Autotrophic respiration	The sum of respiration by all living plant material in an ecosystem
Photorespiration	The oxygenation of ribulose 1,5-bisphosphate (RuBP) by the enzyme RuBisCO in the chloroplast
Dark respiration	The release of CO ₂ in the mitochondria, without the aid of light
Maintenance respiration	Metabolism required to maintain an organism in a healthy, living state
Growth respiration	Metabolism associated with growth processes such as synthesis of new structures, nutrient uptake, N reduction, and phloem loading
Heterotrophic respiration	The respiration rate of all heterotrophic organisms (animals, fungi, and microbes)
Total ecosystem respiration	The sum of autotrophic and heterotrophic respiration
Carbon sequestration	The removal and long-term storage of CO₂ from the atmosphere
Carbon sink or source	The balance of flows of carbon between an ecosystem and the atmosphere over a given period of time
Net ecosystem carbon balance	The balance of carbon entering and leaving an ecosystem through all pathways
Net biome production	The net ecosystem carbon balance for a large ecological and temporal grouping, explicitly including effects from disturbances and management
The residual terrestrial sink	The residual of anthropogenic emissions (including land-use change) minus the oceanic sink and atmospheric CO ₂ growth
Net ecosystem production	Gross primary production minus ecosystem respiration
Net ecosystem exchange	Ecosystem respiration minus gross primary production

is above the canopy, the bottom is the transition between the vadose zone and the water table, and the sides are defined by the spatial scale of interest. NECB represents the total carbon that enters the volume, minus the total carbon that exits, over a specified time interval (**Figure 1**). Carbon can be lost from the volume through respiration, fire (12), photodegradation (13), emissions of methane (14), and volatile organic compounds (15), along with erosion and the leaching of dissolved organic and inorganic carbon (16), or gained through processes such as photosynthesis, wet and dry deposition (17), animal activity (18), and methane consumption (19). A full consideration of an ecosystem source or sink strength requires the quantification of each term. When quantified over large spatial scales, NECB is commonly referred to as net biome productivity (10).

Photosynthesis and respiration dominate the flows of carbon into and out of this volume for the majority of ecosystems (**Figure 1**). Gross photosynthesis refers to the sum of carbon fixed through carboxylation within the leaf chloroplasts (2), and it is commonly referred to as true photosynthesis (20). As the process of carboxylation occurs concurrently with photorespiration in the chloroplast, the term apparent photosynthesis is used to describe the observed carbon assimilated after accounting for photorespiration. A second respiration term, mitochondrial respiration (commonly

referred to as dark respiration), also occurs in photosynthetic cells (2). The net cellular carbon assimilation is called net photosynthesis, defined as true photosynthesis minus photorespiration and dark respiration (20). These terms are typically used to refer to processes at the cellular and leaf scales.

At the ecosystem scale, the photosynthetic flux of carbon is referred to as gross primary productivity (GPP), which, due to methodological considerations, is equivalent to true photosynthesis minus photorespiration (i.e., not to be confused with gross photosynthesis) (2), assuming that dark respiration is not inhibited by light. When considered over longer timescales, GPP is often referred to as gross primary production, to distinguish between a short-term flux and longer-term production.

Gross primary production supplies the carbon needed to build and maintain biomass. A proportion of gross primary production is used to support the construction of new tissue, whereas another proportion contributes to the respiration required to maintain living biomass. The net balance between gross primary production and autotrophic respiration (AR) is termed net primary production (or net primary productivity when relating to GPP), and it represents the rate of biomass production (i.e., the difference between gross primary production and the rate at which plants use energy through AR, the sum of growth and maintenance respiration by all living plant material in an ecosystem).

Heterotrophic respiration (HR) is the respiration rate of all heterotrophic organisms (animals, fungi, and microbes) summed per unit ground or water area and time. AR and HR combined gives total ecosystem respiration ($RE = AR + HR$), which balances gross primary production to give net ecosystem production [$NEP = GPP - RE$ (10)]. NEP is considered from the perspective of the ecosystem, with positive values indicating a larger carbon uptake through production than release through respiration. Conversely, the atmospheric perspective considers positive net ecosystem production to be negative net ecosystem exchange, as positive production implies carbon leaving the atmosphere. In contrast to GPP and RE, which must be inferred from measurements of the net carbon flux, NEP is directly observable at the ecosystem scale.

The terrestrial carbon sink is thus most accurately quantified by considering the NECB for global land ecosystems, including estimates of the spatial and temporal distribution of the components of net ecosystem production ($NEP = GPP - RE$), along with the secondary terms of carbon releases through fire, land-use change emissions, non- CO_2 carbon emissions, and terrestrial-aquatic carbon transfers. Due to difficulties in quantifying NECB, and the conceptual separation of direct and indirect anthropogenic influences on natural ecosystems, research often also focuses on the residual terrestrial sink (RTS), which is defined as the total annual accumulation of carbon in the terrestrial biosphere after accounting for the net effect of land-use change (3), and typically calculated as the residual of fossil, cement production, and land-use change emissions minus the oceanic sink and the atmospheric CO_2 growth.

3. ECOSYSTEMS AND EQUILIBRIUM

Global ecosystems are in a state of constant flux, with growth and reproduction competing against consumption and mortality (**Figure 2**); however, fundamental ecosystem characteristics persist. Before considering the processes responsible for today's terrestrial carbon sink, it is pertinent to examine the intrinsic characteristics of how carbon flows through ecosystems and the implications for an ecosystem's sink-source state.

The primary characteristic of a terrestrial ecosystem is the flow of carbon from photosynthesis through various pools and ultimately back into the atmosphere. CO_2 fixed through photosynthesis is transferred to biomass through growth, passed to soil microbes through root exudates, or

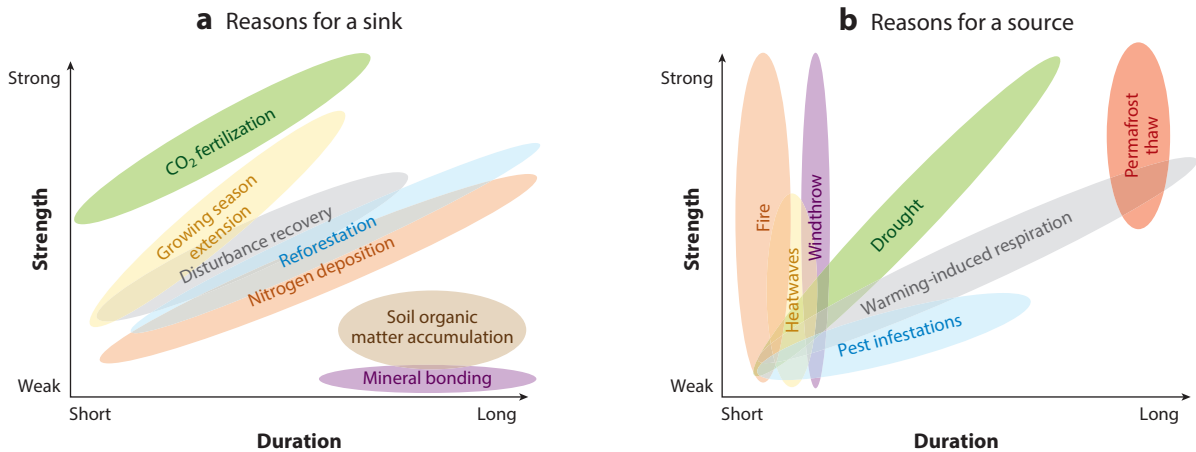


Figure 2

A schematic of the multiple influences responsible for an ecosystem's (a) sink or (b) source magnitude, separated by their strength and duration. Processes such as CO₂ fertilization, growing season extension, and recovery from disturbance have been identified as causes of the current global sink, while drought, warming-induced respiration, and disturbances contribute to sink reductions.

removed from the ecosystem through respiration and other pathways. The carbon stored as biomass can persist from several seasons, as is the case of leaf tissue and fine roots, to several centuries, as is the case of wood in long-living trees. And when a plant dies, much of the biomass carbon is transferred into soil organic matter, where it can be stored for thousands of years more before it is finally released back into the atmosphere (21).

The transfer of carbon from one pool to another in ecosystems is typically dominated by the donor pool (22). The concept of donor pool-dominated transfers is one of the most fundamental characteristic of carbon exchange in ecosystems, and it mathematically provides convergent and predictable dynamics. In the absence of perturbations, such a system inevitably tends toward a quasi-equilibrium state, in which carbon inflows are matched by carbon outflows, and the net carbon sink is at or very near zero. For example, if the photosynthetic influx is higher than the respiratory CO₂ release, this leads to an increase in the NECB. The resulting larger carbon pools imply higher respiration, which over time brings the ecosystem closer to equilibrium. Similarly, if the photosynthetic influx is lower than the CO₂ released through respiration, this leads to declines in the carbon pool size. Smaller carbon pools reduce the carbon available for respiration, bringing the ecosystem closer to equilibrium. The idea was first proposed by Odum (23), who highlighted that respiration approximated productivity over different successional stages. It has since been verified empirically by studies showing that ecosystem carbon stocks recover toward equilibrium during secondary forest succession and following disturbances (24).

An ecosystem in approximate equilibrium should have near constant carbon pools (although oscillatory dynamics persist; 25), but carbon pool sizes differ widely between ecosystems in equilibrium. The equilibrated size of carbon pools in an ecosystem is a combination of the rate of carbon input (photosynthesis and carbon transfers) and the time the carbon spends in each pool (i.e., the residence time; 26). We consider the equilibrated carbon pool's size as an ecosystem's intrinsic carbon holding capacity. A high rate of input does not necessarily equate to a large carbon holding capacity, as it can be offset by large carbon losses. For example, arid ecosystems such as savannahs or grasslands often maintain high rates of photosynthesis, but also have fast turnover times driven by high respiration rates and especially fires, and typically have small carbon pools.

In contrast, tropical ecosystems are characterized by high rates of input and fast turnover times, but also large carbon pools given turnover times are not sufficiently high to compensate for the high input rates. In other systems, such as wetlands and peatlands, low input rates are balanced by low turnover times, which can give exceptionally high carbon pools. Carbon residence times were recently identified to be the dominant source of uncertainty in future projections of the terrestrial carbon cycle (27).

Although ecosystems naturally converge to equilibrium, ecosystems at equilibrium are rarely found in nature, especially in the postindustrial world. Instead, ecosystems exist in a state of dynamic disequilibrium (28), continuously striving to approximate equilibrium but never quite getting there. The reasons for this are both natural and anthropogenic, all of which lead to an ecosystem being either a source or a sink, over a defined period of time, due to disturbance and environmental change (**Figure 2**). Disturbance, either from natural causes such as wildfire or anthropogenic impacts such as deforestation, alter carbon pool sizes and ecosystem function, and thus affect the time required to get to equilibrium and can even keep ecosystems far from equilibrium through periodically repeated disturbance events. Environmental change, which encapsulates both natural cycles in the global climate system and anthropogenically induced changes, such as warming, elevated atmospheric CO₂, and nitrogen deposition, changes the levels of equilibrium carbon storage by changing carbon inputs and residence times. Ecosystems are thus in a perpetual cycle of being knocked away from equilibrium by disturbance, while at the same time the natural equilibrium point is changing due to environmental change. Changes in the disturbance regime, and persistent environmental change can also completely change the playing field by altering ecosystem structure sufficiently to create a regime shift to a new stable equilibrium state. Whether such state changes are more likely to occur as gradual shifts or tipping points is widely debated (29), but they would undoubtedly have profound impacts on the future terrestrial carbon sink.

4. TOOLS FOR EXAMINING THE TERRESTRIAL SINK

The past decade has seen a large increase in the tools and sources of information that can be used to estimate the terrestrial sink and its response to environmental change. Particular advances include satellite and near-surface remote sensing efforts [e.g., solar-induced fluorescence, airborne light detection and ranging (LiDAR), hyperspectral retrievals], distributed and coordinated measurement networks (30), repeated national inventories (5), atmospheric observations (31, 32), and inversion capabilities (33), combined with innovative modeling strategies (34) and the development of novel theory (35). Although the variety of approaches is too vast to cover in this review, here we highlight those that have changed most and offer the greatest potential.

At the integrated global scale, the most influential advances in estimating the global terrestrial sink over the past decade have arguably come from the Global Carbon Project. The first data release in 2007 (36) collated annual time series of regional fossil and nonfossil global anthropogenic emission with estimates of land-use change emissions, economic activity, and atmospheric CO₂ dynamics. Since then, the Global Carbon Project has expanded to include improved data sources and treatment, and multimodel ensemble estimates of oceanic and terrestrial carbon fluxes (3). Key advances include the incorporation of inverse model estimates (3) and a large increase in community contribution through the submission of results from process-based dynamic vegetation models. Challenges remain, however. For instance, historic land-use change emissions are highly uncertain (37). Advances are also needed to develop a meaningful land sink estimate, and the resulting budget imbalance estimate, from the model ensemble given the large structural uncertainty of terrestrial ecosystem models (38). Combined with recent advances in both the theoretical interpretation of atmospheric isotopes (32) and in the use of other tracers and proxies (39), these

data sources form a key benchmark for our understanding of long-term changes in the global carbon cycle, and the different components involved, as well as the likely implications of emissions trajectories for climate stabilization targets.

Atmospheric transport models, coupled with observations from a network of more than 100 atmospheric sampling stations distributed around the world, allow for the inverse calculation of surface carbon cycle dynamics responsible for observed changes in atmospheric CO₂ concentrations (40). Inverse modeling can be used to distinguish terrestrial versus oceanic carbon sinks by incorporating atmospheric measurements on variations in O₂, CH₄, and the isotopic composition of CO₂, and it provides information on broad regional differences (e.g., 33), with increasingly fine spatial resolution (41). It can also allow for the identification of likely sources and magnitudes of anthropogenic emissions, which are key to ensuring mitigation commitments are met (42) but which can only be measured directly at discrete times and locations (e.g., 43). As the observational network expands (44) and the statistical and numerical methods become more sophisticated (e.g., 45), inverse methods are beginning to provide insight into the driving factors responsible for changes in terrestrial carbon cycling (e.g., 46, 47). The current sampling network is still not sufficient to avoid diagnostic ambiguities, however (48), although an increase in horizontal resolution may allow for the incorporation of a large body of surface flux observations in the near future (49).

Satellite remote sensing has advanced over the past decade at a rapid pace (50). The field has moved from the limited-band retrievals available in the 1980s and 1990s, which were focused on the visible spectrum and the near infrared and primarily provided indices of vegetation greenness, to a large range of sensing capabilities and associated products, providing information on photosynthetic activity, canopy temperature, soil moisture, canopy water content, aboveground biomass, fire and phenology, to name but a few (e.g., 51–53). The emerging capabilities promise to provide satellite-derived information on important regions and ecosystems that are poorly represented in current measurement networks, such as tropical and high-latitude ecosystems (33). Recent advances promise to use spaceborne imaging spectroscopy to remotely estimate diversity, relative abundance, and community change over large spatial scales (e.g., 54), allowing for a quantification of functional ecosystem diversity necessary for the next generation of terrestrial carbon cycle modeling (55). Linking remotely sensed information to the carbon cycle is nontrivial, however, as both functional and structural characteristics combine to generate whole ecosystem reflectance (56). Despite the progress and promise of satellite-based observations of the terrestrial carbon cycle (50), near surface and ground-based observations remain essential for carbon cycle research.

Near surface remote sensing has brought a suite of ecosystem-scale observations within reach, spurred by the confluence of advances in drone technology, increased processor speed, and advanced instrumentation. Unmanned aerial systems in particular have emerged as valuable sources of information on the relation between structure, function, and the carbon cycle (57). Over the past decade, improvements to navigation technology, declining costs of unmanned aerial vehicles, and the miniaturization of instrumentation are providing exciting new avenues for carbon cycle research (e.g., 58). Example applications include the characterization of fine-scale temporal changes in land cover using visible spectrum reflectance (59), the classification and quantification of structural characteristics of individual canopies by fusing LiDAR and hyperspectral imagery (60), and assessing trait diversity and ecosystem function (61). In tandem, larger payloads aboard manned aerial systems are providing an unprecedented view of landscape-scale ecosystem properties (e.g., 62, 63), whereas networks of automated near-surface remote sensing instruments such as digital repeat photography (64) are helping link retrievals to canopy physiology (65).

Direct observations of the terrestrial carbon cycle are made using the eddy-covariance technique, which provides high-frequency measurements of the exchange of carbon, water, and energy

between ecosystems and the atmosphere (66). The unique spatial and temporal coverage of these measurements positions them to help answer a broad range of questions about the relationship between ecosystems and climate, and also to bridge gaps between field observations, remote sensing, and models. Over the past decade, many regional networks have improved their data collection, processing, and sharing standards (e.g., 67, 68). Key regions remain underrepresented, however. For example, few sites provide publicly available data in tropical and high-latitude regions (33). In fact, only a small proportion of global eddy-covariance researchers share their data publicly (69). Efforts to improve data sharing are ongoing in each of the regional flux networks, which should help develop a beneficial research culture and an improved global database for use by the carbon cycle research community. Work over the past decade has culminated in the third release of a global FLUXNET eddy-covariance database (30), which contains standardized measurements, and a detailed characterization of uncertainty, from regional networks around the world. The data set includes more than 1,500 site years of data at 30-minute intervals from 212 sites. The volume of data has opened the door to novel machine-learning techniques, providing unprecedented insights into global carbon cycling by scaling distributed and disparate point-based observations to the global scale (e.g., 70, 71). It has also opened the door to new questions. For example, gap-filled eddy-covariance measurements from sites around the world suggest large sinks in the world's forests, with mixed forests, broad-leaved deciduous forests, and evergreen broad-leaved forests being annual carbon sinks of on average 390, 410, and 505 gC m⁻² year⁻¹, respectively (**Figure 3**). Scaling these observations to the globe, however, gives a global annual NEP of 17 Pg C year⁻¹ (72), which is roughly five times higher than the 10-year average RTS (3). The large overestimation of the land sink from flux towers, which is consistent across plant functional types when compared to land surface models (**Figure 3**), suggests a bias in the flux tower measurements (73), a consistent bias in the sampling distribution of the flux towers, missing components that involve the release of carbon from ecosystems to the atmosphere (e.g., fires, crop harvest, volatile organic compound emissions), or a lack of appropriate information for scaling (72). Issues such as surface energy imbalance (74) and missing advection fluxes (75) could potentially contribute. Interestingly, with a globally estimated photosynthetic flux of ~128 Pg C year⁻¹ (70; but see 39), and a similar respiratory flux required to balance the global carbon budget, only a ~10% bias in

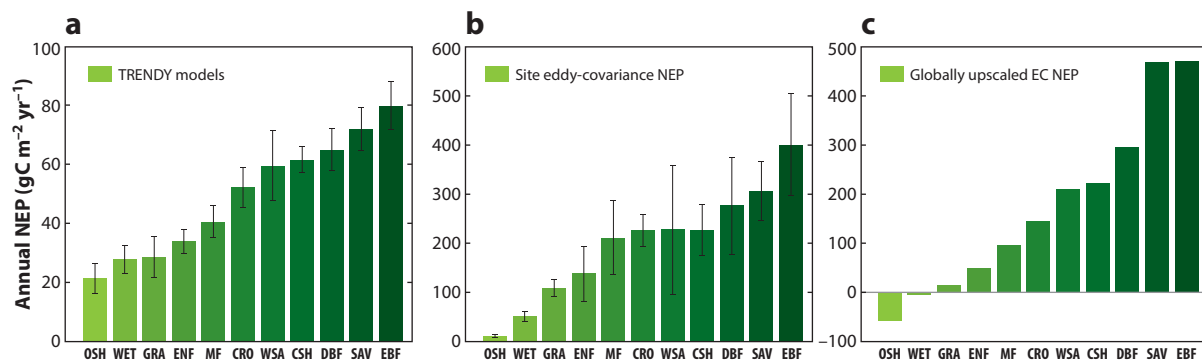


Figure 3

Net ecosystem production (NEP) estimated using land surface models from (a) the TRENDY model intercomparison project, (b) the FLUXNET2015 eddy-covariance data set (30), and (c) an empirical upscaling data product (72). NEP is provided for the major plant functional types (PFTs) around the world, with TRENDY and the upscaled NEP representing the global PFT distribution, whereas FLUXNET2015 NEP is measured at individual sites. PFT denominations: CRO, croplands; CSH, closed shrublands; DBF, deciduous broad-leaved forests; EBF, evergreen broad-leaved forests; EC, eddy covariance; ENF, evergreen needle-leaved forests; GRA, grasslands; MF, mixed forests; OSH, open shrublands; SAV, savannah; WET, wetlands; WSA, woody savannah.

either photosynthesis or respiration could lead to the large bias between the tower observed NEP and the modeled RTS (**Figure 3**), a magnitude not inconsistent with recent findings comparing eddy-covariance and biometric methods (73). New approaches are being developed to address potential biases; for example, online isotopic measurements are providing additional insights into the components of the net flux (76).

Models of the terrestrial biosphere seek to describe spatial and temporal changes in ecological function, and the resulting implication for the global exchanges of carbon, water, and energy between the land surface and the atmosphere (77). The past decade has seen three distinct but related efforts in the design strategies for terrestrial biosphere models. The first is the development of detailed process descriptions, spanning the entire spectrum of ecological function from soil carbon processes (78) to vegetation dynamics (55). The second is focused on the rigorous integration of models and data, through either formal model-data integration techniques (79) or model-directed experiments (80). The third is the development of model benchmarking platforms, such as the International Land Model Benchmarking project (<https://www.ilamb.org>), which seeks to provide standardized tests of model performance applicable across a wide range of global observations and versioned model structures. These three strategies have been fundamental to advancing the field of terrestrial biosphere modeling. Despite these efforts, however, there is limited evidence that terrestrial biosphere models have improved over the past decade, and there has been no reduction in the divergence of model projections over the coming century (81). This has led to calls for a reevaluation of model design strategy, focused on striking a balance between model realism, reliability, and robustness (82). Others have suggested the need for a focus on the intrinsic predictability of ecological processes, to set standards for the expected predictive ability of terrestrial biosphere models (22). Despite the ubiquity and utility of terrestrial biosphere models, much work is needed to attain a predictive science of the biosphere.

5. THE TERRESTRIAL CARBON BUDGET

Over the past decade (2007–2017), the terrestrial carbon sink has removed an estimated 32.6% of anthropogenic fossil fuel and industrial emissions from the atmosphere—28.5% of total emissions, when accounting for the effects of land-use change (3). Combined with the world's oceans, which removed 25.3% and 22.1% of industrial and total emissions, these biological sinks have served to greatly slow the accumulation of CO₂ in the atmosphere, and thus the rate of temperature change (9).

Perhaps the clearest observation-based evidence for a strong biospheric sink comes from measurements of the rate of change in the concentration of CO₂ in the atmosphere. The atmospheric CO₂ concentration exhibits large seasonal cycles, from which biospheric sink strength can be inferred (83). Importantly, the annual growth of atmospheric CO₂ concentrations is much lower than the total annual anthropogenic emissions. For example, for the 10-year period between 2007 and 2016, anthropogenic activities emitted an estimated 10.69 Pg C year⁻¹ into the atmosphere, from fossil fuel burning (8.87 Pg C year⁻¹), cement production (0.48 Pg C year⁻¹), and land-use change (1.33 Pg C year⁻¹). Over the same period, however, atmospheric CO₂ concentrations grew by only 4.71 Pg C year⁻¹ (3). The ratio between the atmospheric CO₂ growth rate and anthropogenic emissions, termed the airborne fraction, is proportional to the biospheric sink strength. The airborne fraction is highly variable, exhibiting large year-to-year swings (84), decadal trends (8), and a sensitivity to emissions estimates (85), which are subject to some uncertainty (37). Nonetheless, the airborne fraction has maintained a long-term mean of close to 40% over the past 50 years. This imbalance between emissions and the growth rate of atmospheric CO₂ suggests a large and persistent biospheric sink.

The strength of the global terrestrial carbon sink is estimated in various ways, but the two primary methods estimate it either as the residual from other better-known terms in the carbon budget (hence the term residual terrestrial sink; 86), or as the mean estimate from an ensemble of process-based dynamic vegetation models (3). Early carbon budget estimates from the Global Carbon Project used the residual approach, where the RTS was calculated as anthropogenic CO₂ emissions minus the observed atmospheric CO₂ growth and model estimates of the oceanic sink (87). The adoption of this residual approach was in acknowledgment of the large differences evident between estimates provided by different vegetation models (81). In 2017, the Global Carbon Project policy changed, and the terrestrial sink was estimated as the mean of an ensemble of dynamic vegetation models (3). The difference between this model-based estimate of the terrestrial sink and the other terms in the carbon budget was then referred to as the budget imbalance. This change has proven controversial. The models used are known to have different sensitivities to various drivers, and there is little evidence that a large ensemble performs better than a subset of models (38, 88). These criticisms appear to be supported by the Global Carbon Project data, as there has been no improvement in the relationship between the model ensemble mean and the budget-based RTS between the first estimates published in 2013 [$r^2 = 0.47$, $p < 0.01$ (89)] and those published in 2018 [$r^2 = 0.47$, $p < 0.01$ (3)], despite an increase in the ensemble size from 9 to 15 models. We prefer to use the budget-based residual estimates for global-scale inference of terrestrial sink behavior and model evaluation. That said, dynamic vegetation models remain effective tools for examining the spatial distribution and dynamics of the sink; and the budget imbalance term is a useful diagnostic for evaluating model uncertainty.

The RTS is estimated to have removed an average of 3.61 Pg C year⁻¹ over the past decade (see 3), roughly 52.7% larger than the oceanic sink of 2.36 Pg C year⁻¹ over the same period, but only 34% of the combined anthropogenic emissions from fossil fuel burning, industrial activities, and land-use change emissions (10.69 Pg C year⁻¹) (3). Dynamic vegetation models suggest large net ecosystem production in tropical and subtropical regions, along with temperate zones of North America (**Figure 4**). Interestingly, they suggest that most regions of the world are sinks for CO₂, net of land-use change, with the tropics seeing the largest uptake followed by humid midlatitudes, which is in general agreement with estimates from large-scale atmospheric inversion models (33). Model estimates are associated with large uncertainty, however, as evidenced by the between model spread (**Figure 4**), which is of comparable magnitude to the model mean. These uncertainties are compounded by uncertainties in the remaining terms required to accurately quantify whether an ecosystem is a sink or a source for carbon, such as net fire emissions, land-use change emissions, and the fate of laterally transported carbon.

More detailed comparisons that attempt to account for all vectors of carbon exchange that contribute to NBP suggest that sink estimates are highly dependent on the region of interest and the methodology used, and are subject to a large amount of uncertainty. For instance, take North America, which is perhaps the most extensively studied region, with the densest network of atmospheric CO₂ concentration and flux sampling towers. Most methods indicate that the North American land surface is a sink for atmospheric CO₂, with a net transfer from the atmosphere to land, but estimates range from anywhere between 280 to 890 Tg C year⁻¹, with inversion methods producing much larger sinks than inventory-based estimates (90). Although North America is densely sampled on average, key regions such as Mexico and Canada remain understudied. In contrast, estimates for Europe, which has a more uniform sampling network, show good agreement between flux, inversion and inventory methods (91) and suggest a terrestrial sink of 891 Tg C year⁻¹. That said, for eastern Europe and Russia, regions that have a relatively sparse sampling network and a lack of recent forest inventories, sink estimate methods also agree quite well, with a mean annual NBP from inventory, eddy-covariance, and inversion methods of 615,

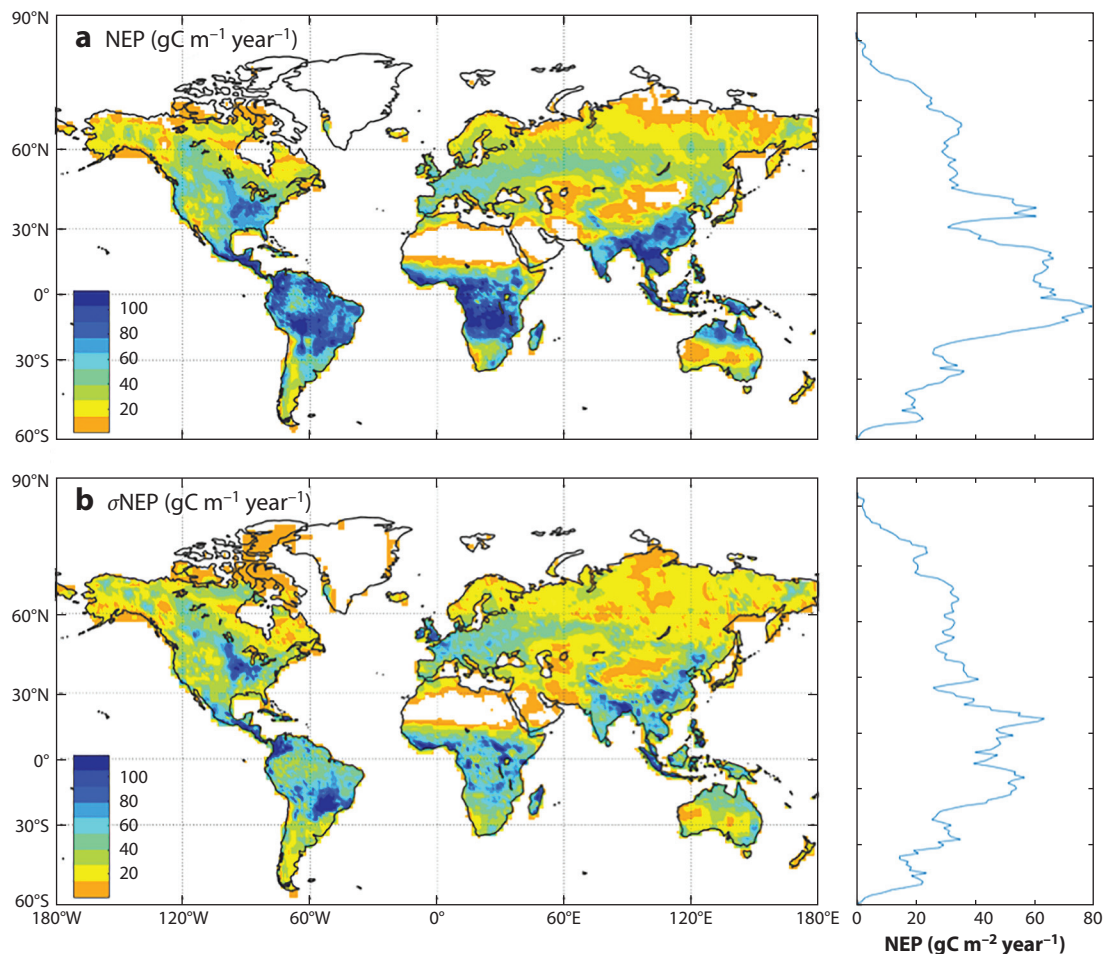


Figure 4

The global distribution of annual net ecosystem production (NEP, $\text{gC m}^{-2} \text{ year}^{-1}$) estimated using land surface models from the TRENDY model intercomparison project over the period 2000–2010. The top panel (a) presents the mean of the multimodel ensemble, along with the latitudinal distribution. The bottom panel (b) presents the between-model standard deviation (σ) of NEP estimates, along with the latitudinal distribution. Note that NEP does not include potentially important terms in the terrestrial ecosystem carbon balance such as land-use change.

662, and 554 Tg C year^{-1} , respectively, although dynamic vegetation models predict a much lower sink (92). Sampling density is therefore not likely the only cause for the lack of agreement between methods.

Asia is estimated to have a total carbon sink of about 500 Tg C year^{-1} , the large majority of which is due to increases in the East Asia sink over recent decades (93). Large uncertainties remain regarding land-use change emissions (94) and whether top-down or bottom-up approaches are used (95), with uncertainty estimates commonly of a similar order of magnitude as the mean sink (96) and larger for inversion estimates than for bottom-up model estimates (97). The sink of the African continent is of similar magnitude and estimated to be $\sim 600 \text{ Tg C year}^{-1}$ (98), whereas the Australian sink is an order of magnitude smaller, with an estimated NBP of $\sim 59 \text{ Tg C year}^{-1}$ (99) in which the largest contributions to uncertainty are NEP, fire and land-use change.

The magnitude and distribution of the sink in South America is particularly debated. Inverse models have shown both that the continent is a net source of CO₂ to the atmosphere from 2000–2010 (100) and a strong carbon sink (33). Ground-based observations suggest a weak and declining sink (101). Carbon dynamics in tropical regions are particularly difficult to quantify, due to methodological difficulties associated with sampling in such complex ecosystems.

From the above, it is clear that conclusions regarding the regional-scale distribution of global sinks are somewhat dependent on the method and model used. A large degree of uncertainty remains (102, 103), which is only likely to be reduced through the integration of knowledge and evidence from diverse disciplines, such as forestry, plant physiology, and ecosystem and atmospheric modeling. On a global scale, however, atmospheric measurements tell us that the terrestrial sink is large and increasing (3). It varies on practically all timescales, depending on weather, anthropogenic interventions, and atmospheric composition. The sink also varies depending on the temporal scale of interest, from diel to interannual scales (104), and on the spatial scale considered (71). Large climatic anomalies, such as El Niño, can lead to large regional perturbations (105, 106), whereas temporary temporal changes can lead to shifts in sink strength (8). To understand the terrestrial carbon sink, and its future potential, it is therefore imperative to understand not just its regional distribution but also the governing processes involved. Note also that here we are considering only CO₂, but the terrestrial biosphere is a net source of greenhouse gases to the atmosphere when other greenhouse gases such as methane and nitrous oxide are included (107).

6. SINK DYNAMICS ACROSS BIOCLIMATIC SETTINGS: CURRENT ESTIMATES AND FUTURE PROSPECTS

The leading drivers of today's terrestrial carbon sink can be classified as (*a*) direct climate effects (changes in precipitation, temperature, and radiation regime, including effects of droughts, heatwaves, and hydraulic stress from rising vapor pressure deficit), (*b*) atmospheric composition effects (CO₂ fertilization, nutrient deposition, and damage by pollution), (*c*) land-use change effects (deforestation, afforestation, agricultural practices, and their legacies over time), and (*d*) natural disturbance effects (changing rates from hurricanes and high winds, wildfires, pests, and pathogens). Impacts on ecosystem carbon balance are manifested differently all over the world, but some broad patterns are reviewed sequentially across biome and climate settings.

Forests contribute a large fraction of the global terrestrial CO₂ sink (**Figure 3**; see also Reference 5), as they experience enhanced growth from improved environmental and resource conditions, and as some regrow following historical, mostly temperate, clearing (108, 109). Forests tend to have larger carbon sink capacity than most other biomes because trees store carbon in woody tissues that are protected from decomposition and respiratory release, whereas nonwoody plants allocate a larger share of their productivity to leaves and fine roots, which turn over more rapidly. Accelerated growth in forest carbon stocks is reported for tropical, temperate, and even boreal settings (110–112), with elevated CO₂ being a plausible driver (113, 114). However, not all forests respond equally to elevated CO₂ (115), particularly if they are nutrient limited (116). Nitrogen deposition is also contributing to accelerated growth in some regions (117, 118). For northern latitude forests, warming has been linked to longer growing seasons (119) and increased carbon uptake (120), although atmospheric observations suggest that the sensitivity to spring warming is weakening (121). Uncertainties remain, however, with disagreement regarding sink strength between methods. For example, atmospheric measurements and models suggest a strong and increasing tropical sink (8, 33), whereas ground observations suggest either a source (122) or small and weakening sink (123).

Responses to the key drivers vary across species and environments, with patterns continuing to be discovered. Forest lands recovering from historical clearing for pasture or agriculture constitute

a contemporary forest carbon sink (124), and ongoing forest management activities such as species selection and thinning treatments that are common in plantations are also stimulating net carbon uptake within forests (125). Whether today's forest sink will persist in the future depends on several uncertain factors. For example, it is unclear whether growth enhancements from elevated CO₂ augment a stand's maximum capacity to store carbon, or simply result in a faster approach to an otherwise-bounded capacity (126). We also do not know how the changing climate will unfold, and what influences it is likely to have on patterns of growth and decomposition. There is a clear risk of increased physiological stresses with warming and drying, compounded by expansion of natural disturbances, all of which may accelerate mortality and carbon losses with potentially large implications for landscape to continental-scale carbon budgets (127). Nonetheless, the present data suggest a strong current carbon sink (RTS) in the world's forests (**Figure 3**; see also Reference 5), although one that is greatly offset by anthropogenic activities such as logging (128).

Grasslands, too, have the potential to contribute to the terrestrial carbon sink (129), with attention turned to soil carbon accumulation because carbon stocks in their living tissues tend to be modest with rapid turnover of the carbon allocated to these living tissues (e.g., leaves and roots). Root decomposition has been identified as important for generating soil organic matter in grasslands, but studies indicate that soil carbon storage in grasslands can involve contributions from both above- and belowground litter (130). Precipitation is well known to be a major determinant of grassland productivity (131), with carbon uptake responding to interannual variability and trends (132). Temperature, of course, also influences productivity, through controls on growing season length (129), and grassland productivity may be responding to recent warming trends. Although grassland production can also respond to elevated CO₂ (133), particularly C3 grasslands with ample nutrient and water supplies (134), C4 grasses common to tropical and semiarid regions may respond more modestly because of their already-efficient utilization of leaf intercellular CO₂ (135). However, in some cases, even C4 grasses have been reported to respond positively to elevated CO₂ (136).

Even if grassland productivity is stimulated by elevated CO₂, it does not necessarily yield lasting effects on soil carbon (137), which is the most persistent carbon stock in grassland systems. Fire and herbivory also act as rapid carbon release pathways (e.g., 138), capping carbon accumulation in aboveground tissues and limiting the build-up of live, and even dead, carbon stocks. Fire may convert a small amount of carbon to long-lived charcoal (139), but the associated carbon sink is expected to be small over annual to decadal timescales. Intensive grassland management with grazing or mowing tends to release carbon to the atmosphere (140), even if it stimulates a regrowth response onsite (141). Some grasslands in select regions are recovering carbon stocks after historical use for agriculture or overgrazing (142), whereas others are experiencing invasion by non-native grasses or woody species (143); however, the global-scale impacts are poorly known. Taken together, grasslands have a modest potential for contemporary sequestration of atmospheric carbon.

Cropland expansion and intensification, with irrigation and nutrient fertilization, has enhanced primary productivity in agricultural belts around the world, with global-scale effects as far-reaching as altering the amplitude of the seasonal cycle of atmospheric CO₂ (144, 145). Elevated CO₂ also boosts the growth and yields of some crops particularly when not constrained by low nitrogen or water stresses (135). However, the turnover of live carbon stocks in croplands tends to be rapid, with soil carbon constituting the primary enduring carbon store. Thus, production-driven carbon sequestration in croplands is mainly generated through stimulation of belowground production, crop residues, or root exudation (146). Furthermore, cropland management tends to also accelerate the release of ecosystem carbon to the atmosphere through harvesting, plowing, tilling, fallowing, burning, and other interventions (147), in some cases causing sizeable releases of soil carbon, which may also be combined with legacy emissions from conversion of forest or grassland to cropland

(148). Management practices can be guided to increase soil carbon sequestration (149); however, global croplands are unlikely to contribute substantially to today's global terrestrial carbon sink (146).

Tundra in arctic and alpine environments is generally cold limited, with short growing seasons, low productivity, and a correspondingly minor share of global live carbon stocks (150). However, these ecosystems are experiencing rapid warming (151) that is lengthening growing seasons (152). These changes are expected to enhance productivity (153), expand vegetation cover, and yield net carbon storage (154). In situ empirical evidence remains limited, however, and models predict a modest current sink (**Figure 3**; see also Reference 4). At the same time, warming is threatening to destabilize permafrost carbon (155), causing its release to the atmosphere that could tip tundra, and some boreal, ecosystems toward significant carbon sources (154). Associated hydrologic changes in tundra landscapes, such as thermokarst lake formation and loss, may also be increasing carbon releases via accelerated export as dissolved inorganic and organic carbon as well as particulate organic carbon transported into continental and coastal waters (156). Thus, although a recent synthesis report suggests a sizeable carbon sink in arctic ecosystems that are likely to sequester carbon ($\text{NBP} = 290 \text{ to } -80 \text{ Tg C year}^{-1}$) (157), there are large uncertainties with potentially large net sources on the way in the near future.

Global drylands, spanning open savannas and shrublands to sparsely vegetated areas and deserts, have low primary productivity but cover such a large area of global lands that they still contribute meaningfully to global terrestrial carbon stocks (150). Elevated CO_2 is a likely driver of reported greening trends in many of the world's drylands as plants experience water savings from improved water-use efficiency (136, 158); however, water is still a prevailing limit in these ecosystems, and this constrains their potential to respond to global change drivers. In addition, trends toward warmer, dryer air may significantly offset water-use savings from elevated CO_2 (159). Trends in grazing, woody encroachment, and desertification all have the potential to alter the carbon balance of dryland landscapes, but consequences for the global terrestrial sink remain uncertain (140). Being so widespread, even small responses to global change drivers may add up, and drylands have the potential to contribute sizably to the interannual variability and trend of the land CO_2 sink (160, 161). Even so, most indications are that semiarid and arid regions of the world are not the largest component of the contemporary long-term mean global terrestrial carbon sink (161).

Each of the global biomes is subject to interannual variability in weather, which translates to different degrees of variability in the terrestrial carbon sink (104, 162). Tropical forests and semiarid ecosystems in particular are predicted to have large variability (161), with interannual variations in the growth rate of atmospheric CO_2 tightly coupled to both variations in air temperature over tropical land (163) and anomalous precipitation in semiarid regions (160). These sensitivities could in theory be used to better understand the processes that govern the terrestrial carbon cycle and the likely future response to climate change. However, doing so is nontrivial. For example, the inferred temperature sensitivity of the terrestrial carbon sink has greatly increased over recent decades (164). The reasons for the reported increase remain unclear, highlighting the difficulty associated with deriving process-relevant information from variability at large scales. Recent results suggest that the inferred responses are indeed scale dependent (71) due to the heterogeneous nature of specific forcings. Models of the terrestrial carbon cycle tend to capture interannual variability in the terrestrial carbon sink relatively well at the global scale (8), but few if any capture observed variability when tested at specific sites (165). Combined, these results suggest either that models mischaracterize ecosystem responses to forcings, particularly those that are spatially heterogeneous, or that the uncertainty associated with annual site-scale observations is underestimated. A detailed consideration of scale-dependent factors should help with the former, and a more seamless integration of models and observations through data assimilation (166)

should help with the latter. Regardless of the dominant drivers, or our ability to reproduce the responses to them, the large variability of the terrestrial carbon cycle relative to the oceanic carbon cycle (3) highlights the sensitivity of terrestrial ecosystems to variability in climate, and it suggests continued disruptions from future climate change.

7. IMPLICATIONS FOR THE PRESENT AND THE FUTURE OF THE EARTH SYSTEM

A strong terrestrial sink has important implications for the atmosphere and thus for policy design. In particular, it lends support to the potential use of forestry and the protection of ecosystems with large sink capacities as potential mitigation strategies. The Paris Agreement, negotiated by representatives of 196 parties at the 21st Conference of the Parties of the United Nations Framework Convention on Climate Change (UNFCCC) and adopted in 2015, includes strategic Nationally Determined Contributions (NDCs) aimed at developing pathways toward low net greenhouse gas emissions. Approximately two-thirds of the signatories indicated they will use the land sink to meet their mitigation targets (167). International programs such as the Reducing Emissions from Deforestation and forest Degradation in developing countries (REDD+) have been established, and the potential role of land-focused negative emission technologies [e.g., large-scale afforestation, bioenergy combined with carbon capture and storage (BECCS), biochar formation, soil carbon sequestration] is being explored (168).

Estimating the resulting climate mitigation potential from changing land practices is nontrivial, however, and current estimates are widely debated (169–171). A common approach relies on estimates of the equilibrium climate sensitivity, which are themselves uncertain (172), and provide only the response of warming to CO₂ forcing but rely on known or assumed CO₂ concentrations. Other metrics such as the Transient Climate Response to cumulative carbon Emissions (173), similarly rely on a known CO₂ forcing, are temporally variable, and do not include effects of any other greenhouse gases, aerosols, or changes in historical forcings. Moreover, the Earth system is highly coupled, and the strengths of carbon sources and sinks depend on the rate of change in the atmospheric CO₂ concentration (174). Accounting for land-atmosphere feedbacks is essential for accurately quantifying the influence of changes in land management practices (175). Earth System Models are designed to account for such feedbacks, by simulating the transient physical climate, and processes that govern the exchanges of CO₂ among land, oceans, and the atmosphere (176). Studies that incorporate such feedbacks through Earth System Models suggest that the postindustrial land sink has lowered the atmospheric CO₂ concentration by 85 ppm, avoiding an additional $0.31 \pm 0.06^{\circ}\text{C}$ of warming (9), but future multifactor responses are less well known, especially for regions such as high latitudes and tropical areas (81). UNFCCC NDC commitments that use the land sink therefore need to do so on a sound scientific basis, fully considering the uncertainties involved.

Despite debates over the potential for the land sink to mitigate anthropogenic emissions, it is worth noting the implications of a carbon sink for the ecosystems involved. For oceans, an increased carbon sink is an unequivocal negative for ecosystem health, leading to reduced metabolic rates and immune responses in some organisms, and causing widespread coral bleaching (177). For terrestrial ecosystems, the situation is different. Increased carbon in terrestrial ecosystems primarily leads to improved soil health, through the effects of increased organic matter on soil structure, soil water holding capacity, microbial diversity and activity, and soil nutrient retention (178).

Although land practices have the potential to offset a small but significant portion of anthropogenic emissions (3, 171), they should ultimately be seen (with the exception of geological

sequestration through BECCS) as a short-term stopgap measure. The natural processes that are now leading to an increase in the land sink could potentially saturate under higher CO₂ concentrations, and even reverse if global temperatures continue to rise (179), or if negative emissions technologies (NETs) manage to reduce atmospheric CO₂ (180). Model projections diverge greatly, however (81), and the possibility of tipping points in the Earth system remains debated (29). Ultimately, the true potential of ecosystems in NET approaches remains underexplored (181). Decarbonization of the energy system, through renewable energy developments, enhanced energy efficiency, and transport electrification, are without doubt the most effective pathways to stabilizing atmospheric CO₂ concentrations (182), but enhancing the land sink and protecting existing sinks now could also greatly reduce the long-term marginal abatement costs for CO₂ emissions (183).

SUMMARY POINTS

1. We review advances from 2008–2018 in understanding of the terrestrial carbon cycle.
2. Evidence suggests that the land surface is a large and increasing sink for CO₂.
3. The regional distribution of the sink is very uncertain, with disagreement between methods.
4. Largest uncertainty is in tropical regions, where estimates diverge greatly.

FUTURE ISSUES

1. Better frameworks are needed to merge disparate observations and models to fully synthesize current understanding.
2. More proxies for process understanding, such as solar-induced fluorescence and carbon isotope flux measurements, are needed.
3. More formal model-data synthesis methods are needed to identify and improve model deficiencies.
4. A renewed focus on processes over patterns should help, using first-principles theory to understand ecological responses to change.

DISCLOSURE STATEMENT

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

ACKNOWLEDGMENTS

T.F.K. acknowledges support by the Director, Office of Science, Office of Biological and Environmental Research of the US Department of Energy under Contract DE-AC02-05CH11231 as part of the Rubisco SFA, and by the NASA Terrestrial Ecology Program IDS Award NNH17AE86L. C.A.W. acknowledges financial support from NASA's Carbon Monitoring System program (NNH14ZDA001N-CMS) under award NNX14AR39G. This work used eddy-covariance data acquired and shared by the FLUXNET community, including the following networks: AmeriFlux,

AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia, and USCCC. The ERA-Interim reanalysis data are provided by ECMWF and processed by LSCE. The FLUXNET eddy-covariance data processing and harmonization was carried out by the European Fluxes Database Cluster, AmeriFlux Management Project, and the Fluxdata project of FLUXNET, with the support of CDIAC and ICOS Ecosystem Thematic Center and the OzFlux, ChinaFlux, and AsiaFlux offices. We thank the TRENDY team, Stephen Sitch, Pierre Friedlingstein, Chris Huntingford, Ben Poulter, Anders Ahlström, Mark Lomas, Peter Levy, Sam Levis, Sönke Zaehle, Nicolas Viovy, Ning Zeng, and Phillipe Peylin, for the provision of the DGVM simulations and the researchers of the Global Carbon Project for making their data available. We also acknowledge the numerous relevant papers not cited given space constraints.

LITERATURE CITED

1. The Core Writing Team, Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, eds. 2014. *IPCC Climate Change 2014: Synthesis Report. Contributions of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC
2. Laisk A, Nedbal L, Govindjee, eds. 2009. *Photosynthesis in Silico*, Vol. 29. Dordrecht, Neth.: Springer
3. Le Quéré C, Andrew RM, Friedlingstein P, Sitch S, Pongratz J, et al. 2018. Global carbon budget 2017. *Earth Syst. Sci. Data* 10(1):405–48
4. Chapin FS, Matson PA, Vitousek PM. 2011. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer
5. Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333(6045):988–93
6. Ballantyne AP, Alden CB, Miller JB, Tans PP, White JWC. 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488(7409):70–72
7. Rayner PJ, Stavert A, Scholze M, Ahlström A, Allison CE, Law RM. 2015. Recent changes in the global and regional carbon cycle: analysis of first-order diagnostics. *Biogeosciences* 12:835–44
8. Keenan TF, Prentice IC, Canadell JG, Williams CA, Wang H, et al. 2016. Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake. *Nat. Commun.* 7:13428
9. Shevliakova E, Stouffer RJ, Malyshev S, Krasting JP, Hurtt GC, Pacala SW. 2013. Historical warming reduced due to enhanced land carbon uptake. *PNAS* 110(42):16730–35
10. Chapin FS, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9(7):1041–50
11. Randerson JT, Chapin FS III, Harden JW, Neff JC, Harmon ME. 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. *Ecol. Appl.* 12(4):937–47
12. Van Der Werf GR, Randerson JT, Giglio L, Van Leeuwen TT, Chen Y, et al. 2017. Global fire emissions estimates during 1997–2016. *Earth Syst. Sci. Data* 9(2):697–720
13. Austin AT, Méndez MS, Ballaré CL. 2016. Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *PNAS* 113(16):4392–97
14. Saunio M, Bousquet P, Poulter B, Peregon A, Ciais P, et al. 2016. The global methane budget 2000–2012. *Earth Syst. Sci. Data* 8(2):697–751
15. Sindelarova K, Granier C, Bouarar I, Guenther A, Tilmes S, et al. 2014. Global data set of biogenic VOC emissions calculated by the MEGAN model over the last 30 years. *Atmos. Chem. Phys.* 14(17):9317–41
16. Li M, Peng C, Wang M, Xue W, Zhang K, et al. 2017. The carbon flux of global rivers: a re-evaluation of amount and spatial patterns. *Ecol. Indic.* 80(Sept.):40–51
17. Iavorivska L, Boyer EW, DeWalle DR. 2016. Atmospheric deposition of organic carbon via precipitation. *Atmos. Environ.* 146:153–63
18. Sobral M, Silvius KM, Overman H, Oliveira LFB, Raab TK, Fragoso JMV. 2017. Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. *Nat. Ecol. Evol.* 1(11):1670–76
19. Kirschke S, Bousquet P, Ciais P, Saunio M, Canadell JG, et al. 2013. Three decades of global methane sources and sinks. *Nat. Geosci.* 6(10):813–23

20. Wohlfahrt G, Gu L. 2015. The many meanings of gross photosynthesis and their implication for photosynthesis research from leaf to globe. *Plant Cell Environ.* 38(12):2500–7
21. Trumbore S. 2009. Radiocarbon and soil carbon dynamics. *Annu. Rev. Earth Planet. Sci.* 37(1):47–66
22. Luo Y, Keenan TF, Smith M. 2015. Predictability of the terrestrial carbon cycle. *Glob. Chang. Biol.* 21(5):1737–51
23. Odum EP. 1969. The strategy of ecosystem development. *Science* 164:262–70
24. Matamala R, Jastrow JD, Miller RM, Garten CT. 2008. Temporal changes in C and N stocks of restored prairie: implications for C sequestration strategies. *Ecol. Appl.* 18(6):1470–88
25. Wang YP, Chen BC, Wieder WR, Leite M, Medlyn BE, et al. 2014. Oscillatory behavior of two nonlinear microbial models of soil carbon decomposition. *Biogeosciences* 11(7):1817–31
26. Carvalhais N, Forkel M, Khomik M, Bellarby J, Jung M, et al. 2014. Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* 514(7521):213–17
27. Friend AD, Lucht W, Rademacher TT, Keribin R, Betts R, et al. 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. *PNAS* 111(9):3280–85
28. Luo Y, Weng E. 2011. Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends Ecol. Evol.* 26(2):96–104
29. Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L. 2013. Does the terrestrial biosphere have planetary tipping points? *Trends Ecol. Evol.* 28(7):396–401
30. Pastorello GZ, Papale D, Chu H, Trotta C, Agarwal DA, et al. 2017. A new data set to keep a sharper eye on land-air exchanges. *Eos* 98. <https://doi.org/10.1029/2017EO071597>
31. Welp LR, Patra PK, Rödenbeck C, Nemani R, Bi J, et al. 2016. Increasing summer net CO₂ uptake in high northern ecosystems inferred from atmospheric inversions and comparisons to remote-sensing NDVI. *Atmos. Chem. Phys.* 16(14):9047–66
32. Keeling RF, Graven HD, Welp LR, Resplandy L, Bi J, et al. 2017. Atmospheric evidence for a global secular increase in carbon isotopic discrimination of land photosynthesis. *PNAS* 114:10361–66
33. Schimel D, Stephens BB, Fisher JB. 2015. Effect of increasing CO₂ on the terrestrial carbon cycle. *PNAS* 112(2):436–41
34. Weng ES, Malyshev S, Lichstein JW, Farrior CE, Dybzinski R, et al. 2015. Scaling from individual trees to forests in an Earth system modeling framework using a mathematically tractable model of height-structured competition. *Biogeosciences* 12(9):2655–94
35. Wang H, Prentice IC, Keenan TF, Davis TW, Wright IJ, et al. 2017. Towards a universal model for carbon dioxide uptake by plants. *Nat. Plants* 3(9):734–41
36. Raupach MR, Marland G, Ciais P, Le Quéré C, Canadell JG, et al. 2007. Global and regional drivers of accelerating CO₂ emissions. *PNAS* 104(24):10288–93
37. Arneth A, Sitch S, Pongratz J, Stocker BD, Ciais P, et al. 2017. Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed. *Nat. Geosci.* 10(2):79–84
38. Lovenduski NS, Bonan GB. 2017. Reducing uncertainty in projections of terrestrial carbon uptake. *Environ. Res. Lett.* 12(4):101001
39. Campbell JE, Berry JA, Seibt U, Smith SJ, Montzka SA, et al. 2017. Large historical growth in global terrestrial gross primary production. *Nature* 544(7648):84–87
40. Ciais P, Rayner P, Chevallier F, Bousquet P, Logan M, et al. 2010. Atmospheric inversions for estimating CO₂ fluxes: methods and perspectives. *Clim. Change* 103(1–2):69–92
41. Bagley JE, Jeong S, Cui X, Newman S, Zhang J, et al. 2017. Assessment of an atmospheric transport model for annual inverse estimates of California greenhouse gas emissions. *J. Geophys. Res.* 122(3):1901–18
42. Pacala SW, Breidenich C, Brewer PG, Fung IY, Gunson MR, et al. 2010. *Verifying Greenhouse Gas Emissions*. Washington, DC: Nat. Acad. Press
43. Subramanian R, Williams LL, Vaughn TL, Zimmerle D, Roscioli JR, et al. 2015. Methane emissions from natural gas compressor stations in the transmission and storage sector: measurements and comparisons with the EPA greenhouse gas reporting program protocol. *Environ. Sci. Technol.* 49(5):3252–61

44. Andrews AE, Kofler JD, Trudeau ME, Williams JC, Neff DH, et al. 2014. CO₂, CO, and CH₄ measurements from tall towers in the NOAA Earth System Research Laboratory's Global Greenhouse Gas Reference Network: instrumentation, uncertainty analysis, and recommendations for future high-accuracy greenhouse gas monitoring efforts. *Atmos. Meas. Tech.* 7(2):647–87
45. Miller SM, Michalak AM. 2017. Constraining sector-specific CO₂ and CH₄ emissions in the US. *Atmos. Chem. Phys.* 17(6):3963–85
46. Fang Y, Michalak AM. 2015. Atmospheric observations inform CO₂ flux responses to environmental drivers. *Glob. Biogeochem. Cycles* 29(5):555–66
47. Miller SM, Commane R, Melton JR, Andrews AE, Benmergui J, et al. 2016. Evaluation of wetland methane emissions across North America using atmospheric data and inverse modeling. *Biogeosciences* 13(4):1329–39
48. Michalak AM, Randazzo NA, Chevallier F. 2017. Diagnostic methods for atmospheric inversions of long-lived greenhouse gases. *Atmos. Chem. Phys.* 17(12):7405–21
49. Broquet G, Chevallier F, Bréon FM, Kadyrov N, Alemanno M, et al. 2013. Regional inversion of CO₂ ecosystem fluxes from atmospheric measurements: reliability of the uncertainty estimates. *Atmos. Chem. Phys.* 13(17):9039–56
50. Schimel D, Pavlick R, Fisher JB, Asner GP, Saatchi S, et al. 2015. Observing terrestrial ecosystems and the carbon cycle from space. *Glob. Chang. Biol.* 21(5):1762–76
51. Barnes ML, Breshears DD, Law DJ, Van Leeuwen WJD, Monson RK, et al. 2017. Beyond greenness: detecting temporal changes in photosynthetic capacity with hyperspectral reflectance data. *PLOS ONE* 12(12):e0189539
52. Konings AG, Yu Y, Xu L, Yang Y, Schimel DS, Saatchi SS. 2017. Active microwave observations of diurnal and seasonal variations of canopy water content across the humid African tropical forests. *Geophys. Res. Lett.* 44(5):2290–99
53. Sun Y, Frankenberg C, Wood JD, Schimel DS, Jung M, et al. 2017. OCO-2 advances photosynthesis observation from space via solar-induced chlorophyll fluorescence. *Science* 358:6360
54. Jetz W, Cavender-Bares J, Pavlick R, Schimel D, Davis FW, et al. 2016. Monitoring plant functional diversity from space. *Nat. Plants* 2(3):16024
55. Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, et al. 2018. Vegetation demographics in Earth System Models: a review of progress and priorities. *Glob. Chang. Biol.* 24(1):35–54
56. Migliavacca M, Perez-Priego O, Rossini M, El-Madany TS, Moreno G, et al. 2017. Plant functional traits and canopy structure control the relationship between photosynthetic CO₂ uptake and far-red sun-induced fluorescence in a Mediterranean grassland under different nutrient availability. *New Phytol.* 214(3):1078–91
57. Anderson K, Gaston KJ. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Front. Ecol. Environ.* 11(3):138–46
58. Kunz M, Lavric JV, Gerbig C, Tans P, Neff D, et al. 2018. COCAP: a carbon dioxide analyser for small unmanned aircraft systems. *Atmos. Meas. Tech.* 11(3):1833–49
59. Klosterman S, Melaas E, Wang J, Martinez A, Frederick S, et al. 2018. Fine-scale perspectives on landscape phenology from unmanned aerial vehicle (UAV) photography. *Agric. For. Meteorol.* 248(Oct. 2017):397–407
60. Sankey T, Donager J, McVay J, Sankey JB. 2017. UAV lidar and hyperspectral fusion for forest monitoring in the southwestern USA. *Remote Sens. Environ.* 195:30–43
61. Van Der Meij B, Kooistra L, Suomalainen J, Barel JM, De Deyn GB. 2017. Remote sensing of plant trait responses to field-based plant-soil feedback using UAV-based optical sensors. *Biogeosciences* 14(3):733–49
62. Asner GP, Martin RE, Knapp DE, Tupayachi R, Anderson CB, et al. 2017. Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science* 355(6323):385–89
63. Kampe TU. 2010. NEON: the first continental-scale ecological observatory with airborne remote sensing of vegetation canopy biochemistry and structure. *J. Appl. Remote Sens.* 4(1):43510
64. Richardson AD, Hufkens K, Milliman T, Aubrecht DM, Chen M, et al. 2018. Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery. *Sci. Data* 5:1–24
65. Keenan TF, Darby B, Felts E, Sonnentag O, Friedl MA, et al. 2014. Tracking forest phenology and seasonal physiology using digital repeat photography: a critical assessment. *Ecol. Appl.* 24(6):1478–89

66. Baldocchi D. 2008. “Breathing” of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Aust. J. Bot.* 56(1):1–26
67. Novick KA, Biederman JA, Desai AR, Litvak ME, Moore DJP, et al. 2018. The AmeriFlux network: a coalition of the willing. *Agric. For. Meteorol.* 249(15):444–56
68. Metzger S, Durden D, Sturtevant C, Luo H, Pinging-Durden N, et al. 2017. eddy4R 0.2.0: a DevOps model for community-extensible processing and analysis of eddy-covariance data based on R, Git, Docker, and HDF5. *Geosci. Model Dev.* 10(9):3189–206
69. Dai S-Q, Li H, Xiong J, Ma J, Guo H-Q, et al. 2018. Assessing the extent and impact of online data sharing in eddy covariance flux research. *J. Geophys. Res. Biogeosci.* 123:129–37
70. Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, et al. 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329(5993):834–38
71. Jung M, Reichstein M, Schwalm CR, Huntingford C, Sitch S, et al. 2017. Compensatory water effects link yearly global land CO₂ sink changes to temperature. *Nature* 541(7638):516–20
72. Jung M, Reichstein M, Margolis HA, Cescatti A, Richardson AD, et al. 2011. Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *J. Geophys. Res.* 116:1–16
73. Wang X, Wang C, Bond-Lamberty B. 2017. Quantifying and reducing the differences in forest CO₂-fluxes estimated by eddy covariance, biometric and chamber methods: a global synthesis. *Agric. For. Meteorol.* 247(July):93–103
74. Stoy PC, Mauder M, Foken T, Marcolla B, Boegh E, et al. 2013. A data-driven analysis of energy balance closure across FLUXNET research sites: the role of landscape scale heterogeneity. *Agric. For. Meteorol.* 171–172:137–52
75. Aubinet M. 2008. Eddy covariance CO₂ flux measurements in nocturnal conditions: an analysis of the problem. *Ecol. Appl.* 18(6):1368–78
76. Wehr R, Munger JW, McManus JB, Nelson DD, Zahniser MS, et al. 2016. Seasonality of temperate forest photosynthesis and daytime respiration. *Nature* 534(7609):680–83
77. Fisher JB, Huntzinger DN, Schwalm CR, Sitch S. 2014. Modeling the terrestrial biosphere. *Annu. Rev. Environ. Resour.* 39:91–123
78. Bradford MA, Wieder WR, Bonan GB, Fierer N, Raymond PA, Crowther TW. 2016. Managing uncertainty in soil carbon feedbacks to climate change. *Nat. Clim. Change* 6(8):751–58
79. Post H, Vrugt JA, Fox A, Vereecken H, Hendricks Franssen HJ. 2017. Estimation of Community Land Model parameters for an improved assessment of net carbon fluxes at European sites. *J. Geophys. Res. Biogeosci.* 122(3):661–89
80. Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, et al. 2015. Using ecosystem experiments to improve vegetation models. *Nat. Clim. Change* 5(6):528–34
81. Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, et al. 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J. Clim.* 27(2):511–26
82. Prentice IC, Liang X, Medlyn BE, Wang YP. 2015. Reliable, robust and realistic: the three R’s of next-generation land-surface modelling. *Atmos. Chem. Phys.* 15(10):5987–6005
83. Graven HD, Keeling RF, Piper SC, Patra PK, Stephens BB, et al. 2013. Enhanced seasonal exchange of CO₂ by northern ecosystems since 1960. *Science* 341(6150):1085–89
84. Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, et al. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494(7437):341–44
85. Gloor M, Sarmiento JL, Gruber N. 2010. What can be learned about carbon cycle climate feedbacks from the CO₂ airborne fraction? *Atmos. Chem. Phys.* 10(16):7739–51
86. Le Quéré C, Andrew RM, Canadell JG, Sitch S, Ivar Korsbakken J, et al. 2016. Global carbon budget 2016. *Earth Syst. Sci. Data* 8(2):605–49
87. Canadell JG, Le Quéré C, Raupach MR, Field CB, Buitenhuis ET, et al. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *PNAS* 104(47):18866–70
88. Schwalm CR, Huntzinger DN, Fisher JB, Michalak AM, Bowman K, et al. 2015. Toward “optimal” integration of terrestrial biosphere model ensembles. *Geophys. Res. Lett.* 42:4418–28

89. Le Quéré C, Andres RJ, Boden T, Conway T, Houghton RA, et al. 2013. The global carbon budget 1959–2011. *Earth Syst. Sci. Data* 5(1):165–85
90. King AW, Andres RJ, Davis KJ, Hafer M, Hayes DJ, et al. 2015. North America's net terrestrial CO₂ exchange with the atmosphere 1990–2009. *Biogeosciences* 12(2):399–414
91. Luyssaert S, Abril G, Andres R, Bastviken D, Bellassen V, et al. 2012. The European land and inland water CO₂, CO, CH₄ and N₂O balance between 2001 and 2005. *Biogeosciences* 9(8):3357–80
92. Dolman AJ, Shvidenko A, Schepaschenko D, Ciais P, Tchebakova N, et al. 2012. An estimate of the terrestrial carbon budget of Russia using inventory-based, eddy covariance and inversion methods. *Biogeosciences* 9:5323–40
93. Thompson RL, Patra PK, Chevallier F, Maksyutov S, Law RM, et al. 2016. Top-down assessment of the Asian carbon budget since the mid 1990s. *Nat. Commun.* 7:10724
94. Calle L, Canadell JG, Patra P, Ciais P, Ichii K, et al. 2016. Regional carbon fluxes from land use and land cover change in Asia, 1980–2009. *Environ. Res. Lett.* 11(7):074011
95. Patra PK, Canadell JG, Houghton RA, Piao SL, Oh NH, et al. 2013. The carbon budget of South Asia. *Biogeosciences* 10(1):513–27
96. Cervarich M, Shu S, Jain AK, Arneth A, Canadell J, et al. 2016. The terrestrial carbon budget of South and Southeast Asia. *Environ. Res. Lett.* 11(10):1–11
97. Piao SL, Ito A, Li SG, Huang Y, Ciais P, et al. 2012. The carbon budget of terrestrial ecosystems in East Asia over the last two decades. *Biogeosciences* 9(9):3571–86
98. Valentini R, Arneth A, Bombelli A, Castaldi S, Cazzolla Gatti R, et al. 2014. A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities. *Biogeosciences* 11(2):381–407
99. Haverd V, Raupach MR, Briggs PR, Canadell JG, Davis SJ, et al. 2013. The Australian terrestrial carbon budget. *Biogeosciences* 10(2):851–69
100. Gloor M, Gatti L, Brien R, Feldpausch TR, Phillips OL, et al. 2012. The carbon balance of South America: a review of the status, decadal trends and main determinants. *Biogeosciences* 9(12):5407–30
101. Brien RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, et al. 2015. Long-term decline of the Amazon carbon sink. *Nature* 519(7543):344–48
102. Enting IG, Rayner PJ, Ciais P. 2012. Carbon cycle uncertainty in regional carbon cycle assessment and processes (RECCAP). *Biogeosciences* 9(8):2889–904
103. Peylin P, Law RM, Gurney KR, Chevallier F, Jacobson AR, et al. 2013. Global atmospheric carbon budget: results from an ensemble of atmospheric CO₂ inversions. *Biogeosciences* 10(10):6699–720
104. Baldocchi D, Ryu Y, Keenan T. 2016. Terrestrial carbon cycle variability. *F1000Research* 5:2371
105. Liu J, Bowman KW, Schimel DS, Parazoo NC, Jiang Z, et al. 2017. Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. *Science*. 358(6360):5690
106. Kim JS, Kug JS, Yoon JH, Jeong SJ. 2016. Increased atmospheric CO₂ growth rate during El Niño driven by reduced terrestrial productivity in the CMIP5 ESMs. *J. Clim.* 29(24):8783–805
107. Tian H, Lu C, Ciais P, Michalak AM, Canadell JG, et al. 2016. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. *Nature* 531(7593):225–28
108. Bellassen V, Viovy N, Luyssaert S, Le Maire G, Schelhaas MJ, Ciais P. 2011. Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. *Glob. Chang. Biol.* 17:3274–92
109. Williams CA, Collatz GJ, Masek JG, Goward S. 2012. Carbon consequences of forest disturbance and recovery across the conterminous United States. *Global Biogeochem. Cycles* 26:GB1005
110. Lewis SL, Lopez-Gonzalez G, Sonké B, Affum-Baffoe K, Baker TR, et al. 2009. Increasing carbon storage in intact African tropical forests. *Nature* 457(7232):1003–6
111. Salzer MW, Hughes MK, Bunn AG, Kipfmüller KF. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *PNAS* 106(48):20348–53
112. McMahon SM, Parker GG, Miller DR. 2010. Evidence for a recent increase in forest growth. *PNAS* 107(8):3611–15
113. Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE. 2010. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *PNAS* 107(45):19368–73
114. Cole CT, Anderson JE, Lindroth RL, Waller DM. 2010. Rising concentrations of atmospheric CO₂ have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Glob. Chang. Biol.* 16:2186–97

115. van der Sleen P, Groenendijk P, Vlam M, Anten NPR, Boom A, et al. 2015. No growth stimulation of tropical trees by 150 years of CO₂ fertilization but water-use efficiency increased. *Nat. Geosci.* 8:24–28
116. Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, et al. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *PNAS* 104(35):14014–19
117. Thomas RQ, Canham CD, Weathers KC, Goodale CL. 2009. Increased tree carbon storage in response to nitrogen deposition in the US. *Nat. Geosci.* 3:13–17
118. Wang R, Goll D, Balkanski Y, Hauglustaine D, Boucher O, et al. 2017. Global forest carbon uptake due to nitrogen and phosphorus deposition from 1850 to 2100. *Glob. Change Biol.* 23:4854–72
119. Friedl MA, Gray JM, Melaas EK, Richardson AD, Hufkens K, et al. 2014. A tale of two springs: using recent climate anomalies to characterize the sensitivity of temperate forest phenology to climate change. *Environ. Res. Lett.* 9(5):054006
120. Keenan TF, Gray J, Friedl MA, Toomey M, Bohrer G, et al. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nat. Clim. Change* 4(7):598–604
121. Piao S, Liu Z, Wang T, Peng S, Ciais P, et al. 2017. Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nat. Clim. Change* 7(5):359–63
122. Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D, Houghton RA. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* 358(6360):230–34
123. Brien RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, et al. 2015. Long-term decline of the Amazon carbon sink. *Nature* 519(7543):344–48
124. Birdsey R, Pregitzer K, Lucier A. 2006. Forest carbon management in the United States: 1600–2100. *J. Environ. Qual.* 35(4):1461–69
125. Erb K-H, Kastner T, Luyssaert S, Houghton RA, Kuemmerle T, et al. 2013. Bias in the attribution of forest carbon sinks. *Nat. Clim. Change* 3:854–56
126. Körner C. 2017. A matter of tree longevity. *Science* 355(6321):130–31
127. Anderegg WRL, Kane JM, Anderegg LDL. 2012. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3(1):30–36
128. Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D, Houghton RA. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* 358(6360):230–34
129. Hufkens K, Keenan TF, Flanagan LB, Scott RL, Bernacchi CJ, et al. 2016. Productivity of North American grasslands is increased under future climate scenarios despite rising aridity. *Nat. Clim. Change* 6(7):710–14
130. Sander J, Amundson R. 2008. A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soils. *Biogeochemistry* 89(3):309–27
131. Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291(5503):481–84
132. Biederman JA, Scott RL, Goulden ML, Vargas R, Litvak ME, et al. 2016. Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America. *Glob. Change Biol.* 22(5):1867–79
133. Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, et al. 2016. Impacts of warming and elevated CO₂ on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. *Ecol. Lett.* 19(8):956–66
134. Reich PB, Hobbie SE. 2012. Decade-long soil nitrogen constraint on the CO₂ fertilization of plant biomass. *Nat. Clim. Change* 3:278
135. Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.* 165:351–72
136. Morgan JA, LeCain DR, Pendall E, Blumenthal DM, Kimball BA, et al. 2011. C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476(7359):202–5
137. Luo YQ, Hui DF, Zhang DQ. 2006. Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology* 87(1):53–63
138. Pellegrini AFA, Ahlström A, Hobbie SE, Reich PB, Nieradzik LP, et al. 2017. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553(7687):194–98

139. Skjemstad JO, Reicosky DC, Wilts AR, McGowan JA. 2002. Charcoal carbon in U.S. agricultural soils. *Soil Sci. Soc. Am. J.* 66(4):1249–55
140. Klumpp K, Fontaine S, Attard E, Le Roux X, Gleixner G, Soussana J-F. 2009. Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. *J. Ecol.* 97(5):876–85
141. Owensby CE, Ham JM, Auen LM. 2006. Fluxes of CO₂ from grazed and ungrazed tallgrass prairie. *Rangel. Ecol. Manag.* 59(2):111–27
142. Conant RT, Cerri CEP, Osborne BB, Paustian K. 2017. Grassland management impacts on soil carbon stocks: a new synthesis. *Ecol. Appl.* 27(2):662–68
143. Naito AT, Cairns DM. 2011. Patterns and processes of global shrub expansion. *Prog. Phys. Geogr.* 35(4):423–42
144. Gray JM, Frohling S, Kort EA, Ray DK, Kucharik CJ, et al. 2014. Direct human influence on atmospheric CO₂ seasonality from increased cropland productivity. *Nature* 515(7527):398–401
145. Zeng N, Zhao F, Collatz GJ, Kalnay E, Salawitch RJ, et al. 2014. Agricultural Green Revolution as a driver of increasing atmospheric CO₂ seasonal amplitude. *Nature* 515:394–97
146. Post WM, Kwon KC. 2000. Soil carbon sequestration and land-use change: processes and potential. *Glob. Change Biol.* 6(3):317–27
147. Del Grosso SJ, Baranski M. 2016. *USDA agriculture and forestry greenhouse gas inventory 1990–2013*. Off. Chief Economist, Tech. Bull. 1943, US Dep. Agric. https://www.usda.gov/oce/climate_change/AFGG_Inventory/USDA_GHG_Inventory_1990-2013_9_19_16_reduced.pdf
148. Sanderman J, Hengl T, Fiske GJ. 2017. Soil carbon debt of 12,000 years of human land use. *PNAS* 114(36):9575–80
149. Cardinael R, Chevallier T, Cambou A, Béral C, Barthès BG, et al. 2017. Increased soil organic carbon stocks under agroforestry: a survey of six different sites in France. *Agric. Ecosyst. Environ.* 236:243–55
150. Chapin FS III, Matson PA, Vitousek P. 2012. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer. 2nd ed.
151. Overland JE, Wang M, Walsh JE, Stroeve JC. 2014. Future arctic climate changes: adaptation and mitigation time scales. *Earth's Future* 2(2):68–74
152. Mao J, Ribes A, Yan B, Shi X, Thornton PE, et al. 2016. Human-induced greening of the northern extratropical land surface. *Nat. Clim. Change* 6(10):959–63
153. Myers-Smith IH, Elmendorf SC, Beck PSA, Wilkening M, Hallinger M, et al. 2015. Climate sensitivity of shrub growth across the tundra biome. *Nat. Clim. Change* 5(9):887–91
154. McGuire AD, Koven C, Lawrence DM, Clein JS, Xia J, et al. 2016. Variability in the sensitivity among model simulations of permafrost and carbon dynamics in the permafrost region between 1960 and 2009. *Glob. Biogeochem. Cycles* 30(7):1015–37
155. Schuur EAG, Bockheim J, Canadell JG, Euskirchen E, Field CB, et al. 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience* 58(8):701–14
156. Anthony KMW, Zimov SA, Grosse G, Jones MC, Anthony PM, et al. 2014. A shift of thermokarst lakes from carbon sources to sinks during the Holocene epoch. *Nature* 511:452–56
157. McGuire AD, Christensen TR, Hayes D, Heroult A, Euskirchen E, et al. 2012. An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences* 9(8):3185–204
158. Ukkola AM, Prentice IC, Keenan TF, van Dijk AIJM, Viney NR, et al. 2015. Reduced streamflow in water-stressed climates consistent with CO₂ effects on vegetation. *Nat. Clim. Change* 6(1):75–78
159. Novick KA, Ficklin DL, Stoy PC, Williams CA, Bohrer G, et al. 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nat. Clim. Change* 6(11):1023–27
160. Poulter B, Frank D, Ciais P, Myneni RB, Andela N, et al. 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509(7502):600–3
161. Ahlström A, Raupach MR, Schurgers G, Smith B, Arneth A, et al. 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science* 348(6237):895–99
162. Niu S, Fu Z, Luo Y, Stoy PC, Keenan TF, et al. 2017. Interannual variability of ecosystem carbon exchange: from observation to prediction. *Glob. Ecol. Biogeogr.* 26(11):1225–37
163. Wang W, Ciais P, Nemani RR, Canadell JG, Piao S, et al. 2013. Variations in atmospheric CO₂ growth rates coupled with tropical temperature. *PNAS* 110(32):13061–66

164. Wang X, Piao S, Ciais P, Friedlingstein P, Myneni RB, et al. 2014. A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature* 506(7487):212–15
165. Keenan TF, Baker I, Barr A, Ciais P, Davis K, et al. 2012. Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange. *Glob. Change Biol.* 18(6):1971–87
166. Niu S, Luo Y, Dietze MC, Keenan TF, Shi Z, et al. 2014. The role of data assimilation in predictive ecology. *Ecosphere* 5(5):65
167. Grassi G, House J, Dentener F, Federici S, Den Elzen M, Penman J. 2017. The key role of forests in meeting climate targets requires science for credible mitigation. *Nat. Clim. Change* 7(3):220–26
168. Fuss S, Jones CD, Kraxner F, Peters GP, Smith P, et al. 2016. Research priorities for negative emissions. *Environ. Res. Lett.* 11(11):115007
169. Houghton RA, Byers B, Nassikas AA. 2015. A role for tropical forests in stabilizing atmospheric CO₂. *Nat. Clim. Change* 5(12):1022–23
170. Griscom BW, Adams J, Ellis PW, Houghton RA, Lomax G, et al. 2017. Natural climate solutions. *PNAS* 114(44):11645–50
171. Mackey B, Prentice IC, Steffen W, House JI, Lindenmayer D, et al. 2013. Untangling the confusion around land carbon science and climate change mitigation policy. *Nat. Clim. Change* 3(6):552–57
172. Cox PM, Huntingford C, Williamson MS. 2018. Emergent constraint on equilibrium climate sensitivity from global temperature variability. *Nature* 553:319–23
173. Leduc M, Damon Matthews H, De Elía R. 2016. Regional estimates of the transient climate response to cumulative CO₂ emissions. *Nat. Clim. Change* 6(5):474–78
174. Boer GJ, Arora V. 2009. Temperature and concentration feedbacks in the carbon cycle. *Geophys. Res. Lett.* 36(2):1–6
175. Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320(5882):1444–49
176. Bonan GB, Doney SC. 2018. Climate, ecosystems, and planetary futures: the challenge to predict life in Earth system models. *Science* 359(6375):8328
177. Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, et al. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359(6371):80–83
178. Coleman DC, Crossley DA, Hendrix PF. 2004. *Fundamentals of Soil Ecology*. Cambridge, MA: Elsevier
179. Peñuelas J, Ciais P, Canadell JG, Janssens IA, Fernández-Martínez M, et al. 2017. Shifting from a fertilization-dominated to a warming-dominated period. *Nat. Ecol. Evol.* 1(10):1438–45
180. Jones CD, Ciais P, Davis SJ, Friedlingstein P, Gasser T, et al. 2016. Simulating the Earth system response to negative emissions. *Environ. Res. Lett.* 11(9):95012
181. Jackson RB, Canadell JG, Fuss S, Milne J, Nakicenovic N, Tavoni M. 2017. Focus on negative emissions. *Environ. Res. Lett.* 12:11
182. Field CB, Mach KJ. 2017. Rightsizing carbon dioxide removal. *Science* 356(6339):706–7
183. Williams JH, Haley B, Kahrl F, Moore J, Jones AD, et al. 2014. *Pathways to Deep Decarbonization in The United States. The U.S. Report of the Deep Decarbonization Pathways Project of the Sustainable Development Solutions Network and The Institute for Sustainable Development and International Relations*. San Francisco: Energy Environ. Econ. Inc. https://ethree.com/publications/index_US2050.php