Reconciling carbon-cycle processes from ecosystem to global scales

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Understanding carbon (C) dynamics from ecosystem to global scales remains a challenge. Although expansion of global carbon dioxide (CO_2) observatories makes it possible to estimate C-cycle processes from ecosystem to global scales, these estimates do not necessarily agree. At the continental US scale, only 5% of C fixed through photosynthesis remains as net ecosystem exchange (NEE), but ecosystem measurements indicate that only 2% of fixed C remains in grasslands, whereas as much as 30% remains in needleleaf forests. The wet and warm Southeast has the highest gross primary productivity and the relatively wet and cool Midwest has the highest NEE, indicating important spatial mismatches. Newly available satellite and atmospheric data can be combined in innovative ways to identify potential C loss pathways to reconcile these spatial mismatches. Independent datasets compiled from terrestrial and aquatic environments can now be combined to advance C-cycle science across the land–water interface.

Carbon (C) is the building block of life. Global photosynthesis generates approximately 100 terawatts (TW) of energy each year by converting solar radiation into stored chemical energy (Barber 2009). Photosynthesis also represents

In a nutshell:

- From a societal perspective, there has never been a more urgent time to advance our understanding of the carbon (C) cycle, given that the atmospheric growth rate of carbon dioxide (CO_2) has reached record levels
- From a scientific perspective, however, there has never been a better time to be a global ecologist, because global C observing systems are becoming more expansive and intensive, allowing scientists to make innovative insights at ecosystem, macrosystem, and global scales
- A fundamental goal of macrosystems research is to reconcile important processes from ecosystem to continental scales, which is now achievable using long-term and consistent measurements of C-cycle dynamics
- Comparisons across scales also reveal many CO_2 loss pathways other than respiration that may not be included in ecosystem-process models

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the largest global annual C flux, of ~125 petagrams (Pg; where 1 Pg equals 10^{15} grams [g] and 1 Pg C is roughly equivalent to 0.47 parts per million [ppm] of CO_2), with the second greatest flux consisting of the subsequent release of CO_2 via respiration (~122 Pg C/year). Both of these fluxes are an order of magnitude greater than fossil-fuel emissions (Ballantyne *et al.* 2015). The atmospheric CO_2 that is fixed during photosynthesis is subsequently stored and transferred as chemical energy, which in turn fuels the metabolic reactions of most autotrophs and heterotrophs. Although C is the most common element in the terrestrial biosphere, representing approximately 50 parts per hundred (%) of all organic matter, CO_2 represents only a very small fraction of the atmosphere and is therefore measured in ppm (~415 ppm in 2020). Given the abundance of C in the terrestrial biosphere and the massive fluxes of C occurring between the biosphere and the atmosphere, it is no surprise that scientists have developed a myriad of innovative ways for measuring and simulating C-cycle processes across a range of scales in time and space. For example, chloroplast CO_2 fluxes are estimated over millimeters per second, whereas biome CO_2 fluxes may be estimated over thousands of kilometers per year. There have been many advances in C-cycle science over the past 60 years at leaf, plant, ecosystem, and global scales, but both challenges to and opportunities for scientific advancement remain. Progress is necessary, however, especially at the macrosystem scale, where human management and ecological processes are often at odds and create interesting interactions of C dynamics.

One of the greatest impediments to accurate predictions of future climate is the uncertain response of the terrestrial C cycle to impending changes in temperature, precipitation, and atmospheric CO_2 concentrations (Friedlingstein *et al.* 2013). Even though land-surface models have become increasingly realistic in their mechanistic representation of C-cycle processes by including nutrient limitation (Thornton *et al.* 2007),

surface hydrology (Wang *et al.* 2013), and microbial processes (Wieder *et al.* 2013), this increased complexity does not necessarily reduce the range of uncertainty in projections of C uptake among models (eg see Friedlingstein *et al.* [2006] compared to Friedlingstein *et al.* [2013]). In parallel, there is now a globally nested CO_2 observation network that allows for unprecedented measurements of changes in CO_2 concentrations and fluxes (Schimel *et al.* 2015). These continuous measurements allow estimates to be made of net CO_2 exchange from ecosystem to global scales, but not necessarily the underlying processes that regulate this net exchange (Ciais *et al.* 2019). In contrast, land-surface models simulate the underlying processes that result in net CO_2 exchange, but these are difficult to benchmark due to a lack of process-level data at the appropriate scale (Luo *et al.* 2012; Anav *et al.* 2013).

Although enhanced net C accumulation in the terrestrial biosphere can be inferred from the global C budget, identifying the ecosystems in which C is accumulating is still difficult. For example, at the global scale, it can be concluded with confidence that ~25% of CO_2 emitted to the atmosphere from fossil-fuel and land-use emissions has been taken up by the terrestrial biosphere (Ballantyne *et al.* 2015; Le Quéré *et al.* 2016), but biomass datasets are too sparse in extent or too short in duration to document which ecosystems continue to accumulate C. More detailed ocean and land measurements now make it possible to identify specific processes affecting the net CO_2 atmospheric exchange between the marine biosphere (Landschützer *et al.* 2015) and terrestrial biosphere (Anderegg *et al.* 2015), in some instances at regional scales (Ciais *et al.* 2019). However, partitioning net C fluxes into their component gross fluxes of photosynthesis and respiration remains a challenge (Wehr *et al.* 2016).

Another vexing problem in global C-cycle research is that top-down global estimates of net terrestrial C uptake do not agree with bottom-up ecosystem estimates when integrated globally. For instance, top-down estimates of global net terrestrial C uptake in 2010 are an order of magnitude less (2.2 ± 2.1 Pg C/year; Ballantyne *et al.* 2015) than eddy covariance estimates up-scaled globally (22 ± 5 Pg C/year; Jung *et al.* 2011). Although some of the discrepancy between top-down and bottom-up estimates of net terrestrial C uptake may be due to issues associated with eddy covariance methods (Keenan *et al.* 2019) – particularly regarding measurement of nighttime respiration, which often violates eddy covariance requirements of turbulent flux and biases in the sampling network – a portion can also be explained by non-respiratory CO_2 loss pathways (~7 Pg C/year; Randerson *et al.* 2002). This suggests that there are many C transformation and transport pathways that ultimately lead to a loss of CO_2 from ecosystems back to the atmosphere. Approximately 90% of inland lakes and streams are net sources of CO_2 to the atmosphere (Cole *et al.* 1994), and at a global scale approximately 2 Pg C/year is returned to the atmosphere via CO_2 loss from rivers and lakes (Raymond *et al.* 2013). Although this estimate of CO_2 loss from aquatic ecosystems is comparable to the magnitude of net C uptake by terrestrial ecosystems, it is

less than 2% of total inferred CO_2 respiration from the terrestrial biosphere back to the atmosphere (Ballantyne *et al.* 2017). As such, characterizing the C balance at the macrosystem scale for direct comparison with different biomes in Earth system models remains difficult (Peylin *et al.* 2013).

Although from a societal perspective there has never been a more urgent time to study the C cycle and its sensitivity to climate change (Obama 2017), from a scientific perspective there has never been a more exciting time to study C-cycle processes. The global C observation network supports innovative analyses and syntheses across scales from ecosystems to the entire planet. Currently, there are over 800 eddy covariance sites operating around the world that contribute measurements of net CO_2 exchange, as well as estimates of primary productivity and total respiration across a wide array of ecosystems (Chu *et al.* 2017). However, in the US, fewer than half of the ecosystem functional types are represented in the combined core sites of the AmeriFlux Network and the National Ecological Observatory Network (NEON) (Villarreal *et al.* 2018), and many ecosystems remain underrepresented, especially in climate-sensitive Arctic tundra and tropical rainforests. Other C flux databases have continued to expand, such as a recently updated database on soil respiration that has been used to identify the climate sensitivity of soil respiration over time (Bond-Lamberty and Thomson 2010), which is critical for evaluating how C supply, soil temperature, and moisture interact to regulate soil respiration (Hursh *et al.* 2017).

Global measurement networks and satellite observations of atmospheric CO_2 now allow for the characterization of biome-scale C fluxes at greater temporal and spatial resolutions (Figure 1). The global greenhouse observation network has grown sporadically, with approximately 90 in situ sites now in operation worldwide (GLOBALVIEW-CO_2 1999). Several of these sites also provide atmospheric profile measurements that are essential for estimating latitudinal differences in CO_2 exchange (Stephens *et al.* 2007), in addition to seasonal differences in regional uptake (Gatti *et al.* 2014). Regional atmospheric CO_2 monitoring networks often engage in intensive atmospheric campaigns to better define regional C fluxes in urban continental settings (Corbin *et al.* 2010) or to determine recent changes in the C balance of ecosystems in climate sensitive regions, such as the Arctic (Commane *et al.* 2017). When combined with three-dimensional atmospheric transport modeling and estimates of surface fossil-fuel emissions, these so-called "atmospheric inversions" deliver critical information about the net exchange of CO_2 at biome scales (Peylin *et al.* 2013). The array of Earth observing satellites has also grown tremendously, providing better spatiotemporal coverage of vegetation indices that are useful for assessing patterns and trends of global productivity since ~1982 (Pinzon and Tucker 2010), as well as valuable information on changes in vegetation cover (Song *et al.* 2018) and ecosystem stress (Anderegg *et al.* 2018). Recent advances in satellite observations facilitate quantification of concentration estimates integrated over the entire total atmospheric column for CO_2 (ie XCO_2) and

CH_4 (ie XCH_4). Although potentially less precise than those relying on surface measurements using infrared gas analyzers, these estimates provide more continuous global coverage, improving characterization of regional flux anomalies and attribution to specific C-cycle processes (Liu *et al.* 2017).

Innovative ways to combine ecosystem measurements with satellite observations have made it possible to quantify how different ecosystems are responding to concomitant changes in atmospheric composition, including CO_2 concentration, surface temperatures, and regional precipitation. Moreover, these top-down and bottom-up observations are helping researchers to disentangle net C exchange into its component processes of photosynthesis and respiration across various scales, which provides important diagnostics for models that are designed to simulate the concurrent ecological processes and not just net CO_2 exchange. For instance, combined satellite and meteorological observations have been used in a machine-learning framework to up-scale eddy covariance measurements to provide spatially and temporally continuous estimates of global primary productivity (Jung *et al.* 2011). Likewise, global atmospheric CO_2 measurements have been used to constrain net CO_2 exchange in combination with satellite data to constrain primary productivity to infer the uncoupling of photosynthesis and respiration on decadal timescales (Ballantyne *et al.* 2017). The challenge for the scientific community is figuring out ways in which emergent patterns of net CO_2 exchange can be used (Cox *et al.* 2013) to identify underlying mechanistic processes that can be diagnosed in models (Anderegg *et al.* 2015). Ultimately, this will lead to scientific advances and societal benefits through improved Earth system models with less uncertainty in future climate predictions.

Theoretical representation of C-cycle processes

Although the global C observing system has been greatly expanded and advanced over the past six decades, the theoretical and conceptual framework for understanding C-cycle dynamics has not necessarily kept pace (Figure 2). There has been extensive discussion over the past several decades concerning how the biosphere–atmosphere C exchange can best be defined. The challenges in defining C exchange lie across several axes, including time, space, and C form. Additional issues arise from the different processes occurring in and the transfer of C between aquatic and terrestrial ecosystems. Although we focus solely on terrestrial processes occurring from the ecosystem to biome scale here, we acknowledge the importance of the aquatic interface (Butman *et al.* 2018). The evolution of C-cycle measurements and key issues regarding terminology was described by Chapin *et al.* (2006), who defined net ecosystem C balance (NECB) simply as the change in C per unit time, but then broke this measure down into its component fluxes:

$$NECB = NEE - F_{CO} - F_{VOC} - F_{CH4} - F_{DIC} - F_{DOC} - F_{PC}$$

(Equation 1).

Figure 1. Image of airborne observations combined with eddy flux observations of carbon (C) fluxes to measure ecosystem–atmosphere exchanges of carbon dioxide (CO_2).

In this formulation, net ecosystem exchange (NEE) is a measure of the net ecosystem CO_2 exchange as the difference between gross primary productivity (GPP) and total ecosystem respiration (TER), and at the ecosystem scale is typically measured using eddy covariance techniques (Wofsy *et al.* 1993). Although the CO_2 flux associated with NEE is usually the dominant form of net C exchange in many ecosystems, it cannot be assumed that transformations of C do not occur as a result of ecosystem processes. For instance, fluxes of carbon monoxide (F_{CO}), volatile organic compounds (F_{VOC}), methane (F_{CH4}), dissolved inorganic C (F_{DIC}), dissolved organic C (F_{DOC}), and particulate C (F_{PC}) all represent C loss pathways that may affect the net C balance over time. Although NEE is sometimes used synonymously with NECB, it is an approximation that can, under certain circumstances, leave out quantitatively important non-respiratory processes that contribute to ecosystem C balance.

A second key issue in C balance terminology emerges at larger spatial or temporal scales when other factors can become major contributors to C balance. Notably, large disturbances like wildfire, landslides, and insect infestations can cause large or punctuated redistributions of C. In human managed ecosystems, activities such as logging, harvest, and other forms of C transfer can result in C taken up at the ecosystem scale being lost at the biome scale, and this transfer can actually cause NECB to shift from a net C sink to a net C source. The net biome productivity (NBP) concept was first introduced by Schulze *et al.* (2000) to account for C transfer and subsequent
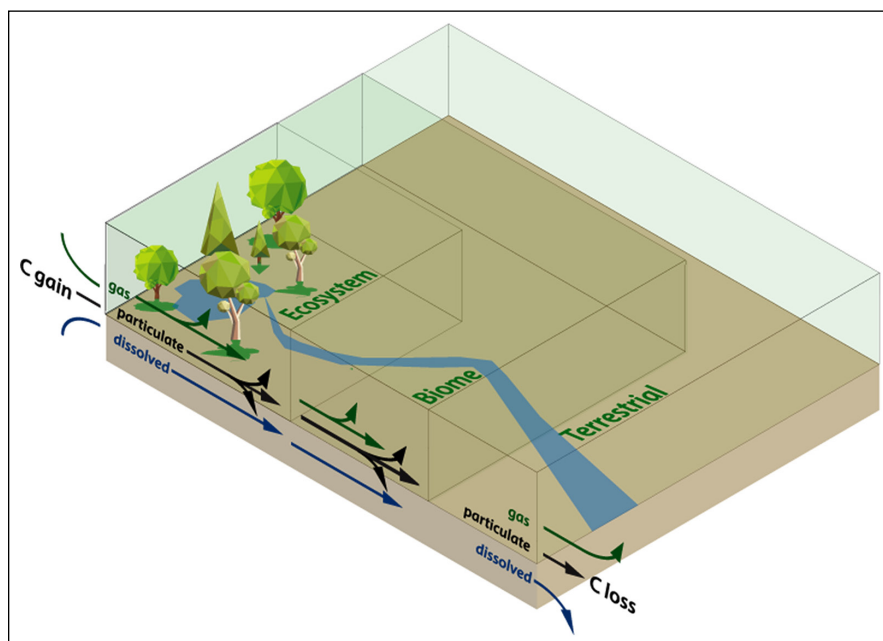
Figure 2. Conceptual figure showing pathways of C gain and loss from ecosystem to biome to terrestrial scales within the biosphere. Although it is often assumed that very little change occurs among the gas, particulate, and dissolved phases of C, ecosystems are very effective at transforming C, such that C gain pathways may not correspond with C loss pathways, leading to an apparent C imbalance across scales. Furthermore, C can be transported across scales via either advection through the atmosphere or fluvial processes in aquatic ecosystems.

loss at regional scales. In Chapin *et al.* (2006), NECB represents NBP integrated over fixed space and time domains, with the assumption that additional processes analogous to those shown in Equation (1) may need to be added to account for C fluxes driven by periodic events. At the global scale, we can assume that CO_2 mass is conserved in the atmosphere and thus, given fossil-fuel emissions to the atmosphere and estimates of net CO_2 uptake by the oceans, net CO_2 uptake by the terrestrial biosphere can be inferred (Le Quéré *et al.* 2016). More importantly, the atmosphere and oceans provide constraints on global C exchange because these are relatively well-mixed homogenous reservoirs as compared to ecosystem C pools and fluxes that tend to be much more spatially and temporally heterogeneous. Resolving C-cycle processes from ecosystem to global scales may therefore require an update to C-cycle nomenclature (see WebPanel 1).

◼ Spatial scale differences in C balance

The "C exchange efficiency" (CEE = NEE/GPP) may provide a useful framework (see WebFigure 1) for comparing relative fluxes across ecosystem to global scales. At the global scale, only ~2% of C fixed annually through GPP remains in the biosphere as a result of NEE (2.5/125 Pg C/year), suggesting that CEE of the terrestrial biosphere is remarkably low. At the scale of the continental US, approximately 5% of C fixed annually through photosynthesis remains in the terrestrial biosphere (Figure 3). However, estimates of CEE derived from eddy

covariance methods reveal very large differences among terrestrial ecosystems. Ecosystems with lower levels of GPP tend to fall on the CEE line at the continental scale, whereas more productive ecosystems tend to deviate from the CEE line. For example, grasslands have very low CEE (~2%), a level consistent with the global CEE, whereas evergreen needleleaf forests and deciduous broadleaf forests appear to have quite high CEE values (~31% and ~24%, respectively). Therefore, our ecosystem-scale measurements suggest that these forests are strong C sinks, whereas our global-scale measurements suggest that much of this apparent forest C uptake is lost, indicating that these forests may be acting more like "C sieves". Moreover, croplands vary considerably, with less productive croplands falling on the continental CEE line and more productive croplands deviating considerably, with an overall CEE of 23%. It should be noted, however, that according to mass balance, the integral of NEE across all ecosystems (aquatic and terrestrial) should be equal to global NEE; in other words, CEE estimates from the different ecosystems shown in Figure 3 should all fall on the continental CEE line (Chapin *et al.* 2006). Therefore, measurements of net CO_2 exchange at the ecosystem scale are biased, or CO_2 loss pathways at the continental scale are offsetting the apparent net uptake of CO_2 by certain ecosystems.

Measurement biases of ecosystem C fluxes stem from the location of eddy flux sites or systematic biases in NEE measurements. In the US, this network bias should be reduced with the addition of more observation sites, such as NEON sites; however, there remain notable gaps in the intermountain west, north-central plains, and parts of the Southeast. Also noteworthy is that eddy flux sites are often situated in rapidly regenerating ecosystems and as such may not capture the full trajectory of ecosystem C dynamics (Luyssaert *et al.* 2008). Furthermore, the eddy flux approach only measures the net ecosystem CO_2 exchange (ie NEE) directly, whereas photosynthetic fluxes and total ecosystem respiration fluxes are estimated, resulting in the potential for systematic biases to occur in these measurements. Eddy covariance methods are inherently challenging in ecosystems with dense canopies (Thomas *et al.* 2013), which can lead to nocturnal C storage within the canopy (Fu *et al.* 2018) and decoupling of the canopy and the atmosphere that may vary seasonally (Jocher *et al.* 2017). This may help explain the strong divergence between both deciduous broadleaf and evergreen needleleaf forests and the CEE line at the continental scale (Figure 3). If daytime respiration is reduced with respect to nighttime respiration, large overestimates of both photosynthetic gains and respiration losses at the ecosystem scale may result, which would increase relative ecosystem CEE (Keenan *et al.* 2019).

The discrepancy between CEE at the biome scale and the ecosystem scale can also be explained by the lack of measurements of non-respiratory loss pathways of CO_2 back to the atmosphere (Figure 2). For example, aquatic ecosystems, which are effective at transporting dissolved and particulate forms of inorganic and organic C and transforming it to CO_2 such that it may be lost to the atmosphere (Neff and Asner 2001; Hotchkiss *et al.* 2015), were not plotted on our diagnostic CEE plot (Figure 3). There are many measurements of the partial pressure of CO_2 in aquatic environments, which determine whether CO_2 is diffusing in or out of aquatic ecosystems, but these are not always combined with productivity estimates (albeit see Hotchkiss *et al.* 2015; Bernhardt *et al.* 2018). Volatile organic C (VOC) compounds are another major source of C loss from ecosystems, which may help to reconcile the discrepancy between ecosystem- and biome-scale C exchange efficiencies. Estimates of VOC production are tightly coupled to primary productivity and range around 450 teragrams (Tg) C/year, making them a very small fraction of terrestrial GPP (less than 0.4%) but an appreciable fraction of NEE (~15%), assuming that VOCs are rapidly oxidized to form CO_2 (Unger *et al.* 2013). Finally, the only ecosystem-scale C loss pathways that can help reconcile ecosystem- and global-scale estimates of CEE are oxidative pathways that ultimately lead to atmospheric CO_2 (eg CO_2 emissions from wildfires), meaning that other loss pathways leading to reduced C (eg CH_4 emissions) will not help reconcile these discrepancies of scale.

We can also look at the spatial distribution of CEE from the biome to ecosystem scale (Figure 4). At the continental scale in the US, it is apparent that high CEE in the midwestern region near the Great Lakes is driven primarily by high mean annual NEE, and very high CEE in the intermountain west is driven by low GPP and modest NEE. In contrast, highly productive regions, such as the Pacific Northwest and the Southeast, do not necessarily retain a large fraction of GPP as NEE, as reflected in their relatively low CEE values. These regional differences in CEE seem to be corroborated by eddy covariance sites in certain biomes, such as the Northeast and parts of the Southwest, but less so in other regions. There appears to be a strong mismatch in CEE near the Great Lakes, with regional estimates suggesting a relatively high CEE, whereas eddy flux sites indicate a much lower CEE. This may be due to the specific locations of eddy flux sites that may not capture the diverse array of midwestern ecosystems. A similar mismatch is evident in the Pacific Northwest, where regional CEE values are extremely low – and in some instances negative – due to an apparent net source of CO_2 to the atmosphere,
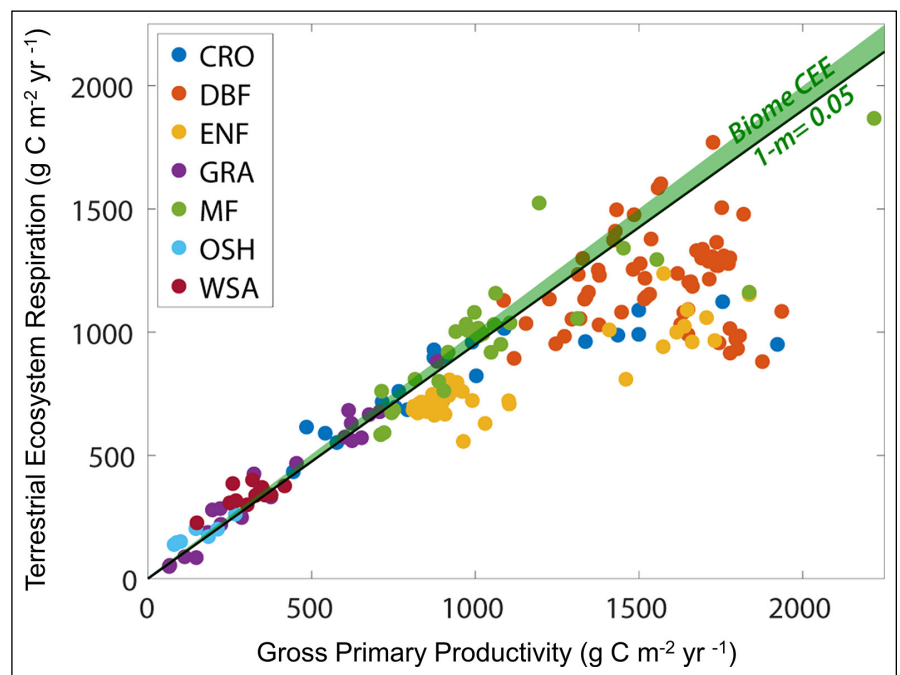

Figure 3. Comparison of C exchange efficiency (CEE) at ecosystem to biome scales across the continental US. Each point represents the mean annual gross ecosystem productivity and total ecosystem respiration for cropland (CRO), deciduous broadleaf forests (DBF), evergreen needleleaf (ENF), grassland (GRA), mixed forest (MF), open shrubland (OSH), and woody savanna (WSA) eddy covariance sites across the US. The diagonal line was derived from satellite estimates of gross primary productivity (GPP) and atmospheric estimates of net CO_2 exchange at the scale of the continental US and indicates that 95% of C fixed during photosynthesis is lost to the atmosphere through respiration, or that CEE is only 5% (1 − 0.95 = 0.05), represented by the green wedge.

while eddy flux measurements from central Oregon suggest high CEE.

■ Climate sensitivity of C-cycle processes

At the continental scale in the US, mean annual primary productivity and net CO_2 exchange do not necessarily covary spatially and appear to occupy different climate spaces at regional scales (Figure 5; Liu *et al.* 2018). GPP is highest in the relatively warm and wet Southeast (Figure 5a), corresponding with high levels of mean annual precipitation (MAP, >1200 mm) across a range of mean annual temperatures (MAT, ~10–20°C; Figure 5c). In contrast, NEE is more variable, with the highest values in the Midwest (Figure 5b) at intermediate to high levels of MAP (~750–1200 mm) and lower MAT (<10°C) (Figure 5d). The spatial covariance of GPP and NEE becomes decoupled as water availability increases. We found a strong precipitation threshold of ~700 mm/year over the continental US, below which NEE is regulated by photosynthetic gains and above which NEE is regulated to a greater degree by respiration losses (Liu *et al.* 2018). This result is consistent with ecosystem-scale studies that show the greatest response in productivity to precipitation anomalies in semiarid grassland and shrubland ecosystems (Knapp and Smith 2001). However, the lateral transport of C through river flow
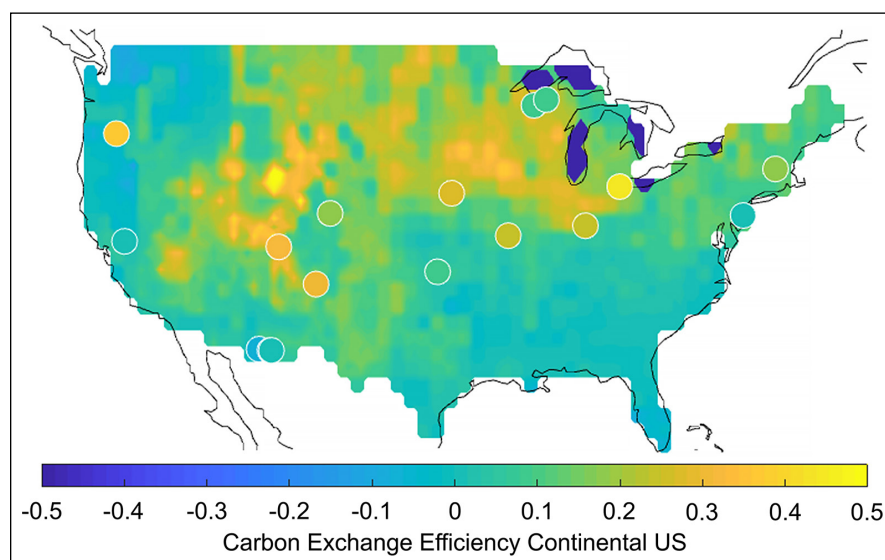
Figure 4. CEE for the continental US. Spatially continuous estimates of GPP derived from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite estimates and continuous estimates of net ecosystem exchange derived from atmospheric inversions over the continental US (Peters *et al.* 2007) are compared with in situ ecosystem-scale measurements made at 16 different eddy covariance core sites within the AmeriFlux Network (circle points). Positive values indicate regions where ecosystems are a net sink of C from the atmosphere, whereas negative values indicate regions where ecosystems are a net source of C to the atmosphere.

and human harvest may also be important in uncoupling GPP from NEE at continental scales. This spatial mismatch is an important finding because it is often assumed that anomalies in photosynthesis directly result in anomalies in net CO_2 exchange. In fact, it is impossible in standard eddy covariance approaches for partitioning fluxes to have increases in net exchange without increases in photosynthesis (Reichstein *et al.* 2005), and net C exchange in land-surface models is dominated by photosynthetic inputs (Liu *et al.* 2018).

At the global scale, the relationship between the interannual variability of the atmospheric CO_2 growth rate and tropical land-surface temperatures has been identified as an emergent constraint, such that higher surface temperatures diminish NEE (Cox *et al.* 2013). However, identifying the processes associated with this diminished NEE is difficult because increased tropical temperatures suppress photosynthesis and/or promote respiration, both of which lead to reduced net C exchange. It has been suggested that total respiration is the
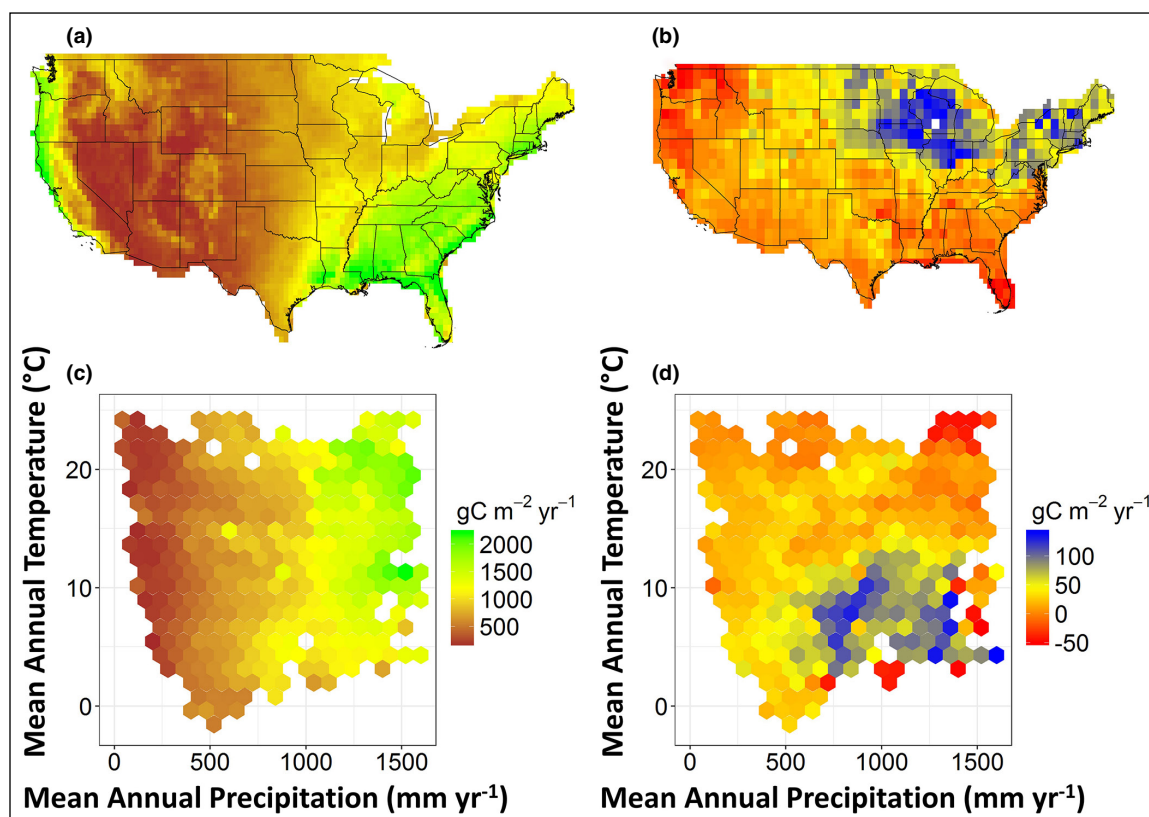

Figure 5. Continental-scale estimates of mean annual GPP and net CO_2 exchange (ie NEE) and their sensitivities to climate factors. (a) Continental-scale estimates of GPP from MODIS satellite observations plotted within (c) their climate space of mean annual precipitation and mean annual temperature. (b) Continental-scale estimates of NEE from atmospheric CO_2 inversion methods plotted within (d) their climate space. All flux estimates are reported as g C/m²/year and have been projected to ecosystem area (modified from Liu *et al.* [2018]; see WebTable 1).

most likely mechanism explaining the emergent relationship between interannual variability in the atmospheric growth rate and tropical surface temperature (Anderegg *et al.* 2015) and that water limitation is important in regulating net CO_2 exchange at the local scale, whereas temperature becomes more important at global scales (Jung *et al.* 2017). Recent satellite evidence suggests that terrestrial water availability that integrates temperature and precipitation variability may be the ultimate mechanism regulating interannual NEE at the global scale (Humphrey *et al.* 2018). However, evidence derived from satellite estimates of XCO_2 and solar induced fluorescence during the recent 2015/2016 El Niño event suggest that net tropical C uptake was reduced by different processes in different tropical regions – such as reduced photosynthesis in South America, increased respiration in Africa, and increased fire emissions in Southeast Asia (Liu *et al.* 2017). Therefore, even though we are gaining new insight on the climate sensitivity of important C-cycle processes, ecosystem-scale observations are still lacking in certain regions to help reconcile different C-cycle processes operating at different spatial scales.

Conclusions and frontiers in C-cycle research

A central goal of ecology at the macrosystem scale is to understand biosphere processes and their complex interactions with climate, land use, and changes in species distribution at regional to continental scales This has also been a central challenge of C-cycle research because there is a long history of atmospheric CO_2 observations that have enabled a better understanding of the C cycle at the global scale and a network of eddy covariance measurements of CO_2 exchange at the ecosystem scale. However, reconciling differences in net CO_2 exchange measured at these different scales continues to be difficult. We are now acquiring data from aircraft and satellites that allow important C-cycle processes to be resolved at the biome scale. The terrestrial and aquatic ecological research communities are also compiling databases to elucidate important C-cycle processes that may be merged to provide an integrated understanding of C transport and transformations across watersheds. Collectively, we are identifying missing pieces of the global C puzzle that now make it possible to reconcile and understand processes that help to explain discrepancies in C dynamics across scales.

Acknowledgements

References

Anav A, Friedlingstein P, Kidston M, *et al.* 2013. Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth system models. *J Climate* **26**: 6801–43.

Anderegg WRL, Ballantyne AP, Smith WK, *et al.* 2015. Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink. *P Natl Acad Sci USA* **112**: 15591–96.

Anderegg WRL, Konings AG, Trugman AT, *et al.* 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* **561**: 538–41.

Ballantyne AP, Andres R, and Houghton R. 2015. Audit of the global carbon budget: estimate errors and their impact on uptake uncertainty. *Biogeosciences* **12**: 2565–84.

Ballantyne A, Smith W, Anderegg W, *et al.* 2017. Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. *Nat Clim Change* **7**: 148.

Barber J. 2009. Photosynthetic energy conversion: natural and artificial. *Chem Soc Rev* **38**: 185–96.

Bernhardt ES, Heffernan JB, Grimm NB, *et al.* 2018. The metabolic regimes of flowing waters. *Limnol Oceanogr* **63**: S99–118.

Bond-Lamberty B and Thomson A. 2010. Temperature-associated increases in the global soil respiration record. *Nature* **464**: 579–82.

Butman DE, Striegl RG, Stackpoole SM, *et al.* 2018. Inland waters. In: Cavallaro N, Shrestha G, Birdsey R, *et al.* (Eds). Second State of the Carbon Cycle Report (SOCCR2): a sustained assessment report. Washington, DC: US Global Change Research Program.

Chapin FS, Woodwell GM, Randerson JT, *et al.* 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* **9**: 1041–50.

Chu H, Baldocchi DD, John R, *et al.* 2017. Fluxes all of the time? A primer on the temporal representativeness of FLUXNET. *J Geophys Res-Biogeo* **122**: 289–307.

Ciais P, Tan J, Wang X, *et al.* 2019. Five decades of northern land carbon uptake revealed by the interhemispheric CO_2 gradient. *Nature* **568**: 221–25.

Cole JJ, Caraco NF, Kling GW, and Kratz TK. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* **265**: 1568–70.

Commane R, Lindaas J, Benmergui J, *et al.* 2017. Carbon dioxide sources from Alaska driven by increasing early winter respiration from Arctic tundra. *P Natl Acad Sci USA* **114**: 5361–66.

Corbin KD, Denning AS, Lokupitiya EY, *et al.* 2010. Assessing the impact of crops on regional CO_2 fluxes and atmospheric concentrations. *Tellus B* **62**: 521–32.

Cox PM, Pearson D, Booth BB, *et al.* 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**: 341–44.

Friedlingstein P, Cox P, Betts R, *et al.* 2006. Climate–carbon cycle feedback analysis: results from the C4MIP model intercomparison. *J Climate* **19**: 3337–53.

Friedlingstein P, Meinshausen M, Arora VK, *et al.* 2013. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J Climate* **27**: 511–26.

Fu Z, Gerken T, Bromley G, *et al.* 2018. The surface–atmosphere exchange of carbon dioxide in tropical rainforests: sensitivity to environmental drivers and flux measurement methodology. *Agr Forest Meteorol* **263**: 292–307.

Gatti LV, Gloor M, Miller JB, *et al.* 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* **506**: 76–80.

GLOBALVIEW-CO_2. 1999. Cooperative atmospheric data integration project – carbon dioxide. Boulder, CO: National Oceanic and Atmospheric Administration.

Hotchkiss ER, Hall Jr RO, Sponseller RA, *et al.* 2015. Sources of and processes controlling CO_2 emissions change with the size of streams and rivers. *Nat Geosci* **8**: 696.

Humphrey V, Zscheischler J, Ciais P, *et al.* 2018. Sensitivity of atmospheric CO_2 growth rate to observed changes in terrestrial water storage. *Nature* **560**: 628–31.

Hursh A, Ballantyne A, Cooper L, *et al.* 2017. The sensitivity of soil respiration to soil temperature, moisture, and carbon supply at the global scale. *Glob Change Biol* **23**: 2090–103.

Jocher G, Ottosson Löfvenius M, De Simon G, *et al.* 2017. Apparent winter CO_2 uptake by a boreal forest due to decoupling. *Agr Forest Meteorol* **232**: 23–34.

Jung M, Reichstein M, Margolis HA, *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-Biogeo* **116**: G00J07.

Jung M, Reichstein M, Schwalm CR, *et al.* 2017. Compensatory water effects link yearly global land CO_2 sink changes to temperature. *Nature* **541**: 516–20.

Keenan TF, Migliavacca M, Papale D, *et al.* 2019. Widespread inhibition of daytime ecosystem respiration. *Nature Ecol Evol* **3**: 407–15.

Knapp AK and Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**: 481–84.

Landschützer P, Gruber N, Haumann FA, *et al.* 2015. The reinvigoration of the Southern Ocean carbon sink. *Science* **349**: 1221–24.

Le Quéré C, Andrew RM, Canadell JG, *et al.* 2016. Global carbon budget 2016. *Earth Syst Sci Data* **8**: 605–49.

Liu J, Bowman KW, Schimel DS, *et al.* 2017. Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. *Science* **358**: eaam5690.

Liu Z, Ballantyne AP, Poulter B, *et al.* 2018. Precipitation thresholds regulate net carbon exchange at the continental scale. *Nat Commun* **9**: 3596.

Luo YQ, Randerson JT, Friedlingstein P, *et al.* 2012. A framework for benchmarking land models. *Biogeosciences* **9**: 3857–74.

Luyssaert S, Schulze E-D, Börner A, *et al.* 2008. Old-growth forests as global carbon sinks. *Nature* **455**: 213–15.

Neff JC and Asner GP. 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* **4**: 29–48.

Obama B. 2017. The irreversible momentum of clean energy. *Science* **355**: 126–29.

Peters W, Jacobson AR, Sweeney C, *et al.* 2007. An atmospheric perspective on North American carbon dioxide exchange: CarbonTracker. *P Natl Acad Sci USA* **104**: 18925–30.

Peylin P, Law RM, Gurney KR, *et al.* 2013. Global atmospheric carbon budget: results from an ensemble of atmospheric CO_2 inversions. *Biogeosciences* **10**: 6699–720.

Pinzon JE and Tucker CJ. 2010. GIMMS 3g NDVI set and global NDVI trends. In: Second Yamal Land-Cover Land-Use Change Workshop; 8–10 Mar 2010; Rovaniemi, Finland. Fairbanks, AK: University of Alaska.

Randerson JT, Chapin III FS, Harden JW, *et al.* 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. *Ecol Appl* **12**: 937–47.

Raymond PA, Hartmann J, Lauerwald R, *et al.* 2013. Global carbon dioxide emissions from inland waters. *Nature* **503**: 355–59.

Reichstein M, Falge E, Baldocchi D, *et al.* 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Glob Change Biol* **11**: 1424–39.

Schimel D, Pavlick R, Fisher JB, *et al.* 2015. Observing terrestrial ecosystems and the carbon cycle from space. *Glob Change Biol* **21**: 1762–76.

Schulze E-D, Wirth C, and Heimann M. 2000. Managing forests after Kyoto. *Science* **289**: 2058–59.

Song X-P, Hansen MC, Stehman SV, *et al.* 2018. Global land change from 1982 to 2016. *Nature* **560**: 639–43.

Stephens BB, Gurney KR, Tans PP, *et al.* 2007. Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO_2. *Science* **316**: 1732–35.

Thomas CK, Martin JG, Law BE, and Davis K. 2013. Toward biologically meaningful net carbon exchange estimates for tall, dense canopies: multi-level eddy covariance observations and canopy coupling regimes in a mature Douglas-fir forest in Oregon. *Agr Forest Meteorol* **173**: 14–27.

Thornton PE, Lamarque J-F, Rosenbloom NA, and Mahowald NM. 2007. Influence of carbon–nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. *Global Biogeochem Cy* **21**: GB4018.

Unger N, Harper K, Zheng Y, *et al.* 2013. Photosynthesis-dependent isoprene emission from leaf to planet in a global carbon–chemistry–climate model. *Atmos Chem Phys* **13**: 10243–69.

Villarreal S, Guevara M, Alcaraz-Segura D, *et al.* 2018. Ecosystem functional diversity and the representativeness of environmental networks across the conterminous United States. *Agr Forest Meteorol* **262**: 423–33.

Wang T, Ottlé C, Boone A, *et al.* 2013. Evaluation of an improved intermediate complexity snow scheme in the ORCHIDEE land surface model. *J Geophys Res-Atmos* **118**: 6064–79.

Wehr R, Munger JW, McManus JB, *et al.* 2016. Seasonality of temperate forest photosynthesis and daytime respiration. *Nature* **534**: 680–83.

Wieder WR, Bonan GB, and Allison SD. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nat Clim Change* **3**: 909.

Wofsy SC, Goulden ML, Munger JW, *et al.* 1993. Net exchange of CO_2 in a mid-latitude forest. *Science* **260**: 1314–17.

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Frontiers**EcoPics**

The ghost orchid mooching off fungi

The color green is a defining feature of the plant kingdom, and plants are mostly assumed to be autotrophs that can make their own food from simple inorganic substances like carbon dioxide. However, in Yokohama, Japan, we observed that a non-photosynthetic or "ghost" variant of the golden orchid *Cephalanthera falcata* reached almost the same size as its photosynthetic green counterpart, suggesting that the ghost orchid was obtaining nutrients from symbiotic fungi.

Over evolutionary time, several lineages of terrestrial plants have independently lost their photosynthetic ability and have become totally dependent on mycobionts. Intriguingly, recent studies have shown that the presence of chlorophyll is insufficient to confirm full autotrophy. Some green plants, including *Cephalanthera* species, not only are photosynthetically active but also obtain carbon from mycorrhizal fungi. These "mixotrophic" plants showcase intermediate stages of the evolutionary transition from autotrophy to heterotrophy. Photosynthesis is one of the processes we think of as fundamental to plants. Therefore, the loss of photosynthesis is one of the most interesting topics within plant evolution.

The non-photosynthetic variants of *C falcata* are presumably more dependent on fungi than their photosynthetic counterparts. Comparisons between the two varieties – albino and green – of this same species would be an elegant way to investigate the evolution of the loss of photosynthesis, given that they share a nearly identical genetic background. Do achlorophyllous plants in general provide benefits to their mycorrhizal partners? If not, why does this "cheating" strategy, at least in *C falcata*, appear to be stable from an evolutionary perspective? These are important questions for future research.

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