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Yoichi P Shiga^{1,2,9}, Anna M Michalak¹, Yuanyuan Fang¹, Kevin Schaefer³, Arlyn E Andrews⁴, Deborah H Huntzinger⁵, Christopher R Schwalm^{6,7}, Kirk Thoning⁴ and Yaxing Wei⁸

¹ Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, United States of America

² Department of Civil and Environmental Engineering, Stanford University, Stanford, CA 94305, United States of America

³ National Snow and Ice Data Center, Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO, 80305, United States of America

⁴ Earth Science Research Laboratory, National Oceanic and Atmospheric Administration, Boulder, CO, 80305, United States of America

⁵ Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, United States of America

⁶ School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ, 86011, United States of America

⁷ Woods Hole Research Center, Falmouth, MA, 02540, United States of America

⁸ Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, 37831, United States of America

⁹ Author to whom any correspondence should be addressed.

E-mail: yshiga@carnegiescience.edu

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Supplementary material for this article is available [online](#)

Abstract

Understanding what drives the interannual variability (IAV) of the land carbon sink is crucial for improving future predictions of this important, yet uncertain, component of the climate system. While drivers of global and hemispheric-scale net ecosystem exchange (NEE) IAV have been investigated, our understanding of the drivers of NEE IAV at regional scales (e.g. sub-continental, biome-level) is quite poor. Here we explore the biome-level attribution and drivers of North American NEE using inverse estimates derived from a dense network of atmospheric CO₂ observations. We find that deciduous broadleaf and mixed forests are the primary regions responsible for North American NEE IAV, which differs from the ecoregions identified for the globe and Northern Hemisphere. We also find that a suite of terrestrial biosphere models (TBMs) do not agree on the dominant biome contributing to NEE IAV, with TBMs falling along an apparent spectrum ranging between those with IAV dominated primarily by forested ecosystems to those with IAV dominated by non-forested ecosystems. Furthermore, this regional trade-off in TBM NEE IAV is found to be linked to differing regional responses to environmental drivers among TBMs. This work displays the importance of extra-tropical forests in driving continental NEE IAV and also highlights the challenges and limitations of using TBMs to inform regional-scale carbon flux dynamics.

Introduction

The terrestrial biosphere absorbs approximately a quarter of anthropogenic carbon dioxide (CO₂) emissions, thereby acting as a natural buffer against rising atmospheric CO₂ levels and the resulting changes in climate (IPCC 2013). This net sink of CO₂ can vary considerably from year to year, however, from over double the long term global average to becoming a net source of CO₂ to the atmosphere (Le Quéré *et al* 2016). Understanding the contemporary interannual variability (IAV) in the land sink is a crucial step toward

better predicting the future buffering capabilities of the terrestrial biosphere and the subsequent fate of the climate system. The uncertainty in estimates of the future land sink by state-of-the-science models remains too large to discern whether, at a global scale, lands will be a net source or sink of CO₂ in the future (Friedlingstein *et al* 2006, 2014). The uncertainty in carbon flux dynamics at finer regional-to-continental scales has been even harder to address (Schimel 2007). Understanding regional-to-continental scale carbon cycle-climate responses is arguably even more critical as they offer relevant information for land management

and climate-change mitigation decisions (Michalak *et al* 2011) and are key for improving the representation of climate controls in carbon cycle model development (Schimel 2007).

North America plays an integral role in the global carbon cycle, representing a quarter of the global land sink (Le Quéré *et al* 2016). North America spans primarily boreal and temperate zones and consists of a variety of biomes, including evergreen needle-leaf forests, deciduous broadleaf forests, mixed forests, grasslands, croplands, and shrublands. At the plot level ($\sim 1 \text{ km}^2$), flux tower studies have indicated that air temperature, precipitation, solar radiation, and disturbance (Baldocchi 2008, Baldocchi *et al* 2017) all play major roles in controlling North American NEE IAV. Site-level findings for North America indicate that the dominant drivers of NEE IAV vary by biome type (Baldocchi *et al* 2017) and can be rather complex (Desai *et al* 2010) as they are not easily correlated with annual climate anomalies but rather seasonal climate anomalies (Fu *et al* 2017b) or transient favorable climate conditions (Zscheischler *et al* 2016). At the continental scale, studies have estimated the total carbon budget and IAV of North American NEE (Hayes *et al* 2012, King *et al* 2015) using TBMs and inverse models, yet they have not examined sub-continental or regional (down to $\sim 100 \text{ km}^2$) NEE IAV nor have they explored regional attribution and drivers of NEE IAV. While TBMs can provide estimates of carbon fluxes at regional scales and have been the primary tool for exploring regional carbon flux IAV dynamics (Ahlström *et al* 2015, Jung *et al* 2017), TBMs have been shown to perform poorly in terms of predicting IAV at the plot level $\sim 1 \text{ km}^2$ (Keenan *et al* 2012, Raczka *et al* 2013). Even at larger scales, the use of TBMs to examine IAV could be problematic as a given TBM may be simulating historical IAV accurately for the ‘wrong reasons,’ i.e. with differing responses to environmental conditions (Fang *et al* 2017, Huntzinger *et al* 2017). Hence, a need exists to explore North American NEE IAV at the intermediate or regional scale with a suitable large scale observational constraint.

One reason for the gap in understanding IAV at intermediate scales is the difficulty in estimating carbon fluxes at these scales. This gap in understanding is not specific to North America, but rather emblematic of regional scale IAV, which is generally poorly understood (Niu *et al* 2017). Analyzing multiple flux towers within a given biome has emerged as a key tool for providing information on carbon flux dynamics representative of a specific biome or ecosystem (e.g. Baldocchi *et al* 2017). However, due to the limited footprint ($\sim 1 \text{ km}^2$) of individual flux towers, interpolation and extrapolation is needed to examine the integrated carbon flux response of a region or biome, which can pose its own set of challenges (e.g. Hoffman *et al* 2013, Kumar *et al* 2016). TBMs can provide estimates of carbon fluxes at intermediate scales, although these estimates are hard to validate due to the lack of an

observational constraint at compatible scales. Regional inverse models leverage atmospheric CO_2 observations and an atmospheric transport model to investigate surface fluxes at regional scales. Atmospheric data have been used to infer regional carbon fluxes through inverse modeling for a variety of studies (e.g. Gourdji *et al* 2012, Lauvaux *et al* 2012, Miller *et al* 2013, Schuh *et al* 2013, Alden *et al* 2016), yet these studies have typically focused on just one or two years. This limitation is primarily related to the relatively recent development of more dense atmospheric observation networks, which previously were only supported via short-term measurement campaigns (e.g. Miles *et al* 2013). In North America, the number of continuous in-situ CO_2 measurement sites has expanded from nine sites in 2004 to ~ 35 by 2007 (Shiga *et al* 2013, ObsPack 2016). Thus, the dense multi-year atmospheric CO_2 monitoring network across North America offers an observational constraint that enables the investigation of regional carbon flux IAV.

The main aim of this study is to explore the regional attribution and drivers of IAV in the annual North American carbon sink from a top-down atmospheric-data perspective. We estimate North American CO_2 NEE for the period 2007–2012 using a network of atmospheric CO_2 observations and a geostatistical inversion, quantify NEE IAV at the continental and biome scales, and identify the biome-level contributions to NEE IAV. We compare results from the atmospheric inversion to estimates from an ensemble of TBMs to explore and highlight any difference between these two approaches. Finally, we investigate possible reasons for the large spread in TBM based IAV contributions.

Methods and data

To analyze flux estimates at the regional-scale, we implement an atmospheric inverse approach specifically designed to account for the challenges of a regional analysis. Peylin *et al* (2013) list several recommendations for exploring regional carbon flux dynamics. We address three pertinent topics here: (1) the network of observations must be sufficiently dense and constant, (2) fluxes must be estimated at relatively high resolution, and (3) a realistic awareness of the impact of prior fluxes must be taken into account. The set-up of the regional inversion utilized in this study addresses each of these goals.

Six years (2007–2012) of continuous atmospheric CO_2 concentration observations are used from a network of towers across North America. CO_2 concentrations are averaged over a three hour interval centered on 3 pm and filtered in the same manner as Gourdji *et al* (2012) and Fang and Michalak (2015) to account for various data anomalies (e.g. outliers, transport model issues, ± 30 ppm spikes from the background). CO_2 concentration data are obtained from the ObsPack GLOBALVIEWplus v2.1 product (Masarie *et al* 2014, ObsPack 2016) with the addition of the site at Har-

vard Forest, Massachusetts (HFM) (Urbanski *et al* 2007) and several sites that were part of the Mid-Continent Intensive project (Miles *et al* 2012, 2013) located in Austin Cary Memorial Forest, Gainesville, Florida (AAC); Chestnut Ridge, Tennessee (ACR); Canaan Valley, West Virginia (ACV); Mead, Nebraska (AME); Missouri Ozark, Missouri (AOZ) (Stephens *et al* 2011); Centerville, Iowa (RCE); Galesville, Wisconsin (RGV); Kewanee, Illinois (RKW); Mead, Nebraska (RMM); Round Lake, Minnesota (RRL) (Richardson *et al* 2012); and Rosemount, Minnesota (KCMP) (Griffis *et al* 2008). Over the six years, 21 sites (~60% of the data) have a 6 year record, seven sites (~15% of the data) have a 5 year record, four sites (~9% of the data) have a 4 year record, nine sites (~10% of the data) have a 3 year record, and 14 sites (~6% of the data) have a 1 or 2 year record (for additional site information see table S1 available at stacks.iop.org/ERL/13/084015/mmedia). While the network has fluctuated over time, a majority of the sites and ~75% of the data (Andrews *et al* 2014, ObsPack 2016) span at least 5 years. Additionally, the integrated sensitivity or footprint of the network covers a relatively consistent area from year to year (figure S1) and sensitivity tests (supplementary materials) showed results were not impacted by the network composition.

We use the Stochastic Time Inverted Lagrangian Transport model (STILT) (Lin *et al* 2003) driven by winds from the Weather Research and Forecasting model (WRF) (Skamarock and Klemp 2008, Nehr Korn *et al* 2010) using an inner 10 km grid over the continental US (~25°–55°N; 135°–65°W) and an outer 30 km grid surrounding the continent (~10°–80°N; 170°–50°W) to derive the footprint or sensitivity [$\text{ppm}/(\mu\text{mol m}^{-2} \text{s}^{-1})$] of each observation to upwind surfaces fluxes at a spatial resolution of $1^\circ \times 1^\circ$ and a 3 hourly temporal resolution. These footprints are derived from a footprint library available as a part of the NOAA CarbonTracker Lagrange regional inversion framework (www.esrl.noaa.gov/gmd/ccgg/carbontracker-lagrange/).

NEE fluxes are estimated at a relatively high spatial and temporal resolution ($1^\circ \times 1^\circ$ in space, 3 hourly in time) for each individual year using the geostatistical inverse modeling (GIM) formulation (Michalak *et al* 2004, Gourdji *et al* 2012) and the WRF-STILT transport model. GIM incorporates covariates that are selected based on their skill in explaining the atmospheric data (Gourdji *et al* 2008, 2012, Fang and Michalak 2015), eliminating the need for a traditional prior flux estimate based on a TBM. The selection of covariates is informed by a statistical model selection framework (e.g. Gourdji *et al* 2012, Shiga *et al* 2014, Fang and Michalak 2015) which has been adapted to derive a consistent multi-year set of variables, namely solar-induced fluorescence (SIF) (Joiner *et al* 2013), specific humidity, and precipitation (Mesinger *et al* 2006) (for more details for the specific inversion set-up see Shiga *et al* 2018 and the supplementary materials). The GIM approach thus removes the dependence of the prior

term on any given TBM and, when combined with the dense atmospheric network over North America and high resolution inverse framework, provides a unique platform for investigating continental-scale IAV.

Carbon flux output from ten TBMs participating in the Multi-scale Terrestrial Model Intercomparison Project (MsTMIP) (Huntzinger *et al* 2013) are used to compare with the inverse estimates of NEE. MsTMIP uses a consistent set of environmental drivers (Wei *et al* 2014a, 2014b) for all models as well as a uniform protocol and experimental design so as to focus on structural differences between models. The ten models with output scaled to the monthly temporal and $1^\circ \times 1^\circ$ spatial scale used here mirror those used by Fang *et al* (2017) and Zscheischler *et al* (2014), and include Biome-BGC (Thornton *et al* 2002), CLM4 (Mao *et al* 2012, Oleson *et al* 2010), CLM4VIC (Li *et al* 2011), DLEM (Tian *et al* 2011, 2012), GTEC (King *et al* 1997, Ricciuto *et al* 2011), ISAM (Jain *et al* 1996, Barman *et al* 2014), LPJ-wsl (Sitch *et al* 2003), ORCHIDEE-LSCE (Krinner *et al* 2005), VEGAS (Zeng *et al* 2005), and VISIT (Ito 2010).

The analysis uses the contribution framework developed by Ahlström *et al* (2015) to explore the portion of North American IAV attributable to a specific region.

$$c_j = \frac{\sum_t \frac{f_{ij}|F_t|}{F_t}}{\sum_t |F_t|} \quad (1)$$

where f_{ij} represents the flux anomaly in region j and year t , and F_t is the North American continental-scale flux anomaly for year t . This formulation weighs a given region's flux anomaly by the similarity to the large-scale North American flux anomaly, thus defining the contribution, c_j , of a given region j to North American IAV. This framing enables the identification and comparison of the relative importance of a region in driving continental-scale North American IAV.

We further calculate the biome-level response or sensitivity of a given flux component annual anomalies to seasonal temperature, precipitation, or radiation anomalies. This is done by first calculating the seasonal anomalies at each $1^\circ \times 1^\circ$ grid cell for each driver variable (e.g. temperature, precipitation) as well as the annual flux anomaly. Next, for each biome (defined using a modified IGBP landcover classification map from Frankenberg *et al* (2011), figure 2(b)), the slope of the linear regression line between the grid cell flux anomalies and the corresponding grid cell anomalies for the given environmental variable is used to quantify the sensitivity. The temperature and precipitation data used here are the same CRU-NCEP data used to drive the MsTMIP simulations covering 1981–2010 (Wei *et al* 2014a, 2014b) extended to 2012 (https://vesg.ipsl.upmc.fr/thredds/catalog/work/p529viov/cruncep/V8_1901_2016/catalog.html) (Le Quéré *et al* 2016), thus seasonal anomalies are defined as deviations from the long-term seasonal means.

Results and discussion

We estimate North American NEE IAV, defined here as the standard deviation of annual net flux estimates (figure 1), to be 0.35 PgC yr^{-1} , which is consistent with the range of previous inverse estimates of North American NEE IAV, $0.36 \pm 0.13 \text{ PgC yr}^{-1}$ (King *et al* 2015). The North American region used here encompasses the five biomes shown in figure 2(b) (see table S2 for IAV estimates for the combined Boreal and Temperate North America TransCom3 regions used by King *et al* (2015)). The continental level IAV found here is comparable in magnitude to the total annual North American net carbon sink for 1990–2009, $-0.47 \pm 0.28 \text{ PgC yr}^{-1}$ (King *et al* 2015), where here and throughout the paper a negative flux represents a net uptake of carbon. Additionally, the average IAV from the 10 MsTMIP TBMs at the continental scale $\sim 0.20 \text{ PgC yr}^{-1}$ (table S2) is approximately 60% of the IAV estimated here using an atmospheric constraint, which is also consistent with King *et al* (2015) who found that TBMs exhibited less IAV than atmospheric observation-based estimates.

The biome-level estimates of IAV derived from atmospheric observations are 1.6–4.4 times larger than the average of TBM-based estimates (figure 1, table S2). Previous studies have suggested that TBMs underestimate IAV at the site level (Keenan *et al* 2012, Raczka *et al* 2013) and at the continental level (King *et al* 2015) due to missing or poorly represented processes in TBMs. Here we show that, at the biome level, TBMs on average underestimate IAV in Deciduous broadleaf & mixed forests and Shrublands, by factors of 3.1 and 4.4, respectively. In these two biomes, the largest IAV predicted by a TBM is less than 60% of the corresponding atmospheric observation-based estimate of IAV.

We identify Deciduous broadleaf & mixed forests as the largest overall contributors ($\sim 40\%$) to North American NEE IAV (figure 2), the largest contributor per unit area, and the biome with the largest NEE IAV magnitude. This is in contrast to the global scale, where Ahlström *et al* (2015) found that semi-arid ecosystems are the dominant contributor to IAV (39%), according to an ensemble of TBM simulations from the TRENDY model intercomparison project (Sitch *et al* 2015). Similarly, for the northern hemisphere, Fu *et al* (2017a) found semi-arid ecosystems (39%) and Grasslands and Croplands (39%) to be the dominant contributors to IAV, based on the Monitoring Atmospheric Composition and Climate (MACC-II) inversion system (www.ecmwf.int/en/research/projects/macc-ii). While Deciduous broadleaf forests have been identified at the site level as an ecosystem with relatively large IAV when compared to other North American biomes (Yuan *et al* 2009, Baldocchi *et al* 2017), our results demonstrate that at the North American continental scale these ecosystems are dominating IAV. Addi-

tionally, we find that TBMs appear to consistently underestimate the contribution of IAV from Deciduous broadleaf & mixed forests, which may be linked to the documented underestimation of IAV across forested sites by TBMs (Keenan *et al* 2012, Raczka *et al* 2013).

The Shrublands biome, while having the second largest overall IAV magnitude (Table S2) shows the lowest relative contribution to North American IAV (figure 2). This is due to the metric defined by Ahlström *et al* (2015), equation (1), which quantifies the contribution based both on the magnitude of and the ‘synchronicity’ between regional anomalies and the ‘global’ anomaly (in this case continental anomaly). Put another way, although Shrublands exhibit high IAV, there is a difference in phasing between Shrublands and the rest of continental North American IAV. Likely Shrublands, which represent 60% of the North American semi-arid ecosystems by area, are more responsive to global drivers of semi-arid ecosystems (e.g. drought (Huang *et al* 2016)) rather than drivers of the forested biomes that make up a large portion of continental North America. Therefore, these findings may indeed be consistent with previous findings recognizing the role of semi-arid regions on global IAV (Poulter *et al* 2014, Ahlström *et al* 2015). Interestingly, the MsTMIP TBMs also show a low contribution of the Shrublands biome to North American IAV, however the low IAV contribution in TBMs is largely due to a smaller magnitude of Shrublands IAV, rather than the phasing difference.

We find the spread across IAV contributions from the various TBMs in the MsTMIP ensemble to be quite large (figure 2). Consequently, no dominant biome can be clearly identified for the MsTMIP TBMs. The large spread in biome-level IAV contributions in TBMs can in part be linked to an apparent trade-off between forested (Needleleaf and Deciduous broadleaf & mixed forests) vs. non-forested (Grasslands and Shrublands) biomes (figure 3). For the following analysis, we group the biomes into these two broader categories. This is done based on the notion that the response of TBMs to the climatic controls related to drought stress (e.g. temperature, water availability) in these two broad categories (e.g. Li *et al* 2017) may be linked to IAV dynamics. Drought plays a key role in the IAV of Shrublands and Grasslands (i.e. semi-arid ecosystems) (Poulter *et al* 2014, Huang *et al* 2016, Ma *et al* 2016) as well as temperate and boreal ecosystems (Wilson and Baldocchi 2001, Ciais *et al* 2005, Kljun *et al* 2007). We exclude Croplands in the subsequent analysis because Croplands are highly-managed and these management practices are likely not represented in TBMs (Lokupitiya *et al* 2016).

TBM responses to anomalies in summertime temperature and precipitation help to explain the IAV trade-off between forested and non-forested regions

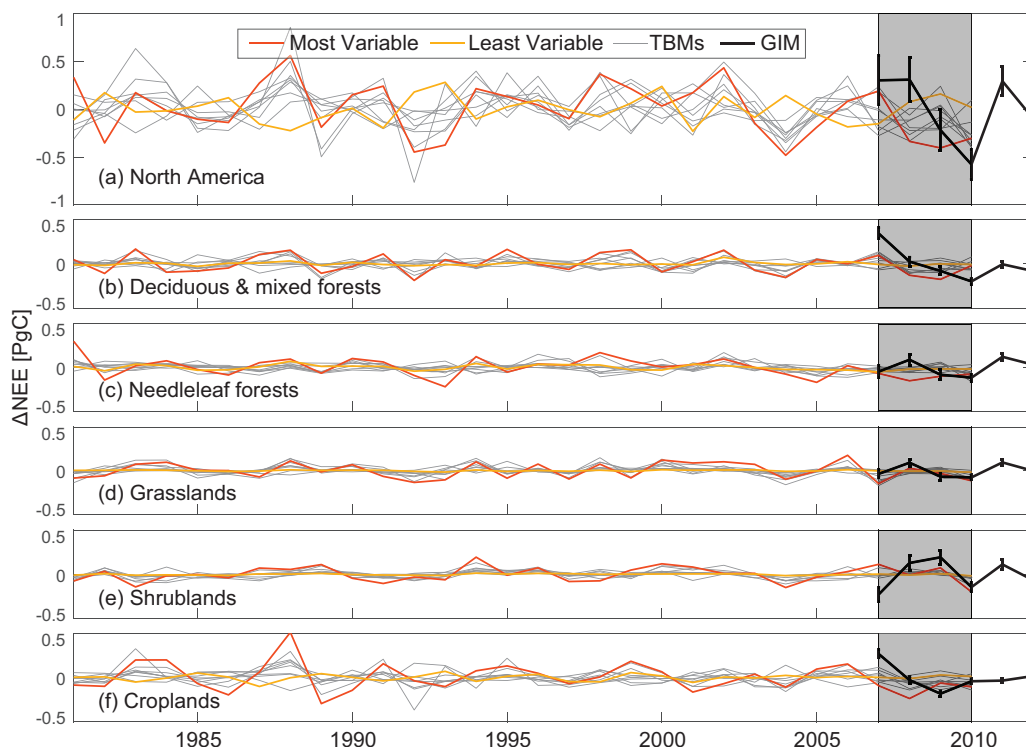


Figure 1. Atmospheric observation-constrained (GIM—black line) North American NEE IAV is found to be larger than that from a suite of ten TBMs (grey lines). The most and least variable TBM for each region are shown in red and yellow, with biome definitions shown in figure 2(b). The shaded area shows the overlap period between inverse and TBM estimates. The North American domain here represents the area encompassing the five biomes listed here and shown in figure 2(b).

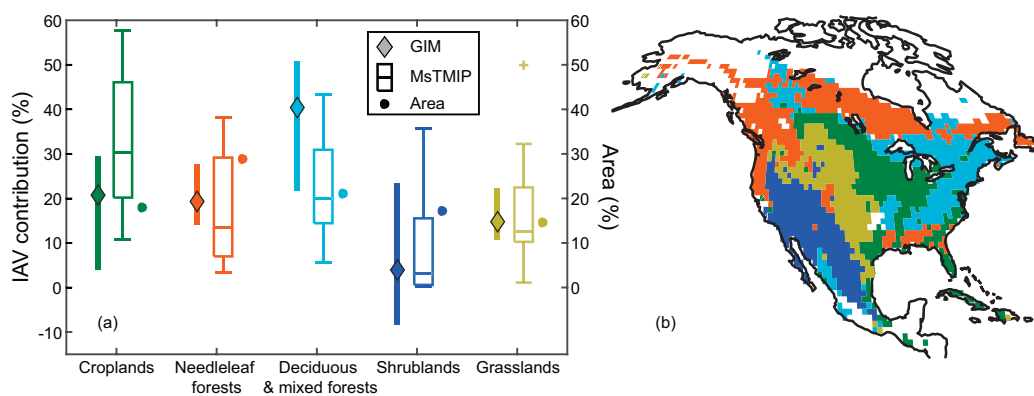


Figure 2. Deciduous & mixed forests are the dominant contributor to North American NEE IAV based on atmospheric observations (diamonds), both in terms of the percent contribution (40%) and relative to the biome's area (circles). TBMs (box-plots) show croplands (30%) as the largest contributor, although the spread among TBMs is too large to identify a dominant biome. For TBMs, boxes show interquartile range and median of the ten TBMs, whiskers represent TBMs within 1.5 times the interquartile range of either box edge, and plus signs represent outliers. For the atmospheric inversion results, the diamond represents the contribution estimate over the full time domain while the solid bar represents the range based on leave-one-year-out bootstrap estimates. The corresponding biome map is shown in panel (b).

(figure 3) (similar responses observed for radiation, figure S2 and S3). TBMs with stronger NEE sensitivities to temperature and precipitation in forested biomes (relative to their sensitivities in non-forested biomes) predict that forested regions dominate North American NEE IAV, while TBMs with stronger sensitivities in non-forested biomes have higher NEE IAV contributions from non-forested biomes (figure 3). This result shows that, for some TBMs, there are clear differ-

ences between how forested and non-forested biomes respond to environmental driver anomalies (figure 4), but that there is little agreement about which regions are more or less sensitive to temperature and precipitation anomalies. Hence, the environmental driver sensitivity differences appear to impact the biome-level attribution of NEE IAV in a given TBM, implying a potential indirect tuning effect where a TBM either has a strong NEE sensitivity in forested biomes or a strong NEE

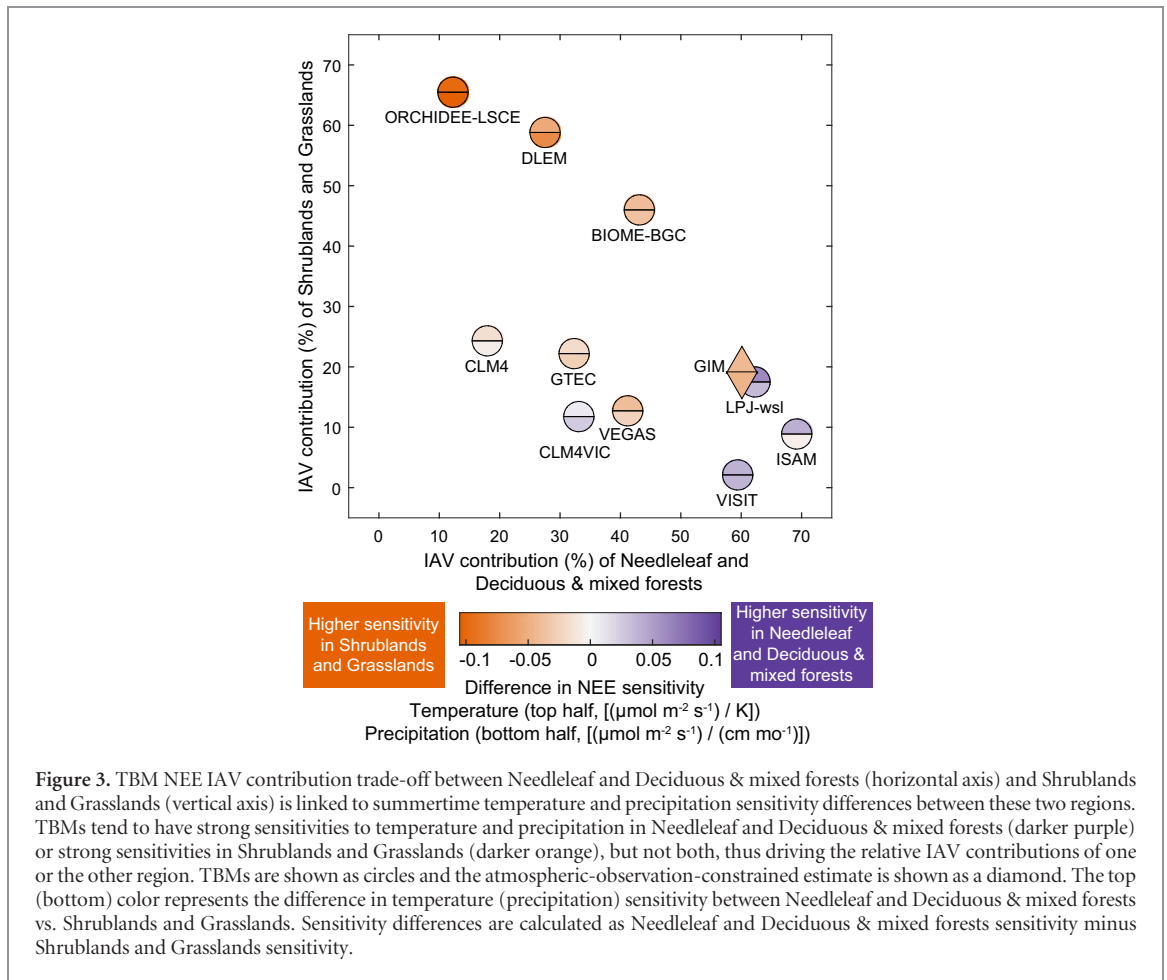


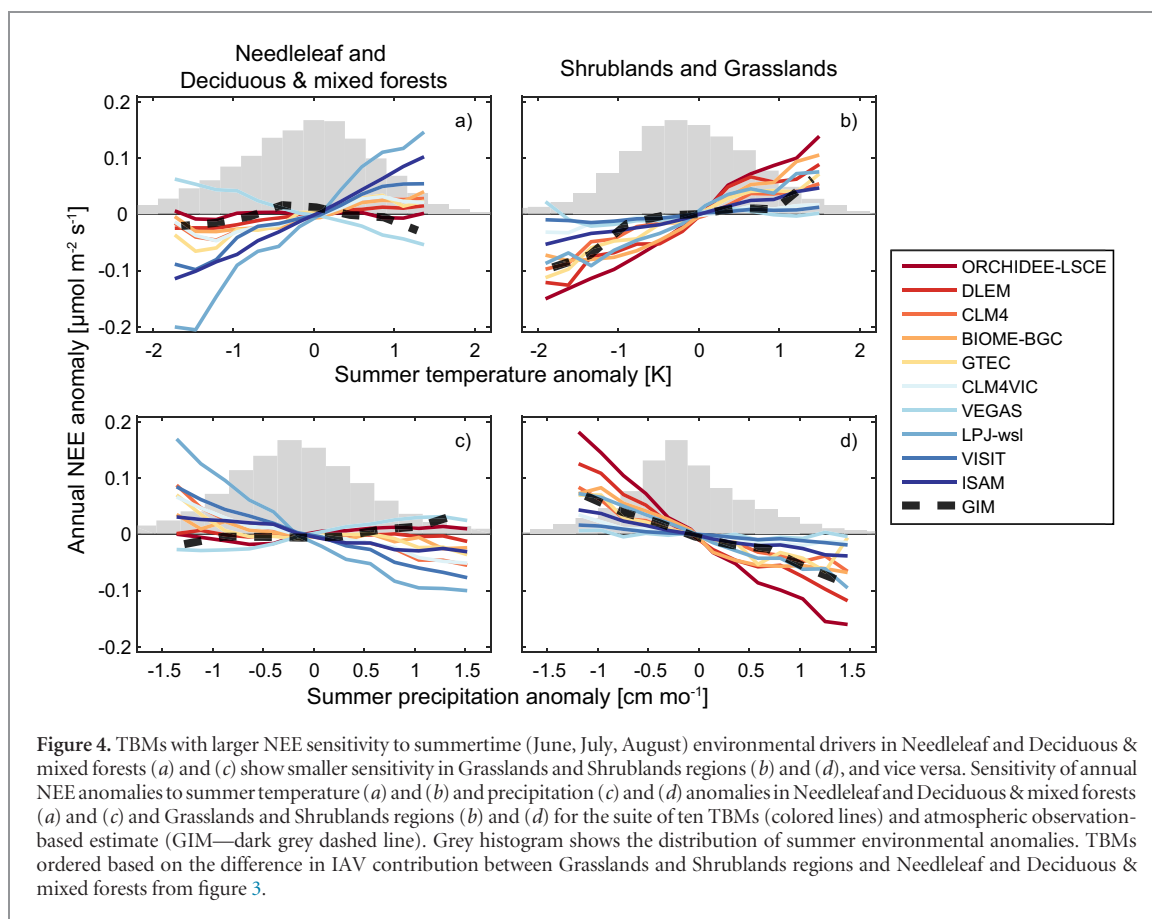
Figure 3. TBM NEE IAV contribution trade-off between Needleleaf and Deciduous & mixed forests (horizontal axis) and Shrublands and Grasslands (vertical axis) is linked to summertime temperature and precipitation and precipitation sensitivity differences between these two regions. TBMs tend to have strong sensitivities to temperature and precipitation in Needleleaf and Deciduous & mixed forests (darker purple) or strong sensitivities in Shrublands and Grasslands (darker orange), but not both, thus driving the relative IAV contributions of one or the other region. TBMs are shown as circles and the atmospheric-observation-constrained estimate is shown as a diamond. The top (bottom) color represents the difference in temperature (precipitation) sensitivity between Needleleaf and Deciduous & mixed forests vs. Shrublands and Grasslands. Sensitivity differences are calculated as Needleleaf and Deciduous & mixed forests sensitivity minus Shrublands and Grasslands sensitivity.

sensitivity in non-forested biomes but not both. Indirect tuning effects have been observed previously at the global scale, for example in TBMs' climate vs. CO₂ sensitivity (Huntzinger *et al* 2017), but are seen here at the biome level.

The atmospheric observation-based results show a large portion of IAV in forested biomes (figure 3, diamond position) but a stronger relative sensitivity of NEE to summer temperature and precipitation anomalies in Shrublands and Grasslands (as compared to Needleleaf and Deciduous broadleaf & mixed forests) (figure 3, diamond color). The sign of the relationship between NEE anomalies and environmental driver anomalies in Shrublands and Grasslands (figures 4(b) and (d)) for TBMs and atmospheric observation-based estimates aligns with site-level findings, which show positive precipitation anomalies lead to more carbon uptake while positive temperature anomalies lead to less carbon uptake (e.g. Scott *et al* 2015, Baldocchi *et al* 2017, Fu *et al* 2017b). The low sensitivity of atmospheric observation-based NEE estimates in Needleleaf and Deciduous broadleaf & mixed forests to summertime temperature (figure 4(a), dark grey dashed line) and the small positive sensitivity to precipitation anomalies (figure 4(c), dark grey dashed line) also aligns with site level findings (e.g. Fu *et al* 2017b) showing a smaller and opposite relationship between summertime precipitation and NEE, compared to non-forested

sites, and an overall weaker relationship to summertime environmental conditions. This result also reinforces the notion that the relationship between summertime environmental drivers and NEE anomalies in forested ecosystems is not as clear as those in grassland or shrubland ecosystems (Zscheischler *et al* 2016, Fu *et al* 2017b, Baldocchi *et al* 2017). While atmospheric-observation based NEE sensitivities seem to fall in the middle of the range of TBM sensitivities in grassland and shrubland ecosystems (figures 4(b) and (d)), for forested ecosystems the atmospheric-observation based sensitivities of NEE anomalies appear to be a lower end-member relative to most of the TBMs (figures 4(a) and (c)). One explanation for this is that TBMs may be overly sensitive to summertime environmental driver anomalies in forests. Annual NEE anomalies in forested ecosystems are often more complex than a simple relationship with growing season environmental conditions and can involve a variety of multifaceted responses (e.g. counteracting seasonal anomalies (e.g. Wolf *et al* 2016), accumulation of favorable conditions (e.g. Zscheischler *et al* 2016), lagged drought effects (e.g. Anderegg *et al* 2015), growing season length, disturbance, soil conditions (e.g. (Baldocchi *et al* 2017)).

As NEE is ultimately the result of two opposing processes, gross primary production (GPP) and ecosystem respiration (RE), we further probed the TBMs to investigate which component drives the trade-off in



relative IAV contributions between the forested and non-forested regions. The correspondence of GPP sensitivity differences with regional NEE IAV contribution differences (figures S3(d)–(f)) is in contrast to the lack of a clear relationship in the corresponding RE sensitivity difference (figure S3(g)–(i)). Thus, we conclude that the regional IAV trade-off is primarily explained by GPP, rather than RE sensitivity differences. This may be somewhat expected as summertime NEE dynamics in the biomes examined are largely driven by GPP, however it suggests that at the component level TBM formulation/parameterization appears to be linked to regional IAV dynamics.

Conclusions

Overall, this work explores North American NEE IAV dynamics at scales that bridge the gap between the site-level and global-level using a dense network of atmospheric CO₂ measurements, which provides a top-down regionally sensitive observational constraint. These findings address one of the fundamental questions regarding the terrestrial carbon cycle, namely quantifying the variability of carbon fluxes from year to year. The regional atmospheric observation-constrained estimates show that North America has larger variability in NEE than TBMs predict, at both the biome and continental level. We also identify Decidu-

ous broadleaf & mixed forests as the main sources of North American NEE IAV, which differs from the main global and northern hemisphere drivers. These findings underscore the importance of North American extratropical forests in regulating continental carbon flux variability, and stress the critical need to improve our understanding of the processes driving regional NEE IAV.

Across North America, we find that current state-of-the-art TBMs disagree about the main regions responsible for NEE IAV, as well as about the NEE, GPP, and RE responses to climate drivers. In TBMs, a trade-off between whether forested or non-forested regions dominate continental IAV is found to be linked to a given TBM's sensitivity to environmental drivers. TBMs with a stronger sensitivity of NEE to environmental drivers in forested (relative to non-forested) regions have a larger contribution of NEE IAV from forested regions and vice versa. The regional differences in NEE responses to environmental drivers in TBMs has important implications for future predictions of the regional and biome-level behavior of the terrestrial biosphere as temperature and precipitation regimes shift and as extreme events become more likely (Seneviratne *et al* 2012, Reichstein *et al* 2013). The ensemble of TBMs examined here, for example, would likely yield divergent predictions about the fate of the carbon sink in forested vs. non-forested regions of North America

under changing temperature and precipitation conditions. Hence, more research is needed to understand and observationally constrain the carbon cycle response to climatic conditions at the regional scale.

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ORCID iDs

Yoichi P Shiga  <https://orcid.org/0000-0001-8569-6841>

Anna M. Michalak  <https://orcid.org/0000-0002-6152-7979>

Yuanyuan Fang  <https://orcid.org/0000-0001-7067-7103>

Kevin Schaefer  <https://orcid.org/0000-0002-5444-9917>

Arlyn Andrews  <https://orcid.org/0000-0002-8552-3999>

Deborah Huntzinger  <https://orcid.org/0000-0003-2998-099X>

Christopher Schwalm  <https://orcid.org/0000-0002-5035-5681>

Yaxing Wei  <https://orcid.org/0000-0001-6924-0078>

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