

Outsized contribution of the semi-arid ecosystems to interannual variability in North American ecosystems

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Key Points:

- GPP and NEE IAV in western North America is characterized by amplification in spring-summer, with enhance uptake in cooler-wetter conditions.
- GPP and NEE IAV in eastern North America is characterized by compensating anomalies between spring and summer, reducing annual net anomalies.
- Observation-based NEE and GPP IAV give greater sensitivity to temperature and moisture anomalies than MsTMIP mean in western North America.

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23 **Abstract**

24 Across North America, interannual variability (IAV) in gross primary production
 25 (GPP) and net ecosystem exchange (NEE), and their relationship with environmental
 26 drivers, are poorly understood. Here, we examine IAV in GPP and NEE and their re-
 27 lationship to environmental drivers using two state-of-the-science flux products: NEE
 28 constrained by surface and space-based atmospheric CO₂ measurements over 2010–2015
 29 and satellite up-scaled GPP from FluxSat over 2001–2017. We show that the arid west-
 30 ern half of North America provides a larger contribution to IAV in GPP (104% of east)
 31 and NEE (127% of east) than the eastern half, in spite of smaller magnitude of annual
 32 mean GPP and NEE. This occurs because anomalies in western North America are tem-
 33 porally coherent across the growing season leading to an amplification of GPP and NEE.
 34 In contrast, IAV in GPP and NEE over eastern North America are dominated by sea-
 35 sonal compensation effects, associated with opposite responses to temperature anom-
 36 alies in spring and summer. Terrestrial biosphere models in the MsTMIP ensemble par-
 37 tially capture these differences between eastern and western North America, but gen-
 38 erally underestimate the sensitivity of flux anomalies in western North America to vari-
 39 ations in soil temperature and moisture by 0–31%. This suggests that ecosystems in west-
 40 ern North America may be more sensitive to warming and increasing aridity than mod-
 41 els predict, and that reductions in growing season productivity and carbon sequestra-
 42 tion under climate change may be larger than predicted by models.

43 **1 Introduction**

44 Interannual variations (IAV) in carbon fluxes between terrestrial ecosystems and
 45 the atmosphere drive variations in the growth rate of atmospheric CO₂. Understanding
 46 the drivers of IAV in the carbon cycle is critical for understanding the response of ecosys-
 47 tems to climate change (Cox et al., 2013; Baldocchi et al., 2016; Niu et al., 2017). In this
 48 study, we examine the drivers of IAV in gross primary production (GPP) and net ecosys-
 49 tem exchange (NEE) over subtropical and temperate North America. In particular, we
 50 contrast IAV in the semi-arid western regions of North America with the wetter east-
 51 ern areas of North America.

52 Semi-arid ecosystems are moisture limited ecosystems, and cover large portions of
 53 western North America. Globally, semi-arid ecosystems have been shown to play an out-
 54 sized role in interannual variability (IAV) of the atmospheric CO₂ growth rate (Poulter
 55 et al., 2014; Ahlström et al., 2015; Huang et al., 2016; Z. Fu et al., 2017), relative to what
 56 would be expected given their productivity. The reason that these ecosystem experience
 57 such large IAV in CO₂ net uptake is thought to be linked to moisture availability (Huang
 58 et al., 2016). In these ecosystems, negative GPP anomalies are driven by warm-dry con-
 59 ditions and positive GPP anomalies are driven by cool-wet conditions (Ahlström et al.,
 60 2015). In turn, NEE anomalies in these ecosystems are strongly associated with varia-
 61 tions in GPP (Ahlström et al., 2015). Still, the relative impact of these ecosystems on
 62 North American carbon fluxes is not well characterized.

63 Eastern North America is generally wetter than the west and is dominated by for-
 64 est and cropland ecosystems. IAV in these ecosystems has been shown to have season-
 65 ally compensating effects, defined as temporally anti-correlated anomalies during a grow-
 66 ing season. For example, a number of studies have found that enhanced GPP early in
 67 the growing season is associated with reduced GPP later in the growing season over mid-
 68 latitude cropland and forest ecosystems (Buermann et al., 2013; Wolf et al., 2016; Buer-
 69 mann et al., 2018). There are several possible mechanisms for explaining seasonal com-
 70 pensation effects. Enhanced spring GPP is associated with warmer spring temperatures
 71 (Angert et al., 2005; Wolf et al., 2016). Warmer temperatures early in the growing sea-
 72 son result in increased evapotranspiration leading to reduced soil moisture later in the
 73 growing season, which adversely impacts productivity (Parida & Buermann, 2014; Wolf

et al., 2016). Direct phenological mechanisms may also contribute to seasonal compensation effects, as the timing of spring budburst and autumn senescence has been found to be correlated on the scale of individual organisms and the landscape (Y. S. Fu et al., 2014; Keenan & Richardson, 2015). The impact of seasonal compensation effects on annual GPP anomalies has been studied across northern forests and croplands using up-scaled FLUXNET GPP (Buermann et al., 2013), NDVI (Buermann et al., 2018) and solar-induced fluorescence (SIF), while seasonal compensation in NEE has been examined for the 2012 North America drought (Wolf et al., 2016; J. Liu et al., 2018). However, the implications of seasonal compensation effects on variability in the carbon balance across multiple years over North America have not yet been examined.

In this study, we take advantage of two newly developed GPP and NEE products to examine IAV over North America. NEE fluxes are obtained from the inversion analyses of Byrne, Liu, et al. (2019). They estimated 14-day NEE globally over 2010–2015 in a flux inversion assimilating both surface-based and space-based CO₂ measurements. This combination of surface- and space-based measurements provides unprecedented observational coverage for a multi-year flux inversion and is expected to mitigate artifacts in the NEE fluxes that are introduced due to uneven observational coverage (J. Liu et al., 2014; Byrne et al., 2017). Using these NEE estimates in combination with 17 years (2001–2017) of satellite-based GPP calibrated on eddy covariance sites from FluxSat (Joiner et al., 2018), we examine the importance of seasonal compensation effects in GPP and NEE across North America. First, we examine the extent to which seasonal compensation effects impact growing season GPP and NEE anomalies across North America, and their dependence on temperature and moisture anomalies. Then, we examine the relative contribution of eastern and western North America to the mean seasonal cycle and IAV, and compare our data-driven estimates to modelled fluxes from the Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP).

2 Data

2.1 Carbon data

We employ two state-of-the-science observationally-constrained GPP and NEE products for examining IAV. The FluxSat GPP product (Sec. 2.1.1) (Joiner et al., 2018) is based on an up-scaling of global eddy covariance flux measurements, and has been found to produce more realistic IAV in GPP when compared to FLUXNET sites relative to other up-scaled GPP products (Joiner et al., 2018). The flux inversion NEE product used here (Sec. 2.1.2) is unique in that it assimilates both surface- and space-based CO₂ measurements, providing increased observational constraints relative to other NEE flux inversion products. Atmospheric CO₂ fields simulated using this product have also been extensively evaluated against aircraft-based CO₂ measurements in the northern extratropics (Byrne, Liu, et al., 2019). In addition, we compare these observationally-constrained flux estimates to terrestrial biosphere model (TBM) estimates from the MsTMIP ensemble (Sec. 2.1.3).

2.1.1 FluxSat GPP

FluxSat version 1 (Joiner et al., 2018) estimates GPP based primarily on Nadir BRDF-Adjusted Reflectances (NBAR) from the MODerate-resolution Imaging Spectroradiometer (MODIS) MYD43D product (Schaaf et al., 2002) that uses data from MODIS instruments on National Aeronautics and Space Administration (NASA) Aqua and Terra satellites. The GPP estimates are calibrated with the FLUXNET 2015 GPP derived from eddy covariance flux measurements at Tier 1 sites (Baldocchi et al., 2001). As such, FluxSat can be considered as a global upscaling of the FLUXNET 2015 GPP data. The data set also employs SIF from the Global Ozone Monitoring Experiment 2 (GOME-2) on the EUMETSAT MetOp-A satellite to identify regions of high productivity crops. FluxSat

124 was evaluated by comparison with independent flux measurements (i.e., not used in the
 125 training) and compared very well both in terms of IAV and site-to-site variability. Monthly
 126 mean FluxSat GPP data on a $0.5^\circ \times 0.5^\circ$ spatial grid were downloaded from
 127 https://avdc.gsfc.nasa.gov/pub/tmp/FluxSat_GPP and regridded to a $4^\circ \times 5^\circ$ spatial
 128 grid to for this analysis.

129 **2.1.2 Flux inversion NEE**

130 NEE fluxes are produced from a flux inversion analyses spanning 2010–2015. The
 131 flux inversions assimilate CO_2 measurements from the Greenhouse Gases Observing Satel-
 132 lite (GOSAT), Total Carbon Column Observing Network (TCCON), and the surface in situ
 133 and flask measurements network concurrently. Four dimensional variational (4-DVar)
 134 assimilation was implemented to estimate 14-day scaling factors for prior NEE and ocean
 135 fluxes at $4^\circ \times 5^\circ$ spatial resolution using the Greenhouse gas framework - Flux model (GHGF-
 136 Flux). The optimized fluxes are taken to be the average of three flux inversions that em-
 137 ploy different prior NEE fluxes and errors. NEE fluxes are aggregated to monthly mean
 138 values for this analysis. A detailed description of the experimental set up and evalua-
 139 tion of the fluxes can be found in Byrne, Liu, et al. (2019).

140 **2.1.3 MsTMIP models**

141 MsTMIP is a model inter-comparison experiment conducted by the North Amer-
 142 ican Carbon Program (Huntzinger et al., 2013; Wei et al., 2014). The project is designed
 143 to provide a consistent and unified modeling framework in order to isolate, interpret, and
 144 address differences in process parameterizations among TBMs. In this analysis, we ex-
 145 amine the modelled NEE (defined here as MsTMIP $\text{NEP} \times -1$) and GPP from the MsT-
 146 MIP Version 1 SG3 simulation, in which the models are driven by CRU+NCEP reanal-
 147 ysis on a global $0.5^\circ \times 0.5^\circ$ spatial grid with time-varying land-use history and atmo-
 148 spheric CO_2 , but with nitrogen deposition kept constant. We examine modeled fluxes
 149 over the period 1980–2010. These data were downloaded from the ORNL DAAC (Huntzinger
 150 et al., 2016). A list of models included in this study are shown in Fig. S8.

151 **2.2 Environmental data**

152 Anomalies in CO_2 fluxes are compared with anomalies in environmental variables
 153 that are expected to drive carbon cycle anomalies. In particular, we focus our analysis
 154 on the relationship between anomalies in CO_2 fluxes with anomalies in soil temperature
 155 and soil moisture.

156 **2.2.1 Soil Temperature**

157 Soil temperatures are from the MERRA-2 (Reichle et al., 2011, 2017; Gelaro et al.,
 158 2017) reanalysis. We average the soil temperature over levels 1–3 (TSOIL1, TSOIL2, and
 159 TSOIL3), which reaches a depth of 0.73 m. These data were downloaded from the God-
 160 dard Earth Sciences Data and Information Services Center at monthly temporal reso-
 161 lution and $4^\circ \times 5^\circ$ spatial resolution (regridded from model horizontal resolution of ~ 50 km).

162 **2.2.2 Moisture stress variables**

163 The ESA CCI combined surface soil moisture product (Y. Y. Liu et al., 2011, 2012)
 164 was downloaded from <https://www.esa-soilmoisture-cci.org/>. We use the combined ac-
 165 tive and passive soil moisture product. Daily soil moisture estimates are provided on a
 166 $0.25^\circ \times 0.25^\circ$ longitude–latitude spatial grid, but we regrid to monthly estimates on a
 167 $4^\circ \times 5^\circ$ spatial grid.

168 Additional datasets are used for supplemental analysis of the relationship between
 169 carbon fluxes and moisture stress. We obtain precipitation estimates from the Global
 170 Precipitation Climatology Project (GPCP) Monthly Analysis Product. We use GPCP
 171 Version 2.3 Combined Precipitation Dataset (Adler et al., 2003). We use RL06 monthly
 172 mass grids of terrestrial water storage (TWS) anomalies derived from the Gravity Re-
 173 covery and Climate Experiment (GRACE) mission (Tapley et al., 2004; Flechtner et al.,
 174 2014; Landerer & Swenson, 2012).

175 3 Methods

176 3.1 Definition of anomalies

177 Anomalies are denoted with a “ Δ ” for all quantities (e.g., ΔNEE). To calculate
 178 anomalies, the mean seasonal cycle over a baseline period is removed. The baseline pe-
 179 riod employed is 2010–2015 for flux inversion NEE, 2003–2014 for GRACE TWS, and
 180 2001–2017 for GPP, soil temperature, soil moisture, and precipitation. In addition, a lin-
 181 ear trend is removed for all datasets except the NEE flux inversion (because the flux in-
 182 version timeseries is only six-years). Sensitivity tests found that results were not sensi-
 183 tive to the time period chosen for the baseline.

184 3.2 Quantifying IAV features

185 We focus our analysis on the seasonal compensation component and amplification
 186 component of IAV over the growing season. For NEE, we define the seasonal compen-
 187 sation component (NEE_{comp}) and seasonal amplification component (NEE_{amp}) as,

$$\Delta\text{NEE}_{\text{comp}} = \Delta\text{NEE}_{\text{Jul-Aug-Sep}} - \Delta\text{NEE}_{\text{Apr-May-Jun}}, \quad (1)$$

$$\Delta\text{NEE}_{\text{amp}} = \Delta\text{NEE}_{\text{Jul-Aug-Sep}} + \Delta\text{NEE}_{\text{Apr-May-Jun}}, \quad (2)$$

188 where $\Delta\text{NEE}_{\text{Apr-May-Jun}}$ and $\Delta\text{NEE}_{\text{Jul-Aug-Sep}}$ are the mean anomalies across April-
 189 June and July-September, respectively. A schematic of NEE anomalies leading to posi-
 190 tive and negative amplification and compensation components are shown in Figure S1.
 191 The amplification component indicates a net increase or decrease in carbon uptake over
 192 the growing season. For example, if NEE anomalies are positive across the growing sea-
 193 son (Fig. S1a), this will imply positive amplification and enhanced CO_2 emitted to the
 194 atmosphere ($\Delta\text{NEE}_{\text{amp}} > 0$). The compensation component indicates anti-correlated
 195 anomalies between the spring and summer. For example, if NEE anomalies are positive
 196 in the spring but negative in the summer (Fig. S1b), this will imply a negative compen-
 197 sation over the growing season ($\Delta\text{NEE}_{\text{comp}} < 0$). We define compensation and ampli-
 198 fication for GPP in the same way.

199 We examine the relative magnitudes of these two components by taking the ratio
 200 of the mean absolute seasonal compensation component to the mean absolute ampli-
 201 fication component. For NEE, this ratio is defined as:

$$\text{NEE}_{\text{RATIO}} = \frac{\sum_{y=2010}^{2015} |\Delta\text{NEE}_{\text{comp}}|}{\sum_{y=2010}^{2015} |\Delta\text{NEE}_{\text{amp}}|}. \quad (3)$$

202 The quantity $\text{NEE}_{\text{RATIO}}$ provides a measure of the relative magnitudes of the compen-
 203 sation and amplification components. If the magnitude of compensation is generally larger
 204 than amplification then the ratio will be larger than 1. If amplification dominates then
 205 the ratio will be less than 1.

206 Note that we split the growing season into the spring (April-May-June) and sum-
 207 mer (July-August-September). The spring roughly covers the period from the spring equinox
 208 (March 20) to the summer solstice (June 20), while the summer roughly covers the pe-
 209 riod from the summer solstice to the fall equinox (Sep 22). We note that these defini-
 210 tions are lagged by one month from the meteorological seasons.

211 3.3 Singular value decomposition

212 We employ singular value decomposition (SVD) to examine the modes of variability
 213 in monthly Δ NEE and Δ GPP between years. SVD is a method to decompose a matrix
 214 into a set of singular vectors and singular values (Golub & Reinsch, 1971), where
 215 the singular vectors are a set of orthogonal basis vectors. In this analysis, we perform
 216 SVD on Δ GPP and Δ NEE arranged into month-by-year matrices. Thus, the singular
 217 vectors give the modes of monthly variability between years in Δ GPP and Δ NEE. The
 218 fraction of overall variance explained the leading singular vector “ i ” is then calculated
 219 using the expression $R^2 = s_i^2 / \sum_j s_j^2$, where s_j are the singular values.

220 4 Results

221 4.1 Amplification dominates in the west and compensation dominates 222 in the East

223 We examine the relative magnitudes of seasonal compensation and amplification
 224 in Δ GPP and Δ NEE. Figure 1 shows NEE_{RATIO} for 2010–2015 and GPP_{RATIO} for 2001–
 225 2017 over subtropical and temperate North America (GPP_{RATIO} for 2010–2015 is shown
 226 in Fig. S2). Spatially, seasonal compensation is most dominant in eastern North Amer-
 227 ica (largest ratios), particularly around the Midwest. In contrast, the amplification com-
 228 ponent of IAV is most dominant in western North America, particularly in the south-
 229 west. Figure 1c and 1d show NEE_{RATIO} and GPP_{RATIO} as a function of the mean Apr-
 230 Sep soil moisture and soil temperature for each $4^\circ \times 5^\circ$ grid cell. Larger ratios are found
 231 to cluster in the wetter areas while smaller ratios are generally found in the drier areas,
 232 consistent with the climatological difference between the west and east of North Amer-
 233 ica. In support of these results, similar spatial structure for NEE_{RATIO} is obtained us-
 234 ing the independent NOAA’s CarbonTracker flux inversion, version CT2017 with updates
 235 documented at <http://carbontracker.noaa.gov> (Peters et al., 2007) (Fig. S3). In addi-
 236 tion, the GPP_{RATIO} spatial structure is supported by GOME-2 version 28 (V28) 740
 237 nm terrestrial SIF data (Joiner et al., 2013, 2016), while agreement with FLUXCOM GPP
 238 (Tramontana et al., 2016) is mixed (Fig. S4).

239 To further examine differences in IAV between eastern and western North Amer-
 240 ica, we aggregate gridcells into western and eastern regions (Fig. 2a). We then perform
 241 SVD on matrices of monthly Δ NEE and Δ GPP (with months as the rows and years as
 242 columns) over these two regions. This analysis allows us to compute basis vectors that
 243 explain modes of variability in monthly Δ NEE and Δ GPP between years. The first and
 244 second basis vectors, which explain the majority of variability in Δ NEE and Δ GPP are
 245 shown in Fig. 2. These basis vectors show that the western region is dominated by am-
 246 plification in GPP and NEE, with the first singular value explaining 66% and 76% of the
 247 variance, respectively (Fig. 2). Conversely, the eastern region is dominated by seasonal
 248 compensation in GPP and NEE, with the first singular value explaining 59% and 47%
 249 of the variance, respectively (Fig. 2). Thus, these aggregated regions are generally re-
 250 flective of the IAV seen at the grid cell level.

251 4.2 Relationship between flux anomalies and environmental drivers

252 To a large extent, IAV in the carbon balance of ecosystems is expected to be driven
 253 by IAV in temperature and moisture (Berry & Bjorkman, 1980; Smith et al., 2011; Byrne,
 254 Jones, et al., 2019), thus we examine the relationship between CO_2 flux anomalies and
 255 anomalies in soil temperature (ΔT) and soil moisture (ΔM). Figure 3 shows the corre-
 256 lation between Δ GPP and anomalies in climate variables over 2001–2017. Note that we
 257 correlated Jul–Sep flux anomalies with Apr–Sep climate anomalies to incorporate lagged
 258 effects of spring climate anomalies on summer carbon cycle anomalies. We find spatial
 259 differences in the correlation coefficient between western and eastern North America. In

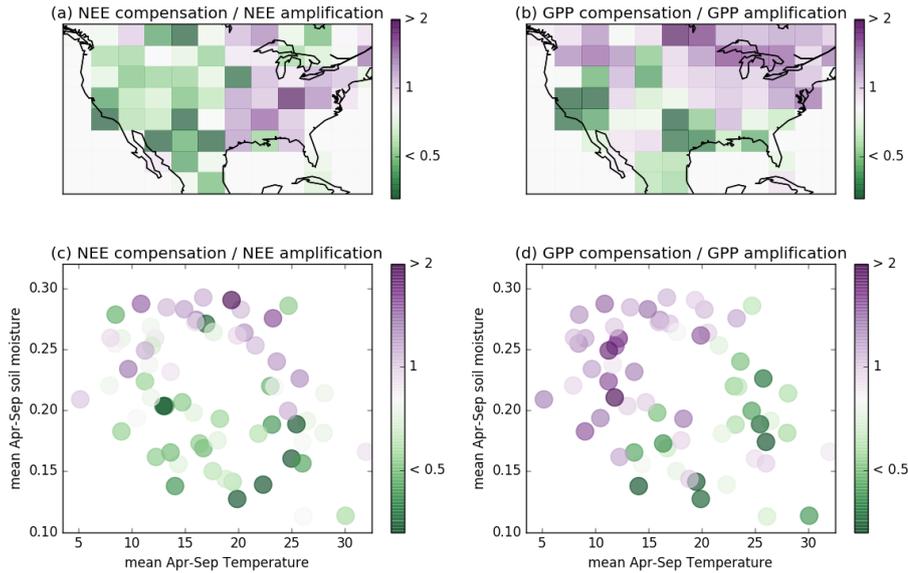


Figure 1. Relative magnitudes of seasonal compensation and amplification. (a) NEE_{RATIO} over 2010–2015 and (b) GPP_{RATIO} over 2001–2017 at $4^\circ \times 5^\circ$. (c) NEE_{RATIO} and (d) GPP_{RATIO} plotted as a function of Apr-Sep mean soil temperature and soil moisture.

260 the west, increased GPP (positive ΔGPP) is found to be correlated with cooler (neg-
 261 ative ΔT) and wetter (positive ΔM) conditions during both Apr–Jun and Jul–Sep. The
 262 temporally coherent relationship between flux anomalies and environmental anomalies
 263 in western North America suggests that cooler-wetter years will lead to an amplification
 264 of carbon uptake. In the east, increased GPP is correlated with warmer conditions dur-
 265 ing Apr–Jun, but cooler and wetter conditions during Jul–Sep. These seasonal variations
 266 in the relationship between flux anomalies and environmental variables suggest that sea-
 267 sonal compensation will occur when climate anomalies persist throughout the year. For
 268 example, warm years would result in increased uptake during the spring but decreased
 269 uptake during the summer. Similar results are found for NEE (Fig. S5) over 2010–2015,
 270 although correlations are generally less statistically significant. This is likely partially
 271 explained by the shorter time period examined and the inability of the flux inversion to
 272 isolate NEE anomalies to $4^\circ \times 5^\circ$ spatial grid cells.

273 We now examine the seasonal cycles of GPP and NEE over the western and eastern
 274 regions of North America. Figure 4 shows the seasonal cycles of GPP (2001–2017)
 275 and NEE (2010–2015) over the western and eastern regions of North America with dif-
 276 ferent years coloured by the corresponding Apr-Sep ΔT or ΔM . An additional plot show-
 277 ing the seasonal compensation and amplification components as a function of ΔT or ΔM
 278 is shown in the supplementary materials (Fig. S6). For western North America, varia-
 279 tions in the seasonal cycle of GPP and NEE are dominated by an amplification compo-
 280 nent over Apr-Sep. Increased GPP and net uptake are associated with cooler and wet-
 281 ter conditions. ΔT and ΔM are strongly correlated with each other ($R = -0.77$ for 2001–
 282 2017), obscuring which variable has the largest impact on IAV. However, the magnitude
 283 of the correlation is slightly larger for ΔM as compared with ΔT for ΔNEE_{amp} (0.91 vs
 284 0.71) and ΔGPP_{amp} (0.66 vs 0.63) (Table S1). IAV is generally weaker in eastern North
 285 America (relative to the mean seasonal cycle). Temporal shifts in the seasonal cycle of
 286 GPP (ΔGPP_{comp}) and NEE (ΔNEE_{comp}) provide the largest component of IAV. Shifts
 287 of GPP and NEE to earlier in the year are associated with positive Apr-Sep ΔT (Fig. 4b
 288 (i) and (iii)), suggesting that a warm spring drives the shift and persistent warming dur-

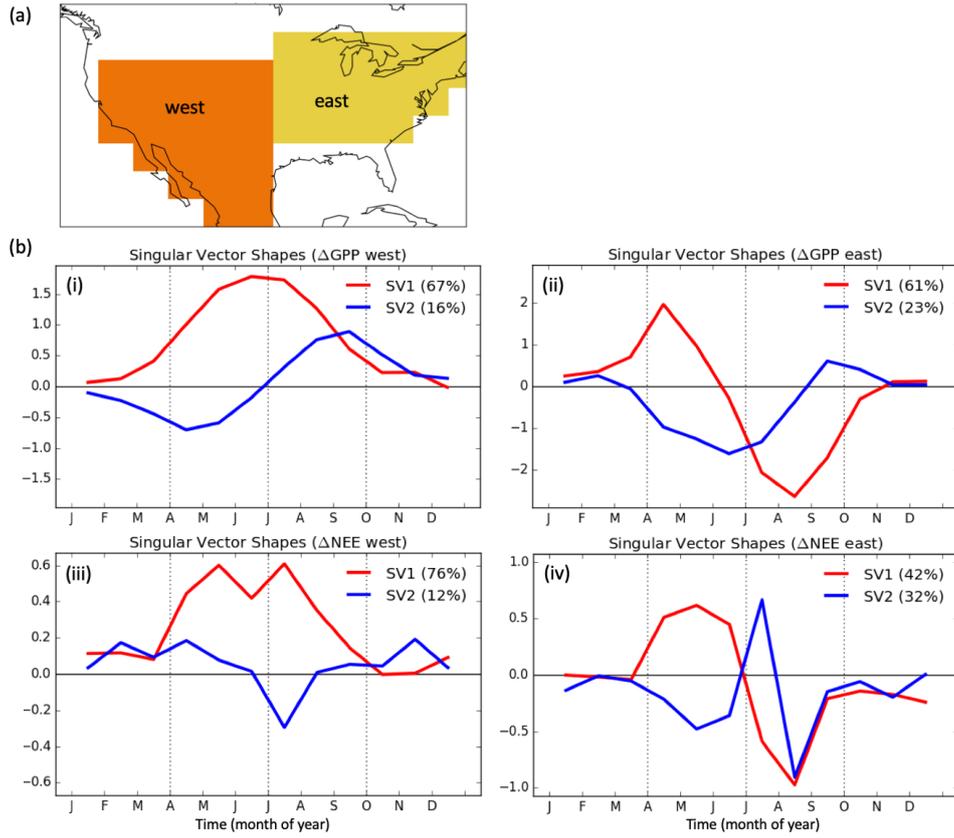


Figure 2. (a) The spatial extent of western (orange) and eastern (yellow) regions of North America. (b) First and second singular vectors resulting from the decomposition of the IAV in GPP over 2001–2017 for the (i) western and (ii) eastern regions of North America, and of the IAV in NEE over 2010–2015 for the (iii) western and (iv) eastern regions of North America.

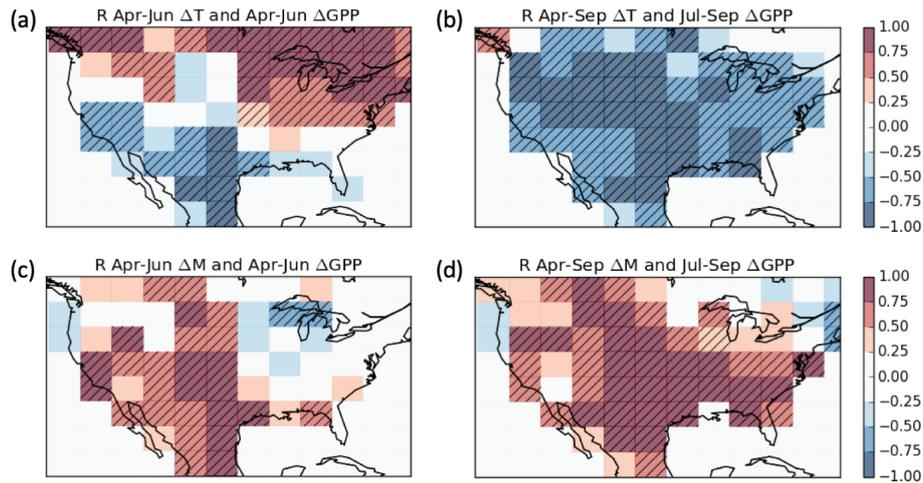


Figure 3. Relationship between Δ GPP and variations in climate. Coefficient of correlation (R) over 2001–2017 for $4^\circ \times 5^\circ$ grid cells between (a) Apr–Jun Δ T and Apr–Jun Δ GPP, (b) Apr–Sep Δ T and Jul–Sep Δ GPP, (c) Apr–Jun Δ M and Apr–Jun Δ GPP and (d) Apr–Sep Δ M and Jul–Sep Δ GPP. Hatching shows grid cells for which $P < 0.05$.

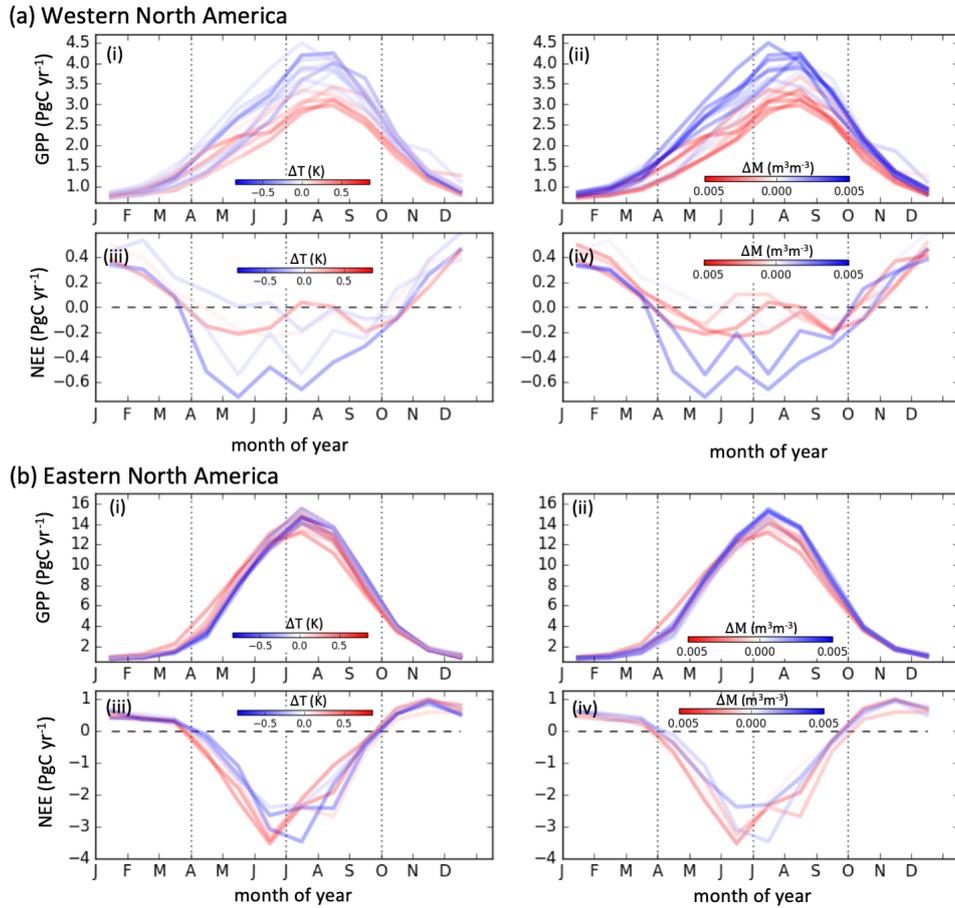


Figure 4. Seasonal cycles of GPP (2001–2017) and NEE (2010–2015) over eastern and western North America. (a) Seasonal cycles of (i–ii) GPP and (iii–iv) NEE over western North America. (b) Seasonal cycles of (i–ii) GPP and (iii–iv) NEE over eastern North America. Colors indicate the Apr–Sep ΔT ((i) and (iii)) or Apr–Sep ΔM ((ii) and (iv)).

289 ing summer reduces the productivity and net uptake. Variations in Apr–Sep ΔM are more
 290 closely tied to an amplification component of ΔGPP ($R=0.72$) and ΔNEE ($R=0.78$) (Ta-
 291 ble S1). This implies that increased soil moisture is associated with increased GPP but
 292 reduced net uptake, suggesting that respiration fluxes increase more than GPP with in-
 293 creased soil moisture. This result is consistent with Z. Liu et al. (2018), but contradicted
 294 (for droughts) by Schwalm et al. (2010). Thus, more research is needed on this topic.

295 4.3 Impact of amplification and compensation for net CO_2 fluxes

296 The presence of temporally coherent spring–summer flux anomalies in western North
 297 America acts to increase the annual net flux anomalies. In contrast, anti-correlated spring–
 298 summer flux anomalies in eastern North America acts to reduce the net annual flux ana-
 299 malies. Here we examine the relative contribution of eastern and western North America
 300 to the mean seasonal cycle and anomalies of GPP and NEE (Figure 5). We find that monthly
 301 NEE and GPP fluxes are larger in eastern North America than in western North Amer-
 302 ica ($7.6\times$ for GPP, $3.5\times$ for NEE), reflecting a more productive carbon cycle. However,
 303 due to seasonal compensating anomalies, annual anomalies in GPP and NEE are larger
 304 in the west than the east ($1.04\times$ for GPP and $1.27\times$ for NEE). Thus, growing season

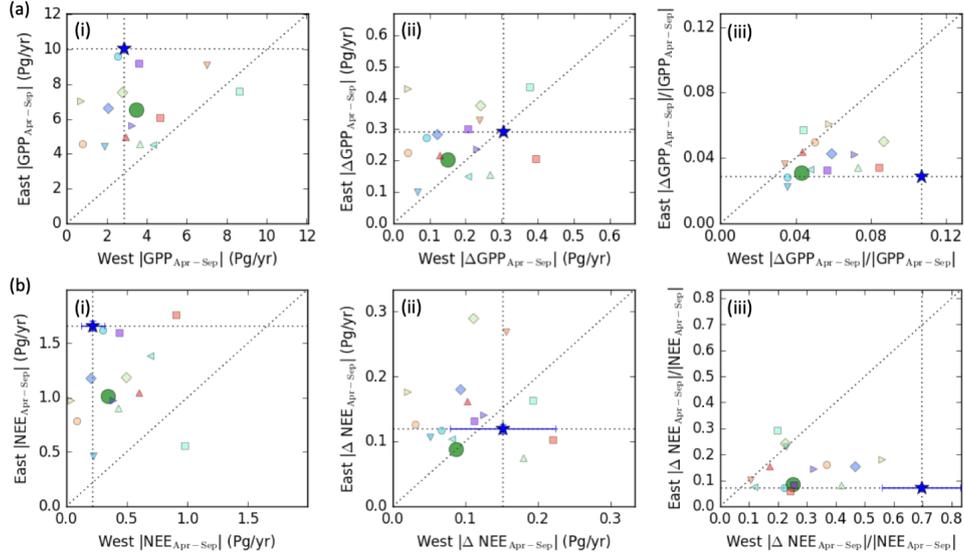


Figure 5. Scatter plots of (a) GPP and (b) NEE fluxes in eastern and western North America. The panels show (i) the magnitude of Apr-Sep mean fluxes, (ii) the magnitude of Apr-Sep mean anomalies, and (iii) the ratio of the anomalies to mean fluxes. The blue star shows the observationally-based estimates from FluxSat GPP and the flux inversion NEE. The error bars on the observationally-constrained NEE estimate show the range in these values between the three flux inversions from (Byrne, Liu, et al., 2019), note error bars are very small for the east. The large green circle shows the GPP and NEE estimate from the MsTMIP model mean. Small circles show the GPP and NEE estimates from individual MsTMIP models.

IAV in NEE and GPP is larger in the western North America, despite a more productive carbon cycle in eastern North America. The impacts of these differences in IAV between these two regions are evident in the timeseries of Δ GPP and Δ NEE anomalies two regions (Fig. S7). Monthly anomalies in western North America are coherent for individual years leading to increased annual anomalies, while anomalies in the east show seasonal compensation, reducing annual net anomalies.

We now investigate the ability of the MsTMIP models to recover observationally-constrained west-east differences in GPP and NEE over 1980–2010. Modeled fluxes are plotted with the observationally-constrained estimates in Fig 5. The MsTMIP models systematically underestimate the magnitude of Apr-Sep GPP and NEE in eastern North America relative to FluxSat GPP and inversion NEE, but closely agree with the observationally-constrained fluxes in western North America. The mean magnitudes of Apr-Sep Δ GPP and Δ NEE are variable between MsTMIP models, but are generally smaller than the observationally-based estimates. The model mean gives similar magnitudes of Δ GPP and Δ NEE in eastern and western North America, suggesting that the models at-least partially capture increased IAV in western North America. The ratio of the magnitudes of Apr-Sep IAV to the Apr-Sep mean are shown in Fig. 5c. The models systematically underestimate this ratio for GPP and NEE in western North America. The MsTMIP models predict that mean magnitude of Apr-Sep Δ GPP is 4% (range of 3–9%) of the Apr-Sep GPP, while FluxSat GPP suggests 11%. Similarly, MsTMIP models predict that mean magnitude of Apr-Sep Δ NEE is 25% (range of 11–56%) of the Apr-Sep NEE, while inversion NEE suggests 70%. The MsTMIP model mean also tends to give weaker sensitivity to soil moisture and temperature anomalies (Table 1). FluxSat Δ GPP is found to be about 30% more sensitive to variations in soil temperature and moisture than the

Table 1. Observationally-based and model based sensitivities. Slope and R^2 values for linear regressions of Apr-Sep Δ GPP and Δ NEE against Apr-Sep Δ T and Δ M for FluxSat GPP (2001–2017), inversion NEE (2010–2016), and MsTMIP model mean GPP and NEE (2001–2010). MsTMIP fluxes are examined over 2001–2010 to isolate comparisons to the period when observational datasets are best constrained by observations. Bold numbers indicate $P < 0.05$.

	West				East			
	Temperature		Soil Moisture		Temperature		Soil Moisture	
	slope (PgC K ⁻¹)	R ²	slope (PgC (m ³ m ⁻³) ⁻¹)	R ²	slope PgC K ⁻¹	R ²	slope (PgC (m ³ m ⁻³) ⁻¹)	R ²
FluxSat Δ GPP	-0.29	0.44	32.6	0.89	-0.04	0.03	52.2	0.09
Model Δ GPP	-0.20	0.55	23.4	0.91	-0.02	0.02	110.6	0.45
Inversion Δ NEE	0.13	0.47	-10.3	0.49	-0.04	0.19	28.6	0.21
Model Δ NEE	0.11	0.53	-10.3	0.71	0.06	0.60	-53.5	0.42

329 MsTMIP model mean, while inversion Δ NEE variations are 15% larger for soil temper-
 330 ature than the MsTMIP model mean but identical for soil moisture. In eastern North
 331 America, the MsTMIP models suggest greater sensitivity to environmental variables than
 332 the observationally-constrained fluxes (Table 1), as previously suggested by Shiga et al.
 333 (2018).

334 5 Discussion

335 5.1 Mechanisms driving IAV

336 5.1.1 Western North America

337 We find that IAV in western North America is dominated by an amplification com-
 338 ponent, wherein increased GPP and net uptake are associated with cooler-wetter con-
 339 ditions. This result is consistent with a number of previous studies investigating south-
 340 west North America (Zhang et al., 2013; Parazoo et al., 2015; Papagiannopoulou et al.,
 341 2017; Shiga et al., 2018; Hu et al., 2019) and in semi-arid regions more broadly (Poulter
 342 et al., 2014; Ahlström et al., 2015; Huang et al., 2016; Z. Fu et al., 2017). Variations in
 343 GPP and NEE over this region are likely primarily due to variations in water availabil-
 344 ity, rather than temperature variability (Papagiannopoulou et al., 2017). Parazoo et al.
 345 (2015) have shown that variability in productivity over the Southern US – Northern Mex-
 346 ico region is linked to El Nino Southern Oscillation (ENSO) and the North Atlantic Os-
 347 cillation (NAO), and suggest that year-to-year variability of carbon net uptake is asso-
 348 ciated with precipitation anomalies in this region. We find Δ P is strongly correlated with
 349 Δ GPP_{amp} ($R=0.78$) and moderately correlated with Δ NEE_{amp} ($R=-0.47$) in western
 350 North America (Table S1). This suggests that IAV in western North America is primar-
 351 ily driven by large scale climate variability. Supporting this result, Hu et al. (2019) found
 352 that North American net uptake is correlated with ENSO phase, which they primarily
 353 attributed to variations in water availability.

354 5.1.2 Eastern North America

355 We find that GPP and NEE IAV in eastern North America are dominated by a sea-
 356 sonal compensation component, where an increase in Apr–Jun is followed by a compen-
 357 sating decrease in Jul–Sep. This is most closely linked to a shift of the seasonal cycle to
 358 earlier in the year with increased temperature. This phenomena has previously been re-
 359 ported for studies of phenology (Y. S. Fu et al., 2014; Keenan & Richardson, 2015), GPP

360 (Buermann et al., 2013, 2018; Parida & Buermann, 2014; Papagiannopoulou et al., 2017)
 361 and NEE (Wolf et al., 2016; J. Liu et al., 2018; Shiga et al., 2018; Rödenbeck et al., 2018;
 362 Hu et al., 2019). Most studies attribute this phenomena to land-atmosphere interactions,
 363 wherein a warm spring results in drying and drought during the summer (Parida & Buer-
 364 mann, 2014; Wolf et al., 2016). This explanation is generally consistent with our results
 365 for GPP but not for NEE. We find that Apr–Jun Δ GPP and Δ NEE are correlated with
 366 Apr–Jun Δ T ($R=0.86$ for GPP, $R=-0.95$ for NEE) but only Jul–Sep Δ GPP is correlated
 367 with Jul–Sep Δ M ($R=0.72$ for GPP, $R=0.16$ for NEE). A further difficulty with this mech-
 368 anism explaining seasonal compensation effects is that Apr–Jun Δ T and Jul–Sep Δ M
 369 are only weakly correlated over eastern North America ($R=-0.28$). This is true for grid
 370 cells with cropland fractions greater than 65% ($R=-0.19$) and less than 35% ($R=-0.28$)
 371 (see Fig. S9). To some extent, the lack of correlation could be due to errors in the ESA
 372 CCI soil moisture product, as somewhat stronger correlations are found between Apr–
 373 Jun Δ T and Jul–Sep GRACE Δ TWS ($R=-0.44$ for 2003–2014, Table S1). Still, these
 374 results suggests that other factors play a role in seasonal compensation effects. Direct
 375 physiological mechanisms linking budburst and senescence, such as leaf structure con-
 376 straints on longevity (Reich et al., 1992) or programmed cell death (Lam, 2004), may
 377 have a significant impact on the length of the growing season (Keenan & Richardson,
 378 2015). However, more research is needed to understand the drivers of seasonal compen-
 379 sation effects.

380 5.2 Implications for North American carbon sink

381 The sensitivity of carbon cycle IAV to environmental drivers may provide infor-
 382 mation on the sensitivity of the carbon cycle to climate change (Cox et al., 2013). Here,
 383 we discuss the implications of the relationships between carbon cycle IAV and environ-
 384 mental drivers for the future carbon balance of North America under anthropogenic cli-
 385 mate change.

386 Changes in temperature and the water cycle of North America have been observed
 387 and are projected into the future. The annual average temperature of the contiguous US
 388 has risen by 0.7–1.0 °C since the start of the 20th century, and is projected to increase
 389 by 1.4 °C (RCP4.5) to 1.6 °C (RCP8.5) for 2021–2050 relative to 1976–2005, based on
 390 Coupled Model Intercomparison Project 5 (CMIP5) simulations (Vose et al., 2017). Warm-
 391 ing is driving a more rapid water cycle (Huntington et al., 2018). This is projected to
 392 cause decreases in soil moisture because increases in evapotranspiration (due to temper-
 393 ature increases) are expected to be larger than precipitation increases (Cook et al., 2015).
 394 Predicted warming and drying in western North America (Seager et al., 2007) could have
 395 profound effects on the carbon cycle (Schwalm et al., 2012), with increasing tempera-
 396 tures and aridity driving reductions in growing season productivity and carbon uptake.
 397 TBMs suggest that carbon loss due to climate change will be partially mitigated by in-
 398 creasing CO₂ (Huntzinger et al., 2018); however, given that the models are found to be
 399 less sensitive to climate variability than the observationally-constrained estimate, car-
 400 bon loss may be underestimated. In eastern North America, the results of this study sug-
 401 gest that temperature increases will result in a shift of the growing season to earlier in
 402 the year, with increased uptake during the spring but decreased uptake during the sum-
 403 mer. However, the observationally-constrained flux estimates do not show sensitivity of
 404 Apr–Sep net GPP and NEE to environmental anomalies, suggesting that eastern North
 405 American ecosystems may be more resilient to climate change than simulated by the mod-
 406 els.

407 6 Conclusions

408 Observationally-constrained FluxSat GPP and CO₂ flux inversion NEE show that
 409 there are substantial differences in IAV between the arid west and wetter east of North

410 America. In western North America, spring and summer anomalies are found to be cor-
 411 related, such that IAV is characterized by an amplification of the mean GPP and NEE
 412 during the growing season. These western ecosystems are generally water limited, such
 413 that increased GPP and net uptake are associated with cooler-wetter conditions. In east-
 414 ern North America, spring and summer anomalies are anti-correlated, leading to com-
 415 pensating anomalies over the growing season. Anomalies in GPP and NEE are closely
 416 associated to temperature, with a shift in the seasonal cycle to earlier in the year dur-
 417 ing warm years, resulting in increased GPP and net uptake in Apr–Jun but decreased
 418 GPP and net uptake in Jun–Sep.

419 Due to the dominance of amplification in the west and seasonal compensation in
 420 the east, western North America contributes more to IAV than the eastern North Amer-
 421 ica in GPP (104% of east) and NEE (127% of east) during the growing season (April-
 422 September), despite the fact that the mean growing season fluxes are larger in the east
 423 ($7.6\times$ for GPP, $3.5\times$ for NEE). Simulated GPP and NEE from the MsTMIP ensemble
 424 partially recover the larger IAV in the west relative to the east, but underestimate the
 425 magnitude of this effect. In particular, the MsTMIP model mean tends to underestimate
 426 the sensitivity of western ecosystems to variation in soil temperature and soil moisture
 427 (by 0–31%). These results suggest that ecosystems in western North America could be
 428 sensitive to increases in temperature and aridity expected under climate change, and that
 429 reductions in growing season productivity and net uptake could be larger than simulated
 430 by TBMs.

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