Evaluating atmospheric CO₂ effects on gross primary productivity and net ecosystem exchanges of terrestrial ecosystems in the conterminous United States using the AmeriFlux data and an artificial neural network approach

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18 Abstract:

19 Quantitative understanding of regional gross primary productivity (GPP) and net ecosystem
20 exchanges (NEE) and their responses to environmental changes are critical to quantifying the
21 feedbacks of ecosystems to the global climate system. Numerous studies have used the eddy flux
22 data to upscale the eddy covariance derived carbon fluxes from stand scales to regional and global
23 scales. However, few studies incorporated atmospheric carbon dioxide (CO₂) concentrations into
24 those extrapolations. Here, we consider the effect of atmospheric CO₂ using an artificial neural
25 network (ANN) approach to upscale the AmeriFlux tower of NEE and the derived GPP to the
26 conterminous United States. Two ANN models incorporating remote sensing variables at an 8-day
27 time step were developed. One included CO₂ as an explanatory variable and the other did not. The
28 models were first trained, validated using eddy flux data, and then extrapolated to the region at a
29 $0.05^{\circ} \times 0.05^{\circ}$ (latitude x longitude) resolution from 2001 to 2006. We found that both models
30 performed well in simulating site-level carbon fluxes. The spatially-averaged annual GPP with and
31 without considering the atmospheric CO₂ were 789 and 788 g C m⁻² yr⁻¹, respectively (for NEE, the
32 values were -112 and -109 g C m⁻² yr⁻¹, respectively). Model predictions were comparable with
33 previous published results and MODIS GPP products. However, the difference in GPP between the
34 two models exhibited a great spatial and seasonal variability, with an annual difference of 200 g C
35 m⁻² yr⁻¹. Further analysis suggested that air temperature played an important role in determining
36 the atmospheric CO₂ effects on carbon fluxes. In addition, the simulation that did not consider
37 atmospheric CO₂ failed to detect ecosystem responses to droughts in part of the US in 2006. The
38 study suggests that the spatially and temporally varied atmospheric CO₂ concentrations should be
39 factored into carbon quantification when scaling eddy flux data to a region.

Keywords: gross primary production, net ecosystem change, eddy flux tower, CO₂, artificial neural network

1. Introduction

Net ecosystem carbon exchange (NEE) and gross primary productivity (GPP) are two major fluxes involved in the ecosystem biogeochemical carbon process. Quantification of GPP and NEE and their responses to environmental changes would improve our understanding of the ecosystem carbon cycling and its feedbacks to the global climate system. At present, GPP and NEE at regional scales are often quantified using atmosphere inverse models (e.g. *Prince and Goward, 1995*), process-based biogeochemical models (e.g. *White et al., 2000*), and satellite remote sensing approaches (e.g. *Running et al., 2000*). The estimation of NEE based on the inverse models is limited by the sparseness of the carbon dioxide (CO₂) observation network (*Tans et al., 1990*); and this approach cannot differentiate the carbon source/sink contributions of each ecosystem (*Janssens et al., 2003*). Process-based models generally first derive the GPP and ecosystem respiration, which are modeled as a function of physical and biological variables and thus can be applied at regional and global scales. However, large uncertainty still exists in current quantification due to complex model structure, uncertain parameters, and model input (*Chen et al., 2011*). Satellite remote sensing approaches have advantages in GPP quantification that is based on a near real-time dataset, instead of broadly parameterized ecosystem models. However, they are highly dependent on the accuracy of the model algorithms and the quality of satellite imageries (*Baldocchi et al., 2001*).

The eddy covariance technique provides direct measurement of net carbon and water fluxes between vegetation and the atmosphere (*Baldocchi et al., 1988; Foken and Wichura, 1996; Aubinet*

62 *et al.* 1999). At present, over 500 flux tower sites have been operated to measure the exchanges of
63 carbon fluxes continuously over a broad range of climate and biome types (FLUXNET
64 <http://daac.ornl.gov/FLUXNET/fluxnet.shtml>). These towers also provide calibrated, validated NEE
65 data and the derived GPP product. To date, numerous studies have been conducted using those flux
66 data to explore the GPP and NEE temporal or spatial variation and their controlling factors in
67 terrestrial ecosystems (*Valentini et al.* 2000; *Law et al.* 2002; *Baldocchi*, 2008; *Hirata et al.* 2008;
68 *Kato and Tang* 2008; *Lund et al.*, 2010; *Bracho et al.*, 2012). Eddy flux data have also been widely
69 used for model calibration (*Baldocchi*, 1997; *Hanan et al.*, 2002; *Reichstein et al.*, 2002; *Hanson et*
70 *al.*, 2004) and to upscale from stands to regional levels. The upscaling exercises generally employ
71 the machine learning algorithm that uses meteorological data, vegetation properties, and remote
72 sensing products, which have been conducted for Asia (*Zhu et al.*, 2014; *Fu et al.*, 2014), Europe
73 (*Jung et al.*, 2008; *Vetter et al.*, 2008), the US (*Yang et al.*, 2007; *Xiao et al.*, 2008; *Xiao et al.*, 2010)
74 and even at global scales (*Beer et al.*, 2010; *Yuan et al.*, 2010).

75 However, few studies have incorporated the atmospheric CO₂ concentrations into regional GPP
76 and NEE extrapolations when using eddy flux tower data. Increasing CO₂, which is mainly due to the
77 burning of fossil fuels and, to a much lesser extent, land-cover change (*Keeling et al.*, 1995;
78 *Hartmann et al.*, 2013), will have substantial direct and indirect effects on the carbon budget
79 (*Canadell et al.*, 2007). Numerous studies have been conducted to understand how plants and
80 ecosystems will respond to elevated CO₂ (*Ainsworth and Long*, 2005). The large-scale free-air CO₂
81 enrichment experiment (FACE) showed that increasing CO₂ would reduce the stomatal conductance
82 (*Curtis and Wang*, 1998; *Medlyn et al.*, 2001; *Ainsworth and Rogers*, 2007) over a short time period,
83 resulting in decreased transpiration, enhanced water-use efficiency (*Conley et al.*, 2001; *Wall et al.*,

2001) and increased soil moisture (Bunce, 2004). In addition, stimulated photosynthesis (e.g. Li et al., 2014) would increase the above and below-ground biomass production (Piao et al., 2006, Los, 2013; Wan et al., 2007; Deng et al., 2010) and hence accelerate the CO₂ loss from heterotrophic respiration (Luo et al., 1996). Generally, long-lived plant biomass (trees) is more responsive to increasing CO₂ than herbaceous species (Ainsworth and Long, 2005). However, increased plant production with high carbon (C) to nitrogen (N) ratio under elevated CO₂ results in low quality litter input and slows the soil N mineralization, thus triggering the negative feedback to plant biomass over time (Oren et al., 2001; Gill et al., 2002; Luo et al., 2004) if there is no extra nitrogen input. This conceptual framework about progressive N limitation is more obvious in long-lived plants (trees) (Luo et al., 2004) and has been supported by few experiments (Oren et al., 2001; Norby et al., 2010). In addition, the climate drivers and their interaction with soil resources (Reich et al., 2014) would also constrain the ecosystem response to CO₂ fertilization. For example, increasing N mineralization due to warming temperature would further promote plant growth (Peltola et al., 2002; Dijkstra et al., 2010) whereas the drought stress may diminish this positive effect under elevated CO₂ condition (Dermody et al., 2007; Larsen et al., 2011). Moreover, altered water, energy balance (Drake et al., 1997, Keenan et al., 2013), and vegetation physiology due to increasing CO₂ would in turn affect the carbon cycling. Therefore, incorporating atmospheric CO₂ concentrations into the regional GPP and NEE estimation should be a research priority. In addition, previous upscaling flux studies that exclude the atmospheric CO₂ concentration assume that CO₂ variations were spatially and temporally uniform in a region. Although atmospheric CO₂ is generally well-mixed globally since it is chemically inert (Eby et al., 2009), it actually exhibits a large seasonal and spatial variability at the regional scale (Miles et al., 2012). The seasonal and spatial characteristics have previously been

106 reported at site and regional levels (*Davis et al.*, 2003; *Haszpra et al.*, 2008; *Miles et al.*, 2012). For
107 example, the summer measurement of the atmospheric boundary layer CO₂ mole fraction from a
108 nine-tower regional network deployed during the North American Carbon Program's Mid-Continent
109 Intensive (MCI) during 2007 to 2009 shows that the seasonal CO₂ amplitude is five times larger than
110 the tropospheric background and the spatial gradient across the region is four times the
111 inter-hemispheric gradient (*Miles et al.*, 2012).

112 In this study, we used an artificial neural network (ANN) approach to upscale the AmeriFlux
113 tower derived GPP and NEE to the conterminous US from 2001 to 2006 by considering the
114 atmospheric CO₂ concentrations as an independent factor. We developed two sets of ANN models
115 linking GPP and NEE and remote sensing variables for each vegetation type: the first considered the
116 atmospheric CO₂ concentration effects (CO₂ incorporated simulation, S0) and the other did not
117 (non-CO₂ incorporated simulation, S1). After the training and validation procedure, we then used
118 the two models to extrapolate GPP and NEE to the conterminous US. We hypothesized that: (1)
119 both models would capture the GPP and NEE variation at the calibration stage; (2) the two
120 simulations would exhibit spatiotemporal differences which associate with climate drivers; and (3)
121 ecosystems with high productivity (e.g., forest, cropland) would show greater differences between
122 the two simulations.

123

124 **2. Method**

125 **2.1 Overview**

126 From the AmeriFlux network, we selected the key ecosystem types in the conterminous US
127 including: evergreen forest, deciduous forest, grassland, mixed forest, savannas, shrubland, and

cropland. Day land surface temperature (D_LST) and night land surface temperature (N_LST), leaf area index (LAI), fraction of absorbed photosynthetically active radiation (fPAR), normalized difference vegetation index (NDVI), enhanced vegetation index (EVI), CO₂ measurement and derived GPP and NEE from the eddy flux towers were organized into an 8-day time step. To explore the atmospheric CO₂ concentrations' effect on the GPP and NEE, we constructed two sets of ANN models for each vegetation type: one incorporated CO₂(S0) in addition to D_LST, N_LST, LAI, fPAR, NDVI and EVI; and the second did not incorporate with CO₂ (S1) with the same explanatory variables in S0. After the training and validation of the two sets of ANN models, the regional estimation of GPP and NEE was driven by the explanatory variables at a spatial resolution of 0.05° × 0.05° on an 8-day time step. The difference between S0 and S1 was then analyzed, considering the controls of environmental variables.

139

2.2 Explanatory variables

NEE is the difference between photosynthesis and ecosystem respiration, which is influenced by a variety of physical, physiological, hydrological, and atmospheric variables. As for the plant photosynthesis, current ecosystem models have incorporated various mechanisms related to these factors to simulate GPP, such as the bio-chemical model (e.g. *Farquhar et al.*, 1980), light use efficiency equation (e.g. *Running et al.*, 2000), and the semi-empirical relationship (e.g. *Raich et al.*, 1991). Ecosystem respiration (Re) includes autotrophic (Ra) and heterotrophic respiration (Rh). Ra is generally modeled as a function of temperature and plant biomass, while Rh is empirically modeled as a function of soil temperature, moisture, and soil organic carbon stocks. Many of these factors influencing GPP and NEE can be assessed by satellite remote sensing products. NDVI is closely

150 correlated to the photosynthetic activity, vegetation biomass, and fractional vegetation cover, which
151 have been widely used in production efficiency models. We also incorporated the EVI to improve
152 the ANNs performance due to the several limitations of normalized difference vegetation index
153 (NDVI), including the saturation in a multilayer closed canopy and sensitivity to atmosphere
154 aerosols and soil background. The LST derived from the Moderate Resolution Imaging
155 Spectroradiometer (MODIS) corresponds the surface soil temperature, which is known to strongly
156 control the Re as both Ra and Rh. Previous studies demonstrated that satellite-derived LST was
157 strongly correlated with Re, especially in dense-vegetated ecosystems (*Rahman et al.*, 2005). The
158 estimation of LAI and fPAR, characterizing the vegetation canopy function and energy absorption
159 capacity, are key parameters in most biogeochemical models due to the high correlation with GPP.
160 Taken together, we selected LST, NDVI, EVI, fPAR, and LAI as explanatory variables to account for the
161 GPP and NEE variation.

162

163 2.3 Data Organization

164 We organized AmeriFlux site-level data of carbon flux and meteorology, MODIS land-cover,
165 spatially and seasonally explicit CO₂, and the remote sensing products derived from MODIS. The
166 AmeriFlux network coordinates regional analyses of observations from eddy covariance flux towers
167 across the US. The Level-3 and Level-4 data for 36 AmeriFlux sites over the period 2000–2006 that
168 contained CO₂ measurements were ultimately organized (Table 1 & Fig.1). In the Level-3 product,
169 the half-hourly CO₂ was aggregated into 8-day time step values. The Level-4 product consists of two
170 types of GPP and NEE data: standardized (GPP_st and NEE_st) and original (GPP_or and NEE_or).
171 Here, we used the same method in *Xiao et al.* (2010) to select the type of GPP and NEE product.

Explanatory variables, GPP and NEE values derived from the selected sites were organized to develop the ANN models for each ecosystem type.

We used the following four MODIS data products (Collection 4), including daytime and nighttime LST (MOD11A2; *Wan et al.*, 2002), EVI (MOD13A1; *Huete et al.*, 2002), and LAI/fPAR (MOD15A2; *Myneni et al.*, 2002). EVI is at a spatial resolution of 500 m x 500m, while LAI, fPAR, and LAI are at spatial resolutions of 1 km x 1km. These MODIS data were resampled to the same resolution of $0.05^{\circ} \times 0.05^{\circ}$ (longitude x latitude). The explicitly spatial and seasonal CO₂ data was obtained from the National Oceanic and Atmospheric Administration (NOAA) gridded CO₂ product (<ftp://aftp.cmdl.noaa.gov/products/carbontracker/co2/>). The product is based on global CO₂ observation network data, employing a novel ensemble assimilation method to accurately model atmospheric CO₂ mole fractions (*Peters et al.*, 2007). Land cover was obtained from the MODIS product Land Cover Types Yearly L3 Global 0.05 Deg CMG (MOD12C1) (Year 2005) from the NASA Goddard Space Flight Center website (<http://modis-land.gsfc.nasa.gov>). The classification of the International Geosphere and Biosphere (IGBP) land-cover classification system was used to reclassify the land-cover map of the conterminous United States into seven major vegetation types in the ANN model. To be more specific, the evergreen needleleaf forest and evergreen broadleaf forest were combined into evergreen forest (same for deciduous forest); and closed shrubland and open shrubland were merged into shrubland. Therefore, the model calibration and simulation were based on the seven vegetation types: evergreen forest, deciduous forest, grassland, mixed forest, savannas, shrubland, and cropland.

2.4 Neural Network Development

194 We used a General Regression Neural Network (GRNN) algorithm (*Specht, 1991*) to represent the
195 input-output relationship between the independent variables and dependent variables. The GRNN
196 scheme can model the nonlinear system without specifying the algebraic relationship or internal
197 mechanism. With the advantage of a fast-learning speed and good convergence with a large
198 number of training datasets, GRNN can be a useful tool to estimate GPP and NEE based on the
199 explanatory environmental variables. The training data set, including input and output values of
200 measurements, is fed into the multilayer neural network. The network is trained to obtain a set of
201 optimized interconnected network weights, which are used to produce the most probable value for
202 the outputs. More details about the GRNN algorithm and optimization procedure are provided in
203 the supplementary information (GRNN algorithm and Fig. S1). To develop the GRNN model for each
204 ecosystem type, we first randomly divided each dataset into two sets: a training set (75% of whole
205 data for each vegetation type) used to construct the GRNN model and a testing set (25% of whole
206 data for each vegetation type) used to evaluate the performance of constructed GRNN. MATLAB
207 codes were used for developing the model (The MathWorks Inc., Natick, MA, USA).

208 The uncertainty of GRNN model prediction is mainly from three sources: input variables, ANN
209 model structure, and model parameters. Here we focused on the uncertainties associated with the
210 model structure because we do not have sufficient knowledge about the uncertainty of input
211 variables. We used the “delete-one” method (*Zhuang et al., 2012*) through developing a number of
212 alternative ANN models to quantify the uncertainty of GPP and NEE due to uncertain model
213 structures. To be more specific, we randomly selected 75% of the observed data for each ecosystem
214 type to develop a new ANN model. The new model was then scaled up to obtain the new GPP and
215 NEE estimation at the regional scale. The process was repeated for 100 times in S0 and S1 for each

ecosystem type, respectively. The averaged GPP and NEE of all estimations were used to analyze the differences among simulations. The 95% confidence intervals were considered to be the range of model uncertainty to define the upper and lower bounds of the GPP and NEE estimation.

3. Results

3.1 Annual GPP and NEE and spatial difference

The simulated GPP, NEE with the two sets of ANN models were both close to the observed GPP and NEE for each ecosystem type (Fig. S2). We applied the two sets of models to calculate the annual averaged GPP and NEE of terrestrial ecosystems for the conterminous US at an 8-day time step from 2001 to 2006 (Fig. 2a, 2c). Both models showed a high spatial variability with a clear gradient from west to east. The Gulf Coast and parts of the Southeastern US were the most productive regions, with GPP greater than $2000 \text{ g C m}^{-2} \text{ yr}^{-1}$. Most parts of the Southeast and coastal Pacific Northwest also possessed high GPP ($1250\text{-}1500 \text{ g C m}^{-2} \text{ yr}^{-1}$). The Northeast had intermediate GPP ($500\text{--}1000 \text{ g C m}^{-2} \text{ yr}^{-1}$), where was mainly dominated by deciduous forest. The Midwest, Southwest and Rocky Mountain areas generally had relatively low GPP ($<500 \text{ g C m}^{-2} \text{ yr}^{-1}$). As for spatial patterns of NEE, the greatest net carbon uptake took place in the Gulf Coast and Mideast, with the annual averaged value of $-800 \text{ g C m}^{-2} \text{ yr}^{-1}$. By contrast, the Rocky Mountain area had the highest contribution to carbon release across the conterminous US. The uncertainty analysis based on the 100 ANN models (Fig. S3) demonstrated that our ANNs models predicted GPP and NEE with a small uncertainty across the whole ecosystem type. Overall, both simulations indicated that the East and Pacific Northwest showed high ecosystem productivity, acting as a carbon sink, while the Rocky Mountain region had the lowest GPP value and acted as a carbon source to the atmosphere.

The two simulations however, diverged in regions including the Pacific Northwest coast, Gulf coast and most parts of Southeast dominated by evergreen forests, savannas and mixed forest (Fig. 2b, 2d). S0 exhibited lower GPP ($-200 \sim -100 \text{ g C m}^{-2} \text{ yr}^{-1}$) and more positive NEE ($100 \sim 250 \text{ g C m}^{-2} \text{ yr}^{-1}$) value in most Southeastern US than that of S1 (Fig. 2b). In contrast, west North Central region had higher GPP ($100 \sim 200 \text{ g C m}^{-2} \text{ yr}^{-1}$) and more negative NEE ($-150 \sim -50 \text{ g C m}^{-2} \text{ yr}^{-1}$) in S0. From the vegetation perspective, the relative difference of GPP and NEE in the mixed forest and cropland showed a spatial variability. Specifically, the lower estimation of GPP in mixed forests and cropland was mainly found in the Southeast and east of South Central, while a higher GPP was observed in the North Central in S0. These patterns were similar to the NEE estimation (Fig. 2d).

3.2 Seasonal GPP and NEE difference

Our 8-day GPP and NEE estimation based on the two ANN models both captured the seasonal flux variability in the conterminous US (Fig.3 and Fig.S4). Take the GPP seasonal pattern, for example; in spring (March to May), the Gulf Coast and the Pacific Northwest region began to assimilate carbon at $100\text{--}200 \text{ g C m}^{-2} \text{ yr}^{-1}$, followed by the Southeast and the South Central. In contrast, most of the Northeast and Rocky Mountain area possessed a low GPP due to the relatively cold weather or late leaf-out. Plants reached the greatest productivity in summer (June–August) with the highest GPP of $300\text{--}400 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Northeast regions. From fall (September–November) to winter (December–February), GPP decreased drastically to either a low level ($50\text{--}100 \text{ g C m}^{-2} \text{ yr}^{-1}$) in the Gulf Coast, Pacific Northwest and South Central or nearly zero in most parts of Rocky Mountains throughout the US.

The obvious difference between seasonal GPP and NEE generally occurred in mixed forests and

croplands (Fig.4 and Fig.S5). In the early spring (March–April), the mixed forest in the Southeast began to exhibit lower GPP and more positive NEE in S0, and this difference was much stronger from late spring (May) to early fall (September). However, for the mixed forest in North Central and the Northeast, the difference only took place in June, July, and August. And this was similar for cropland in North Central, which only showed higher GPP and more negative NEE in these three months. No obvious difference was observed between the two simulations in winter.

266

3.3 GPP and NEE response to CO₂ concentrations under drought condition

Annual GPP and NEE both exhibited positive and negative anomalies each year. The anomalies could have been due to climate variability, disturbances, management practices, or model errors. The severe drought affected over 50% of the country, including the Southwest, the Great Plains, the Gulf Coast, the coastal Southeast, and particularly Texas and Oklahoma. Therefore, we evaluated the GPP and NEE response to the drought condition in 2006. Both models showed negative anomalies in most regions, like the Great Plains (Fig 5). However, as for the Southeast and parts of North Central, the S0 exhibited the negative GPP and positive NEE anomalies when compared with S1. According to the US Drought Monitor (<http://www.drought.unl.edu>) and the PRISM database, these regions showed around 250 mm less precipitation in 2006. Without considering the CO₂ effect in upscaling GPP and NEE, the S1 failed to show the ecosystem response to severe drought condition.

279

4. Discussion

4.1 Comparison of S0 and S1 with other studies

Our estimation of GPP and NEE and their spatial variations agreed well with previous published results. For example, Xiao *et al.* (2010) estimated that the spatially averaged GPP across the conterminous US scaled at $907 \text{ g C m}^{-2} \text{ yr}^{-1}$. Our simulation showed that the Gulf Coast and parts of the Southeast were the most productive regions, with GPP greater than $2000 \text{ g C m}^{-2} \text{ yr}^{-1}$, and was consistent with previous studies (Yang *et al.*, 2007; Xiao *et al.*, 2010; Chen *et al.*, 2011). The total gross carbon uptake estimated in both models was 4.00 and 3.95 Pg yr^{-1} , respectively, and was lower than the results of Xiao *et al.* (2010) because we did not reclassify the cropland/natural vegetation mosaic in MODIS land cover product as cropland ecosystems. In addition, the estimation of GPP ($1250\text{--}1500 \text{ g C m}^{-2} \text{ yr}^{-1}$) in the Southeast was much lower than Xiao's (Xiao *et al.*, 2010) prediction ($>2250 \text{ g C m}^{-2} \text{ yr}^{-1}$), but was comparable with Chen's (Chen *et al.*, 2011) study and the MODIS GPP product (Running *et al.*, 2004). The spatially averaged GPP in two simulations generally agreed well with MODIS GPP (Fig.S6) ($R^2>0.8$). However, MODIS GPP ($<800 \text{ g C m}^{-2} \text{ yr}^{-1}$) was markedly underestimated in cropland compared with our models ($>1000 \text{ g C m}^{-2} \text{ yr}^{-1}$). This large difference may be attributable to that MODIS GPP, which was based on the light use efficiency algorithm while ANN was based on the site-level flux tower data. The key parameter, the maximum light use efficiency in the MODIS GPP algorithm, was always underestimated and thus led to lower estimation in high productivity areas (Turner *et al.*, 2006; Xiao *et al.*, 2010). Recently, Madani *et al.* (2014) used eddy flux carbon data to show that the optimum light use efficiency in cropland was twice as much as that in the MODIS GPP algorithm.

301

302 4.2 Climate controls on the CO_2 effects on GPP and NEE

303 Previous studies have evaluated the interactions between elevated CO_2 and other

304 environmental variables, such as increasing temperature (*Peltola et al.*, 2002; *Tingey et al.*, 2003;
305 *Hovenden et al.*, 2008; *Dijkstra et al.*, 2010) and hydrological conditions (*Morgan et al.*, 2004;
306 *Nowak et al.*, 2004). Increasing CO₂ with enhanced N mineralization at higher temperatures may
307 further promote plant growth (*Kirschbaum et al.* 1994), whereas the positive effect may be
308 ameliorated in a reduced precipitation environment due to the slow turnover rate of N
309 belowground (*Emmett et al.*, 2004; *Sowerby et al.*, 2008). The seasonal GPP and NEE difference in
310 our simulations also indicated there were interactions between CO₂ effect and climate drivers.
311 Obvious GPP and NEE difference can only been observed from late spring to summer in the
312 Northern forest ecosystem (Fig.4 and S5), suggesting that the temperature controlling the plant
313 phenology may play a key role in CO₂ effects on the carbon fluxes. In addition, evergreen forest in
314 Pacific Northwest exhibited lower GPP in May and October (Fig.4), indicating that drought or the
315 soil water deficit (*Law et al.*, 2000; *Schwarz et al.*, 2004) may impact the CO₂ effects. The seasonal
316 variation of NEE difference was slightly different from GPP (Figs.4 and S5). NEE differences were
317 shown earlier than GPP in spring, especially in the Northern forest. The enhanced heterotrophic
318 respiration due to soil warming (*Raich and Schlesinger*, 1992; *Lloyd and Taylor*, 1994) may result in
319 the asynchronicity of GPP and NEE's response to the atmospheric CO₂ effect.

320 We analyzed the causes for the spatial variability of GPP difference using annual averaged air
321 temperature (Ta) and vapor pressure deficit (VPD) (Fig. 6). We obtained the Ta and VPD from North
322 American Regional Reanalysis dataset (*Mesinger et al.*, 2006). The atmospheric CO₂ concentration
323 showed negative effect on the evergreen forest and the effect was more obvious under high
324 temperature condition (>285 K). Both deciduous forest and shrubland did not show a obvious
325 difference across the Ta and VPD ranges. However, for the mixed forests, the difference could be

326 divided by the T_a value around 285 K. The GPP estimation in S0 was generally lower when $T_a > 285$ K
327 but higher when $T_a < 285$ K, when compared with S1. This was similar for the cropland; a lower GPP
328 estimation occurred in S0 when $T_a > 285$ K and it had a higher estimation when $T_a < 285$ K. In
329 addition, the negative effect was much stronger in lower VPD ranges ($VPD < 600$ Pa), indicating that
330 the CO_2 had stronger effect in the humid area. As for the savannas, no obvious T_a threshold was
331 observed and the negative effect generally located in the high T_a range. CO_2 concentration showed
332 complex effect on grassland, but overall, had a small influence on GPP estimation. Figure 5 also gave
333 the statistical values (mean and standard deviation) of the GPP difference between the two
334 simulations in each ecosystem type. Although the spatially averaged GPP difference was generally
335 small ($< 50 \text{ g C m}^{-2} \text{ yr}^{-1}$), the coefficient of variation (the ratio of standard variation to mean value)
336 was great in mixed forest and evergreen forest, followed by cropland and savannas.

337

338 4.3 GPP and NEE response to atmospheric CO_2 under drought condition

339 Remote sensing has been widely used to monitor the spatial patterns of drought and its related
340 changes in global ecosystems. Previous studies implemented the vegetation indices (NDVI, NDWI)
341 from Advanced Very High Resolution Radiometer (AVHRR) (Tucker, 1979) and MODIS to detect
342 drought conditions over the Great Plains in the US (Gu *et al.*, 2007), East Asia (Song *et al.*, 2004),
343 and Amazonian forest (Anderson *et al.*, 2010). Due to the lagged response of vegetation to the
344 drought events, these vegetation indices were combined with land surface thermal infrared
345 information to improve drought detection (Singh *et al.*, 2003; Park *et al.*, 2004; Wan *et al.*, 2004;
346 Son *et al.*, 2012). In this study, the negative anomalies of GPP in the Southeast only occur in S0,
347 although both simulations captured the vegetation response to drought events in 2006, especially

in the low biomass ecosystem (grassland, shrubland), by exploring the vegetation indices and thermal information. The spatial pattern of GPP anomalies in S1 was similar with Xiao *et al.* (2010), which also incorporated MODIS products using the regression tree model. Park *et al.* (2004) demonstrated that soil water-holding capacity affected the drought detection when using MODIS vegetation indices and thermal information. Gu *et al.* (2008) also pointed out that the various correlations between MODIS, NDVI, NDWI and drought events were highly dependent on the vegetation structure and soil types. Drought stress with reduced soil moisture can constrain plant nutrient uptake by reducing nutrient supply through mineralization (Emmett *et al.*, 2004; Sowerby *et al.*, 2008, Larsen *et al.*, 2011), also by reducing nutrient diffusion and mass flow in soils (Lamber *et al.*, 2008). Therefore, the induced drought condition may potentially decouple the soil microbial carbon and soil CO₂ fluxes with canopy photosynthesis (Ruehr *et al.*, 2009), increasing the residence of recent assimilated carbonate in vegetation (Deng *et al.*, 1990; Li *et al.*, 2003) and thus affecting the whole ecosystem carbon and nitrogen cycling. Some studies also pointed out the great contribution of drought to the surface CO₂ variability (Knorr *et al.*, 2005; Keppel-Aleks *et al.*, 2014). The climate of the Southeast is predicted to be warmer and drier in future (Dai, 2013). Therefore, incorporating the atmospheric CO₂ concentration into an upscaling practice using the flux site data should improve the qualification of GPP and NEE and strengthen our understanding of vegetation's response to environmental condition.

4.4 Implication of the CO₂ effect on GPP and NEE

Since atmospheric CO₂ is an important factor related to plant carbon assimilation and water balance, incorporating it is expected to improve our understanding on the ecosystems' response to

370 environmental variables. However, previous studies concerning the degree of climate controls on
371 the spatial and temporal patterns of the eddy covariance derived GPP and NEE (e.g. *Yu et al.*, 2013)
372 or upscale the site-level data to regional estimation (e.g. *Xiao et al.*, 2010) always ignored the
373 atmospheric CO₂ concentration. As our study statistically demonstrated above, including CO₂ as an
374 explanatory variable in upscaling site-level eddy flux data to regional GPP and NEE made an obvious
375 seasonal and spatial difference. Taking the North Central region of US as an example, our results
376 demonstrated that GPP was about 200 g C m⁻² yr⁻¹ higher in S0 due to the overestimation in the
377 growing season; this implied that larger GPP and NEE differences may occur between the two
378 simulations when atmospheric CO₂ showed a greater variability during these periods. Furthermore,
379 excluding the atmospheric CO₂ concentration, the regional GPP and NEE variation may be overly
380 attributed to other climate variables.

381 Up to now, most of the regional and global estimations of terrestrial carbon uptake come from
382 various ecosystem biogeochemistry models, which are mathematical representations of biophysical
383 processes (*Bonan*, 2008). The model constrained with eddy flux towers observation would
384 strengthen the understanding of ecosystem mechanisms. This data-assimilation method provides an
385 alternative way to quantify regional carbon exchanges between the terrestrial biosphere and the
386 atmosphere at regional and global scales (*Xiao et al.*, 2012). Generally, flux measurements are used
387 to calibrate the parameters in ecosystem models, and then the optimized parameters are
388 extrapolated for the estimation over a region. In some process-based ecosystem models which use
389 CO₂ data as an input to compute GPP, the carbon fluxes are routinely calibrated and simulated based
390 on annual CO₂ time series (or to be more specific, the background CO₂ concentration) across a
391 region or globe (*Turner et al.*, 2003; *Chen et al.*, 2011). However, although CO₂ is generally

392 well-mixed globally since it is chemically inert (*Eby et al.*, 2009), it may exhibit a large local
393 variability at short time scales. A recent study by Keppel-Aleks (*Keppel-Aleks et al.*, 2014) also
394 underscored the need to consider the full spatial and temporal distribution of atmospheric CO₂ to
395 accurately separate the climate events' (e.g., warming and drought) influence on carbon cycling.
396 Thus, GPP and NEE estimation should be improved if spatially- and temporally-varied atmospheric
397 CO₂ data are used.

398

399 4.5. Limitation

400 There are a number of limitations in our ANN estimations. First, the gridded CO₂ product was
401 developed using a global inversion model, whose accuracy is highly dependent on the prior CO₂
402 fluxes (*Masarie et al.*, 2011). In addition, inaccurate weather data in complex terrain also introduces
403 errors by using the transport model (TM5) at coarse spatial resolutions (*Geels et al.*, 2007). The
404 uncertain CO₂ product may bias our GPP and NEE estimations. To assess the uncertainty of the
405 NOAA CO₂ products, we did a comparison analysis between the 8-daily averaged NOAA gridded CO₂
406 values and the in-situ CO₂ observation in summer season at seven sites (Fig. S7). Generally, the
407 extracted CO₂ seasonal variations from NOAA products were comparable with the CO₂
408 measurement at forests (Fig. S7a, S7b and S7c) and crop sites (Fig. S7g), with the differences ranging
409 from 5 to 15 ppmv. The site-level sensitivity analysis (Fig.S8) showed that these CO₂ input data
410 differences would change annual GPP by 8 -50 g C (2%-6% relative change) using ANN models. In
411 particular, the GPP changes in the mixed forest and croplands were almost two times larger than in
412 other ecosystems. Despite the uncertainty of the gridded CO₂ product, we used it to gain insight
413 into the effects of CO₂ on regional GPP and NEE prediction when upscaling site-level data. High

414 frequency, stable CO₂ measurements (*Andrews et al.*, 2014) and high-density observation networks
415 (*Lauvaux et al.*, 2012) are needed to accurately quantify the atmospheric CO₂ effects on GPP.

416 Second, the selected AmeriFlux sites can contribute a large uncertainty to our model
417 development, because ANN training and validating are highly associated with the eddy flux data.
418 The representativeness of the AmeriFlux data is crucial to scaling up site-level measurement to large
419 regions. In our study, the criterion to select sites is based on the available CO₂ measurement from
420 2000 to 2006. The representativeness of the flux sites is crucial to scaling up site-level measurement
421 and to understand the carbon dynamics across large spatial scales and quantify uncertainty.
422 Although the global sites well represent variations in climate and ecological regions (*Reichstein et al.*,
423 2014), whether the major ecoregions from North America are well represented by the AmeriFlux
424 network has not been examined (*Hargrove et al.*, 2003). Using a cluster analysis with 25 climatic
425 and physiological forcing variables based on 59 AmeriFlux sites, Hargrove *et al.* (2003) showed that
426 the vast interior of the US was well-represented by the AmeriFlux network, but the Pacific
427 Northwest, Southern, and Southwestern were under represented. In addition, the uncertain eddy
428 flux data—due to system errors, random errors, site selection criteria (*Loescher et al.*, 2006), and
429 the gap-filling method (*Moffat et al.*, 2007; *Desai et al.*, 2008)—may affect the GPP and NEE
430 uncertainty in the model parameterization and simulation.

431 Third, our approach has not considered other controlling factors on the carbon fluxes. The
432 vegetation distribution was constant without any shifts or disturbances during the study period,
433 which might have biased estimation. Lacking the effects of land-cover changes, natural
434 disturbances (e.g., fire, hurricane, insect infestation), economic influences (e.g., harvest) and
435 demographic factors (*Lambin et al.*, 2003) would also introduce uncertainties to our

quantifications. Especially in the US, about half of the forest area is disturbed each decade, including the timber harvesting and grazing (*Birdsey and Lewis, 2003*). The forest age reflects the past disturbance history. Use of the North American forest stand age database (*Pan et al., 2011*) derived from forest inventory, historical fire data, and remote sensing imagery could help reduce our quantification uncertainty (*Deng et al., 2013; Xiao et al., 2014*). For cropland, without considering the effects of crop rotation (such as from corn to soybeans) may also introduce uncertainty. Since C4 photosynthetic capacity is different from C3 plant, explicit C3 versus C4 plant distribution data shall also help reduce the uncertainty of carbon qualification. In addition, the MODIS ecosystem distribution is not consistent with flux tower footprints (*Xiao et al., 2008*) and can be significantly different from the towers' vegetation type. Recent studies by Melton and Arora (2013) showed that the plant function type variability within the one-grid scale is important in simulating ecosystem responses to changing climate and atmospheric CO₂ concentration.

Fourth, using only seven plant functional types (PFTs) derived from the MODIS land use product may also introduce uncertainties to the carbon flux quantification. In the simulations, we assumed that, at each PFT level, the response of carbon fluxes to environmental condition changes is same. The usefulness and accuracy of such assumption has been questioned by field ecologists and there is a significant overlap between PFTs (*Reich et al., 2007*). The PFT-level parameterization could be biased because it may not properly represent the functional and structural characteristics of the species within a region. The parameter values obtained at the PFT level led to diverse significant carbon dynamic quantifications (*Alton, 2011; He et al., 2013*). Additionally, Reichstein *et al.* (2014) showed that the functional biogeographical variations of ecosystem properties were only partially explained by climate and PFTs. The large variability of biogeochemical processes

458 within each PFT (*Kattge et al.* 2011) depended even more on plant traits, such as allocation and
459 stabilization of carbon in the soil. Future studies should explicitly include the site-level information
460 and trait database to test the relation between ecosystem functions and organismic traits to
461 accurately quantify carbon fluxes.

462 Finally, the simplistic aggregation of CO₂ hour by hour into 8-day averages may bias our
463 quantification without considering the influence of the planetary boundary layer (PBL) development.
464 The PBL depth and turbulence intensity have a strong impact on the vertical and horizontal
465 distribution of CO₂ in the atmosphere (*Yi et al.*, 2001). The covariance between surface fluxes of CO₂
466 and the atmospheric mixing process has a strong seasonal character (*Helliker et al.*, 2004). Since the
467 rectifier effect influences the horizontal and vertical distributions of CO₂ in the atmosphere, it can
468 bias carbon flux quantification (*Denning et al.*, 1995). We further noted that we have not explicitly
469 differentiated CO₂ fertilization effects and its indirect effects on CO₂ uptake through affecting
470 stomata openness in these ANN simulations. Process-based ecosystem models shall incorporate
471 both fertilization and indirect effects into regional GPP and NEE quantification.

472

473 **5. Conclusion**

474 When scaling site-level eddy flux data to a region, the atmospheric CO₂ concentration on GPP
475 and NEE has rarely been incorporated. Here we made a step forward by considering this effect in
476 quantifying regional GPP and NEE in the conterminous US. We constructed two sets of artificial
477 neural networks incorporating remote sensing variables to upscale the AmeriFlux site-level data to
478 the region for seven ecosystem types: one that incorporated CO₂ and a second that did not. Our
479 results showed that both sets of models showed good performance and were able to capture the

480 GPP and NEE variation when compared with previous published results and MODIS products.
481 However, the GPP and NEE difference between two models exhibited a great spatial and seasonal
482 variability, which was closely related with climate drivers (air temperature and vapor pressure
483 deficit). In addition, the simulation without considering CO₂ effects fails to detect the ecosystem
484 response to droughts in the southeastern US in 2006, indicating that drought-induced surface
485 CO₂ variation could have more constraint on the regional GPP and NEE qualification. This study is
486 among the first to explore the CO₂ influence on the regional GPP and NEE estimation in upscaling
487 eddy flux data to regional scales. Our study suggests that the spatially and temporally varied CO₂
488 concentration should be factored into GPP and NEE quantification when scaling eddy flux data to a
489 region.

490

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823 Figure1. Selected AmeriFlux tower sites in this study.

824 Figure2. Annual averaged GPP (a) and NEE (c) in S0 and their differences (GPP (b), NEE (d)) between S0 and
825 S1 across the conterminous US scale from 2001 to 2006 (Unit: g C/(yr m²)). The difference is calculated as S0 minus
826 S1. S0 and S1 are the simulations with and without considering the atmospheric CO₂ concentration, respectively.

827 Figure3. Averaged monthly GPP (g C/(month m²)) for the conterminous U.S. from January through December from
828 2001 to 2006 in S0. S0 is the simulation with considering the atmospheric CO₂ concentration.

829 Figure4. Averaged monthly GPP difference (g C/(month m²)) between S0 and S1 for the conterminous U.S. from
830 January through December from 2001 to 2006. The difference is calculated as S0 minus S1. S0 and S1 are the
831 simulations with and without considering the atmospheric CO₂ concentration, respectively.

832 Figure5. Annual GPP (a, b), NEE (c, d), and anomalies in S0 and S1 for the conterminous U.S. at 2006. The
833 anomalies of annual GPP and NEE at 2006 were relative to the 6-year average value. The anomalies difference (e
834 and f) is calculated as S0 minus S1. S0 and S1 are the simulations with and without considering the atmospheric
835 CO₂ concentration, respectively.

836 Figure6. Air temperature and VPD controls on the annual GPP difference (the difference is calculated as S0 minus
837 S1) spatial variability for each vegetation type: (a) Evergreen forest; (b) Deciduous forest; (c) Mixed forest; (d)
838 Shrubland; (e) Savannas; (f) Grassland; and (g) Cropland. The mean values and standard deviations of GPP
839 difference in each vegetation types are presented. S0, and S1 are the simulations with and without considering
840 the atmospheric CO₂ concentration, respectively.

Table. 1 Ameriflux Sites used in ANN models

Site Name	Site ID	Vegetation Type	Data range
ARM SGP Control	US-Arc	Grasslands	2005–2006
ARM SGP Main	US-ARM	Cropland	2003–2006
Bartlett Experimental Forest	US-Bar	Deciduous broadleaf forest	2004–2005
Blodgett Forest	US-Blo	Evergreen needleleaf forest	2000–2006
Duke Forest Hardwoods	US-Dk2	Mixed Forest	2001–2005
Duke Forest Loblolly Pine	US-Dk3	Evergreen needleleaf forest	2001–2005
Fermi Agricultural	US-IB1	Cropland	2005–2006
Fermi Prairie	US-IB2	Grasslands	2004–2006
Fort Dix	US-Dix	Mixed Forest	2005–2006
Freeman Ranch Mesquite Juniper	US-FR2	Woody savannas	2004–2006
Harvard Forest	US-Ha1	Deciduous broadleaf forest	2000–2006
Harvard Forest Hemlock	US-Ha2	Evergreen needleleaf forest	2004
Howland Forest Main	US-Ho1	Evergreen needleleaf forest	2000–2004
Kendall Grassland	US-Wkg	Grasslands	2004–2006
Kennedy Space Center Scrub Oak	US-KS2	Shrubland	2000–2006
Mead Rainfed	US-Ne3	Cropland	2001–2005
Mead Irrigated	US-Ne1	Cropland	2001–2005
Mead Irrigated Rotation	US-Ne2	Cropland	2001–2005
Metolius Intermediate Pine	Us-Me2	Evergreen needleleaf forest	2003,2005
Metolius Second Young Pine	Us-Me3	Evergreen needleleaf forest	2004–2005
Morgan Monroe State Forest	US-MMS	Deciduous broadleaf forest	2000–2005
Lost Creek	US-Los	Shrubland	2001–2005
Missouri Ozark	US-MOz	Deciduous broadleaf forest	2004–2006
North Carolina Loblolly Pine	US-NC2	Evergreen needleleaf forest	2005–2006

Ohio Oak Openings	US_Oho	Deciduous broadleaf forest	2004–2005
Santa Rita Mesquite Savanna	US-SRM	Woody savannas	2004–2006
Sky Oak Old	US-SO2	Shrubland	2005–2006
Sky Oak Young	US-SO3	Shrubland	2005–2006
Sylvania Wilderness	US-Syv	Mixed Forest	2002–2006
Tonzi Ranch	US-Ton	Woody savannas	2001–2006
Univ of Mich Biological Station	USMS	Mixed Forest	2000–2003
Vaira Ranch	US-Var	Grasslands	2001–2006
Willow Creek	US-Wcr	Deciduous broadleaf forest	2000–2006
Wind River Field Station	US-Wrc	Evergreen needleleaf forest	2000–2004
Wisconsin Intermediate Hardwoods	US_Wi1	Deciduous broadleaf forest	2003
Wisconsin Mature Red Pine	US-Wi4	Evergreen needleleaf forest	2002–2005

Figure1

Figure2

Figure3

Figure4

Figure5

Figure6