

# On the difference in the net ecosystem exchange of CO<sub>2</sub> between deciduous and evergreen forests in the southeastern United States

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## Abstract

The southeastern United States is experiencing a rapid regional increase in the ratio of pine to deciduous forest ecosystems at the same time it is experiencing changes in climate. This study is focused on exploring how these shifts will affect the carbon sink capacity of southeastern US forests, which we show here are among the strongest carbon sinks in the continental United States. Using eight-year-long eddy covariance records collected above a hardwood deciduous forest (HW) and a pine plantation (PP) co-located in North Carolina, USA, we show that the net ecosystem exchange of CO<sub>2</sub> (NEE) was more variable in PP, contributing to variability in the difference in NEE between the two sites ( $\Delta$ NEE) at a range of timescales, including the interannual timescale. Because the variability in evapotranspiration (ET) was nearly identical across the two sites over a range of timescales, the factors that determined the variability in  $\Delta$ NEE were dominated by those that tend to decouple NEE from ET. One such factor was water use efficiency, which changed dramatically in response to drought and also tended to increase monotonically in nondrought years ( $P < 0.001$  in PP). Factors that vary over seasonal timescales were strong determinants of the NEE in the HW site; however, seasonality was less important in the PP site, where significant amounts of carbon were assimilated outside of the active season, representing an important advantage of evergreen trees in warm, temperate climates. Additional variability in the fluxes at long-time scales may be attributable to slowly evolving factors, including canopy structure and increases in dormant season air temperature. Taken together, study results suggest that the carbon sink in the southeastern United States may become more variable in the future, owing to a predicted increase in drought frequency and an increase in the fractional cover of southern pines.

**Keywords:** carbon flux, drought, eddy covariance, evapotranspiration, net ecosystem exchange, water use efficiency, wavelet spectra

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## Introduction

The forests of the warm and mesic southeastern United States confer a number of economic benefits and ecological services that are directly linked to patterns of ecosystem carbon and water cycling. Specifically, they produce more timber than any other forestry region in the United States (Wear & Greis, 2012), and they play key roles in controlling the quantity and quality of stream water and water available for human

consumption (Bolstad & Swank, 1997; Oishi *et al.*, 2010; Ford *et al.*, 2011). They are also important sinks for anthropogenic emissions of CO<sub>2</sub> (Brown & Schroeder, 1999; Albani *et al.*, 2006). When surveying previously published estimates of the net ecosystem exchange of CO<sub>2</sub> (NEE) from continental US ecosystems, it is clear that southeastern US forests are among the strongest carbon sinks (Fig. 1, Table S1). For instance, in several southeastern US forests, the minimum observed NEE (representing the strongest observed annual carbon sink) was  $< -700$  g C m<sup>2</sup>, which places these forests within the top 10% of observed annual carbon sinks not only in the continental United States (i.e. Fig. 1) but

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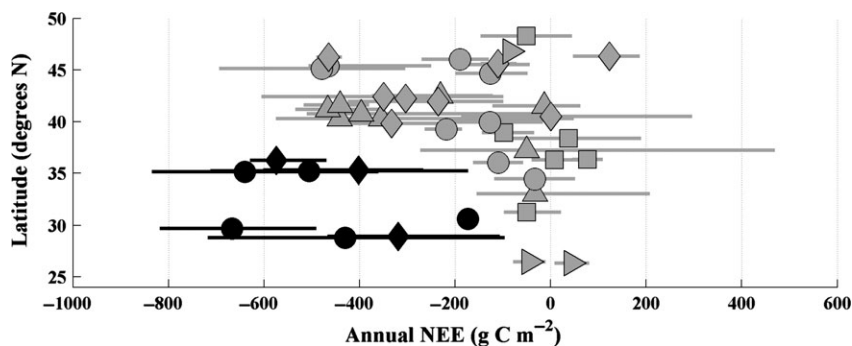
also globally (see Baldocchi, 2008, who reported a mean NEE of  $183 \pm 270$  g C m<sup>2</sup> from 506 site years of data representing a range of global biomes). Further, the mean value of annual NEE in most southeastern US forests is  $< -400$  g C m<sup>2</sup>, which is outside of the range of observed NEE in two-thirds of the ecosystems surveyed.

However, in the southeastern United States, the magnitude of NEE and related ecosystem benefits are sensitive to ongoing shifts in the land cover regime affecting the relative distribution of deciduous and evergreen forests. Much of the eastern United States, which was historically dominated by late-successional hardwood forests and fire-dominated pine woodlands (Stanturf *et al.*, 2002; Abrams, 2003), was cleared and converted to farmland between 1800 and 1930 (Hall *et al.*, 2002; McEwan *et al.*, 2011). Since then, agricultural abandonment beginning in the mid-20<sup>th</sup> century has resulted in an increase in the fractional forest cover of the southeastern United States (Ramankutty *et al.*, 2011; Wear & Greis, 2012). Following well-established patterns of ecological succession (Oosting, 1942), many of these abandoned farm fields have developed into mixed deciduous hardwood forests. However, due to a doubling of softwood timber production in the southeastern United States over the last 40 years (Wear & Greis, 2012), pine plantations now comprise over 160 000 km<sup>2</sup> in the region. The abundance of southern pine forests is expected to increase over coming decades, with an important shift toward establishment on cleared hardwood forest lands (Wear & Greis, 2012). While both southern pine and hardwood forests are capable of assimilating large amounts of CO<sub>2</sub> from the atmosphere, the range of annual NEE can differ considerably between these two ecosystems, even when they

experience similar climate or are located at approximately the same latitude (Fig. 1, Stoy *et al.*, 2008; Powell *et al.*, 2008).

Complicating efforts to predict how these patterns of land-use change will affect regional carbon and water cycling is the fact that NEE in both southeastern US forests types is highly variable from year to year. For instance, the range of annual NEE exceeds 300 g C m<sup>2</sup> in six of the eight southeastern US forests ecosystems surveyed in Fig 1. This variability may reflect patterns of canopy development, but it also may reflect sensitivity to meteorological drivers, which themselves are nonstationary. Indeed, over the past century, changes in annual temperature, atmospheric CO<sub>2</sub> concentration, and hydrologic regime have been observed in the eastern United States (Ford *et al.*, 2011; Laseter *et al.*, 2012; Brzostek *et al.*, 2014) and are predicted to continue in the future (Huntington, 2006; Dai, 2011). Thus, efforts to predict the magnitude and variability in regional NEE in the southeastern United States must consider the extent to which southeastern US hardwood and pine forests differentially respond to climate forcings.

A number of independent investigations have characterized the relation between the carbon and/or water vapor exchange of southeastern US forests and their meteorological drivers (Wilson & Baldocchi, 2001; Lai *et al.*, 2002; Schäfer *et al.*, 2002, 2003; Pataki & Oren, 2003; Clark *et al.*, 2004; Wullschlegel *et al.*, 2004; Palmroth *et al.*, 2005; Mccarthy *et al.*, 2006; Novick *et al.*, 2009a; Noormets *et al.*, 2010; Sun *et al.*, 2010; Ward *et al.*, 2013; Whelan *et al.*, 2013). In general, these studies reveal that the magnitude of NEE tends to be highly sensitive to hydrologic conditions (Baldocchi, 1997; Wilson & Baldocchi, 2001; Stoy *et al.*, 2005; Noormets *et al.*, 2010; Whelan *et al.*, 2013) and to patterns of



**Fig. 1** The mean (symbols) and range (lines) of NEE derived from eddy covariance flux towers in the continental United States. The sites were selected by identifying all sites in the Ameriflux network with at least 4 years of available data, and then extracting previously published estimates of NEE from the literature (see supplementary information for more details). Grasslands and shrublands are identified with squares, agricultural sites with upward pointing triangles, evergreen forests with circles, deciduous forests with diamonds, and wetland sites with right pointing triangles. Southeastern US forests are shown in black. Negative NEE indicates a carbon sink.

canopy development related to disturbance (Clark *et al.*, 2004; McCarthy *et al.*, 2006; Stoy *et al.*, 2008). However, only a few of these studies have attempted such an investigation in colocated pine and hardwood forests, which permits a disentangling of how the two ecosystem types differentially respond to meteorological forcings. Fewer still attempt such an investigation over sufficiently long time periods (i.e. near-decadal) to evaluate the effect of drivers that vary over time scales commensurate with climate change and canopy development.

The principle objective of this study, which leverages long-term flux records collected in colocated pine and hardwood forests in central NC (USA), was to explore how carbon and water fluxes in these important forest types differentially respond to climatic forcings that operate over timescales ranging from hours to years. In meeting this objective, we will specifically address the following research questions:

- To what extent do the magnitude and variability in ecosystem-scale carbon and water fluxes differ between the two principle southeastern US forest types?
- What timescales of variability are associated with the largest differences in fluxes between the two sites?
- What biophysical mechanisms are most likely responsible for observed differences?

The answers to these questions will reflect the relative advantages for ecosystem carbon uptake of deciduousness vs. evergreenness in the warm, mesic southeastern US. Predictions drawn from classic studies on the topic include: (i) greater magnitude of NEE in the evergreen forest, reflecting the relatively large difference between gross ecosystem productivity and ecosystem respiration predicted for mid-successional forests (Odum, 1969), (ii) greater drought tolerance in the deciduous site (Givnish, 2002), and (iii) relatively less seasonal contrast in evergreen forest NEE (Hollinger, 1992; Givnish, 2002).

With this study, we will build upon these previous efforts and extend the scope of analysis to characterize the variability in NEE driven by other factors that vary over time scales commensurate with climate change and canopy development (i.e. near-decadal). At these timescales, we expect that biophysical mechanisms responsible for these differences, if they exist, may include a range of processes already shown to impact long-term forest carbon and water cycling in other ecosystems, including canopy development and recovery from disturbance (Law *et al.*, 2001; Amiro *et al.*, 2010), long-term trends in temperature and the length of the growing season (Dragoni *et al.*, 2011; Keenan *et al.*, 2014), and long-term variation in water use efficiency

(Katul *et al.*, 2010; Manzoni *et al.*, 2011; Keenan *et al.*, 2013).

## Methods

### *The study sites*

The pine plantation (PP) and hardwood forest (HW) study sites were located in the Blackwood Division of the Duke Forest near Durham, North Carolina (35° 58' 41"N, 79° 05' 59"W, 163 m a.s.l.), and the PP site was situated within an ambient CO<sub>2</sub> ring of the Duke Free-Air Carbon Enrichment (FACE) experiment. These ecosystems vary in vegetation cover and canopy structure, but experience nearly identical climatic and edaphic conditions. The pine plantation was established in 1983 following a clear cut and a burn. *Pinus taeda* L. (Loblolly pine) seedlings were planted at a 2.0 m by 2.4 m spacing with pine density reduced to approximately 1100 trees ha<sup>-1</sup> after 15 years. Canopy height increased from 16 meters in 2001 to over 20 meters in 2008. The hardwood forest is classified as an uneven-aged (90–110 year old) oak (*Quercus*)–hickory (*Carya*) forest. The stand is dominated by hickories [*Carya tomentosa* (Poir.) Nutt., *C. glabra* (P. Mill.) Sweet.], yellow poplar (*Liriodendron tulipifera* L.), sweetgum (*Liquidambar styraciflua* L.), and oaks (*Quercus alba* L., *Q. michauxii* Nutt., *Q. phellos* L.). Coniferous species including *Pinus taeda* L. and *Juniperus virginiana* L. make up a minor component of the over- and understory, respectively (Pataki & Oren, 2003; Oishi *et al.*, 2008). The forest was not managed after establishment, and mean canopy height is 25 m. Both ecosystems have little topographic variation and lie on Enon silt loam, and a clay pan underlies the research sites at a depth of ~ 35–50 cm, imposing similar constraints on root-water access for both ecosystems. Long-term mean annual temperature and precipitation are 15.5 °C and 1146 mm. More details about the study sites are available in Stoy *et al.* (2006a,b) and Novick *et al.* (2009a).

### *Eddy covariance, meteorological, and leaf area measurements*

NEE and the latent heat flux (LE) were measured above the canopies from 2001 to 2008 using eddy covariance systems comprised of triaxial sonic anemometers (CSAT3, Campbell Scientific, Logan, UT, USA) and open-path infrared gas analyzers (LI-7500, Li-Cor, Lincoln, NE, USA), with the flux towers decommissioned in 2009. Wind and scalar concentration measurements were collected at 10 Hz, and for most of the study period, fluxes were processed in real time. The gas analyzers were calibrated twice each year (at the beginning and end of the growing season), with little variation in the calibration coefficients observed over time. Half-hourly meteorological and edaphic measurements were also collected in each site, including air temperature ( $T_a$ ), vapor pressure deficit ( $D$ ), photosynthetically active radiation (PAR), soil moisture content ( $\theta$ ) and precipitation (PPT). Friction velocity ( $u^*$ ) was calculated from the high-frequency wind velocity data. In each site for a portion of the study period, a multilayer concentration monitoring

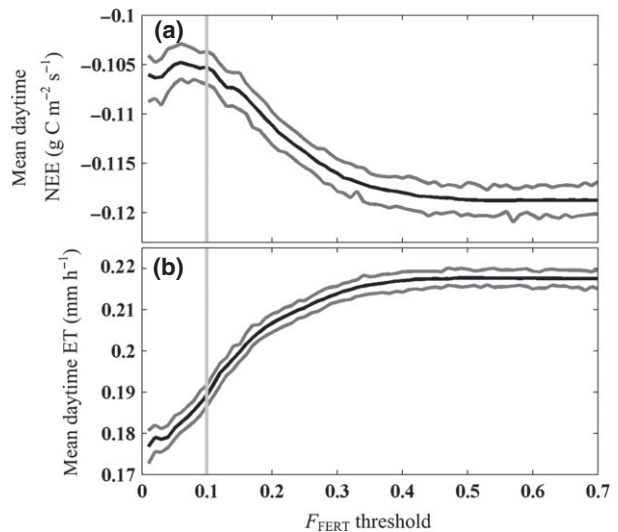
system was installed to measure the mean water vapor and CO<sub>2</sub> concentration at 10 different levels throughout the canopy volume using a Li-Cor 6262 CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer. These profiling systems included a multi-port gas sampling manifold to sample each level for 1 min (45 s sampling and 15 s purging) with a repeated cycle of 10 min. Profile data were recorded as 30 min averages. Evapotranspiration (ET, mm) was derived from the latent heat flux time series using the temperature-dependent latent heat of vaporization.

Ground-based leaf area index (LAI) measurements were made in PP during the entire eight year study period (McCarthy *et al.*, 2007), and from 2001 to 2005 in HW (Oishi *et al.*, 2008) using litterfall and light-penetration measurements, and then interpolated to a daily time step. To generate a complete eight year record of leaf area index in HW, MODIS LAI data (Myneni *et al.*, 2002) were obtained for the pixel that includes the hardwood site. The MODIS data were interpolated and scaled so that the mean minimum and maximum MODIS LAI from 2001 to 2005 match the mean minimum and maximum ground-based LAI from the same time period. The interpolated and scaled MODIS time series from 2006 to 2008 was then appended to the ground-based measurements to generate the eight year record for the HW site. Estimates of the monthly Palmer Drought Severity Index (PDSI) at the study sites were obtained from the National Oceanic and Atmospheric Administration (NOAA, <http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php>).

### Flux footprint considerations

Fluxes were screened to remove measurements collected when the footprint was not representative of the study ecosystem. In PP, the flux records may be contaminated by fluxes originating from a small portion of the study site receiving annual fertilization from 2005 to 2008 as part of FACE protocol. We used the footprint model of Hsieh *et al.* (2000), extended to two dimensions by Detto *et al.* (2006), to estimate the flux footprint for every half-hour averaging period, and then quantified the fraction of the footprint that overlaid the fertilized area ( $F_{\text{FERT}}$ ). We then iteratively estimated the total daytime NEE and ET measured from 2005 to 2008 (i.e. the fertilization period) by progressively increasing the maximum permissible value of  $F_{\text{FERT}}$ . We found that the total NEE remained relatively stable as long as  $F_{\text{FERT}}$  was less than 0.10 (Fig. 2a). A similar relation was not observed in the ET fluxes, though the change in ET as the  $F_{\text{FERT}}$  filter was increased from 0.0 to 0.10 was small (<5%). As  $F_{\text{FERT}}$  increased further, NEE decreased (i.e. became larger sink for CO<sub>2</sub>), and ET continued to increase (Fig. 2b). We note that  $F_{\text{FERT}}$  values greater than 0.5 comprised less than 0.5% of the data record. On the basis of these results, we excluded all PP flux measurements associated with  $F_{\text{FERT}} > 0.10$ . While the results are not shown here, we note that the study results are largely invariant for  $F_{\text{FERT}}$  thresholds as low as 0.03, and also do not change if the fertilization sector filter is applied to data collected before the nutrient amendments began (i.e. years 2001 to 2004).

A clear cut on private land 200 m south of the HW tower occurred in late November 2002. Using the same footprint



**Fig. 2** The average NEE (panel a) and ET (panel b) in PP as a function of the maximum permissible fraction of the flux footprint that overlies the fertilized portion of the study area ( $F_{\text{FERT}}$ ). Gray lines represent 95% confidence intervals determined from a nonparametric bootstrap.

model, Stoy *et al.* (2006b) determined that the effect of this clear cut was evident in the flux records. Thus, the HW flux data were filtered to remove data collected when more than 30% of the flux footprint originated from the clear cut. These data were further adjusted as described in Stoy *et al.* (2006b) to account for the fact that the application of the footprint filter in 2003 also selectively filters ideal climate conditions.

### Eddy covariance data processing – NEE fluxes

The Webb–Pearman–Leuning correction (Webb *et al.*, 1980) for air density fluctuations was applied to the half-hourly NEE and LE fluxes. The NEE data were initially screened to remove any flux measurements whose absolute magnitude exceeded  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The data were then screened to remove measurements collected during suboptimal meteorological conditions using the online eddy covariance processing tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc>), which employs the  $u^*$  filtering method of Reichstein *et al.* (2005).

These filtering and quality control procedures create a number of gaps in the data records that must be gapfilled to derive annual flux estimates (Falge *et al.*, 2001). Furthermore, to understand the processes that control NEE, it is desirable to partition measured NEE fluxes into the primary components GEP and RE, where  $\text{NEE} = -\text{GEP} + \text{RE}$ , and a negative NEE flux denotes carbon assimilation by the ecosystem. We adopted the gapfilling and partitioning methods of Van Gorsel *et al.* (2009), hereafter VG2009, which is designed to exclude data collected when nocturnal vertical and horizontal advection fluxes prevent a straightforward interpretation of measured turbulent fluxes as representative of the integrated ecosystem scalar sources and sinks. The approach assumes



that the contribution of advection to the total ecosystem flux is minimized during early evening hours, when the sum of measured eddy covariance fluxes and canopy storage fluxes should be representative of total ecosystem respiration fluxes. During periods when the gas profile systems were active, storage fluxes of CO<sub>2</sub> were estimated by integrating temporal changes in CO<sub>2</sub> concentration within the canopy (Juang *et al.*, 2006; Novick *et al.*, 2014); otherwise, they were estimated using site-specific relationships between the ratio of storage to turbulent CO<sub>2</sub> fluxes and friction velocity ( $u^*$ ).

Data representing the sum of turbulent and storage fluxes collected within two hours of the time of the observed monthly peak in measured RE were used to parameterize a temperature-dependent model of the form  $RE = \varepsilon_1 \exp(\varepsilon_2 T_a)$ , where  $\varepsilon_1$  is a parameter related to the base respiration rate, and  $\varepsilon_2$  describes the temperature sensitivity of RE. The latter was estimated on an annual time step to avoid situations in which the temperature range of the data used to parameterize the model was much smaller than the temperature range of the data needing to be gapfilled. The base respiration rate parameter was then estimated on a weekly time step using all acceptable, early evening data collected within 3 weeks (i.e. by using a moving 6 week window). This continuous RE record was used to gapfill missing nocturnal data.

Missing daytime data, which represent <5% of all missing data, were gapfilled with the approach of Lasslop *et al.* (2010), hereafter L2010, which is supported by the online flux tool. The L2010 approach links GEP to PAR via:

$$GEP = \frac{\alpha \beta PAR}{\alpha PAR + \beta} \quad (1)$$

where  $\alpha$  is the mean apparent ecosystem quantum yield, and  $\beta$  is the maximum assimilation rate which is modified to account for humidity effects according to:

$$\beta = \beta_0 \quad \text{when } D \leq 1 \text{ kPa} \quad (2)$$

$$\beta = \beta_0 \exp[-k(D - D_0)] \quad \text{when } D > 1 \text{ kPa}$$

where  $\beta_0$  is a reference assimilation rate at low  $D$ ,  $k$  is the humidity response parameter, and  $D_0$  is set to 1 kPa. Following L2010, daytime respiration is modeled as a function of air temperature according to:

$$RE = r_0 \exp \left[ E_0 \left( \frac{1}{T_{ref} - T_0} - \frac{1}{T_a - T_0} \right) \right] \quad (3)$$

The parameter  $r_0$  is a base respiration rate and the parameter  $E_0$  is a temperature response parameter. The reference temperature parameter  $T_{ref}$  was set to 15 °C and the parameter  $T_0$  was set to -46 °C. The parameters were fit using 4–12 day moving windows.

The VG2009 flux records were compared to annual fluxes estimated in an earlier effort by Stoy *et al.* (2006b), hereafter S2006. The S2006 approach does not rely on the Reichstein *et al.* (2005)  $u^*$  filter; rather, data quality control is largely governed by the magnitude of the atmospheric stability parameter (see Novick *et al.*, 2004). The S2006 fluxes were gapfilled and partitioned using a light-response model for NEE that is similar to the L2010 model, but is parameterized at a different time step and does not include a humidity response parameter.

### Eddy covariance data processing – LE fluxes

The same  $u^*$  filter described in the previous section was also applied to the LE flux records. In addition, measured LE fluxes outside of a conservative expectation window of -200 to 800 W m<sup>2</sup> were removed from the time series. For consistency with a previous study, LE records were gapfilled using the marginal distribution methodology (Reichstein *et al.*, 2005) described in Novick *et al.* (2009a). ET flux magnitudes presented here differ slightly (<5%) from those presented Novick *et al.* (2009a) owing to different filtering procedures, and the fact that Novick *et al.* (2009a) did not include the footprint filters, but were nonetheless within the uncertainty bounds of annual ET flux in the study forests (Stoy *et al.*, 2006a; Novick *et al.*, 2009a).

### Spectral analysis of flux records

To explore the timescales of variability in NEE and ET, we relied on a wavelet spectral decomposition. We refer readers to Stoy *et al.* (2005, 2009), Torrence & Compo (1998), and Katul *et al.* (1998) for a thorough discussion of the utility and application of wavelet transforms, which are an appropriate tool for spectral analysis of nonstationary and discontinuous time series (Katul *et al.*, 1998; Stoy *et al.*, 2005; Dietze *et al.*, 2011). Briefly, the purpose of this spectral analysis was to quantify the energetic frequencies/timescales in a signal (i.e. NEE or ET), and to relate those energetic timescales to the timescales of variability in meteorological drivers. Determining the wavelet spectra of a single time series (i.e. NEE or ET) permits an identification of the fraction of the variability in the signal attributable to processes operating at specific timescales/frequencies. The determination of a wavelet cospectra describing interactions between two time series permits an identification of the frequencies at which they most significantly coresonate.

We employed an orthonormal wavelet transformation with the Haar basis function to characterize the energetic frequencies of NEE and ET by relying only on measured data, and not gapfilled data (which were set = 0), so that the spectral decomposition would not be strongly affected by the choice of gapfilling approach. The filtered time series were normalized to have zero mean and unit variance, and were zero-padded to a length equal to the power of 2 greater than the length of the data record (in this case, 2<sup>18</sup>, noting that the 8 year data records contain 140 256 half-hourly data points). The wavelet coefficients were determined and summed within dyadic time scales ranging from 2<sup>1</sup> (hourly) to 2<sup>16</sup> (nearly 4 years) as the wavelet coefficients associated with longer (i.e. ~ 8 year, or 2<sup>17</sup> h) timescales are generally unreliable (Stoy *et al.*, 2005).

We also relied on the wavelet cospectra to explore the extent to which the difference in NEE between the two sites ( $\Delta$ NEE) coresonates with meteorological factors, including PAR,  $T_a$ ,  $D$ ,  $\theta$ , and atmospheric CO<sub>2</sub> concentration. Specifically,  $\Delta$ NEE was determined at the half-hourly timestep and then normalized to have zero mean and unit variance, as were the meteorological drivers. The cross-spectra were determined after Katul *et al.* (1998). All wavelet analyses were performed in Matlab using the Wavelet Toolbox (Mathworks, Natick, MA, USA).

### Phenological and seasonality indices

We relied on an approach for active season delineation that first identifies the days of each year when the time derivative of GEP ( $dGEP/dt$ ) reached a minimum and maximum, respectively, representing the days when GEP was changing most rapidly in spring and in fall. Before identifying the minimum and maximum  $dGEP/dt$ , a smoothed spline curve was fitted to the daily time series of GEP. We choose to use GEP, and not LAI, to delineate the active season for two reasons: (i) ground-based measurements of LAI were not performed at a sufficiently fine temporal frequency in the HW site (i.e. weekly or every 2 weeks) for the duration of the study period, and (ii) recent work has shown that the relation between assimilation capacity and leaf area index varies considerably over the course of the growing season (Bauerle *et al.*, 2012).

### Ecosystem-scale water use efficiency

We considered two approaches for characterizing water use efficiency at each site. The first is the 'inherent water use efficiency' ( $WUE_i$ ) metric proposed by Beer *et al.* (2009) and more recently used by Keenan *et al.* (2013). The inherent water use efficiency recognizes the potential for variation in  $D$  to modify the total water use efficiency (i.e.  $GEP/ET$ , presuming ET is dominated by transpiration, Jasechko *et al.*, 2013), and is formulated as:

$$WUE_i = \frac{GEP}{ET} D \quad (4)$$

The second metric, here termed the 'ecosystem marginal water use efficiency' ( $\lambda_E$ ), is derived from applications of stomatal optimization theory to explore the effect of variations in atmospheric  $CO_2$ ,  $D$ , and hydrologic conditions on leaf gas exchange (Katul *et al.*, 2009, 2010; Manzoni *et al.*, 2011). If stomata are assumed to function so as to maximize carbon gain while minimizing water loss, then the Hamiltonian of the system can be expressed as  $H=A-\lambda T$  and optimality is achieved with respect to the control variable (stomatal conductance  $g$ ) via.

$$\frac{\partial H}{\partial g} = 0 \quad (5)$$

where  $A$  and  $T$  are leaf-level assimilation and transpiration rates, respectively,  $g$  is stomatal conductance to  $CO_2$ , and  $\lambda$  ( $=\partial A/\partial E$ ) is the leaf-level marginal water use efficiency, representing the carbon cost of a unit of transpired water. When Eqn (5) is coupled to a linearized variant of the Farquhar assimilation model (Farquhar *et al.*, 1980; Katul *et al.*, 2010) and to Fickian-diffusion type expressions for  $A$  and  $E$ , it may be shown, following Katul *et al.* (2010), that

$$\lambda = \frac{\partial A}{\partial E} = \frac{1}{ac_a} \left( \frac{A}{E} \right)^2 D, \quad (6)$$

where  $a$  is the ratio of molecular diffusivities between  $H_2O$  and  $CO_2$ , and  $c_a$  is the atmospheric  $CO_2$  concentration. We note that this parameter  $\lambda$  is an important input into a relatively new suite of stomatal conductance models based in optimization theory (Katul *et al.*, 2009; Katul *et al.*, 2010; Manzoni *et al.*, 2011), though here we are principally focused on exploring the utility of a big-leaf (i.e. ecosystem-scale) analog to Eqn (6) (i.e.

$\lambda_E$ ) to explain cross-site differences in the dynamics of GEP and ET. The parameter  $\lambda_E$  is determined from:

$$\lambda_E = \frac{1}{ac_a} \left( \frac{GEP}{ET} \right)^2 D \quad (7)$$

The units of  $WUE_i$  are expressed as  $g C kg^{-1} H_2O/hPa$  for consistency with Keenan *et al.* (2013), and the units of  $\lambda_E$  are expressed as  $\mu mol m^{-2} s^{-1}$  for consistency with Katul *et al.* (2009).

Interpretation of both  $WUE_i$  and  $\lambda_E$  requires that ET be dominated by transpiration. During the growing season, LAI at the two study sites typically exceeds  $5 m^2 m^{-2}$ , such that little radiation reaches the canopy floor, and soil evaporation is assumed to be small (Stoy *et al.*, 2006a; Oishi *et al.*, 2008). Thus, we limit the analysis of water use efficiency to data collected when leaf area index is relatively stationary (May–September), and when at least 2 days have elapsed since a rain event, after which it is assumed that the contribution of canopy interception evaporation to total ET is negligible, and soil evaporation is likely limited not only by radiation but also by soil moisture. Thus, for continued discussions of these water use indices, we assume ET and  $E$  are indistinguishable.

The quantities  $WUE_i$  and  $\lambda_E$  are related, but with some key differences. Mathematically, given Fickian-diffusion type relations for GEP [ $GEP = g/(c_a - c_i)$ ] and ET ( $ET = agD$ ), where  $g$  and  $c_i$  are here interpreted as integrated canopy averages,  $WUE_i$  reduces to

$$WUE_i = \frac{GEP}{ET} D = \frac{g(c_a - c_i)}{agD} D = \frac{c_a - c_i}{a} \quad (8)$$

Or in other words, variations in  $WUE_i$  are due solely to variations in the quantity  $(c_a - c_i)$ . The marginal water use efficiency may then be related to  $WUE_i$  as:

$$\begin{aligned} \lambda_E &= \frac{1}{ac_a} \left( \frac{GEP}{ET} \right)^2 D = \frac{1}{ac_a} \left( \frac{g(c_a - c_i)}{agD} \right)^2 D = \frac{1}{ac_a D} WUE_i^2 \\ &= \frac{1}{a^3 c_a D} (c_a - c_i) WUE_i, \end{aligned} \quad (9)$$

Thus, both  $\lambda_E$  and  $WUE_i$  are sensitive to variations in the quantity  $(c_a - c_i)$ , which could be due to increases in  $c_a$  or increases in  $D$  that induce stomatal closure and thereby reduce  $c_i$ . However, they will become increasing decoupled with increasingly large changes in  $(c_a - c_i)$  and  $D$ , reflecting the fact that these two driving variables may affect the carbon cost of a unit of transpired water beyond their effect on  $WUE_i$ . Both quantities are useful for interpreting how gas exchange dynamics respond to varying climatic conditions, though the parameter  $\lambda_E$  has the advantage of being derived from a theoretical framework grounded in the assumption that stomata function to minimize water loss while maximizing carbon gain.

## Results

### Meteorological and hydrological variability during the study period

The study period was marked by variability in meteorological and hydrological forcing factors operating at a

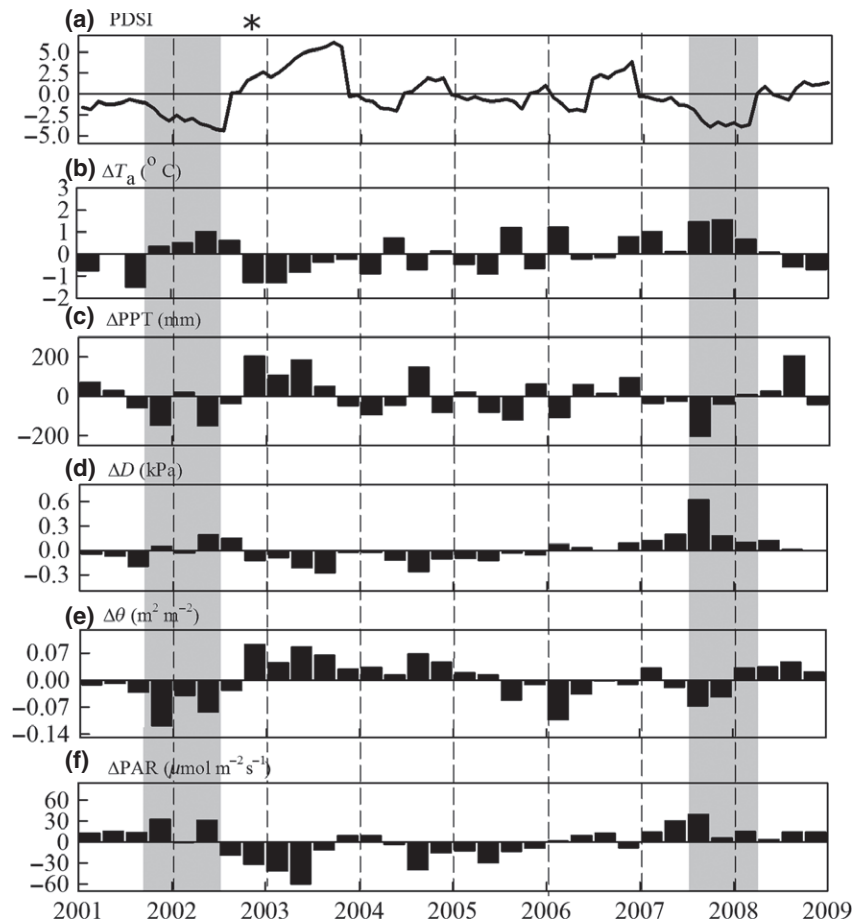
range of time scales, and included two severe drought events. The first began late in 2001 and persisted until the latter part of the growing season in 2002, and the second drought period began early in the 3rd quarter of 2007 and persisted through the 1st quarter of 2008. During both of these drought events, the regional Palmer Drought Severity Index (PDSI) dipped below  $-4$  (Fig. 3), which is considered the threshold for extreme drought. Moderate drought events were experienced in 2001 and 2005 (Fig. 3), when soil moisture, precipitation, and the PDSI were below average, but excursions were not as severe as in 2002 or 2007.

The study sites experienced a severe ice storm event in December 2002. The storm reduced leaf area index in PP by 12–14% in 2003, though the canopy quickly recovered (Mccarthy *et al.*, 2006). The ice storm had little effect on canopy structure in HW, where the absence of leaves during the dormant season reduced branch ice accumulation and thus damage.

The study period was characterized by a long-term increasing trend in active season  $D$  during non-drought years (slope =  $0.05 \text{ kPa yr}^{-1}$ ,  $P = 0.04$ ), and a long-term trend in dormant season air temperature after excluding drought years (slope =  $0.03 \text{ degrees C yr}^{-1}$ ,  $P = 0.03$ ). There was no observed trend in mean annual temperature.

*Annual flux magnitudes and trends within and across sites*

The choice of QC/gapfilling methodology (e.g. VG2009 vs. S2006) affects the magnitudes of the fluxes (Table 1, Fig. 4). We note that while S2006 estimated fluxes for year 2005, we omitted them from this comparison as that study did not employ a footprint filter to remove measurements originating from the fertilized sector of PP. During the years for which fluxes estimated with the VG2009 and S2006 approach were available (2001–



**Fig. 3** Climatic variables measured during the study period. Panel (a) shows the interpolated Palmer Drought Severity Index (PDSI). Other panels show quarterly deviations from the study period mean air temperature ( $T_a$ , b), precipitation (PPT, c), vapor pressure deficit ( $D$ , d), soil moisture content ( $\theta$ , e), and photosynthetically active radiation (PAR, f), as measured in the pine site. The two drought events are highlighted in gray, and the date of the ice storm is indicated with the asterisk.

**Table 1** Annual fluxes of the net ecosystem exchange of CO<sub>2</sub> (NEE), gross ecosystem productivity (GEP), ecosystem respiration (RE) (in g m<sup>-2</sup>), and evapotranspiration (ET, in mm) at the pine plantation and hardwood forest ecosystems in the Duke Forest, NC. The data show the annual fluxes, and the growing season fluxes in parentheses. Carbon fluxes are calculated using two different approaches to gapfilling and partitioning: the Van Gorsel *et al.* (2009) approach (VG2009) and the Stoy *et al.* (2006b) approach (S2006)

Year	VG2009 Approach				S2006 Approach		
	NEE	RE	GPP	ET	NEE	RE	GPP
<b>Pine</b>							
2001	-564 (-492)	1760 (1078)	-2324 (-1570)	740 (508)	-610 (-443)	1340 (907)	-1950 (-1350)
2002	-307 (-142)	1745 (1262)	-2042 (-1406)	678 (416)	-270 (-138)	1610 (972)	-1860 (-1111)
2003	-173 (-165)	1665 (1138)	-1838 (-1303)	832 (526)	-220 (-298)	1730 (888)	-1950 (-1186)
2004	-523 (-302)	1733 (1257)	-2256 (-1558)	860 (551)	-420 (-219)	1760 (1193)	-2190 (-1412)
2005	-635 (-391)	1769 (1233)	-2404 (-1624)	888 (586)			
2006	-712 (-380)	2121 (1557)	-2833 (-1946)	916 (577)			
2007	-547 (-244)	1824 (1159)	-2371 (-1403)	793 (478)			
2008	-561 (-140)	2136 (1490)	-2678 (-1630)	876 (549)			
Mean	-506 (-282)	1844 (1272)	-2344 (-1555)	823 (524)	-381 (-274)	1607 (990)	-1989 (-1265)
SD	173 (131)	181 (169)	317 (197)	81 (56)	173 (130)	189 (140)	130 (140)
<b>Hardwood</b>							
2001	-367 (-455)	1472 (1060)	-1839 (-1516)	622 (452)	-510 (-598)	1200 (650)	-1710 (-1248)
2002	-341 (-411)	1310 (888)	-1651 (-1300)	608 (436)	-390 (-445)	1320 (797)	-1710 (-1232)
2003	-267 (-332)	1430 (1068)	-1696 (-1401)	747 (510)	-400 (-531)	1250 (724)	-1650 (-1254)
2004	-384 (-453)	1415 (985)	-1799 (-1439)	702 (489)	-420 (-573)	1313 (705)	-1750 (-1278)
2005	-422 (-502)	1460 (962)	-1882 (-1464)	814 (599)	-490 (-570)	1230 (700)	-1720 (-1269)
2006	-602 (-666)	1742 (1148)	-2344 (-1815)	783 (553)			
2007	-403 (-494)	1852 (1194)	-2255 (-1688)	691 (490)			
2008	-432 (-634)	1960 (1199)	-2393 (-1832)	794 (562)			
Mean	-402 (-494)	1585 (1063)	-1989 (-1561)	720 (508)	-444 (-543)	1261 (715)	-1705 (-1258)
SD	96 (110)	243 (113)	305 (192)	78 (56)	52 (60)	53 (54)	35 (15)

2005 for HW, 2001 – 2004 for PP), VG2009 and S2006 estimates of mean annual NEE differed by 60 g C m<sup>-2</sup> yr<sup>-1</sup> in the PP and 88 g C m<sup>-2</sup> yr<sup>-1</sup> in HW, on average, representing 14% and 20% of the mean annual NEE, respectively. Over the course of the comparison period, the VG2009 and S2006 estimates of PP GEP and RE agreed to within 200 and 130 g C m<sup>-2</sup> yr<sup>-1</sup>, or 9% and 7%, respectively. The VG2009 and S2006 estimates of HW GEP agreed to within 70 g C m<sup>-2</sup> yr<sup>-1</sup> (or 4%), and to within 160 g C m<sup>-2</sup> yr<sup>-1</sup> (or 11%) for HW RE. Particularly large differences between PP GEP and RE fluxes estimated by the two methods were observed in year 2001, which is not surprising as much of the first 3 months of PP data were missing in 2001 due to a technical problem. In general, variations in the annual NEE fluxes between the two approaches are well correlated in the PP site ( $r = 0.93$ ), and moderately correlated in the HW site ( $r = 0.66$ , Fig. 4), which experienced less annual variability as discussed below. For the remaining analysis, we use the VG2009 flux records unless otherwise noted.

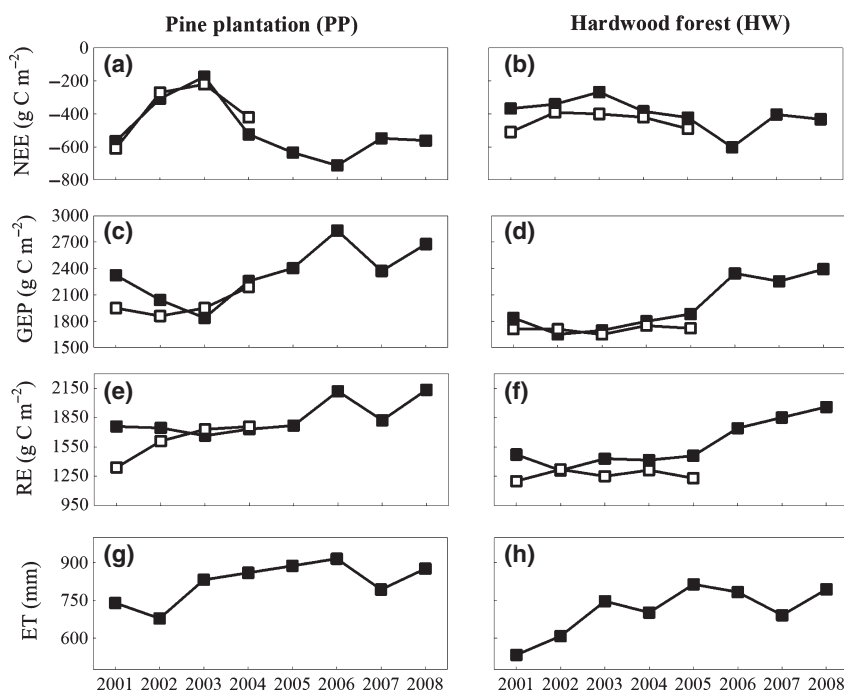
Over the entire study period, both ecosystems were strong carbon sinks. Mean annual NEE in PP

( $\langle \text{NEE} \rangle = -506 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) represented a larger carbon sink than mean annual NEE in HW ( $\langle \text{NEE} \rangle = -402 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), though interannual variation was higher in PP ( $\sigma = 173 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) than HW ( $\sigma = 96 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). The magnitude of both NEE and RE, and thus GEP, was higher in the pine plantation as compared to the hardwood forest (Table 1). The interannual variability in GEP fluxes was similar in the two sites ( $\sigma = 317$  and  $305 \text{ C m}^{-2} \text{ yr}^{-1}$  in PP and HW, respectively), and the variability in RE fluxes was higher in the HW site ( $\sigma = 181$  and  $234 \text{ C m}^{-2} \text{ yr}^{-1}$  in PP and HW, respectively). A stronger coupling between GEP and RE was observed in the hardwood site ( $r^2 = 0.92$ ,  $P = 0.0001$ ) when compared to the pine site ( $r^2 = 0.81$ ,  $P = 0.003$ ). The magnitude of ET was higher in PP (Table 1), and in both sites interannual variability in ET was small relative to the variability in carbon dioxide fluxes.

#### *Spectral characteristics of NEE and ET in the two sites*

The normalized wavelet spectra of PP and HW ET were nearly identical (Fig. 5b); however, significant differ-





**Fig. 4** A comparison between the annual net ecosystem exchange (NEE, a & b), gross ecosystem productivity (GEP, c & d), ecosystem respiration (RE, e & f), and evapotranspiration (ET, g & h) estimated using the VG2009 approach (closed symbols) and those estimated with the S2006 approach (open symbols).

ences emerged in the spectra for NEE (Fig. 5a). In particular, the PP NEE was more sensitive to factors that vary over daily-to-weekly timescales, and to factors that vary over long (i.e. interannual timescales). Indeed, in PP, the fraction of variability attributable to long timescales is similar to that attributable to factors that vary seasonally. In contrast, HW NEE was driven principally by factors varying over seasonal timescales, with relatively little interannual variability.

At daily-to-weekly timescales, the difference in NEE between PP and HW (i.e.  $\Delta$ NEE) was most strongly driven by variables that tend to change during the course of a drought (i.e.  $D$ ,  $\theta$ , and  $T_a$ , Fig. 5c). At seasonal timescales,  $\Delta$ NEE resonates most closely with variation in  $\theta$  and  $T_a$  (Fig. 5c). At interannual timescales, variation in  $\Delta$ NEE resonates most with  $\theta$  and atmospheric  $\text{CO}_2$  (Fig. 5c).

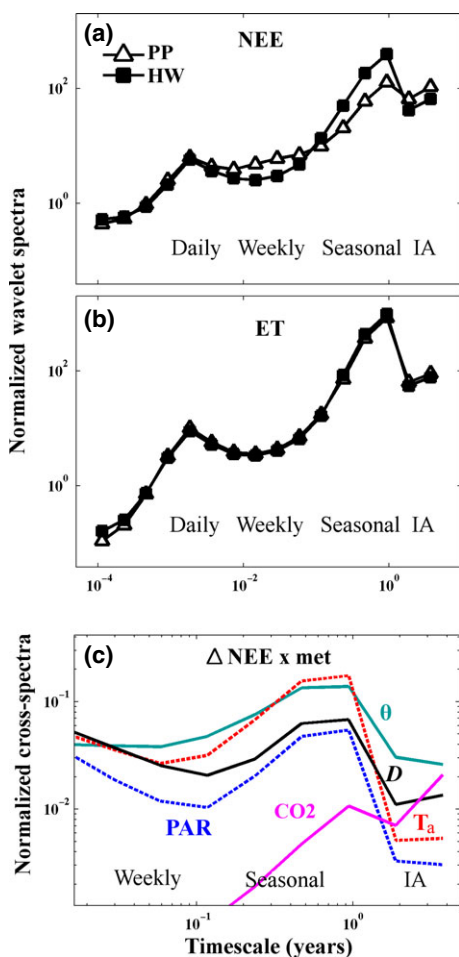
#### *Drought effects on carbon and water fluxes*

The strong linkages between  $\Delta$ NEE and the meteorological variables  $\theta$ ,  $D$ , and  $T_a$  at a range of timescales (e.g. Fig. 5c) motivate a closer examination of the drought effects on NEE in both sites. Toward that end, a nonlinear least-squares regression was used to parameterize the GEP model of Eqn (1) and the RE model of Eqn (3) using observed (i.e. not gapfilled) data from the 2nd and

3rd quarters of the two severe drought years (i.e. years 2002 and 2007). We also parameterized the model for the 2nd and 3rd quarters of the years preceding the drought years to provide a basis for comparison. In this application, we did not include the  $D$  response function [Eqn (2)], so that differences in the model parameters (i.e.  $\beta$ ) reflect variations in  $D$  and  $\theta$ .

During the growing season of 2002 and 2007, the assimilation rate in PP was reduced for all PAR, and was reduced at high PAR by 24% during the 2nd quarter of 2002, 5% during the 3rd quarter of 2002, 14% during the 2nd quarter of 2007, and 48% during the 3rd quarter of 2007 (Fig. 6a–d). These reductions are relative to the modeled assimilation rate during the same quarter of the year preceding each drought year (i.e. 2001 and 2006). The respective reductions in HW assimilation were in general not as large (10–21% reduction, Fig. 6a–d). The effect of the drought events on respiration rate at a given temperature was also not as pronounced (Fig. 6e–h), and only in the 2nd quarter of 2007 was respiration at high air temperatures (i.e.  $T_a > 20^\circ\text{C}$ ) reduced in both PP and HW (by 0.04 to 0.06  $\text{g C m}^{-2} \text{s}^{-1}$ , or by 34% and 24%, respectively, Fig. 6f).

Relative to years preceding the drought events, growing season ET was reduced in both PP and HW (Table 1), though in general, the reductions were not as great as those observed for GEP (relative decreases of



**Fig. 5** The wavelet spectra of (a) NEE and (b) ET in the two forests, illustrating that the timescales of variability in NEE differed considerably between the two ecosystems at weekly to interannual timescales, whereas the timescales of variability in ET are nearly identical. Panel (c) shows the wavelet cospectra between the difference in NEE between PP and HW ( $\Delta$ NEE) and a range of meteorological drivers, including photosynthetically active radiation (PAR), air temperature ( $T_a$ ), soil moisture content ( $\theta$ ), vapor pressure deficit ( $D$ ), atmospheric  $CO_2$  concentration ( $CO_2$ ), and also monotonically increasing time. The abbreviation 'IA' indicates 'interannual' timescales.

8–13% in PP and 3–12% in HW for the drought years as compared to the preceding years).

#### Ice storm effects

Damage from the December, 2002 ice storm was primarily confined to PP. Annual GEP in 2003 was reduced by  $>400 \text{ g C m}^{-2}$  relative to year 2001, and by  $>200 \text{ g C m}^{-2}$  relative to year 2002 (the drought year). However, GEP recovered quickly, and in 2004 and 2005, annual GEP was comparable to that observed in 2001 (Table 1). Neither the S2006 nor the VG2009

estimates of RE showed a large change in 2003 as compared to 2002 or 2004. This is consistent with previous work focused on the effect of ice storms in managed pine plantations (McCarthy *et al.*, 2006), which suggests that the carbon content of downed biomass during an ice storm event is  $\sim 30\%$  of annual net ecosystem productivity, but will take  $>25$  years to decompose, which means the contribution of the decomposition of downed biomass to total RE in any given year is relatively small. It is worth noting that the smallest carbon sink was observed in 2003 in both sites, suggesting that the effects of the ice storm, moderate and severe droughts in 2001–2002, and low PAR in 2003 (Fig. 3) have combined effects among forest types.

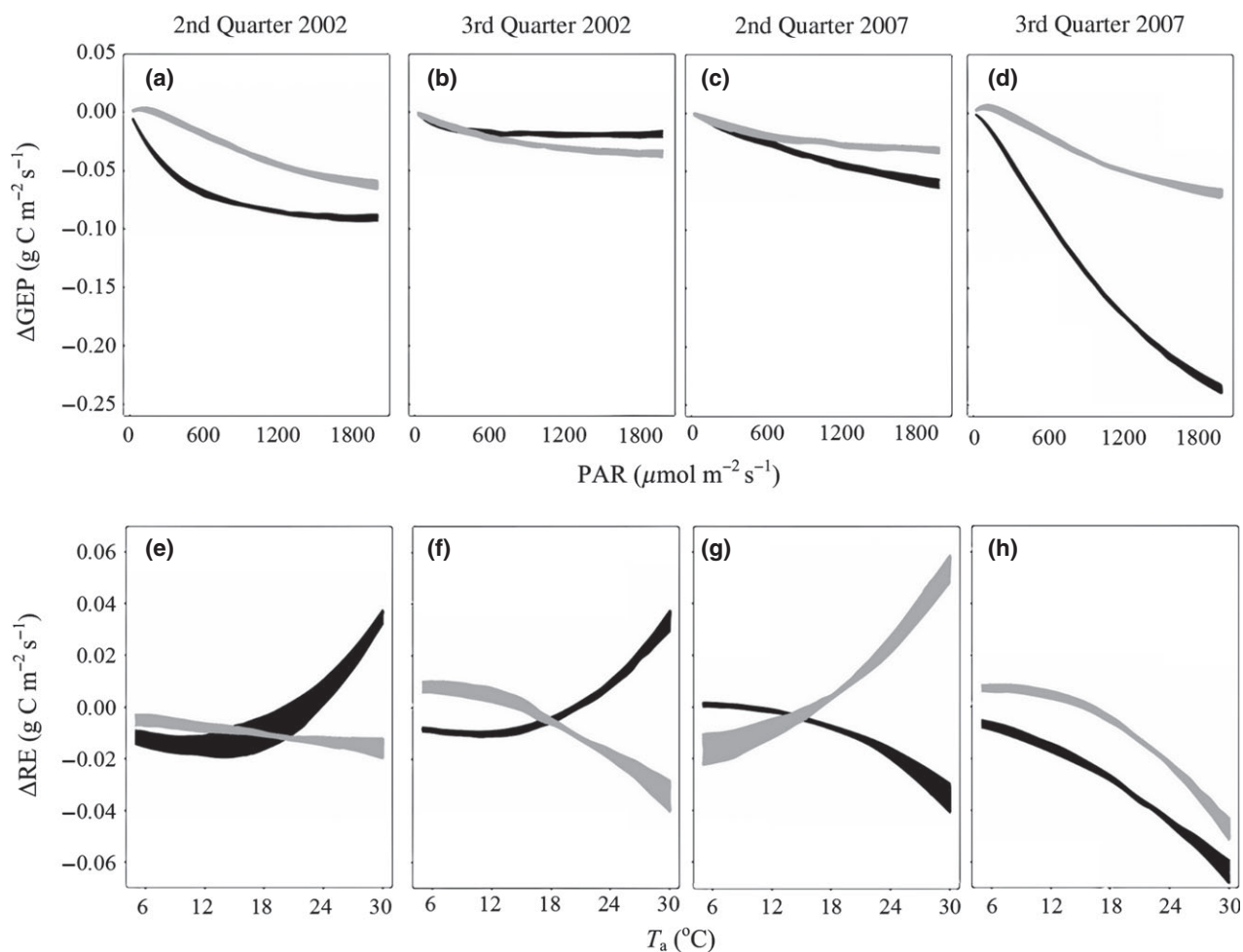
#### Seasonality of the fluxes

Considerable variability was observed in the timing of the start and the end of the active season in the PP site (Fig. 7). The start of the active season in PP (hereafter  $S_{AS}$ ) occurred at DOY 108 on average, with the earliest  $S_{AS}$  observed in 2007 (DOY 96), and the latest  $S_{AS}$  observed in 2003 (DOY 125). The end of the active season (hereafter  $E_{AS}$ ) in the pine site occurred on DOY 286 on average, and was similarly variable (ranging from DOY 258 to DOY 306). In HW, the timing of the  $S_{AS}$  and  $E_{AS}$  were less variable than in PP (DOY 102 to 114 for  $S_{AS}$ , and DOY 268 to 288 for  $E_{AS}$ ). The length of the active season (hereafter  $L_{AS}$ ) was 178 days on average in the pine site, and 167 days on average in the hardwood site. The  $L_{AS}$  alone was not a significant determinant of annual NEE/GEP/RE fluxes in either site, though the interaction between  $L_{AS}$  and drought status was a significant predictor for annual GEP and RE in the HW site ( $P < 0.10$  from an ANOVA considering  $L_{AS}$ , a binary variable for drought status equal to 1 in 2002 and 2007, and 0 otherwise, and their interaction in a linear model).

In PP,  $\sim 25\%$  of annual GEP occurred outside of the active season (Fig. 8), and  $\sim 13\%$  of annual GEP occurred during winter months (January–February, November–December, Fig. 8). Dormant season PP GEP was significantly related to dormant season temperature ( $r^2 = 0.65$ ,  $P = 0.06$ ). PP and HW GEP were relatively similar during the growing season (Table 1, Fig. 8).

#### Trends in water use efficiency

The annual growing season  $WUE_i$  and  $\lambda_E$  were strongly correlated ( $r^2 > 0.94$ ,  $P < 0.001$  in both sites, Fig. 9a,b), and in many years, the magnitude of  $WUE_i$  and  $\lambda_E$  were similar in both sites (Fig. 9). Local maxima in both  $WUE_i$  and  $\lambda_E$  were observed in both sites during the two extreme drought years (Fig. 9 a,b), reflecting the



**Fig. 6** (a–d) The difference in GEP at a given flux of photosynthetically active radiation (PAR) in the 2nd and 3rd quarters of the two severe drought years (2002 and 2007) relative to the GEP in the same quarter of the preceding year. PP data are represented with dark black lines, and HW data with gray lines. The bottom four panels show difference in RE as a function  $T_a$  for the same time periods. The trends shown here were determined from site-specific, quarterly parameterizations of the GEP and RE models of Eqns (1) & (3). The data show the 95% confidence intervals estimated from a nonparametric bootstrap.

direct dependence of both metrics on  $D$ . When the drought years were excluded, both  $WUE_i$  and  $\lambda_E$  tended to increase with atmospheric  $CO_2$  concentration in HW (Fig. 9c,d,  $P = 0.08$  and  $0.14$ , respectively) and in PP ( $P = 0.0011$  and  $0.001$ , respectively). However, in HW at least, the marginal water use efficiency tended to be less sensitive to  $c_a$  than  $WUE_i$ . Specifically, when both were scaled to standard normal variables, the slope of the relationship with  $c_a$  was  $0.76$  for  $WUE_i$  as compared to  $0.68$  for  $\lambda_E$ . Following Eqns. 8 & 9, the trends in the water use efficiency variables may also be affected by the long-term trend in  $D$  over the course of the study period, which is significant even when drought-years were excluded (see Fig. 2d,  $P < 0.05$ ).

In PP, which experienced significant changes in canopy structure during the study period, we also

explored the relationship between the water use efficiency metrics and the allometric index, which is defined as the growing season average sapwood area divided by the product of leaf area and canopy height ( $A_S : A_L/h$ , Ward *et al.*, 2013), and which should be related to stomatal conductance rates at reference environmental conditions (Novick *et al.*, 2009b). We did not find a significant relationship between  $A_S : A_L/h$  and either  $WUE_i$  or  $\lambda_E$  when all years, or even nondrought years, were considered. When the analysis was limited to nondrought years after the ice storm disturbance (2003–2006, and 2008), a significant relationship between  $A_S : A_L/h$  and both  $WUE_i$  and  $\lambda_E$  emerged ( $P = 0.01$  and  $0.01$ , respectively). However, the evolution of  $A_S : A_L/h$  and  $CO_2$  were also strongly correlated during those years ( $r^2 = 0.96$ ).

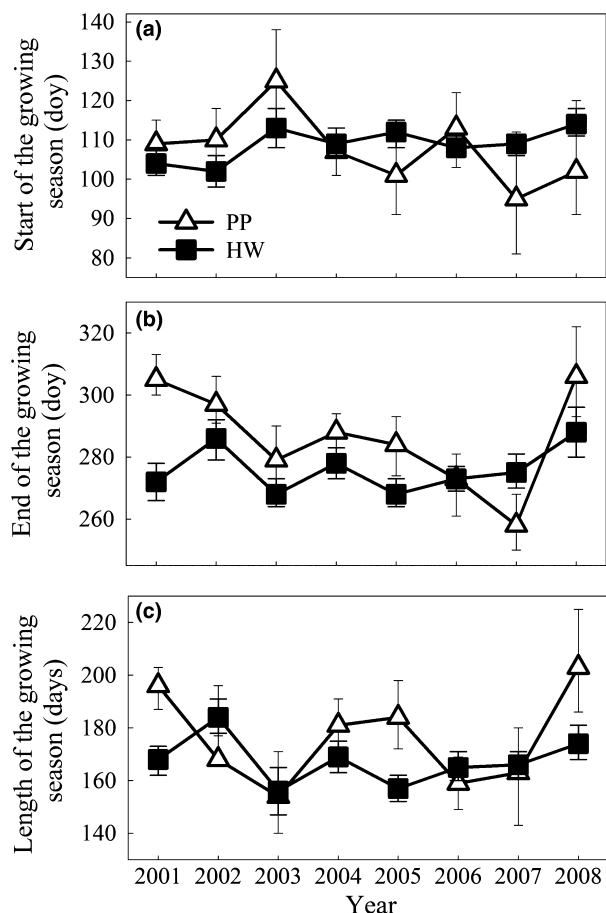


Fig. 7 The day of year (doy) of the start and end of the active seasons (panels a and b), and the resulting length of the active season (panel c) for each year in the study period.

## Discussion

The timescales of variability in NEE differed considerably between the two forests (Fig. 5a), with relatively larger variability in HW NEE at seasonal timescales, and relatively larger variability in PP NEE over interannual timescales. The modes of variability in ET are nearly identical between the two sites (Fig. 5b), which would indicate that ET in both sites is strongly driven by meteorological forcings, and the factors driving variability in  $\Delta$ NEE are limited to eco-physiological processes that tend to decouple the dynamics of NEE and ET. In the following subsections, we will illustrate that those factors are likely: (i) variations in GEP and water use efficiency during drought periods, (ii) cross-site differences in the seasonality of NEE, and (iii) ecosystem-responses to slowly evolving bio-meteorological drivers. Together, the results highlight some of the relative advantages of evergreenness vs. deciduousness in determining NEE in the southeastern United States. In particular, we will discuss how the relative invariability

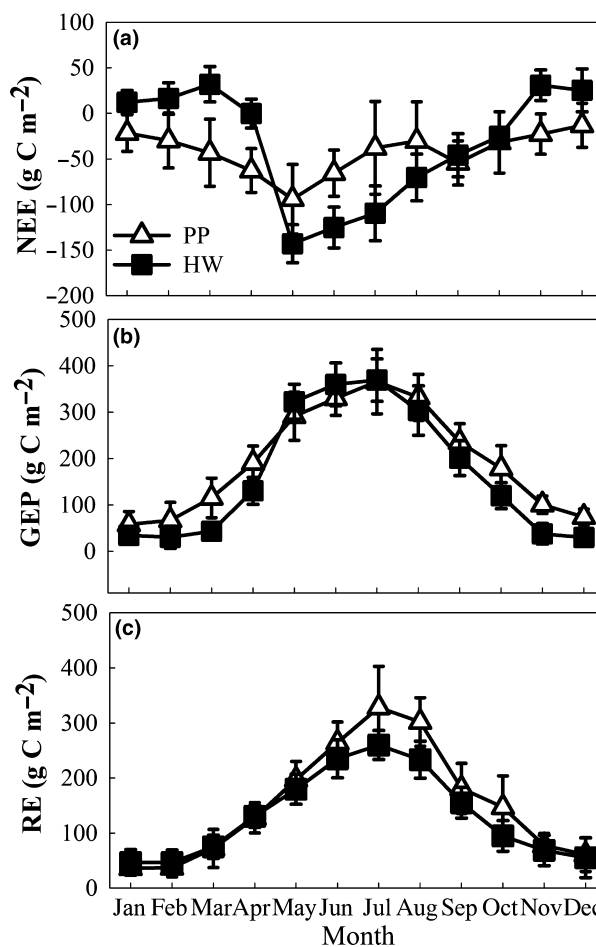


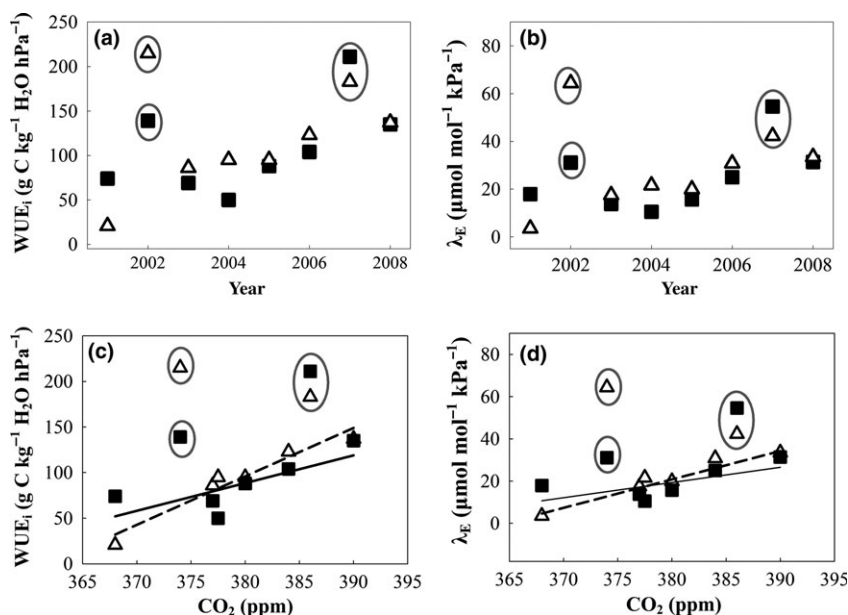
Fig. 8 Mean monthly average NEE (top row), GEP (middle row), and RE (bottom row) in the two study sites.

of PP NEE at seasonal timescales represents a distinct advantage for evergreen forests growing in warm climates; however, increased drought sensitivity of GEP in PP relative to HW represents a disadvantage that may become more important if future climates are characterized by increased frequency or severity of drought (Huntington, 2006; Dai, 2011).

### Differences in the magnitude of carbon fluxes

When aggregated over the entire 8 year study period, PP tended to capture and store more carbon than HW (mean annual  $\Delta$ NEE =  $100 \text{ g C m}^{-2}$ , Table 1). This result refines earlier work based on shorter time series from these sites (Stoy *et al.*, 2008), and generally agrees with theoretical predictions for the carbon storage capacity of late-successional forests (i.e. Odum, 1969; Tang *et al.*, 2014). However, this result is sensitive to the high degree of interannual variability in NEE in both sites (Table 1), and the related fact that the annual  $\Delta$ NEE





**Fig. 9** Trends in annual intrinsic ( $WUE_i$ ) and ecosystem marginal water use efficiency ( $\lambda_E$ ). Panels a & b show the time series for the two variables over the study period. Panels c & d show the relation between mean growing season  $CO_2$  concentration and the water use efficiency variables. Drought years are indicated with gray circles. Regression lines for the relation between  $WUE_i/\lambda_E$  and  $c_a$  for nondrought years are shown with solid lines for HW and dashed lines for PP. They are significant at the 90% confidence levels for all regressions except HW  $\lambda_E$  ( $P = 0.14$ ). Triangles show PP data, and squares show HW data.

was not significantly different from zero ( $P = 0.18$ ). The long-term magnitudes of NEE are also sensitive to the gapfilling and partitioning approach (Table 1, and see also Stoy *et al.*, 2006b). We selected the van Gorsel *et al.* (2009) approach because the annual RE estimated by other approaches in general did not exceed estimates of annual soil respiration alone (determined from chamber-based measurements to be  $1383 \pm 152$  g C m<sup>-2</sup> yr<sup>-1</sup> in PP, Oishi *et al.*, 2013; Palmroth *et al.*, 2005; and  $1209 \pm 99$  g C m<sup>-2</sup> yr<sup>-1</sup> in HW, Oishi *et al.*, 2013). Still, in both PP and HW, the ratio of soil respiration to total respiration estimated by the Van Gorsel approach is near unity in the dormant season ( $\sim 1.06 \pm 0.21$  and  $1.05 \pm 0.25$  for PP and HW, respectively), and thus tower-derived RE fluxes are still likely underestimated in the winter months.

#### Drought effects

The  $\Delta NEE$  resonated most strongly with variables that change most during drought events (i.e.  $D$ ,  $\theta$ ,  $T_a$ ) at daily-to-weekly timescales, and at interannual timescales (Fig. 5), suggesting that variation in hydrologic condition is an important, if not the predominant, factor driving  $\Delta NEE$ . Our results allow us to draw the following conclusions about drought effects in the study sites:

- Drought affects GEP more than RE, and affects PP GEP more than HW GEP: Drought decreased GEP capacity during the severe droughts in both sites, whereas the drought effects on RE were mixed and generally small (Fig. 6), consistent with previous work (Ciais *et al.*, 2005; Schwalm *et al.*, 2010). The relative reduction to growing season PP GEP during drought years ( $\sim 23\%$ ) exceeded that observed in the HW ( $< 14\%$ , Fig. 6).
- Ecosystem marginal water use efficiency mediates drought effects: The ecosystem-scale water use efficiency increased during drought years in both sites, but not identically so (Fig. 9). Thus, water use efficiency is an important variable driving the decoupling between  $\Delta NEE$  and ET.

#### Flux seasonality

Net ecosystem exchange resonated strongly with factors that vary seasonally in the HW, but not the PP (Fig. 5). Further, the length of the active season was not a significant predictor for any of the annual PP carbon fluxes, though its interaction with drought status was related to HW GEP and RE ( $P < 0.10$ ). Thus, with respect to HW, our results confirm previous work showing that  $L_{AS}$  is significant control on interannual

flux variability in deciduous forests (Dragoni *et al.*, 2011), but highlight that the delineation of an active season may not be appropriate in PP. Indeed, given that PP and HW GEP were relatively similar during the growing season (Table 1, Fig. 8), much of the difference in annual PP and HW GEP (which exceeds 300 g C m<sup>2</sup> on average, Table 1) may be attributed to pine physiological functioning when the HW forest is inactive. These results represent an important advantage of evergreen ecosystems growing in warm climates, and refine earlier work proposing that the advantages of an extended photosynthetic period in evergreen trees tend to be offset by relatively low photosynthetic rates during the active season (Hollinger, 1992; Givnish, 2002).

*Relationship between the fluxes and factors that are changing over timescales commensurate with climate change*

At annual to interannual timescales, large variation in  $\Delta$ NEE was observed (Fig. 5) that resonated most closely with variations in soil moisture content (reflecting drought effects that have already been discussed), and with variation in atmosphere CO<sub>2</sub>. It has long been hypothesized that rising CO<sub>2</sub> may increase ecosystem water use efficiency (Field *et al.*, 1995), representing a physiological adaptation to prevent excessive water loss when CO<sub>2</sub> is less limiting (Katul *et al.*, 2010; Medlyn *et al.*, 2011). Consistent with the results of Keenan *et al.* (2013), the WUE<sub>i</sub> and  $\lambda_E$  were correlated with CO<sub>2</sub> in both PP ( $P < 0.0011$  for both metrics) and HW ( $P = 0.08$  and  $.14$  for WUE<sub>i</sub> and  $\lambda_E$ ) when drought years were excluded, with a more rapid increase in PP WUE<sub>i</sub> and  $\lambda_E$  for a given rise in CO<sub>2</sub> (Fig. 9). We considered that changes in canopy structure could also affect the evolution of water use efficiency in PP. No significant trend between the allometric relationship (i.e.  $A_S : A_L/h$ ) and WUE<sub>i</sub> or  $\lambda_E$  was observed during nondrought years, though a significant relationship did emerge when only drought-free years following the ice storm disturbance were considered ( $P = 0.01$  and  $0.02$  for WUE<sub>i</sub> and  $\lambda_E$ ). Thus, variation in canopy structure may be a relatively more important determinant of water use efficiency in years following a disturbance event, though we caution that  $A_S : A_L/h$  and CO<sub>2</sub> were also highly correlated during this time period. The trends in water use efficiency are likely also affected by the observed long-term increase in growing season D in non-drought years ( $P = 0.04$ , slope =  $0.05$  kPa/year). From Eqn. 9, it can be shown that the increases  $c_a$  and  $D$  during the course of the study period should each promote an increase in  $\lambda_E$  on the order of  $3 \mu\text{mol/mol/kPa}$ , excluding drought years and assuming constant  $c_i$ . Finally, we note that the combined rate of increase

( $\sim 6 \mu\text{mol/mol/kPa}$ ) is less than the observed increases in  $\lambda_E$ , which may reflect the influence of an unidentified process, or uncertainty in the data themselves.

The observed agreement between  $\Delta$ NEE and CO<sub>2</sub> at long time scales may be confounded by the effect of other variables like  $T_a$ , which may be slowly evolving in concert with increases in CO<sub>2</sub>. Here,  $T_a$  was relatively poorly related with  $\Delta$ NEE at long-time scales (Fig. 5c, d), and no long-term trend was observed in mean annual  $T_a$  ( $P = 0.20$ ) or the  $L_{AS}$  (Fig. 7). However, there did exist a significant trend in dormant season air temperature (slope =  $0.03$  degrees C yr<sup>-1</sup>,  $P = 0.03$  after excluding drought years), which is related to the variability in dormant season PP GEP ( $r^2 = 0.65$ ,  $P = 0.06$ ).

Factors related to canopy development may also be important in determining  $\Delta$ NEE, even if they do not affect water use efficiency. A direct effect of canopy development on  $\Delta$ NEE would likely be realized as a long-term flux trend that is monotonic from 2003 to 2008 (i.e. during the period after the ice storm disturbance). Such a trend was suggested but not significant for PP NEE ( $P = 0.20$  for years 2003–2008, Fig. 4). Long-term trends in PP GEP and RE were observed, but they were similar to long-term trends observed in the slowly growing HW site (Fig. 4). Thus, while we cannot rule out canopy development as an significant driver of  $\Delta$ NEE, the data do not indicate that it is the predominant controlling variable.

Finally, while we were able to show here that  $\Delta$ NEE is strongly sensitive to factors that vary over interannual timescales, we recognize that our ability to confidently identify these factors would be facilitated by longer data sets. Thus, efforts should be made to lengthen the time series at long-running flux sites, even if such an effort is not possible for PP and HW (which were decommissioned in 2009).

*Implications for the variability in future regional carbon and water fluxes*

Within the context of ongoing climate change and regional land-cover change, this study highlights several processes important to future regional carbon and water cycling. First, the variability in ET is similar in both sites (Fig. 5b) and relatively small, consistent with results from a previous study investigating the relative temporal invariance of ET (Oishi *et al.*, 2010). Second, predicted increases in drought frequency (Dai, 2011), if realized, will likely promote a more variable and generally smaller regional carbon sink, due to the sensitivity of GEP, and in particular PP GEP, to drought (Fig. 6). Third, future increases in atmospheric CO<sub>2</sub> will likely promote increases in water use efficiency, though the extent to which those increases will lead to decreased

transpiration, increased GEP, or both under elevated CO<sub>2</sub> remains an open question (Medlyn *et al.*, 2011; Barton *et al.*, 2012; Ward *et al.*, 2013). And finally, the capacity of PP to assimilate CO<sub>2</sub> year-round (Fig. 8) represents an important carbon uptake advantage of evergreen trees in warm temperature climates, and should motivate future efforts to link regional pine forest functioning to meteorological trends occurring when deciduous forests are dormant.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** The previously published estimates of the annual Net Ecosystem Exchange of CO<sub>2</sub>(NEE) used to create Fig. 1 in the main text are shown in Table S1. These sites were initially selected from among Ameriflux sites with at least five site years of available data, though sites were included in the table even if less than 5 years of reported estimates of NEE were recovered in the literature.