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Differential responses of carbon and water vapor fluxes to climate among evergreen needleleaf forests in the USA

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Abstract

Introduction: Understanding the differences in carbon and water vapor fluxes of spatially distributed evergreen needleleaf forests (ENFs) is crucial for accurately estimating regional or global carbon and water budgets and when predicting the responses of ENFs to current and future climate.

Methods: We compared the fluxes of ten AmeriFlux ENF sites to investigate cross-site variability in net ecosystem exchange of carbon (NEE), gross primary production (GPP), and evapotranspiration (ET). We used wavelet cross-correlation analysis to examine responses of NEE and ET to common climatic drivers over multiple timescales and also determined optimum values of air temperature (T_a) and vapor pressure deficit (VPD) for NEE and ET.

Results: We found larger differences in the NEE spectra than in the ET spectra across sites, demonstrating that spatial (site-to-site) variability was larger for NEE than for ET. The NEE and ET were decoupled differently across ENF sites because the wavelet cospectra between ET and climate variables were similar at all sites, while the wavelet cospectra between NEE and climate variables were higher (i.e., closer coupling between NEE and climatic drivers) in semi-arid and Mediterranean sites than in other sites. Ecosystem water use efficiency (EWUE) based on annual GPP/ET ranged from 1.3 ± 0.18 to 4.08 ± 0.62 g C mm⁻¹ ET, while EWUE based on annual net ecosystem production (NEP)/ET ranged from 0.06 ± 0.04 to 1.02 ± 0.16 g C mm⁻¹ ET among ENFs. Responses of NEE and ET to T_a varied across climatic zones. In particular, for ENF sites in semi-arid and Mediterranean climates, the maximum NEE and ET occurred at lower ranges of T_a than in sites with warm and humid summers. The optimum T_a and VPD values were higher for ET than for NEE, and ET was less sensitive to high values of T_a and VPD.

Conclusions: Large spatial variability in carbon and water vapor fluxes among ENFs and large variations in responses of NEE and ET to major climate variables among climatic zones necessitate sub-plant functional type parameterization based on climatic zones to better represent climate sensitivity of ENFs and to reduce uncertainty in model predictions.

Keywords: Drought, Ecosystem water use efficiency, Net ecosystem CO₂ exchange, Spatial variability, Wavelet cross-correlation analysis

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Introduction

Forest ecosystems play a significant role in global carbon and water cycles because they cover over four billion hectares of the Earth's land surface (Dixon et al. 1994). Evergreen needleleaf forests (ENFs) cover about 57 % of the forested land in the USA (Smith et al. 2009). In the past two decades, eddy covariance (EC) systems have been deployed at several (>20) ENFs across the USA to help understand the seasonality, magnitudes, and processes controlling surface-atmosphere fluxes (Dore et al. 2012; Falk et al. 2008; Hadley and Schedlbauer 2002; Hollinger et al. 1999; Jassal et al. 2009; Monson et al. 2002; Noormets et al. 2007; Noormets et al. 2010; Powell et al. 2008; Schwarz et al. 2004; Stoy et al. 2008). With the exception of the 10–20 years following a stand-replacement disturbance, ENFs are generally net sinks of carbon from the atmosphere (Amiro et al. 2010; Law et al. 2001). These independent site-level studies have reported varying rates of carbon and water vapor exchange and carbon uptake period (CUP) among ENFs due to substantial differences in forest age, land use history, topography, edaphic and climatic conditions, and species composition. Some studies have shown that the magnitudes of fluxes are highly sensitive to hydrologic conditions (Noormets et al. 2010; Stoy et al. 2005; Whelan et al. 2013) and canopy development after a disturbance (Clark et al. 2004). In addition to climate and structural changes, variations in biotic responses (Richardson et al. 2007) also cause variation in forest-atmosphere carbon exchange. Forest carbon cycling and the distribution and composition of forest species are tightly coupled with water availability (Berner and Law 2015). The broad distribution of ENFs across climatic gradients adds to the complexity of estimating fluxes for large regions and widespread vegetation types, since the sensitivity of fluxes for different ENF ecosystems to climate variability is not completely understood. Such understanding is necessary to enhance our ability to predict the potential responses of ENFs to the changing climate.

Direct measurements of carbon uptake and water loss by terrestrial ecosystems using the EC technique make it possible to characterize ecosystem water use efficiency (EWUE) (Arneeth et al. 2006; Law et al. 2002) and to quantify the coupling between carbon and water cycles (Yu et al. 2004). At the ecosystem level, EWUE is generally estimated as the ratio of carbon uptake (gross primary production, GPP or net ecosystem production, NEP) to water loss (evapotranspiration, ET). However, the relationship between carbon gain and water loss is complicated at the ecosystem level. The EWUE is different from the concept of water use efficiency (WUE) that is conventionally calculated at leaf or individual plant level because several additional factors, such as heterotrophic respiration, decomposition of organic materials, and evaporation of soil moisture, can potentially

influence EWUE (Emmerich 2007). The influence of vapor pressure deficit (VPD) on canopy conductance (Bierhuizen and Slatyer 1965; Monteith and Greenwood 1986) can have confounding effects on the individual responses of carbon uptake and water loss to the climatic conditions. Beer et al. (2009) proposed the “inherent water use efficiency (IWUE)” approach to account for the effect of VPD on WUE at the ecosystem level. In addition, higher temperature leads to higher VPD which limits carbon assimilation via stomatal (Turner et al. 1984) or non-stomatal (Morison and Gifford 1983) effects. Elevated temperatures will also increase photorespiration and heterotrophic respiration and, in turn, reduce carbon assimilation (Long 1991). The variability in EWUE among ecosystems reflects the water-use strategy (i.e., trade-off between water loss and carbon gain) of different species (Donovan and Ehleringer 1991) and provides an important insight into the relationships between carbon uptake and water loss. However, understanding of the variations in carbon and water vapor fluxes and EWUE over climatic gradients in ENFs is still lacking.

An increasing number of EC flux towers now allow synthesis, comparative analysis, and modeling of ecosystem-level fluxes (Falge et al. 2002; Gilmanov et al. 2010; Turner et al. 2003; Wagle et al. 2015a; Xiao et al. 2014). Comparison and synthesis of eddy flux data from multiple sites for a plant functional type (PFT) across a large climatic gradient facilitates investigation of complex biophysical controls on carbon and water vapor fluxes (Schwarz et al. 2004; Thornton et al. 2002). However, few studies have investigated the variability in carbon and water vapor fluxes and their differential responses to major climate variables (e.g., rainfall, temperature) at widely distributed diverse ENFs. It is well known that plants adapt to prevailing climatic conditions to optimize their functions under a varying climate (Berry and Bjorkman 1980; Mooney et al. 1978). We hypothesize that carbon and water vapor fluxes of various ENFs in different climatic zones respond differently to major climatic variables. Thus, investigating the response of carbon uptake and ET to major climatic variables at multiple timescales and sites within widely distributed diverse ENFs is necessary to move beyond site-level measurements and into realistic carbon and water budget estimates over regions or continents.

Eddy fluxes are controlled by physical and biological processes that change over a wide range of temporal scales ranging from seconds to decades (Baldocchi and Wilson 2001; Katul et al. 2001; Schimel et al. 2001). Eddy fluxes are governed by complex, turbulent eddy motion (rich in spectral properties) over seconds, while interactions with weather patterns, bulk turbulent flow characteristics, eco-physiological and biochemical characteristics of plant

canopy, and the hydrological conditions induce variability in fluxes at hourly to monthly timescales (Katul et al. 2001). Similarly, synoptic weather patterns superimposed on seasonal variations dominate the variability in fluxes over monthly to annual timescales. Wavelet cross-correlation spectral analysis suitably interprets eddy flux time series data and assesses the contributions of the processes that act on different frequencies (Katul et al. 2001; Ouyang et al. 2014). The spectral analysis quantifies the energetic frequencies/timescales of net ecosystem exchange of carbon (NEE) or ET fluxes and relates them to the timescales of variability in climatic drivers. Descriptions of the use of spectral analysis in investigations of eddy fluxes can be found in previous publications (Baldocchi et al. 2001; Katul et al. 2001; Katul and Parlange 1995; Ouyang et al. 2014; Torrence and Compo 1998). To date, only a few studies have used wavelet cross-correlation analysis to investigate variability in vegetation surface fluxes at a small number of ENF sites (Katul et al. 2001; Novick et al. 2015; Stoy et al. 2005). Thus, this current study investigates the responses of carbon and water vapor fluxes to common climatic drivers by using the wavelet cross-correlation spectral analysis on ten widely distributed ENFs across the USA (Fig. 1).

By analyzing eddy flux and climate data from ten widely distributed ENFs, the following questions are addressed in this study: (1) to what extent do the magnitudes and annual or seasonal sums of carbon and water vapor fluxes differ among sites? (2) how do the relationships between carbon

uptake and water loss and seasonal variations of EWUE differ among sites? (3) how do the responses of NEE and ET to climate forcings differ among sites and over multiple timescales (from week to interannual)? and (4) to what extent do the responses of NEE and ET to T_a and VPD differ among sites? Furthermore, by examining the time series in flux measurements, we assess conditional statistics for carbon and water vapor fluxes associated with changes in seasonal and interannual climatic conditions.

Methods

Study sites

We accessed the eddy flux data from ten AmeriFlux ENF sites (Fig. 1), with each site having a minimum of 4 years of surface flux data over a period from the late 1990s through 2013. The sites are distributed across the conterminous USA (Fig. 1) and cover a broad range of climates (Table 1). Detailed site information is available in previous studies (see references in Table 1) or on the AmeriFlux website (<http://ameriflux.lbl.gov/>).

Flux and climate data

The EC technique was used to measure carbon and water vapor fluxes at all sites. We acquired site-specific gap-filled level 4 eddy flux data (half hourly, daily, and weekly) and climate data, including air temperature (T_a), VPD, photosynthetically active radiation (PAR), soil water content (SWC), and precipitation, from the AmeriFlux data archive (<http://ameriflux.ornl.gov/>) or from

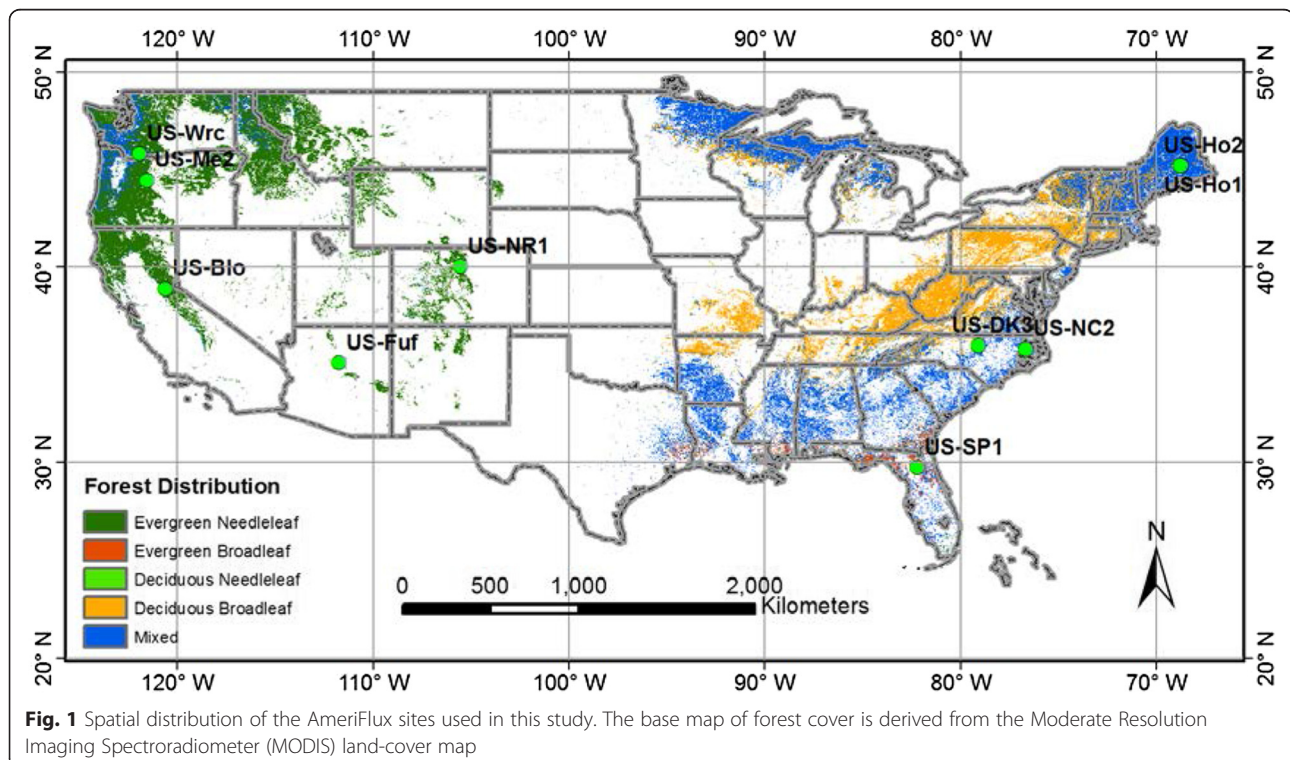


Table 1 Site characteristics of ten evergreen needleleaf forest sites included in this study

Site (symbol)	Latitude longitude elevation (m)	MAT MAP SWC MAR	Study period	Vegetation	Climate	Stand age	References
Austin Cary, FL (US-SP1)	29.7381 −82.2188 44	20.19 833 — 6028	2001–2006 (missing 2002, 2004)	Pine forest (longleaf pine, slash pine)	Warm and humid summers and mild winters	80	(Powell et al. 2008)
Duke Forest Loblolly Pine, NC (US-DK3)	35.9782 −79.0942 163	14.87 1051 29.45 5185	2001–2008	Loblolly pine	Warm and humid summers and mild winters	31	(Novick et al. 2015)
North Carolina Loblolly Pine, NC (US-NC2)	35.8031 −76.6679 12	15.09 1105 25.93 4380	2005–2013	Loblolly pine	Warm and humid summers and mild winters	22	(Noormets et al. 2010)
Howland Forest Main, ME (US-Ho1)	45.2041 −68.7402 60	6.51 809 — 4096	1996–2004	Red spruce, eastern hemlock, other conifers	Continental temperate	100	(Hollinger et al. 1999)
Howland Forest West Tower, ME (US-Ho2)	45.2091 −68.7470 91	6.42 786 — 4132	1999–2004	90 % evergreen needleleaf and 10 % broadleaf deciduous	Continental temperate	100	(Hollinger et al. 1999)
Niwot Ridge, CO (US-NR1)	40.0329 −105.5464 3050	2.41 665 13.37 5972	1999–2007	Subalpine fir, Engelmann spruce, Lodgepole pine	Continental temperate to montane	110	(Monson et al. 2002)
Flagstaff Unmanaged Forest, AZ (US-Fuf)	35.0890 −111.7620 2180	8.59 562 28.83 6661	2006–2010	Ponderosa pine	Semi-arid	100	(Dore et al. 2012)
Metolius Intermediate Pine, OR (US-Me2)	44.4523 −121.5574 1253	7.41 431 22.72 5827	2002–2007 (missing 2003)	Ponderosa pine	Semi-arid	66	(Thomas et al. 2009)
Blodgett Forest, CA (US-Blo)	38.8952 −120.6327 1315	11.16 1306 24.79 5706	2000–2006	Ponderosa pine (mixed evergreen coniferous)	Mediterranean	24	(Kurpius et al. 2002)
Wind River, WA (US-Wrc)	45.8205 −121.9519 371	9.33 2099 29.29 4825	1999–2008 (missing 2005)	Douglas-fir and western hemlock	Mediterranean	~500	(Wharton et al. 2012)

MAT, MAP, SWC, and MAR were determined for each year first, then averaged over the study period

MAT mean annual average temperature (°C), MAP mean cumulative annual precipitation (mm), SWC mean annual average volumetric soil water content (%), MAR mean cumulative annual solar radiation ($\text{MJ m}^{-2} \text{ year}^{-1}$)

site investigators (A. Noormets, US-NC2; K. Novick, US-DK3; S. Dore, US-Fuf; S. Wharton, US-Wrc). Marginal distribution sampling (MDS) (Reichstein et al. 2005) or the artificial neural network (ANN) (Papale and Valentini 2003) was used to fill gaps in the AmeriFlux Level 4 carbon flux data. For the AmeriFlux dataset, we used the gap-filled carbon flux data based on the MDS method. The flux data obtained from site investigators were corrected and gap filled by researchers of each site. Site-specific data gap-filling procedures can be found in site-specific publications (Table 1). For example, site researchers filled the gaps using the MDS method for US-DK3 site. No obvious differences were reported for different gap-filling approaches in comparison studies (Moffat et al. 2007), implying that any differences due to different gap-filling techniques are unlikely to significantly affect the current analysis. The GPP was computed as the balance between ecosystem respiration (ER) and NEE by partitioning NEE data (Lasslop et al. 2010; Reichstein et al. 2005). To compare the responses of NEE and ET to T_a and VPD among sites, we categorized half-hourly daytime (global radiation $>5 \text{ W m}^{-2}$) NEE and ET values in ten classes of increasing T_a and VPD, with class intervals of 3–5 °C for T_a and 0.3–0.5 kPa for VPD depending on the available range of T_a and VPD. The optimum values of T_a and VPD for NEE and ET were determined from the curves relating NEE and ET with T_a and VPD, respectively.

To characterize the seasonality of fluxes and net CUP, we averaged 8-day composite flux data for the entire study period from a single site into a single composite year and produced a mean 8-day time series of flux and climate data. The number of negative NEE days (i.e., carbon gain by the ecosystem) during the growing season was determined as CUP (Churkina et al. 2005; Wagle et al. 2015b). Integrated fluxes (calculated by summing daily values) at the annual (NEE_{yr} , GPP_{yr} and ET_{yr}) and seasonal (NEE_{CUP} , GPP_{CUP} and ET_{CUP} ; for the length of CUP) scales, and maximum daily values (NEE_{max} , GPP_{max} , and ET_{max}) of carbon uptake and ET during the growing season were calculated for each site year.

To quantify the coupling between carbon and water cycles at the ecosystem level, we computed EWUE based on GPP and ET ($EWUE_{GPP_{yr}} = GPP_{yr}/ET_{yr}$) and NEP and ET ($EWUE_{NEP_{yr}} = NEP_{yr}/ET_{yr}$) at the annual scale. Similarly, $EWUE_{GPP_{CUP}}$ and $EWUE_{NEP_{CUP}}$ for the length of CUP were derived from the ratio between GPP_{CUP} and ET_{CUP} and between NEP_{CUP} and ET_{CUP} respectively. Seasonal patterns (8-day averages) of EWUE were determined from the time series of NEP, GPP, and ET.

Statistical analysis

We examined the cross-site relationship between integrated values of NEE, GPP, and ET at the seasonal and

annual timescales. For each site, the relationships between GPP and ET and NEE and ET were also examined using 8-day average values during CUP over the study period.

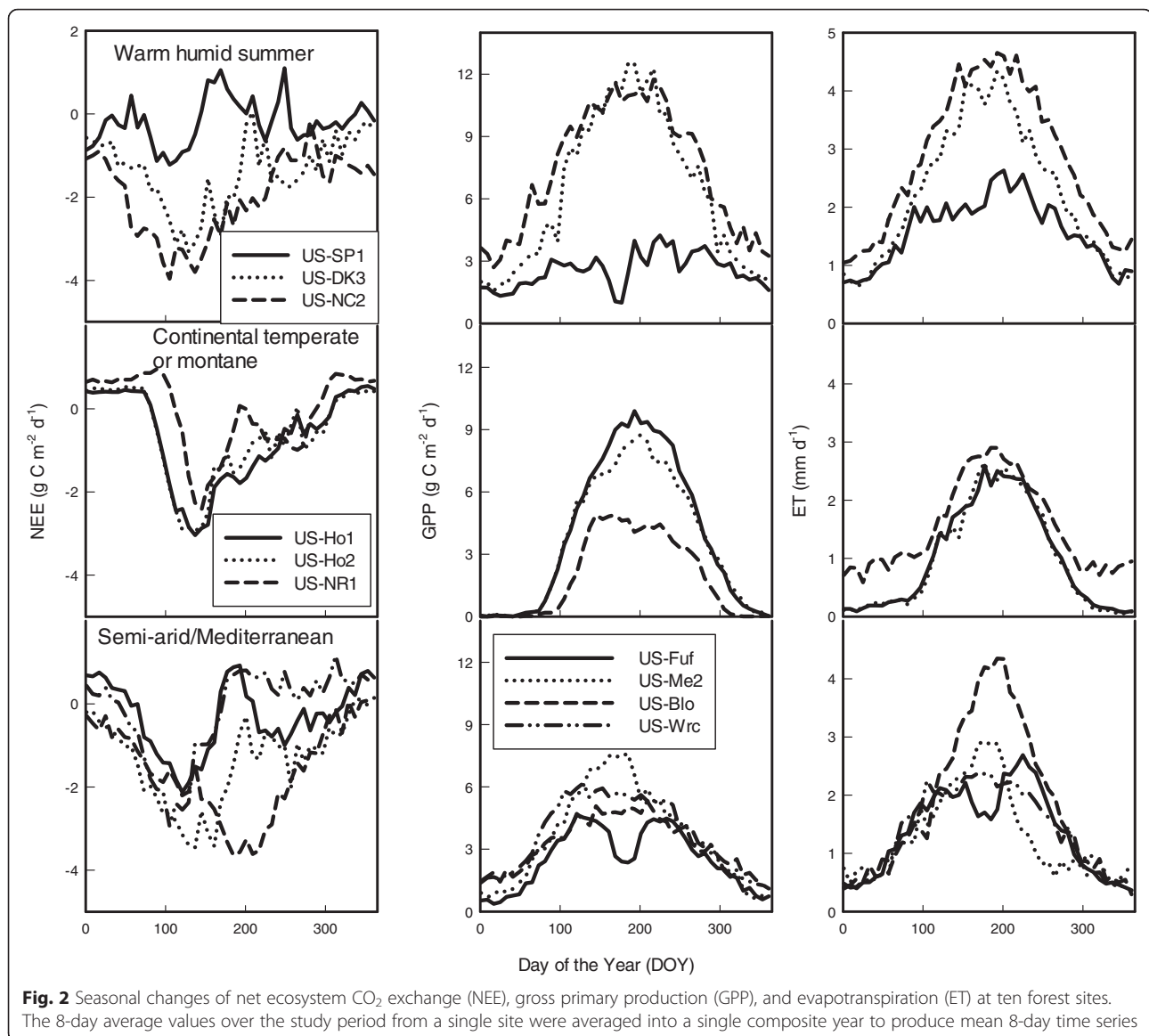
The coefficient of determination (R^2) was calculated to show the strength of relationships between variables and the coefficient of variation (CV) for annual or seasonal integrals, and the maximum rates of fluxes (NEE, GPP, and ET) was calculated to characterize their spatial variations. We used a linear regression to analyze the relationship of the optimum T_a for NEE and ET with mean annual average temperature (MAT). We presented relationships that best fit the data based on highest R^2 values.

We determined the wavelet spectra of NEE or ET time series to identify the proportion of the variability in NEE or ET attributable to processes operating at specific timescales/frequencies. The wavelet cospectra between two time series of fluxes (e.g., NEE, ET) and climatic drivers (e.g., VPD, T_a , PAR, and SWC) were also explored to identify the frequencies at which they significantly co-resonate. An orthogonal wavelet transformation with the Haar basis function was performed to characterize the energetic frequencies/timescales of NEE and ET and to relate those to the timescales of variability in major climatic drivers. Flux and meteorological half-hourly time series data were normalized to have zero mean and unit variance and were zero-padded (gaps in data were also zero-padded) to a length equal to the power of 2 (2^{18} in this case), which is greater than the length of the data record (up to 157,825 half-hourly data points) for any site in this study. We only determined and summed the wavelet coefficients within dyadic timescales ranging from 2^1 (hourly) to 2^{16} (~4 years) because of the unreliability of the wavelet coefficients associated with longer timescales (2^{17} or ~8 years) as in a previous study (Stoy et al. 2005). We performed the wavelet analyses in MATLAB using the Wavelet Toolbox (Mathworks, Natick, MA, USA).

Results

Seasonality and magnitudes of carbon uptake and ET

Seasonal patterns and magnitudes of carbon uptake (NEE and GPP) and ET varied among sites (Fig. 2) because carbon uptake was suppressed during extreme winters, mainly for continental temperate or montane sites where T_a was generally less than 0 °C before DOY 100 and after DOY 300, and dry summers, mainly for US-SP1, US-Wrc, and US-Fuf. Table 2 shows large variations in magnitudes of NEE, GPP, and ET across study sites, with a CV of 26, 34, and 17 %, respectively. Mean net CUP varied from 121 days at US-Wrc to 365 days at US-DK3 and US-NC2, with a CV of 33 % (Table 2). The CUP was longer at sites with higher MAT, except at the US-SP1 site. Consequently, CUP showed a positive



linear correlation ($R^2 = 0.63$, $P = 0.01$) with MAT when the US-SP1 site was excluded from the cross-site analysis (Additional file 1: Figure S1). The length of CUP showed a strong positive linear correlation with spatial variations in mean NEE_{CUP} ($R^2 = 0.81$, $P < 0.001$) and NEE_{yr} ($R^2 = 0.73$, $P = 0.002$) (Additional file 1: Figure S1).

Variability in carbon and water budgets

Large variations in annual and seasonal sums of NEE, GPP, and ET were observed across study sites, with a CV of 83, 45 and 36 %, respectively, on an annual scale and 61, 58, and 52 %, respectively, on the seasonal scale (Table 3). Average NEE_{yr} and NEE_{CUP} over all sites were -314 ± 261 ($\pm$ SD) $g\ C\ m^{-2}$ and -361 ± 222 $g\ C\ m^{-2}$, respectively. In addition to site-to-site variability, ENFs showed large inter-annual variability in the carbon uptake potential in

response to disturbances and climate forcings such as drought. Several sites switched from a net sink to a source of carbon or remained carbon neutral during drought years. For example, the US-SP1 site was a source of carbon in the drought year of 2001 ($64\ g\ C\ m^{-2}\ year^{-1}$) when the extreme drought caused premature senescence and loss of 50 % annual litterfall in May and June of 2000 and 2002, and the site was a large sink of carbon in 2005 ($-200\ g\ C\ m^{-2}\ year^{-1}$) when the site received above-average rainfall ($>1228\ mm$). At the US-Fuf site, NEE_{yr} varied from $-19\ g\ C\ m^{-2}$ in 2009 when annual precipitation was 296 mm to $-174\ g\ C\ m^{-2}$ in 2006 when annual precipitation was 686 mm. At the US-Blo site, NEE_{yr} varied from $-75\ g\ C\ m^{-2}$ in 2001 to $-931\ g\ C\ m^{-2}$ in 2006, with the weak sink in 2001 likely due to pre-commercial thinning and mastication in 2000 that left debris to decompose on-

Table 2 Mean net carbon uptake period (CUP, days) and maximum rates of net ecosystem CO₂ exchange (NEE_{max}, g C m⁻² day⁻¹), gross primary production (GPP_{max}, g C m⁻² day⁻¹), and evapotranspiration (ET_{max}, mm day⁻¹) with the standard deviation and coefficient of variation (CV) at ten forest sites

Site	CUP	NEE _{max}	GPP _{max}	ET _{max}
US-SP1	235	-4.16 ± 0.61	7.97 ± 2.07	4.16 ± 0.47
US-DK3	365	-7.75 ± 0.90	17.48 ± 2.24	5.76 ± 2.57
US-NC2	365	-7.02 ± 1.88	14.98 ± 0.97	6.26 ± 0.68
US-Ho1	217	-5.33 ± 0.72	12.50 ± 0.83	4.2 ± 0.34
US-Ho2	217	-5.12 ± 0.36	11.67 ± 1.30	4.32 ± 0.57
US-NR1	169	-3.78 ± 0.80	7.06 ± 0.77	4.91 ± 0.64
US-Fuf	210	-3.42 ± 0.45	6.71 ± 0.65	3.96 ± 0.50
US-Me2	297	-5.97 ± 0.55	9.75 ± 0.46	4.06 ± 0.43
US-Blo	321	-5.27 ± 1.28	7.65 ± 1.25	5.22 ± 0.92
US-Wrc	121	-5.38 ± 0.49	9.51 ± 1.63	4.31 ± 0.59
CV (%)	33	26	34	17

NEE_{max}, GPP_{max}, and ET_{max} were calculated for each year first, then averaged over the study period. NEE data over the study period were averaged for the same date into a single composite year at each site to determine the CUP

site. The US-Wrc was a net source or a sink of carbon, largely depending on the springtime and early summer climatic conditions (NEE_{yr} varied from 100 g C m⁻² in 2003 to -221 g C m⁻² in 1999).

Relationship between carbon uptake and ET and variability in EWUE

To investigate the relationship between carbon uptake and water loss at individual sites, we performed regression analyses between time series (8-day average) of NEE or GPP and ET during CUP. We observed different (i.e., weak to strong) relationships between GPP and ET (R^2 values ranging from 0.35 to 0.81), while NEE and ET showed weak relationships at most of the sites ($R^2 < 0.20$ in eight out of ten sites) (Additional file 2: Table S1). The cross-site regression analysis also shows that ET was more strongly correlated with GPP than NEE. Spatial variation in ET_{yr} explained 31 and 37 % of spatial variability in NEE_{yr} and GPP_{yr} respectively, while spatial variation in ET_{CUP} explained 54 and 68 % of the spatial variability in NEE_{CUP} and GPP_{CUP} respectively.

We observed large differences in the seasonality and magnitudes of EWUE_{GPP} and EWUE_{NEP} (Fig. 3). The EWUE_{GPP} was nearly constant throughout the year at sites with warm and humid summers. At continental or montane sites, EWUE_{GPP} was around zero in winter and fluctuated greatly during the active growing season when GPP increased more than ET. At the semi-arid US-Me2 pine site, EWUE_{GPP} increased steadily as drought progressed in summer and EWUE_{GPP} peaked in early September when drought stress peaked. At the Mediterranean sites, the seasonal pattern of EWUE_{GPP}

differed from those of GPP and ET, with a maximum in winter when ET is smaller and a minimum in the peak growing season (i.e., dry summer months) when ET increased more than GPP due to drought effects. Seasonal change in EWUE_{NEP} was different from EWUE_{GPP}. In general, EWUE_{NEP} started to increase with increasing T_a , reached maximum values in spring, declined in warm-dry summers, and again rose in fall and declined in winter. As a result of large spatial variability in annually or seasonally integrated NEP, GPP, and ET values, we found a wide range of EWUE_{GPP-yr} (1.3–4.08 g C mm⁻¹ ET), EWUE_{GPP-CUP} (1.71–4.21 g C mm⁻¹ ET), EWUE_{NEP-yr} (0.06–1.02 g C mm⁻¹ ET), and EWUE_{NEP-CUP} (0.32–1.1 g C mm⁻¹ ET), with a CV of 40, 36, 67, and 35 %, respectively (Table 3).

Spectral characteristics of NEE and ET across sites

Large spatial variability in carbon uptake, ET, and EWUE among ENFs calls for a closer examination of the spectral characteristics of NEE and ET and the cospectra and coherence of NEE and ET with governing climate variables such as VPD, T_a , PAR, and SWC from week to interannual timescales using the wavelet analysis. The normalized wavelet spectra show that there were larger differences in the NEE spectra across sites than in the ET spectra at seasonal-to-interannual timescales (Fig. 4). Over longer timescales, variability in NEE and ET was relatively smaller in warm and humid summer sites and larger in semi-arid and Mediterranean sites. The comparison of wavelet spectra of NEE and ET for each site (Fig. 5) shows that they deviated from each other especially at seasonal-to-interannual timescales. The deviation between NEE and ET spectra was relatively larger in temperate continental and warm and humid summer sites and smaller in montane, semi-arid, and Mediterranean sites. The wavelet cospectra of NEE and ET to major governing climate variables showed that climate variables were positively correlated to NEE and ET at all timescales, but climate variables were more positively correlated to ET than NEE at seasonal and interannual timescales (Figs. 6 and 7). In particular, climate variables were less positively correlated to NEE at warm and humid summer sites than at other sites, while the wavelet cospectra between ET and climate variables were of a similar magnitude at all sites, except at the US-SP1 site. Variations in NEE and ET most resonated with VPD at weekly timescales and with T_a at seasonal and interannual timescales.

Responses of NEE and ET to T_a and VPD

The responses of NEE and ET to T_a and VPD differed among ENFs (Fig. 8), but were similar in the same climatic zone with the exception of US-Blo in semi-arid/Mediterranean. The maximum NEE occurred near $T_a =$

Table 3 Annual and seasonal (carbon uptake period, CUP) sums of net ecosystem CO₂ exchange (NEE_{yr} and NEE_{CUP}, g C m⁻²), gross primary production (GPP_{yr} and GPP_{CUP}, g C m⁻²), and evapotranspiration (ET_{yr} and ET_{CUP}, mm) with the standard deviation and coefficient of variation (CV) at ten forest sites. Ecosystem water use efficiency (EWUE, g C mm⁻¹ ET) was derived from the ratio between GPP and ET sums (EWUE_{GPP}) and between net ecosystem production (NEP = -NEE) and ET sums (EWUE_{NEP}) at annual (year) and seasonal (CUP) timescales

Site	NEE _{yr} NEE _{CUP}	GPP _{yr} GPP _{CUP}	ET _{yr} ET _{CUP}	EWUE _{GPP_yr} EWUE _{GPP_CUP}	EWUE _{NEP_yr} EWUE _{NEP_CUP}
US-SP1	-70 ± 127 -118 ± 19	968 ± 344 661 ± 232	581 ± 48 376 ± 44	1.67 ± 0.57 1.74 ± 0.45	0.13 ± 0.23 0.32 ± 0.09
US-DK3	-501 ± 176 Same	2337 ± 319 Same	829 ± 75 Same	2.82 ± 0.31 Same	0.60 ± 0.19 Same
US-NC2	-788 ± 304 Same	2839 ± 282 Same	1053 ± 107 Same	2.81 ± 0.45 Same	0.77 ± 0.35 Same
US-Ho1	-256 ± 49 -313 ± 44	1472 ± 108 1428 ± 98	367 ± 57 343 ± 45	4.08 ± 0.62 4.21 ± 0.54	0.72 ± 0.21 0.93 ± 0.22
US-Ho2	-233 ± 39 -290 ± 37	1347 ± 94 1296 ± 86	361 ± 63 339 ± 52	3.79 ± 0.44 3.87 ± 0.42	0.67 ± 0.18 0.88 ± 0.21
US-NR1	-34 ± 23 -159 ± 16	737 ± 99 666 ± 84	572 ± 77 391 ± 36	1.30 ± 0.18 1.71 ± 0.21	0.06 ± 0.04 0.41 ± 0.04
US-Fuf	-112 ± 70 -188 ± 63	937 ± 94 726 ± 89	506 ± 46 371 ± 40	1.85 ± 0.14 1.96 ± 0.13	0.22 ± 0.14 0.50 ± 0.14
US-Me2	-497 ± 91 -490 ± 74	1335 ± 91 1296 ± 91	484 ± 40 445 ± 39	2.78 ± 0.33 2.93 ± 0.35	1.02 ± 0.16 1.10 ± 0.13
US-Blo	-579 ± 276 -578 ± 268	1195 ± 257 1141 ± 253	681 ± 69 662 ± 67	1.76 ± 0.37 1.72 ± 0.37	0.83 ± 0.36 0.85 ± 0.36
US-Wrc	-66 ± 88 -182 ± 40	1370 ± 233 617 ± 75	517 ± 71 230 ± 35	2.71 ± 0.67 2.74 ± 0.54	0.13 ± 0.15 0.82 ± 0.26
CV (%)	83 61	45 58	36 52	40 36	67 35

NEE, GPP, and ET sums and EWUE were determined for each year first, then averaged over the study period

30 °C at warm and humid summer sites, ~22 °C at continental temperate sites, and ~15 °C at a montane, semi-arid, and Mediterranean (US-Wrc) sites, except at the US-Blo (Mediterranean) site where it occurred at ~25 °C. The ET increased alongside T_a up to 33–35 °C at warm and humid summer sites, while it plateaued beyond 20 °C at continental temperate or montane, semi-arid, and Mediterranean sites, except at the US-Blo (Mediterranean) site where ET continued to rise with increasing T_a up to 30 °C. The optimum T_a values for NEE and ET showed a strong positive correlation ($R^2 = 0.86$, $P < 0.001$). The MAT was positively correlated with the optimum T_a for NEE ($R^2 = 0.68$, $P < 0.01$) and ET ($R^2 = 0.72$, $P < 0.01$) across sites. The maximum NEE occurred near VPD = 1.5 kPa at warm and humid summer, continental temperate or montane sites, and at a semi-arid site (US-Fuf). It occurred at less than 1 kPa at a semi-arid site (US-Me2) and at a Mediterranean site (US-Wrc), but at ~2 kPa at the other Mediterranean site (US-Blo). The

maximum ET occurred near VPD = 2.5 kPa at all sites except US-Fuf where it occurred at slightly less than 2 kPa. Results show that the optimum T_a and VPD values were higher for ET than for NEE, and NEE declined more than ET at high T_a and VPD values.

Discussion

The average NEE_{yr} over all sites was -314 ± 261 (±SD) g C m⁻² year⁻¹, indicating that ENFs in the USA are generally net carbon sinks, except for early seral forests, but there are large variances among sites. The NEE_{yr} was < -450 g C m⁻² year⁻¹ in four out of ten sites, which is outside of the range of observed NEE_{yr} in two thirds of the ecosystems in the continental USA surveyed by Novick et al. (2015). A mean NEE_{yr} of -183 ± 270 g C m⁻² year⁻¹ was reported for 506 site-years of data representing a range of global biomes (Baldocchi 2008). The average NEE_{yr} became more negative (i.e., larger C sinks) with increasing MAT, similar to

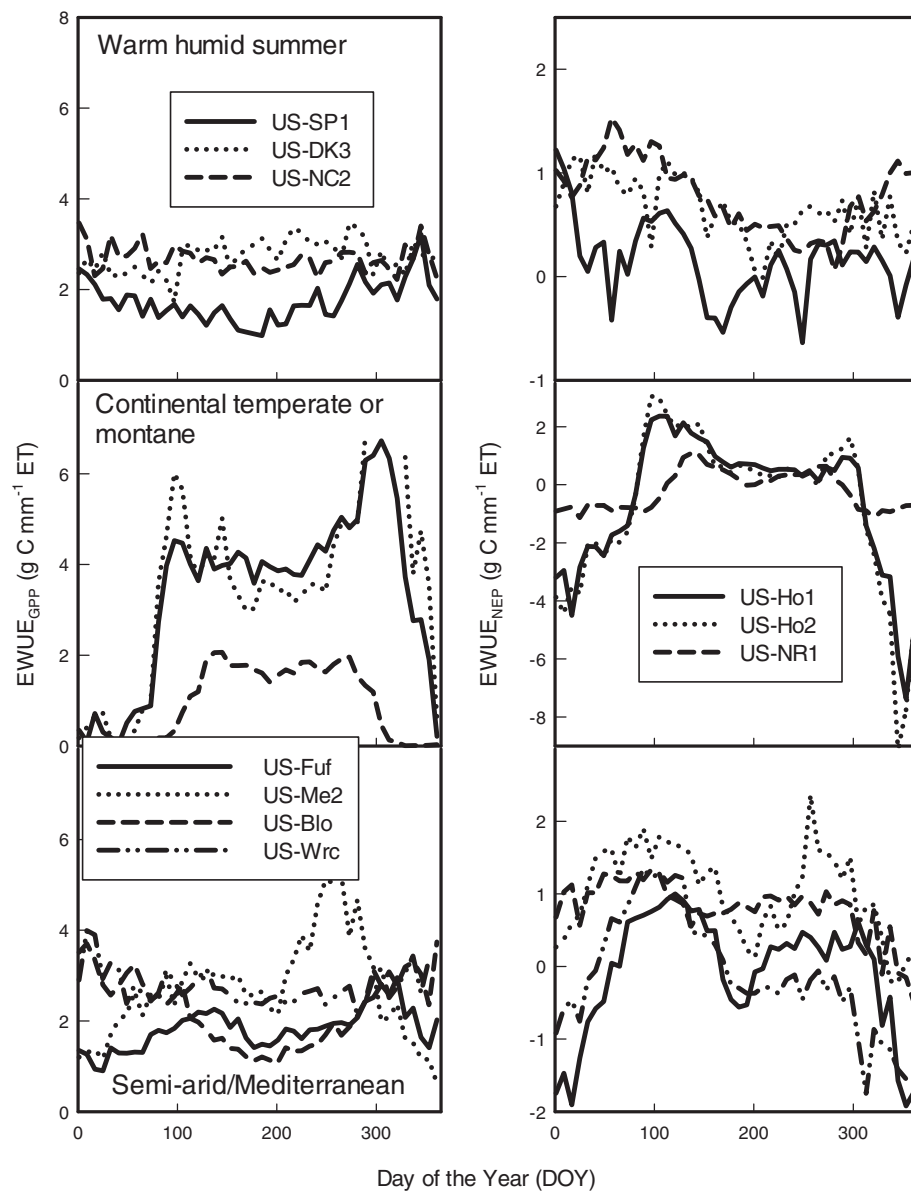


Fig. 3 Seasonal changes (8-day averages) of ecosystem water use efficiency ($EWUE_{GPP}$ and $EWUE_{NEP}$) based on gross primary production (GPP) and evapotranspiration (ET) and net ecosystem production (NEP) and ET at ten forest sites, respectively

previous studies (Lindroth et al. 2008; Valentini et al. 2000), as the length of CUP increased with increasing MAT. The length of CUP was an important determinant of spatial variations in mean NEE_{yr} , which is consistent with the findings of previous studies in boreal and deciduous forests (Baldocchi et al. 2005; Suni et al. 2003).

Despite being in the same PFT type, we observed a large spatial variability in carbon uptake and ET among ENF sites. The spatial variability was larger for carbon uptake than for ET (i.e., larger CV for NEE and GPP than for ET in Tables 2 and 3), which was consistent with findings for grasslands across the USA (Wagle et al.

2015a). Results of the wavelet analysis further support the larger spatial variability of NEE than ET, as we found larger differences in the NEE spectra than in the ET spectra across sites at longer (seasonal-to-interannual) timescales (Fig. 4). Larger spatial variability of NEE than of ET can be partly attributed to the fact that NEE is a more complex process than ET because NEE involves soil respiration, which is greatly influenced by the soil microbial community (Monson et al. 2006) and substrate availability and quality (Raich and Schlesinger 1992), which do not necessarily influence ET. Variation in NEE across multiple spatial and temporal scales is driven by dynamic variation of two biological processes at the

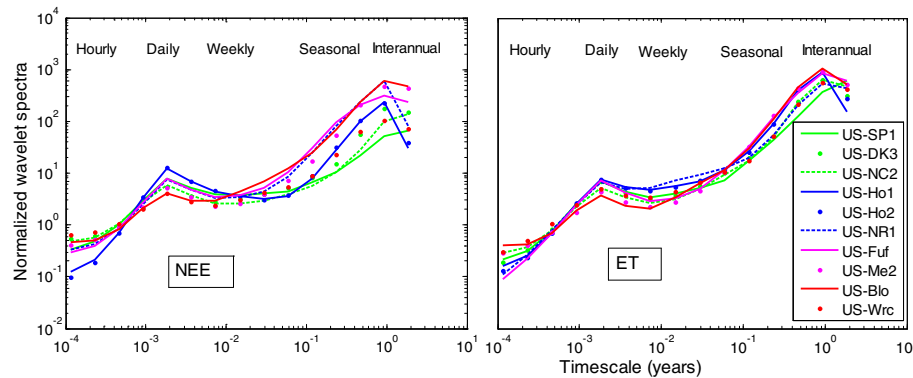


Fig. 4 Normalized wavelet spectra of net ecosystem CO_2 exchange (NEE, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and evapotranspiration (ET, $\text{mm } 30\text{-min}^{-1}$) at ten forest sites. Half-hourly data were used in the analysis

ecosystem level: GPP or ER (which includes both autotrophic and heterotrophic respiration) in response to environmental effects (Stoy et al. 2009). In addition, carbon uptake (NEE or GPP) is constrained more than ET by VPD through restriction of stomatal regulation (Kuglitsch et al. 2008; Wagle and Kakani 2014).

The wavelet analysis showed that NEE and ET deviated from each other at seasonal-to-interannual timescales at all ENFs (Fig. 5) because climate variables were more positively correlated to ET (Fig. 7) than NEE (Fig. 6). However, the deviation between NEE and ET was greater in warm and humid summer and temperate continental sites than in other sites (Fig. 5), indicating that NEE and ET are decoupled differently across study sites. These differences in coupling between NEE and ET across sites can be attributed to differences in the wavelet cospectra of NEE and ET with climate variables. Unlike the wavelet cospectra between ET and climate variables, the wavelet cospectra between NEE and climate variables differed across climatic zones and were generally higher in semi-arid and Mediterranean sites, indicating closer coupling between NEE and climate drivers in these sites. As a result, we observed a relatively larger variability in NEE (Fig. 4) and a smaller deviation between NEE and ET spectra in semi-arid and Mediterranean sites than in warm and humid summer sites (Fig. 5).

The wavelet analysis also indicated that T_a and VPD dominated the variability in NEE and ET over most timescales (Figs. 6 and 7). The responses of NEE and ET to T_a and VPD were very different across climatic zones (Fig. 8). In particular, NEE declined more than ET at high T_a and VPD values, and the maximum NEE occurred at lower ranges of T_a for ENF sites in semi-arid and Mediterranean climate, which would promote greater coupling between NEE and these climate variables. The wavelet analysis further confirms that drivers that vary seasonally or annually were more important

for NEE in semi-arid and Mediterranean sites. Over longer timescales, NEE is influenced by seasonal changes in climatic conditions, leaf dynamics, phenology, rainfall, snow events, and growing season duration (Baldocchi et al. 2001; Stoy et al. 2005). Larger variability in NEE in semi-arid and Mediterranean sites at longer timescales might be related to larger year-to-year variability in soil water availability and drought duration and the length of CUP in these sites. A positive linear relation between annual or seasonal sums of NEE and CUP length in this study suggests that CUP variability has a profound influence on interannual NEE fluxes, which is consistent with an earlier study (Randerson et al. 1999). Unlike the different magnitudes of the wavelet cospectra between NEE and climate variables, the wavelet cospectra between ET and climate variables were similar in magnitude at all sites because the optimum T_a and VPD values were higher for ET than for NEE, and ET was less sensitive to high values of T_a and VPD. The optimum T_a values for NEE and ET increased with increasing MAT, suggesting the thermal acclimation of ecosystem properties (Mooney et al. 1978; Niu et al. 2012).

This study also highlights that the carbon source-sink status of ENFs was conditional upon seasonal changes in climatic conditions and that ENF stands of any age or climatic zone can be either a carbon source or carbon neutral under certain climatic conditions. Such alterations in carbon dynamics have been observed in several grasslands and forests worldwide (Amiro et al. 2006; Barr et al. 2007; Ciais et al. 2005; Wagle et al. 2015a). Although old-growth stands are traditionally viewed as net carbon sources or carbon neutral (DeBell and Franklin 1987) due to increased respiration and decreased photosynthesis, previous studies have suggested that old-growth forests can still be large carbon sinks under favorable climatic conditions (Carey et al. 2001; Luyssaert et al. 2008; Wharton et al. 2012). The carbon source or sink strength of any stand age depends on local climatic

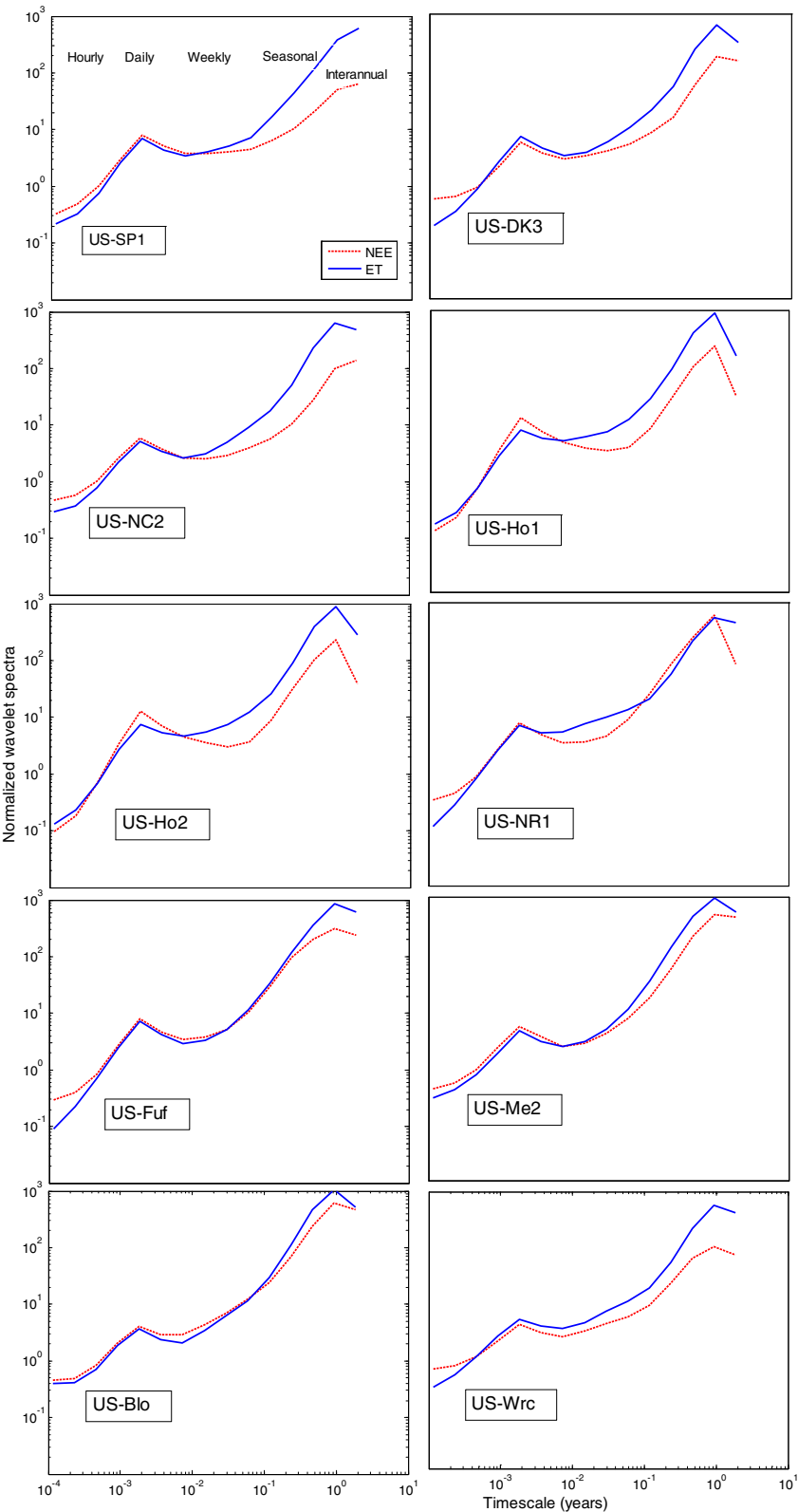


Fig. 5 A comparison of the normalized wavelet spectra of net ecosystem CO₂ exchange (NEE, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and evapotranspiration (ET, mm 30-min^{-1}) at each forest site. Half-hourly data were used in the analysis

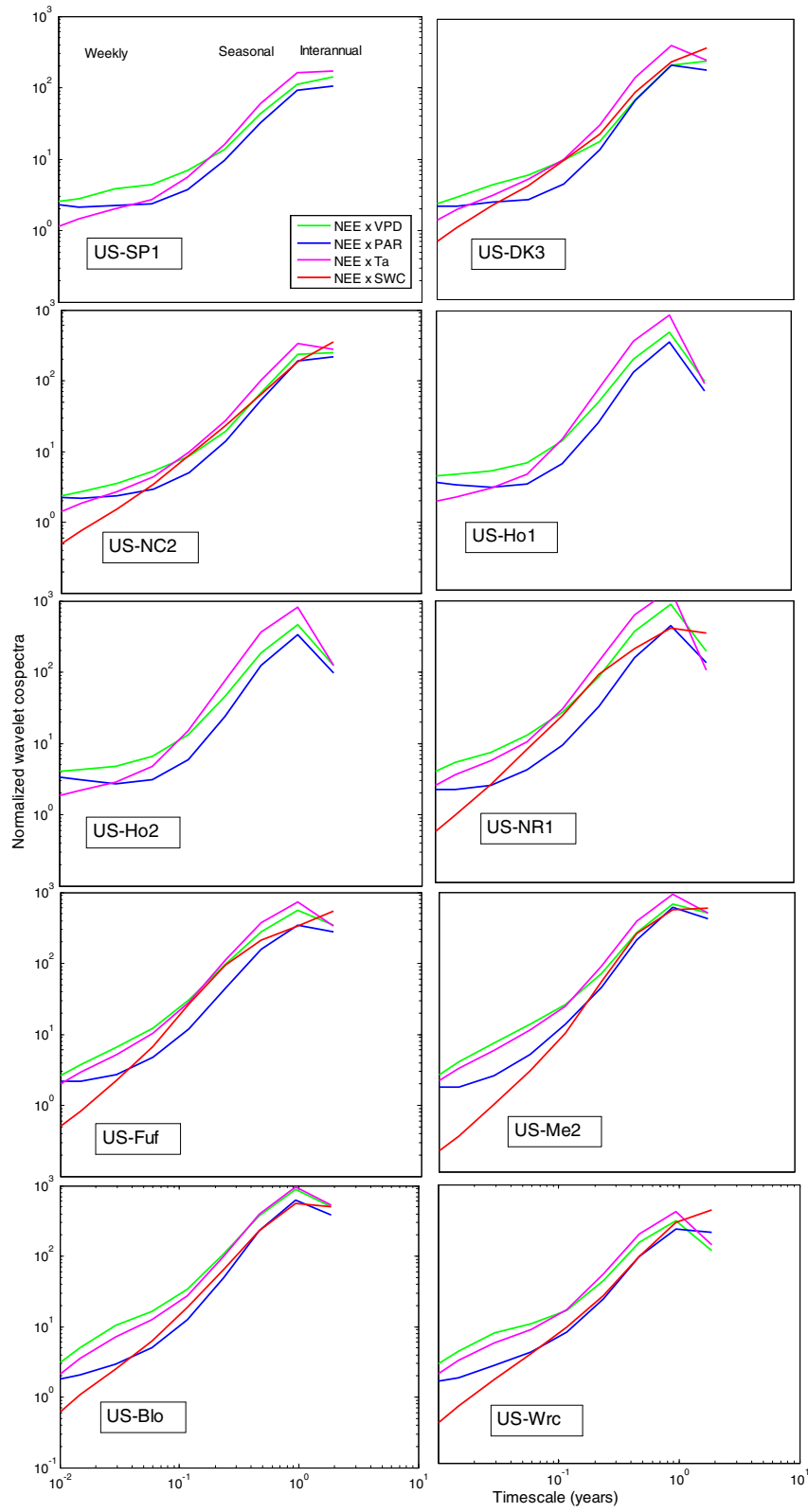


Fig. 6 Normalized wavelet cospectra between net ecosystem CO_2 exchange (NEE) and major climate variables (vapor pressure deficit (VPD), photosynthetically active radiation (PAR), air temperature (T_a), and soil water content (SWC)) at ten forest sites. Half-hourly data were used in the analysis. SWC data were not available in some sites

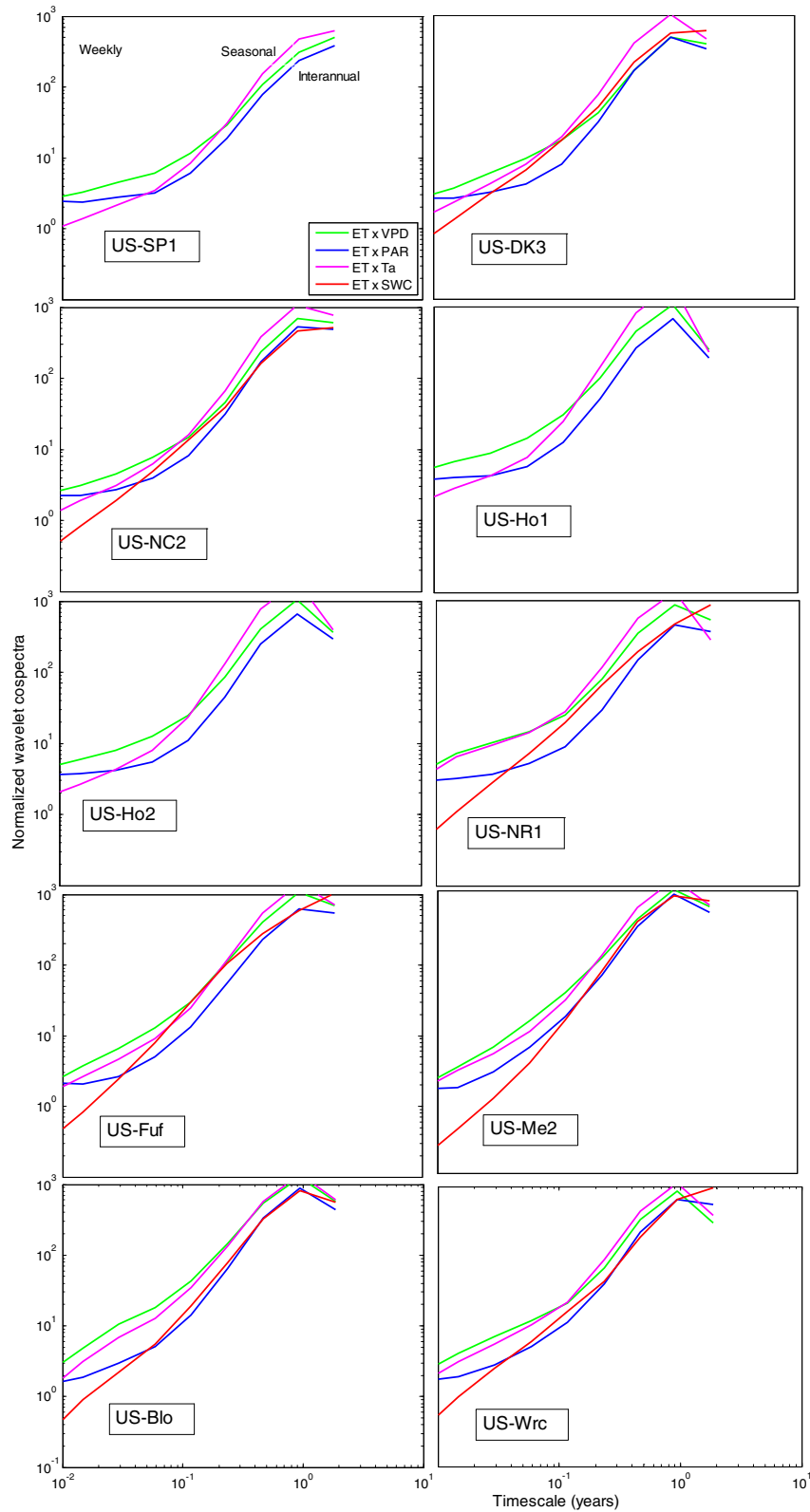
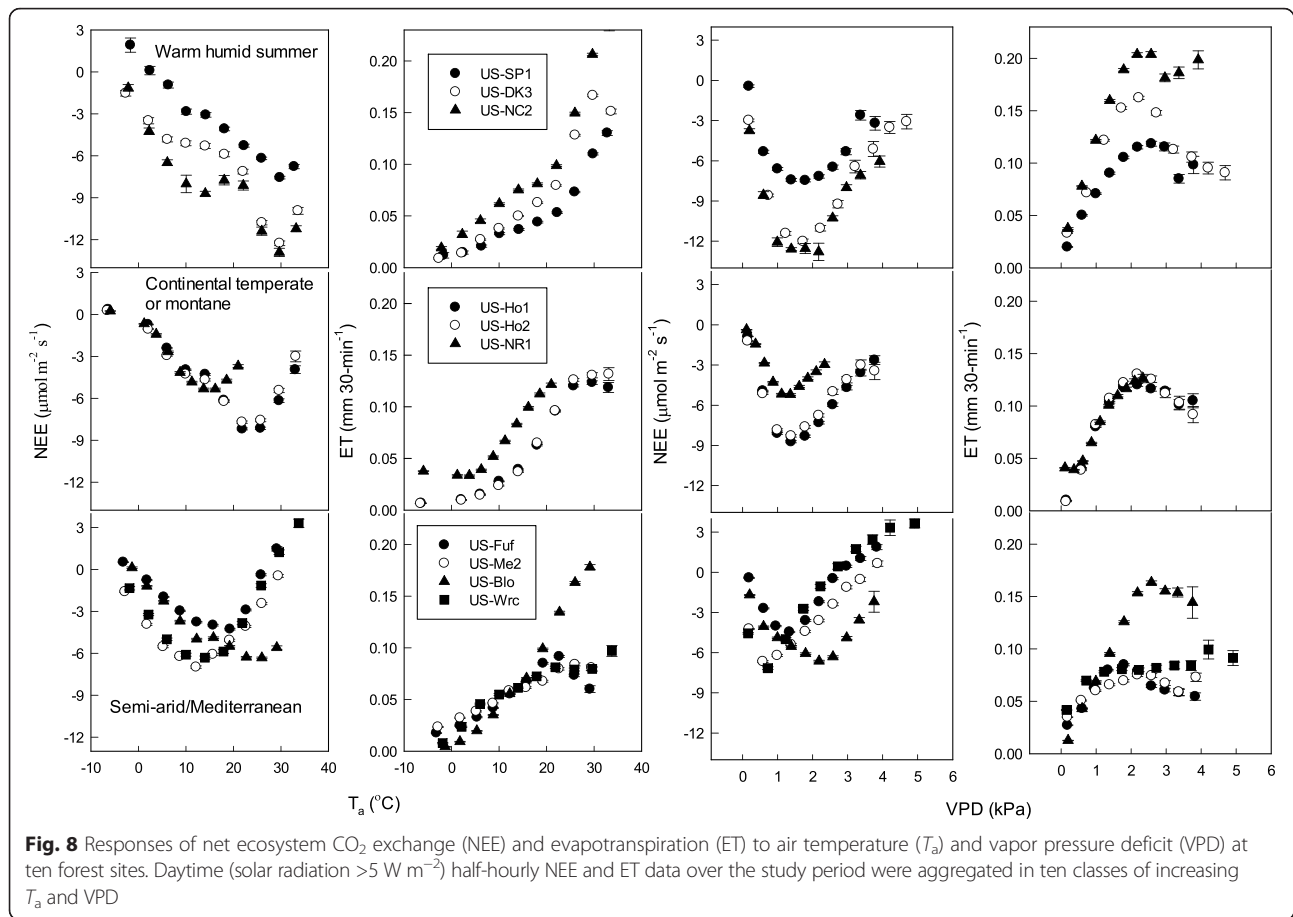


Fig. 7 Normalized wavelet cospectra between evapotranspiration (*ET*) and major climate variables (vapor pressure deficit (*VPD*), photosynthetically active radiation (*PAR*), air temperature (T_a), and soil water content (*SWC*)) at ten forest sites. Half-hourly data were used in the analysis. *SWC* data were not available in some sites



conditions (Chen et al. 2004; Wofsy et al. 1993). However, many studies reported that individual-tree-level carbon and water vapor fluxes varied with tree age and/or height (Bond 2000; Irvine et al. 2004; Law et al. 2001; Novick et al. 2009). For example, different seasonal EWUE trends of three Douglas-fir stands of 7, 19, and 58 years old were observed in similar ecosystems (within 50 km of each other) because of the greater impact of stand age on GPP than ET (Jassal et al. 2009). Our results also demonstrated that the maximum NEE and ET occurred at a higher range of T_a or VPD for younger stands (24 years old) at the US-Blo site compared to older stands in semi-arid and Mediterranean sites (Fig. 8). In addition to climate controls and differences in stand age (varying from ~20 to ~500 years in this study) of ENFs, disturbance history and management practices might have also contributed to some portions of the spatial variability in carbon and water vapor fluxes, but evaluation of those contributions is outside the scope of this study.

Understanding spatial patterns of EWUE is important for elucidating the relationship between carbon uptake and water loss. Different seasonal patterns (Fig. 3) and magnitudes (Table 3) of EWUE_{GPP} and EWUE_{NEP} and the difference in the relationships between NEE or GPP

and ET (Additional file 2: Table S1) across sites indicate differences in trade-off between carbon uptake and water loss by ENFs. Our analyses illustrate that this observed large spatial variability in EWUE can be attributed to a larger spatial variations in carbon fluxes than in ET, a greater sensitivity of carbon fluxes than ET to climate, and differences in the coupling of carbon uptake and ET among sites. Some variations in EWUE among sites can also be attributed to differences in climatic conditions and dominant species (Yu et al. 2008). In addition, ET is composed of evaporation (E) and transpiration (T), and the fractions vary among sites and seasons, which affect EWUE estimations. These results suggest that improved representation of spatial and temporal differences in EWUE among ENFs is necessary in modeling.

Different methods to calculate EWUE complicate comparisons among studies. However, EWUE values in our study were within the reported range from past studies. Annual EWUE_{GPP} of Douglas-fir stands of different ages on the east coast of Vancouver Island, BC, Canada, varied from 0.5 to 5.3 $\text{g C mm}^{-1} \text{ ET}$ (Jassal et al. 2009). The average EWUE_{GPP} (derived from the slope of the relationship between monthly GPP and ET) value

for evergreen conifers in FLUXNET was $0.65 \text{ g C mm}^{-1} \text{ ET}$ (Law et al. 2002). The EWUE_{GPP} of ponderosa pine in central Oregon was $2.9 \text{ g C mm}^{-1} \text{ ET}$ (Law et al. 2002) and EWUE_{GPP} of conifer plantation forest in eastern China was $2.5 \text{ g C mm}^{-1} \text{ ET}$ (Yu et al. 2008).

The same physiological and structural parameters are assigned to all ENF sites based on generalized PFTs for simulation of ecosystem processes. For example, production efficiency models (i.e., light use efficiency models) use a single light use efficiency value and terrestrial ecosystem models use a single optimum T_a value per PFT based on the assumption that PFT-specific physiological parameters do not change with space or time (Raich et al. 1991; Running et al. 1999). Our study highlights large differences in the magnitudes of carbon and water vapor fluxes and their responses to climate among ENFs. Our results are consistent with the findings of previous studies (Law 2014; Van der Molen et al. 2011) that generalized PFTs cannot capture the differences in sensitivity of different species to climate. These results suggest that modeling carbon and water vapor fluxes of ENFs and projections of response of ENFs to climate based on the same PFT parameters can potentially cause extensive errors. Thus, sub-PFT parameterization based on climatic zones is required to better represent climate sensitivity of ENFs and to reduce uncertainty in model predictions.

Conclusions

This study highlights large spatial variability of carbon and water vapor fluxes and EWUE of widely distributed ENFs in the USA. We found large variations in optimum T_a ($15\text{--}30^\circ\text{C}$ for NEE and $20\text{--}35^\circ\text{C}$ for ET) and VPD ($1\text{--}2 \text{ kPa}$ for NEE and $\sim 2.5 \text{ kPa}$ for ET) for NEE and ET among ENFs. Furthermore, NEE showed greater sensitivity to high T_a and VPD than did ET. The NEE and ET responded differently to climate variables as the wavelet cospectra between ET and climate variables were similar in magnitude at all sites, while the wavelet cospectra between NEE and climate variables were generally higher in semi-arid and Mediterranean sites. These results highlight that modeling carbon and water budgets of ENFs based on the same biome-specific parameters can potentially cause extensive errors in model predictions. Therefore, canopy photosynthesis and transpiration models used in predicting responses to future climate and in estimating regional or global carbon and water budgets should be considered using more refined parameterization of ENFs based on climatic zones. Long-term observations and a more complete sample of plant groups within the ENFs of the world are required for further validation of our results and for global application.

Additional files

Additional file 1: Figure S1. Relationships of carbon uptake period (CUP) with mean annual temperature (MAT) and integrated net ecosystem CO_2 exchange (NEE) at annual (yr) and seasonal (CUP) timescales at ten forest sites. (DOCX 20 kb)

Additional file 2: Table S1. The coefficient of determination (R^2) for the relationships of gross primary production (GPP) and net ecosystem CO_2 exchange (NEE) with evapotranspiration (ET) during the carbon uptake period at ten forest sites. (DOCX 12 kb)

Abbreviations

ANN, artificial neural networking; CUP, carbon uptake period; CV, coefficient of variation; E, evaporation; ENF, evergreen needleleaf forests; ET, evapotranspiration; EWUE , ecosystem water use efficiency; $\text{EWUE}_{\text{GPP_CUP}}$, EWUE based on GPP and ET for the length of CUP; $\text{EWUE}_{\text{GPP_yr}}$, EWUE based on GPP and ET at annual scale; $\text{EWUE}_{\text{NEP_CUP}}$, EWUE based on NEP and ET for the length of CUP; $\text{EWUE}_{\text{NEP_yr}}$, EWUE based on NEP and ET at annual scale; GPP, gross primary production; MAT, mean annual temperature; MDS, marginal distribution sampling; NEE, net ecosystem CO_2 exchange; NEE_{CUP} , NEE based on CUP; GPP_{CUP} and ET_{CUP} , integrated NEE, GPP, and ET for the length of CUP; NEE_{yr} , GPP_{yr} , and ET_{yr} , integrated NEE, GPP, and ET at the annual scale; NEP, net ecosystem production; PAR, photosynthetically active radiation; PFT, plant functional type; R^2 , coefficient of determination; SWC, soil water content; T, transpiration; T_a , air temperature; VPD, vapor pressure deficit; WUE, water use efficiency.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

PW did this research work and developed the entire draft manuscript. XX and PG provided the financial support for this study. AN, KN, SD, and SW provided site-specific climate and eddy flux data. XX, TK, BL, SW, RM, JC, PB, KN, and AN provided many edits on the manuscript. All authors read and approved the final manuscript.

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