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An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration

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Abstract

We measured net ecosystem CO_2 exchange (NEE) using the eddy covariance (EC) technique for 4 years at adjoining old field (OF), planted pine (PP) and hardwood forest (HW) ecosystems in the Duke Forest, NC. To compute annual sums of NEE and its components – gross ecosystem productivity (GEP) and ecosystem respiration (RE) – different 'flux partitioning' models (FPMs) were tested and the resulting C flux estimates were compared against published estimates from C budgeting approaches, inverse models, physiology-based forward models, chamber respiration measurements, and constraints on assimilation based on sapflux and evapotranspiration measurements. Our analyses demonstrate that the more complex FPMs, particularly the 'non-rectangular hyperbolic method', consistently produced the most reasonable C flux estimates. Of the FPMs that use nighttime data to estimate RE, one that parameterized an exponential model over short time periods generated predictions that were closer to expected flux values. To explore how much 'new information' was injected into the data by the FPMs, we used formal information theory methods and computed the Shannon entropy for: (1) the probability density, to assess alterations to the flux measurement distributions, and (2) the wavelet energy spectra, to assess alterations to the internal autocorrelation within the NEE time series. Based on this joint analysis, gap-filling had little impact on the IC of daytime data, but gap-filling significantly altered nighttime data in both the probability and wavelet spectral domains.
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1. Introduction

A primary goal of the United States Global Change Research Program (USGCRP) is to quantify the role of vegetation in controlling the magnitude and variability of the terrestrial carbon sink (Sarmiento and Wofsy, 1999). Eddy covariance (EC) estimates of the net ecosystem exchange of CO_2 (NEE) are ideally suited for addressing this goal (Baldocchi et al., 2001) with an important caveat. To evaluate the processes that control NEE, EC data rely on models that partition NEE into its components—gross ecosystem productivity (GEP) and ecosystem respiration (RE). These 'flux partitioning' models (FPMs) can be used in turn to 'gap-fill' missing or rejected data, thereby allowing estimates of CO_2 flux over long periods (Falge et al., 2001). Hence, FPMs are

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an essential tool for interpreting EC data, yet no study to date has critically examined how the choice of a given FPM affects the magnitude and variability of carbon (C) flux estimates by comparison with independent estimates of C flux for different ecosystems that experience similar climatic and edaphic conditions.

Here, we used the EC technique to measure NEE for 5 years at adjoining old field (OF), planted pine (PP) and broadleaf-deciduous ('hardwood', HW) ecosystems that represent a typical post-agricultural successional sequence in the southeastern United States (SE, Oosting, 1942). The study ecosystems offer a unique set-up for a comparison of FPMs because, although they experience the same climatic (*e.g.*, geostrophic winds, cloud cover, precipitation history, air temperature) and edaphic (*e.g.*, soil type, rooting depth) conditions, they differ substantially in friction velocity (u_*, Fig. 1; Stoy et al., 2006), which is often used as the primary filter for nighttime EC measurements (Falge et al., 2001; Gu et al., 2005; Reichstein et al., 2005). These differences in u_* are attributable to differences in roughness properties that reflect differences in foliage drag and leaf area density among the ecosystems (Poggi et al., 2004). Five-year EC time series from these three ecosystems were used to generate NEE, GEP, and RE estimates using four FPMs that differ substantially in the data source employed (*i.e.*, daytime versus nighttime data) and complexity of the modeling procedure. These estimates were compared against the best available independent data and model results from a range of other studies that provide estimates of the magnitude and interannual variability of net primary productivity (NPP), RE, and gross primary productivity (GPP). In this way, we ensure that EC-based estimates are defensible and independently constrained to the extent that ecosystem flux inter-comparison was possible. We then diagnosed the FPMs using both direct comparison and information theory via the Shannon entropy to assess which FPM generated the most reasonable flux estimates across dissimilar vegetative types. After choosing the optimal FPM, we provide error estimates on the flux values that are obtained.

With respect to the inter-comparison, it is important to note that the independent and model-based estimates themselves are naturally prone to random and systematic errors and do not represent the unknown 'true' flux. Regardless, alongside EC-based estimates, these techniques represent the state of the art for estimating C flux. Therefore, estimates generated using these methods provide 'expected' flux values in the logical rather than the statistical sense. If a given FPM fails to reproduce the approximate mean and long-term variability of the independent or model-based estimates, or delivers results that conflict with logical expectations (*e.g.*, if the fast-growing PP ecosystem is found to be a long-term source of C to the atmosphere), we can conclude that this FPM should not be used for generating EC-based estimates across different vegetation types. Below we briefly describe the methods that have been employed by different studies to estimate C flux from the study ecosystems.

At OF, Novick et al. (2004) combined EC and leaf-level physiological measurements with a 'big-leaf' assimilation model to estimate NEE, GEP, and RE for 2001 (Table 1), and used the model to predict C fluxes in the absence of soil moisture (θ) limitations. Combined with other studies, their findings suggest that the interannual variability of NEE in grassland ecosystems may be driven by changes in GEP rather than RE, and that grassland ecosystems can switch from C source to C sink with increasing θ content. The interannual variability of GEP at OF is expected to be large due to reductions in leaf

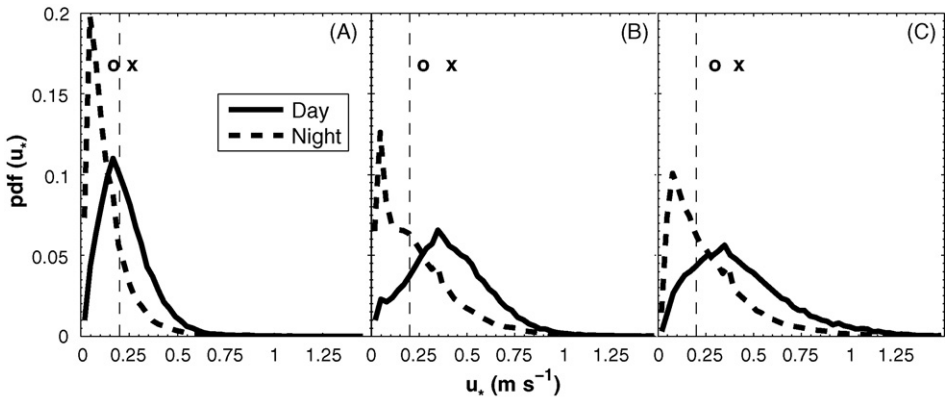

Fig. 1. The probability distribution of measured friction velocity (u_*) for OF (A), PP (B) and HW (C). The symbols o and x indicate median u_* for nighttime and daytime distributions, respectively. $u_* = 0.2$ m s^{-1}, a common threshold for data filtering, is indicated by vertical dashed lines for reference.

Table 1
Estimates of net ecosystem exchange (NEE), ecosystem respiration (RE) and gross primary productivity (GPP) at the old field (OF) and planted pine (PP) ecosystems in the Duke Forest, NC

Ecosystem	Period	NEE	GEP	RE	References
OF	11 April 2001–11 April 2002	97	−1202	1299	Novick et al. (2004)

Ecosystem	Year	NEE	GPP	RE	References
PP	1997		−1224[a]		Luo et al. (2001)[a], Katul et al. (2001b)[b]
	1998	−580 to −650[b], −585[c], −428[d]	−1250[a], −2371[f]	1920[f]	Falge et al. (2001)[c]
	1999	−666[c], −605[d], −661[e], −746[h]	−1808[d], −2287[e]	1203[d]	Lai et al. (2002)[d]
	2000	−792[e]	−2486[e]		Schäfer et al. (2003)[e]
	2001	−355[g]	−2122[g]	1767[g]	Hamilton et al. (2002)[f]
	2002	−410[g]	−2033[g]	1623[g]	Juang et al. (2006)[g]
	2003	−449[g]	−2471[g]	2022[g]	Hui et al. (2004)[h]

All flux units are g C m^{-2} $year^{-1}$. Gross ecosystem productivity (GEP) differs from GPP as described in the text.

area index (LAI) induced by drought and anthropogenic management, namely hay removal, and corresponding changes in canopy conductance. Stoy et al. (2006) showed that EC-measured evapotranspiration (ET) increased by nearly 50% between severe drought and wet years, and used a simple radiation attenuation model after Campbell and Norman (1998) to model transpiration (T), which varied by over 200% among years. Given that GEP is controlled in part by T due to the role of the stomata in coupling canopy H_2O losses with CO_2 gains, we expect that GEP will be highly sensitive to hydrologic forcing at OF, and thus highly variable given the wide range of climatic conditions observed over the measurement period.

Estimates of GPP and/or RE at PP are available from ecosystem carbon budgeting (Hamilton et al., 2002), canopy conductance-based assimilation models (Schäfer et al., 2003), physiology-based assimilation models (Luo et al., 2001), and inverse methods using mean CO_2 and mean air temperature (T_a) profiles within the canopy (Table 1, Lai et al., 2002; Juang et al., 2006). Earlier studies used EC data to estimate NEE and/or its components at PP (Table 1, Falge et al., 2001; Katul et al., 2001b; Law et al., 2002), but did not conduct a sensitivity analysis of different FPMs as performed here. We expect that the magnitude and variability of C fluxes at PP should approximate the independent estimates, noting that at PP the sensitivity of ET and modeled T to severe drought and ice storm damage (McCarthy et al., 2006; Stoy et al., 2006) may inject more variability in GEP during 2001–2005 than in previous years.

There are no independent estimates of NEE at HW at the present, but we expect that interannual C flux variability will be small in a drought-tolerant (Pataki et al., 1998; Pataki and Oren, 2003) closed canopy forest that sustained minor ice storm damage and showed little interannual variability in measured ET or modeled T from 2001 to 2005 (Stoy et al., 2006). The difference in chamber measured soil respiration at HW between mild and severe drought years was ca. 100 g C m^{-2} $year^{-1}$ (6%), and the magnitude of soil respiration at HW was between 10 and 26% larger than at PP (Palmroth et al., 2005). Ecosystem respiration is dominated by forest floor efflux at both ecosystems, but Mortazavi et al. (2005) used δC^{13} measurements to show that soil respiration provides a greater proportion of RE at HW compared to PP. Thus, to a first order, we expect RE at HW to be similar to PP given the similarities in forest floor efflux and the larger contribution of foliage respiration to ecosystem respiration at PP. A complication arises due to an 11.9 ha clear-cut that occurred 200 m south of the HW EC tower on private land in November 2002 (see Fig. 1 in Stoy et al., 2006). We conducted a two-dimensional footprint analysis to determine the impact of this clear-cut on annual flux estimates at HW (Appendix A), which was estimated to be on the order of ca. 200 g C m^{-2} $year^{-1}$ for NEE and RE but less than 50 g C m^{-2} $year^{-1}$ for GEP during 2003 and negligible during other years.

For the purposes of our study, it is important to distinguish between GEP (also called gross ecosystem exchange, GEE) and gross primary productivity (GPP). GEP does not take into account recycling of CO_2 within the ecosystem, such as within the leaf via re-assimilation of metabolic ('dark') respiration, or within the canopy volume and below the plane of the EC instrumentation. GEP is thus analogous, but not identical, to GPP (Goulden et al., 1997). Note also that all EC-based methods that use nighttime RE estimates to extrapolate daytime RE assume that the ratio of photorespiration – energy expended by the oxygenase function of Rubisco – to RE is small. The relative role of photorespiration is likely to be lower in OF which contains a small

proportion of C4 plants (Novick et al., 2004). Our goal was not to quantify differences between GEP and GPP or to attempt to quantify the photorespiratory term in EC-measured RE. Rather, our criteria for success in employing an ideal FPM is its ability to estimate GEP, RE, and NEE values that are consistent with the mean and interannual variability determined by C flux estimates that are independent of eddy covariance, or based on models that assimilate multiple data sources.

We restrict our analysis of FPMs to those that have a basis in ecosystem physiology, namely those that parameterize known relationships between RE and temperature or between GEP (or NEE) and light. These methodologies employ the basic equations used by many ecosystem models, and thus can generate transferable information (*e.g.*, terms of their parameters) for future studies of C dynamics both across time at the ecosystems studied here, and across space with respect to ecosystems with similar characteristics. To this end, we do not explore statistical methods such as multiple imputation (Hui et al., 2004) or more complex algorithms such as neural networks (Hagen et al., 2006), whose 'black-box' nature can complicate the analysis of relationships between driving variables and flux. Commonly used 'look-up tables' do not provide a formal mechanism for generating error estimates – as explored for the case of PP by Oren et al. (2006) – and are likewise not investigated here. After choosing the ideal FPM, we provide error estimates for all flux terms for each ecosystem-year of measurement.

2. Methods

2.1. Site description

Ecological characteristics of the study sites have been described extensively (Ellsworth et al., 1995; Oren et al., 1998; Lai and Katul, 2000; Pataki and Oren, 2003; Novick et al., 2004). Briefly, OF is dominated by the grass *Festuca arundinacea* Shreb., with contributions from other C3 and C4 grasses and various herbs, and is mowed at least once annually for forage (Novick et al., 2004). PP is a 22-year-old (in 2005) planted *Pinus taeda* L. forest (Ellsworth et al., 1995; Oren et al., 1998; Katul et al., 1999). HW is an 80–100-year-old mixed deciduous forest dominated by late-successional shade-tolerant *Quercus* (oak) and *Carya* (hickory) species with fewer shade-intolerant individuals of *Liquidambar styraciflua* L. and *Liriodendron tulipifera* L. positioned in the upper canopy (Pataki and Oren, 2003; Palmroth et al., 2005).

Measurement details are listed in Table 2. Flux measurements were made with open path LI-7500 IRGAs (Li-Cor, Lincoln, NE) coupled with CSAT-3 sonic anemometers (Campbell Scientific, Logan, UT). A closed path system with a LI-6400 was employed at PP before 1 May 2001. Corrections to fluxes measured by the closed path system that resulted from an experiment with both open and closed path systems are described in Oren et al. (2006).

2.2. Measurement period

The 2001–2005 measurement period was notable for an extended drought that began in the latter part of the growing season (April–September) in 2001 (hereafter 'mild drought') and continued through most of the 2002 growing season ('severe drought', Table 3). Mean T_a was higher during the severe drought than during the other growing seasons measured here. A severe ice storm event in December 2002 sharply reduced leaf area index (LAI) at PP (McCarthy et al., 2006), but resulted in little observed damage to canopy structure and canopy conductance at OF and HW (Stoy et al., 2006). The 2003 growing season was wetter than average ('wet year') and the 2004 growing season experienced

Table 2
Summary of ancillary measurements and sensor locations

Variable	Instrument	Company	Height (m)		
			OF	PP	HW
T_a/RH/D	HMP 35C/45C	Campbell Scientific, Logan, UT	2.0	12	23
PAR	LI-190SA	Li-Cor, Lincoln, NE	4.8	22.2	41.8
R_n	Q7[a], CNR1	REBS, Seattle, WA; Kipp and Zonen, Delft, The Netherlands	4.8	22.2	41.8
u/u_*	CSAT3 triaxial sonic anemometer	Campbell Scientific, Logan, UT	2.8	20.2	39.8
LAI	LAI-2000, litter baskets	Li-Cor, Lincoln, NE			
NEE/LE	LI 7500[b]	Li-Cor, Lincoln, NE	2.8	20.2	39.8

Negative height values denote distance belowground.
[a] Q7 radiometers were employed before 1 January 2004 and the CNR1 radiometers thereafter.
[b] Coupled to CSAT3. Corrections for the effects of air density on flux measurements were calculated after Webb et al. (1980).

Table 3
Interannual variation in the sum (Σ) of precipitation (P) and photosynthetically active radiation (PAR) and mean air temperature (T_a) during the April–September growing season (gs) across the 2001–2005 measurement period

Year	$\sum P$ (mm gs^{-1})	Hydrologic signature	$\sum$ PAR (mol photons m^{-2} gs^{-1})	Mean T_a (°C)
2001	529 (-1σ)	Mild late-season drought	7274	20.3
2002	371 (-2σ)	Severe drought	7135	21.9
2003	790 ($+1\sigma$)	Wet	6472	20.4
2004	661	Normal	6692	21.0
2005	359 (-2σ)	Severe late-season drought	6669	21.2

Numbers in parentheses are the standard deviation (σ) of the measurements from the long-term (110 years) mean. Monthly climatic and hydrologic variability for the 2001–2004 period is detailed in Stoy et al. (2006).

precipitation (P) commensurate with the long-term (110 years) mean ('average year'). P during the 2005 growing season was extremely low as in 2002, but the effects of this drought were constrained to the latter months as in 2001. The cloudier conditions during the 2003–2005 growing seasons resulted in lower photosynthetically active radiation (PAR) than during the previous years (Table 3). Macroclimatic conditions were identical among ecosystems because they are adjacent; flux towers lie within 750 m of each other. Some micrometeorological drivers, including vapor pressure deficit (D), soil temperature (T_s) and θ, varied slightly among ecosystems and across seasons due to inter-ecosystem differences in LAI and evapotranspiration (Stoy et al., 2006).

2.3. Flux partitioning methods

We explored four methods of varying complexity to partition NEE into its RE and GEP components. We restricted our analysis to methods that parameterize known relationships between meteorological driving variables and flux to maximize information transfer with modeling efforts as mentioned. Two methods, one based on the annual Q_{10} model (AQ10) and another on short-term exponential fits (STE), use measured nighttime fluxes (defined here as periods in which the solar zenith angle exceeds 90°) to model RE as a function of temperature. The other two methods, one based on the rectangular hyperbolic fit (RH) and the other on a non-rectangular hyperbolic fit (NRH), use the intercept of the relationship between PAR and daytime NEE (NEE_d) to model RE. GEP was then calculated by definition:

$$\mathrm{GEP} = \mathrm{NEE} - \mathrm{RE} \tag{1}$$

We use the micrometeorological convention where fluxes from biosphere to atmosphere are denoted as positive. The NRH was used to gap-fill missing NEE_d measurements for the AQ10 and STE; these methods as employed here only gap-fill nighttime RE measurements, a far larger source of missing EC data. All model parameters were determined using non-linear least squares via an unconstrained Gauss–Newton algorithm (MATLAB, Natick, MA). Optimization via the Levenburg–Marquardt algorithm was also investigated but did not result in substantial differences in annual flux estimates. We note that the error distribution of EC measurements may be better approximated as double exponential (Laplacian), rather than normal (Gaussian), and thus least absolute regression may be preferred for estimating model parameters (Hollinger and Richardson, 2005; Richardson and Hollinger, 2005; Richardson et al., 2006). We employed least-squares optimization here for comparisons with previous studies.

2.4. Annual Q_{10} (AQ10)

One of the simplest methods for gap-filling missing nighttime data is to model RE measurements collected under nighttime conditions of sufficient turbulence (*e.g.*, $u_* > 0.2$ m s^{-1}, Fig. 1) as a function of a physical driver, usually T_a or T_s, or to use a slightly more complex model that might include, for example, θ. Morgenstern et al. (2004) found 29 studies between 1993 and 2001 that employed different methods to relate RE to T. Here, we use the commonly employed Q_{10} model:

$$\mathrm{RE_{AQ10}} = R_{10} Q_{10}^{(T_a - 10)/10} \tag{2}$$

where R_{10} is base RE at a reference temperature, here 10 °C, and Q_{10} describes the exponential temperature response of RE. At both PP and HW, the frequency characteristics of RE estimated from Eq. (2) better matched the frequency characteristics of observed RE when T_a rather than T_s was used as the driving variable (Stoy et al., 2005). The parameter values of R_{10} and Q_{10} were determined for each ecosystem at the annual time scale. Seasonal variations in u_* are likely to result in a data set that is biased towards colder periods when

parameterizing Eq. (2) (Gu et al., 2005; Reichstein et al., 2005). This is in part attributable to the fact that summer-time nocturnal runs experience smaller mean u_* than their winter-counterpart at these ecosystems (see Juang et al., 2006 or Stoy et al., 2006 for time series of u_* measurements at the study sites).

2.5. Short-term exponential (STE)

Reichstein et al. (2005) noted that the parameters in Eq. (2) may vary along the annual cycle (cf. Janssens and Pilegaard, 2003; Palmroth et al., 2005) and suggested a strategy by which the parameter values of the base respiration and the temperature response can be estimated over the time scales at which they might vary using the 'short-term exponential' (STE) method. They used the Arrhenius (1889) equation after Lloyd and Taylor (1994):

$$\mathrm{RE_{STE}} = R_{10,\mathrm{STE}} \exp\left(E_0\left[\frac{1}{283.15 - T_0} - \frac{1}{T_\mathrm{a} - T_0}\right]\right) \tag{3}$$

with a constant T_0 parameter (227.13 K, Lloyd and Taylor, 1994) and a 15-day moving window to determine variability in the temperature sensitivity parameter (E_0), then a 4-day window to estimate the base respiration parameter ($R_{10,\mathrm{STE}}$). More methodological details are discussed in Reichstein et al. (2005).

2.6. Rectangular hyperbola (RH)

Lee et al. (1999) noted that the relationship between accepted nighttime flux data and T was statistically significant but considerably scattered. To investigate the seasonal dynamics of RE in a way that was less subject to the constraints of nighttime EC data quality, they used the intercept parameter (γ) of the rectangular hyperbolic model (RH, *i.e.*, the Michaelis–Menten model), which for NEE can be written as (Ruimy et al., 1995):

$$\mathrm{NEE_{RH}} = -\frac{\alpha\,\beta\,\mathrm{PAR}}{\alpha\,\mathrm{PAR} + \beta} + \gamma \tag{4}$$

where α is the mean apparent ecosystem quantum yield, β is GEP at light saturation, and signs follow the micrometeorological convention. Lee et al. (1999) used a 15-day window to estimate the parameters in Eq. (4), and then regressed γ, as a measure of RE, against T_s. We determined the parameters of Eq. (4) for monthly periods because some gaps in the 15 site-year measurement period were greater than 15 days, and used monthly γ as an estimate of RE.

2.7. Non-rectangular hyperbola (NRH)

Gilmanov et al. (2003) proposed a method that employs a non-rectangular hyperbolic fit (NRH):

$$\mathrm{NEE_{NRH}} = -\frac{1}{2\eta}\left(\alpha\,\mathrm{PAR} + \beta - \sqrt{(\alpha\,\mathrm{PAR} + \beta)^2 - 4\alpha\beta\eta\,\mathrm{PAR}}\right) + \gamma \tag{5}$$

where α, β and γ have the same definition as in Eq. (4), and the parameter η describes model curvature as the NEE/PAR relationship approaches saturation. Eq. (4) is a special case of Eq. (5) when $\eta = 1$. A major methodological difference between the NRH and the RH methods is that in the NRH, parameters were estimated for daily periods according to the original use of Eqs. (4) and (5) (Gilmanov et al., 2003), and missing data were gap-filled using Eq. (5) with mean monthly parameter values in the former. Because an unconstrained nonlinear optimization was performed, daily parameter sets were rejected if parameter values were not realistic (*i.e.*, if α, γ or η were less than zero and if η was greater than unity), or if the root mean squared error between model and measurements exceeded 0.001 mg C m^{-2} s^{-1}. Parameter sets were also rejected in instances where the Gauss–Newton algorithm did not converge to a solution within the specified tolerance (here 10^{-6}) within the maximum admissible number of iterations (here 4000). In these cases, the four-parameter NRH model was a poor descriptor of the data for that day of the measurement record.

2.8. Thresholds

FPM parameters, and thus annual NEE estimates, may be sensitive to extreme data values. An added advantage of the NRH is that it can recursively provide inference into realistic flux data thresholds that otherwise might have to be selected subjectively, because extreme values may result in non-convergence of the curve-fitting algorithm on a daily basis. We explored the population of data points from daily data sets when the Gauss–Newton algorithm converged to an optimum and determined the minimum admissible NEE measurement to be −0.7, −0.85, and −0.8 mg C m^{-2} s^{-1} for OF, PP, and HW, respectively, and the maximum NEE threshold to be 0.5 mg C m^{-2} s^{-1} for all ecosystems. Measurements that exceeded these thresholds were removed. The maximum NEE threshold is larger than the maximum

soil respiratory fluxes reported in Palmroth et al. (2005) for PP and HW, as expected for whole ecosystem respiration.

To minimize subjectivity in determining a u_* threshold to filter nighttime data (Barford et al., 2001), we used the atmospheric stability threshold after Novick et al. (2004), which requires near-neutral atmospheric stability for nighttime data acceptance. There are three reasons for adopting this threshold: (1) Day-time and night-time footprint sizes become comparable (though not identical). This is an important consideration if footprint size may exceed ecosystem dimensions, as is the case here, or if there is a large spatial component in ecosystem flux activity, as discussed for the case of PP by Oren et al. (2006). (2) The flux-transporting eddies under near-neutral conditions are dominated by ramp-like structures that appear insensitive to rapid transients such as passage of clouds during nocturnal conditions (Cava et al., 2004). (3) Storage fluxes are likely to be small under near-neutral conditions when compared to the fluxes above the canopy (Juang et al., 2006). We note that u_* thresholds are employed in the original usage of the STE. These thresholds are determined over 3-month periods for each ecosystem based on the original algorithm described in Reichstein et al. (2005). Briefly, flux data are sorted into temperature and u_* classes and the threshold for each class is taken to be the u_* value for which mean flux exceeded 95% of the mean flux at higher values of u_*. Because the intent of this method is similar to one of the goals of the atmospheric stability method – to make flux estimates independent of turbulent statistics – we adopted the atmospheric stability threshold for the STE as well.

2.9. Information content

In addition to the comparison among FPMs, we explored the information content (IC) of raw and gap-filled flux data in both the probability and frequency domains using the Shannon entropy and a wavelet variant thereof. We undertook this analysis to investigate how the process of gap-filling generates differences in the IC relative to that contained in raw data (Katul et al., 2001a). The Shannon-entropy ($\mathrm{ENT_S}$; Shannon, 1948) is a formal method for assessing the IC and is calculated as

$$\mathrm{ENT_S} = -\sum_{i}^{N} p_i(\hat{x}) \ln(p_i(\hat{x})), \tag{6}$$

where p_i is the discrete probability density function (here estimated from a histogram defined over N bins) of an arbitrary time series having zero mean and unit variance, *i.e.*, if x denotes the original time series, then $\hat{x} = (x - \bar{x})/\sigma_x$ where the over bar denotes time averaging and $\sigma = \overline{((x-\bar{x})^2)}^{1/2}$ is the standard deviation. Maximum entropy (or minimum IC) is attained when $p_i = 1/N$, which represents random (white) noise. We further normalized our entropy estimates by this maximum theoretical value such that when $p_i = 1/N$, $\mathrm{ENT_S} = 1$. This normalization provides entropy estimates that are independent of N provided N is sufficiently large (here 200).

$\mathrm{ENT_S}$ integrates the IC over time through the pdf and hence is primarily sensitive to the frequency of occurrence of excursions in NEE measurements from their mean state. To quantify whether gap-filling results in a change in the frequency characteristics of NEE (or alternatively their auto-correlation), we computed the 'wavelet entropy' ($\mathrm{ENT_W}$) of normalized raw and gap-filled flux time series after computing orthonormal wavelet coefficients using the Haar wavelet basis. In this application, p (Eq. (6)) represents the spectral energy of the Haar wavelet coefficients computed over a sequential doubling of frequencies i and $N = \log_2(87648) - 1 \cong 15$, where 87,648 is the number of 1/2 h periods in the 5-year measurement records. Note that because of the strong locality of the Haar wavelet basis in the temporal domain, p can be readily computed for both gap-filled and gap-infected time series. More details on the application of the wavelet transformation for flux analysis can be found elsewhere (Katul et al., 2001b; Braswell et al., 2005; Stoy et al., 2005).

3. Results and discussion

3.1. Flux partitioning methods

The salient results of the FPM analyses (Fig. 2) are that (1) flux estimation is highly sensitive to the method employed, and (2) the simpler methodologies return unrealistically high interannual mean flux magnitude (the AQ10 and RH) or variation in flux (AQ10). For example, mean $\mathrm{NEE_{RH}}$ at HW is less than -700 g C m^{-2} year^{-1} (Fig. 2A), a stronger C sequestration rate than predicted by all methods for all ecosystems, even the fast-growing PP. In contrast, the AQ10 predicts that OF is a C source of 400 g C m^{-2} year^{-1} on average, a situation that would not be sustainable over the long term. Also, the interannual variability of $\mathrm{NEE_{AQ10}}$ is higher by over

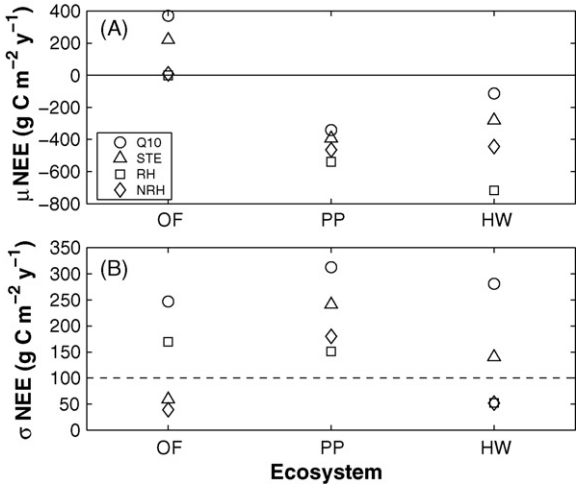

Fig. 2. The mean (A) and standard deviation (B) of annual NEE at old field (OF), planted pine (PP) and hardwood forest (HW) ecosystems for the 2001–2005 measurement period. Negative values represent flux from atmosphere to biosphere. A comprehensive spatial variability study combined with a flux error analysis by Oren et al. (2006) suggested that NEE error at PP is on the order of 100 g C m^{-2} year^{-1}, as indicated by the dashed line.

50 g C m^{-2} year^{-1} for all ecosystems, in part because it results in unreasonable values for certain ecosystem-years (Appendix B). For example, observe the strong C source predicted for PP in 2002, and the positive NEE estimates at HW during the drought years of 2001 and 2002 but negative estimates during the drought year of 2005 (see Appendix B). We, therefore, concentrate on the contrast between the STE and the NRH, both of which generated more realistic estimates of NEE, RE, and GEP (Fig. 2, Table 4). (Flux estimates for each site year generated by the AQ10 and RH methods are listed in Table B1 for completeness.) We note that minor differences in the output of two different techniques is expected and may fall within the range of error quantified in the case of NEE at PP to be over 100 g C m^{-2} year^{-1} for some years (Oren et al., 2006), as indicated by the dashed line in Fig. 2. Therefore, we interpret the results from periods in which estimates differed from expectations by at least that amount. We begin with the STE method and discuss only the major findings of the comparisons.

The STE estimated that OF lost nearly 1100 g C m^{-2} year^{-1} (Table 4A) to the atmosphere over the measurement period, a value that is difficult to reconcile with the amount of C removed as biomass during the annual mow, which represented an additional loss of ca. 100, 100, 400, 200 and 100 g C m^{-2} year^{-1} for 2001–2005, respectively. Despite anomalous NEE_{STE} values at OF, annual GEP_{STE} was strongly related to ET (r^2 = 0.78, Stoy et al., 2006), as expected due to the coupling of these two fluxes via stomatal function.

NEE_{STE} at PP followed an interannual pattern that was broadly consistent with the drought sensitivity of *P. taeda* and the *P* record during the 5-year study period (Oren et al., 1998; Pataki and Oren, 2003; Stoy et al., 2005; Stoy et al., 2006), and the ice storm-induced reduction in LAI (McCarthy et al., 2006). GEP_{STE}

Table 4
Estimates of net ecosystem exchange (NEE), ecosystem respiration (RE), and gross ecosystem productivity (GEP) in old field (OF), pine plantation (PP) and hardwood forest (HW) ecosystems from (A) the short-time exponential method (STE) of Reichstein et al. (2005) and (B) the non-rectangular hyperbolic (NRH) method of Gilmanov et al. (2003)

Ecosystem	Year	NEE	GEP	RE
(A) STE				
OF	2001	200	−1720	1920
	2002	200	−1270	1470
	2003	320	−2170	2490
	2004	200	−1770	1980
	2005	170	−1310	1480
PP	2001	−360	−2410	2050
	2002	20	−2440	2460
	2003	−220	−2080	1860
	2004	−520	−2190	1670
	2005	−770	−2690	1920
HW	2001	−230	−2240	2000
	2002	−100	−2220	2120
	2003	−240	−1980	1740
	2004	−350	−2000	1650
	2005	−470	−1850	1380
(B) NRH				
OF	2001	−40	−1270	1230
	2002	20	−970	980
	2003	−30	−1520	1500
	2004	30	−1360	1390
	2005	60	−1050	1110
PP	2001	−610	−1950	1340
	2002	−270	−1880	1610
	2003	−230	−1950	1730
	2004	−420	−2180	1760
	2005	−740	−2580	1840
HW	2001	−510	−1710	1200
	2002	−390	−1710	1320
	2003	−170 (−400)	−1610 (−1650)	1440 (1250)
	2004	−430	−1750	1310
	2005	−490	−1720	1230

Numbers in parentheses represent adjusted estimates of 2003 HW fluxes after accounting for clear-cut effects using the footprint thresholding methodology described in Appendix A. Units are g C m^{-2} year^{-1}. NEE estimates using the NRH for the 2001–2004 period for PP were given in Oren et al. (2006). They are reproduced here for completeness.

ranged from ca. 2000 to 2700 g C m^{-2} $year^{-1}$ (Table 4A) largely within the range predicted by the independent estimates (1800–2500 g C m^{-2} $year^{-1}$, Table 1). However, NEE_{STE} was positive in 2002 and RE_{STE} during 2003 was 600 g C m^{-2} $year^{-1}$ less than during severe drought (2002) despite the substantial production of needle and branch litter by the ice storm, which is an unexpected result.

GEP_{STE} differed by less than 20% among years at HW, as expected at a late successional hardwood forest comprised largely of drought-tolerant species (Pataki et al., 1998; Oren and Pataki, 2001; Pataki and Oren, 2003; Palmroth et al., 2005). However, RE_{STE} differed by nearly 35% among years; the 2001 and 2002 RE_{STE} estimates were over 600 g C m^{-2} $year^{-1}$ greater than 2005 despite similar drought conditions. Consequently, the magnitude of NEE_{STE} during 2005 was more than twice that in 2001 and nearly five times the 2002 estimate. In summary, whereas the STE largely agreed with expectations of ecosystem flux given prior knowledge, there were a number of instances where results may be considered unreasonable.

At OF, mean annual NEE_{NRH} was not significantly different from zero as determined by a two-tailed unequal variance t-test ($p = 0.69$, $t = 0.43$; Ruxton, 2006). However, adding biomass removed by the mow to NEE_{NRH} resulted in a distribution that is significantly different from zero ($p = 0.24$, $t = 3.5$) with a mean of ca. −200 g C m^{-2} $year^{-1}$. This is the imbalance in the C budget that cannot be explained by combining EC and harvest estimates, and represents either measurement uncertainty or an annual loss of soil C to the atmosphere or to groundwater via dissolved organic carbon (DOC) dissolution. At PP, growing nearby on the same soil, DOC represents a trivial ecosystem C loss compared to other fluxes (ca. 10 g C m^{-2} $year^{-1}$, Schäfer et al., 2003). Other soil C losses can be inferred by comparison with PP because both ecosystems shared common management practices and ecosystem composition across a large portion of their current extents. Preliminary estimates of belowground C show similar values (∼4500 g C m^{-2}, K. Johnsen, unpublished) at both sites. Thus, it is unlikely that soil C loss explains the imbalance, which appears to be attributable to measurement uncertainty. Whereas a lack of closure of 200 g C m^{-2} $year^{-1}$ appears large compared to the near zero NEE estimates, this term is within the range of error of GEP_{NRH} and RE_{NRH} as discussed below. The lack of closure that results from using NRH estimates is approximately half of that which arises when using the STE.

Annual GEP_{NRH} at OF was strongly related to ET ($r^2 = 0.84$), but averaged over 400 g C m^{-2} $year^{-1}$ less than GEP_{STE} due to lower RE estimates. The 2001 GEP and RE estimates using the NRH and STE were on the order of −1300 and 1200 and −1700 and 1900 g C m^{-2} $year^{-1}$, respectively. The GEP_{NRH} and RE_{NRH} estimates for 2001 are closer to those of Novick et al. (2004), who used a combination of EC and porometry measurements in conjunction with a big leaf model to estimate GEP and RE values of −1200 and 1300 g C m^{-2} $year^{-1}$, respectively.

At PP, the magnitude of NEE_{NRH} was largest in the years with late-season droughts, 2001 and 2005. Although at first glance this appears puzzling, the finding is reasonable when considering that in both years growing conditions were ideal until the latter part of the growing season when the drought intensified; Palmroth et al. (2005) demonstrated that in both stands low θ greatly reduced soil respiration. Thus, high NEE in these years is due to high GEP early in the season followed by low RE later in the season. GEP_{NRH} and RE_{NRH} for PP were slightly larger in magnitude than estimates for an earlier period (1998–1999) obtained with an inverse modeling approach (Lai et al., 2002, Tables 1 and 4B), consistent with the fact that the PP canopy closed only at the end of 1999. GEP_{NRH} and RE_{NRH} for 2001–2003 at PP were approximately equal to or slightly lower than estimates from a similar inversion approach that accounted for local thermal stratification (Juang et al., 2006). GEP is expected to be lower than GPP due to the C 'recycling' issues mentioned in Section 1. GEP_{NRH} was equal to or slightly lower than GPP from budgeting approaches (Hamilton et al., 2002) and estimates based on sap flux constraints (Schäfer et al., 2003), with a similar degree of interannual variability (Tables 1 and 4). NEE_{NRH} at PP was lowest in 2003 (−225 g C m^{-2} $year^{-1}$), as expected after ice storm canopy damage, but its magnitude was over 200 g C m^{-2} $year^{-1}$ less than estimates from Juang et al. (2006).

Excluding 2003, interannual variability of NEE_{NRH}, GEP_{NRH}, and RE_{NRH} at HW were low, on the order of 50–100 g C m^{-2} $year^{-1}$. A two-dimensional footprint analysis suggests that fluxes during 2003 were impacted by the December 2002 private land clear-cut (see Appendix A). After accounting for the clear-cut effects, HW had the lowest NEE variability among the methods for all three ecosystems, as expected based on results from previous sap flux and soil respiration studies (Pataki and Oren, 2003; Palmroth et al., 2005). This low interannual flux variability at HW is consistent with recent findings from a HW site at Walker Branch, TN by Hanson et al. (2004), who also found NEE variability on the order of 100 g C m^{-2} $year^{-1}$ for 1993–2000. These

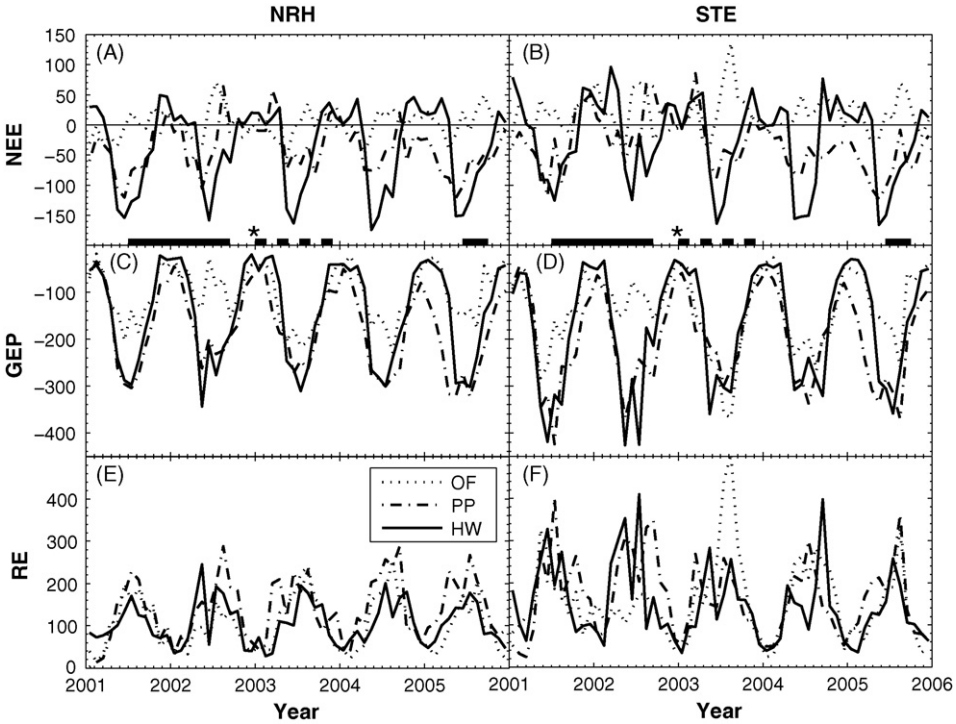

Fig. 3. Monthly net ecosystem exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (RE) at the old field (OF), planted pine (PP) and hardwood forest (HW) ecosystems in Duke Forest. NRH refers to estimates using the non-rectangular hyperbolic method of Gilmanov et al. (2003) and STE to estimates using the short-time exponential method of Reichstein et al. (2005). Drought and wet conditions are indicated by solid and dashed bars, respectively. The severe ice storm in December 2002 is indicated by an asterisk. Flux units are g C m^{-2} $month^{-1}$.

values were gap-filled using the 'look-up table' method, incorporating a temperature response curve for RE similar to the AQ10; we showed earlier that such approach tends to amplify interannual variability. In summary, annual flux estimates using the NRH largely matched independent estimates with the possible exception of the low 2003 NEE estimate at PP. We proceed to compare monthly estimates from the STE and NRH approaches.

Monthly NEE, GEP, and RE estimates from the NRH and STE generally followed a logical seasonal pattern (Fig. 3) with the most notable deviation being the extremely high RE_{STE} estimates during late summer in 2003 at OF. This period was marked with vigorous grass growth (Stoy et al., 2006), but a monthly respiratory flux of 500 g C m^{-2} $month^{-1}$ seems unlikely and exceeds many of the annual RE estimates for grassland ecosystems worldwide as summarized in Novick et al. (2004). The dramatic decrease in GEP at OF during the peak of the 2002 drought is also apparent in both methods. Grasses were largely dead during this period. Interestingly, both methods predict that PP is a C sink during the winter between 2004 and 2005 as ice storm recovery was nearing completion, but wintertime NEE was slightly positive or near zero on a monthly basis during other years. HW exhibits later leaf-on phenology than the other two ecosystems (one of which is coniferous), and this effect can be observed in the GEP dynamics of both methods. Finally, the STE estimates show a decline in peak monthly GEP and RE through time at PP and HW (Fig. 3); the magnitude of maximum monthly component fluxes is higher in 2001 and 2002 than in 2003 and 2004 excluding a spike in RE_{STE} at HW in late 2004. This result is difficult to reconcile with the fact that the 2001 and 2002 period experienced drought; the pattern is inconsistent with estimates based on the NRH approach.

3.2. Information content

The IC of gap-filled NEE_d was similar to the IC in the gap-infested time series in both the Shannon entropy (ENT_S) and wavelet entropy (ENT_W) sense; raw and gap-filled NEE_d data differed by a maximum of 2 and 7% for ENT_S and ENT_W, respectively (Table 5, note that ENT as defined here exists between 0 and 1). Gap-filled

Table 5
The Shannon entropy (ENT_S) and wavelet entropy (ENT_W) values for daytime net ecosystem exchange (NEE_d) and ecosystem respiration (RE) for the 2001–2005 measurement period at the old field (OF), pine plantation (PP) and hardwood forest (HW) study ecosystems

NEE_d	Ecosystem	Raw data	Gap-filled data
ENT_S	OF	0.72	0.71
	PP	0.81	0.80
	HW	0.80	0.78
ENT_W	OF	0.27	0.33
	PP	0.41	0.39
	HW	0.33	0.26

RE	Ecosystem	Raw data	Gap-filled STE	Gap-filled NRH
ENT_S	OF	0.66	0.74	0.51
	PP	0.73	0.74	0.54
	HW	0.60	0.73	0.46
ENT_W	OF	0.55	0.29	0.32
	PP	0.28	0.28	0.27
	HW	0.38	0.41	0.39

Raw data refers to eddy covariance data filtered using the atmospheric stability thresholding approach of Novick et al. (2004). NRH refers to nighttime data gap-filled using the non-rectangular hyperbola after Gilmanov et al. (2003) and STE refers to the short-term exponential approach of Reichstein et al. (2005). Missing NEE_d data was gap-filled using the NRH. All entropy estimates are normalized by the maximum theoretical value.

data closely matched the frequency characteristics of the total NEE time series for all ecosystems (Fig. 4) with the exception of the higher frequencies, those on the time scale of hours on the left hand side of the abscissa in Fig. 4. This result was expected given the known spatial distribution of ecosystem activity (Oren et al., 2006). The FPMs did not seek to capture the scale of variability due to hourly shifts in footprint direction and extent because we focused on examining the longer-term estimates more relevant to the ecosystem C cycling questions referred to in the introduction. Therefore, gap-filling does not inject new information to the complete NEE time series in the probability domain, and in the spectral domains at time scales longer than approximately 1 day. Despite success in replicating the time domain and frequency characteristics of measured NEE data, the special case of nighttime NEE data (*i.e.*, RE) is a focus of the present study and warrants more investigation.

The ENT_S of NRH-gap-filled RE was on average 16% lower than that of raw nighttime flux data, and the ENT_S of STE-gap-filled data averaged 23% higher than RE_{NRH} (Table 5). From this analysis, it is clear that gap-filling using the NRH adds 'organization' to the pdf of nighttime NEE, and that RE_{STE} is more random than its NRH counterpart. This result follows from the fact that the NRH models RE as a constant that varies monthly and the STE models RE as an exponential function of T_a, itself highly variable on diurnal and seasonal time scales.

In contrast to the ENT_S, both the NRH and STE decreased the ENT_W of RE on average (Table 5). In other words, gap-filling RE adds order to (or filters out randomness of) the time series in the spectral domain. This spectral imbalance is unavoidable unless far more nighttime runs are accepted, which would reduce data quality. This result may not be surprising given the highly stochastic nature of nighttime EC flux measurements, as indicated by the relatively high degree of spectral energy on the hourly time scale (Fig. 4). At OF and HW the power spectra of nighttime data increase at high frequencies, and exhibit the characteristics of high frequency noise when compared to hourly flux data from the entire NEE time series. However, the direct comparison of flux magnitudes indicates that the magnitude of annual RE was similar to independent estimates, especially when using the NRH. For these reasons and those discussed above, the NRH is the preferable FPM for gap-filling NEE data in the case of these ecosystems. This finding agrees with the comparison of EC and inverse model estimates at PP (Juang et al., 2006) in which RE estimates based on the intercept of the light response curve compared well at the annual basis with RE estimates from a Eulerian version of a constrained source optimization inverse model (Lai et al., 2002).

3.3. Flux error

We undertook an analysis of error (ε) in flux estimates generated by the NRH to provide a complete description of flux findings for the 2001–2005 period at the Duke Forest AmeriFlux ecosystems, noting that the largest component of flux ε may be FPM selection itself (Hagen et al., 2006), which in part motivated this study. The choice of the NRH after comparison with independent and model estimates is intended to decrease this uncertainty in model selection.

A full analysis of random, instrument, and spatial ε was provided for PP NEE data by Oren et al. (2006). We expand on this analysis by providing ε estimates for annual NEE, GEP, and RE for all ecosystem-years of measurement using a variation of the approach of Goulden et al. (1997) as discussed in greater detail in Stoy et al. (2006) and Oren et al. (2006). Briefly, ε in NEE and RE due to gap-filling ('sampling uncertainty') was estimated by randomly selecting NRH parameters

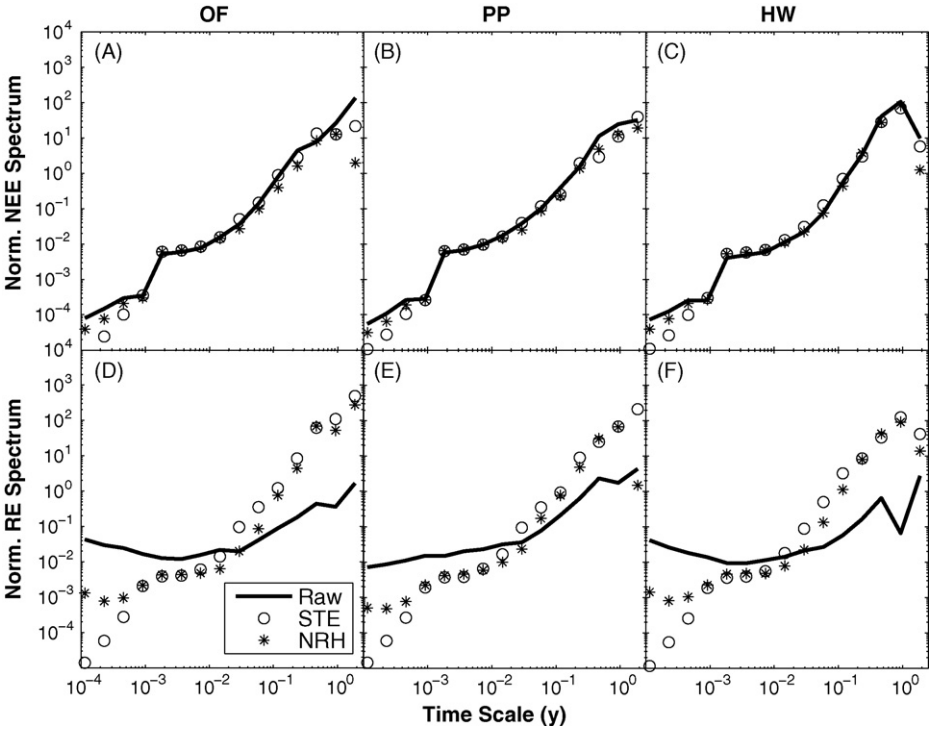

Fig. 4. Orthonormal wavelet spectra using the Haar wavelet basis for raw and gap-filled normalized (Norm.) net ecosystem exchange (NEE) and ecosystem respiration (RE) data for the Duke Forest old field (OF), pine plantation (PP) and hardwood forest (HW) ecosystems. STE and NRH refer to the short-term exponential gap-filling method of Reichstein et al. (2005) and the non-rectangular hyperbolic gap-filling method of Gilmanov et al. (2003), respectively.

Table 6
Error estimates for net ecosystem exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (RE) generated using the non-rectangular hyperbolic method (NRH) of Gilmanov et al. (2003)

Ecosystem	Year	NEE	GEP	RE
OF	2001	68	274 (22)	265 (21)
	2002	48	290 (30)	286 (29)
	2003	49	241 (16)	236 (16)
	2004	42	253 (19)	249 (18)
	2005	48	177 (17)	170 (15)
PP	2001	92 [108]	188 (11)	165 (13)
	2002	100 [111]	235 (16)	214 (19)
	2003	96 [95]	183 (11)	156 (14)
	2004	84 [69]	167 (9)	146 (11)
	2005	53	204 (11)	198 (12)
HW	2001	108	255 (15)	229 (19)
	2002	113	309 (18)	287 (21)
	2003	84	224 (14)	206 (16)
	2004	90	243 (14)	225 (17)
	2005	90	231 (13)	211 (17)

Numbers in square brackets are from Oren et al. (2006) and the percent error of GEP and RE is listed in parentheses. Flux units are g C m^{-2} $year^{-1}$.

based on the variance of monthly parameter values using a Monte Carlo simulation with 100 realizations. ε in the EC system ('uniform systematic ε') was estimated using the variance of nighttime ET measurements made under non-turbulent conditions in the absence of radiative perturbations (Cava et al., 2004), a situation that should result in zero flux. These two ε sources were combined to provide an estimate of total error; unlike Oren et al. (2006), the spatial component of EC ε is not considered here. We used the variance calculated from the beta parameter of the Laplacian distribution in this analysis (Richardson and Hollinger, 2005); thus, NEE ε terms (ε_{NEE}) are in general slightly smaller than those reported in Oren et al. (2006) (Table 6).

RE is a component of NEE and the covariance between ε_{NEE} and ε_{RE} must be taken into account when estimating ε_{GEP} error. Calculated this way, ε_{GEP} averaged 16% of GEP and ε_{RE} averaged 17% of RE, noting that the magnitude of the former is generally greater because the forested ecosystems represented a strong C sink. These relative error estimates are broadly consistent with but slightly greater than estimates from other flux studies (Meyers, 2001; Wilson and Meyers,

2001) and represent a conservative ε estimate for NRH-generated GEP and RE values.

4. Summary and conclusion

This study is the first to explore the effect of vegetation cover, and thereby different momentum roughness properties and u_* characteristics (Fig. 1), on C flux estimates generated by a suite of FPMs with the goal of determining which FPM is most robust across ecosystem type given prior flux estimates. We demonstrated that the choice of FPM can influence understanding of long-term variation in C flux – including the ability to estimate whether an ecosystem acts as a C source or sink in a given year – and can change the apparent ecosystem response to climatic events such as droughts and ice storms (Fig. 2, Table 4). Results showed that simpler FPMs (namely, the AQ10 and RH) produced estimates of C flux magnitude or variability that were not substantiated by independent measurements. The 'non-rectangular hyperbolic method' of Gilmanov et al. (2003) generated NEE, GEP, and RE estimates that best matched the magnitude and interannual variability of independent estimates across ecosystem types. Thus, a complex method that employs daytime EC data to estimate RE was the most robust in the case of these three ecosystems. These results agree with Juang et al. (2006), who found that nighttime RE measurements from the intercept of the light response curve agreed with estimates from a constrained source optimization on CO_2 profile data from PP. However, across EC research sites, simpler methodologies based on nighttime data are more commonly used (*e.g.*, Falge et al., 2001). If the use of nighttime data for RE estimation is preferred, the short-time exponential method of Reichstein et al. (2005) provided flux estimates that were nearer to the expected magnitudes, although in some cases interannual flux variability was unexpectedly large.

The information content (IC) of NEE_d was not altered by gap-filling in both the probability and wavelet domains, but nighttime gap-filling altered both the probabilistic and spectral structure of the RE time series. In particular, the wavelet analysis suggests that RE gap-filling added a high degree of 'organization' originating from the surrogate variables or assumptions used in the gap-filling and did not replicate the variability of the time series, which exhibited some characteristics of noise at high frequencies. Despite these limitations, EC-based RE estimates roughly matched the magnitude of independent data estimates over longer-term (*e.g.*, annual) time scales when an appropriate FPM (namely, the NRH) was used. Based on this analysis, we suggest that more focus be placed on methods that use daytime NEE data for RE (and thereby GEP) estimation when interpreting EC data when possible.

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Appendix A. Estimating the contribution of the clear-cut to C exchange at HW

A clear-cut on private land within the extent of HW 200 m south of the tower occurred in late November 2002 (see Fig. 1 in Stoy et al., 2006). We restrict the analysis of its effects on flux measurements beginning January 2003, as December 2002 was dominated by the ice storm and cold conditions that resulted in low observed RE. We used the two-dimensional representation of the footprint model of Hsieh et al. (2000) after Detto et al. (2006) to quantify the fraction of the HW flux footprint encompassed by the private land clear-cut for each 30-min measurement period. We then conducted a sensitivity analysis by filtering data for which the percent of the footprint in the clear-cut exceeded certain thresholds. In this way, we estimated the NEE, GEP, and RE that would have resulted had the clear-cut not occurred.

Measurements taken when the wind comes from the south or southwest are more likely to experience footprint contamination due to the clear-cut, but these conditions commonly occur during the growing season and are usually associated with a favorable climate. To test for any effects of selectively removing data, we also applied the footprint filtering procedure on 2001 and 2002 NEE data as a control, and expected that the

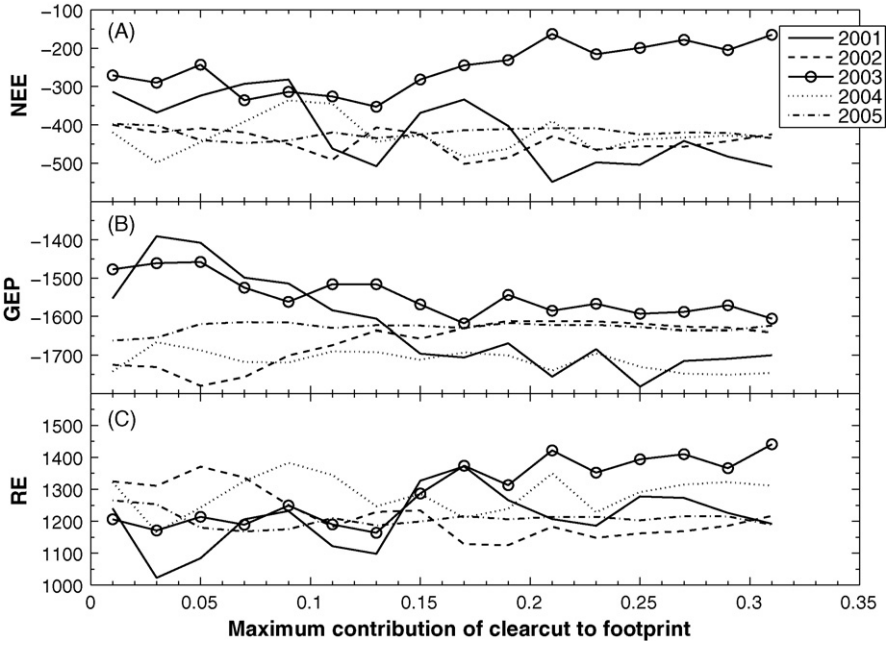

Fig. A1. The impacts of selectively filtering the clear-cut contribution to the flux footprint on annual net ecosystem exchange (NEE, A), gross ecosystem productivity (GEP, B) and ecosystem respiration (RE, C) at the hardwood forest ecosystem (HW). The analytical footprint model of Hsieh et al. (2000) extended to two dimensions by Detto et al. (2006) is used. 'Maximum contribution of footprint to clear-cut' is the fraction of footprint area within the dimensions of the clear-cut.

magnitude of NEE would decrease when measurements collected under relatively ideal climactic conditions were selectively removed.

Fig. A1 shows the impact of filtering fluxes on NEE, GEP, and RE estimates (using the NRHM). The right hand side of Fig. A1 displays flux estimates without filtering (*i.e.*, the area of the clear-cut is allowed to comprise over 30% of the footprint) and the left hand side represents a strong filter (*i.e.*, measurements are filtered if the clear-cut comprises only 1% of the footprint). Strengthening the filter to remove fluxes with <1% potential clear-cut contamination had the potential to retain too few points with which to obtain stable estimates of annual flux.

NEE during 2001, 2002, 2004 and 2005 showed a similar response to selective filtering; the magnitude of NEE estimates decreases, although not monotonically, as the strength of filter is increased (from right to left on the abscissa). The reduction in NEE was expected because favorable climate is primarily associated with south and southwesterly prevailing winds from the direction of the clear-cut as mentioned. NEE estimates for 2003 differ from other years in that their magnitude increases from −150 to −300 g C m^{-2} year^{-1} as the strength of the clear-cut filter increases. The increase in NEE magnitude was attributable to a ca. 100 g C m^{-2} year^{-1} decrease in the magnitude of GEP (Fig. A1B) and a 250 g C m^{-2} year^{-1} decrease in RE (Fig. A1C). After applying the clear-cut filter, GEP estimates in 2001 and 2003 are similar and 200 g C m^{-2} year^{-1} smaller in magnitude than 2002 and 2004. RE estimates are also similar and within 100 g C m^{-2} year^{-1} for all years. Taking into account the fact that the magnitude of NEE estimates in other years decreased between 25 and 175 g C m^{-2} year^{-1} from the weakest to strongest filter, the best estimate of 2003 NEE at HW is on the order of −400 g C m^{-2} year^{-1} (Table 4). This accounts for the observed NEE of −150 g C m^{-2} year^{-1}, adds −150 g C m^{-2} year^{-1} from filtering out clear-cut effects, and −100 g C m^{-2} year^{-1} to account for the fact that ideal climatic conditions were selectively filtered. Accordingly, adjusted 2003 HW RE and GEP estimates are on the order of 1250 and −1650 g C m^{-2} year^{-1}, respectively (Table 4).

Appendix B. Flux estimates from the AQ10 and RH methods

C flux estimates from the AQ10 and RH for each ecosystem and measurement year are presented in Table B1.

Table B1
Estimates of net ecosystem exchange (NEE), ecosystem respiration (RE), and gross ecosystem productivity (GEP) at the old field (OF), pine plantation (PP) and hardwood forest (HW) ecosystems

Ecosystem	Year	AQ10	RH
NEE			
OF	2001	570	150
	2002	670	60
	2003	220	−220
	2004	70	−140
	2005	320	150
PP	2001	−240	−530
	2002	210	−420
	2003	−170	−290
	2004	−610	−580
	2005	−840	−740
HW	2001	170	−680
	2002	190	−680
	2003	−160	−740
	2004	−370	−690
	2005	−390	−800
GEP			
OF	2001	−1690	−1290
	2002	−1490	−920
	2003	−1820	−1330
	2004	−1860	−1160
	2005	−1530	−1000
PP	2001	−2910	−1900
	2002	−3170	−1680
	2003	−2080	−1860
	2004	−2180	−2050
	2005	−2510	−2560
HW	2001	−2160	−1610
	2002	−2360	−1470
	2003	−2000	−1430
	2004	−2140	−1540
	2005	−1970	−1750
RE			
OF	2001	2270	1430
	2002	2160	980
	2003	2040	1110
	2004	1930	1020
	2005	1850	1150
PP	2001	2670	1370
	2002	3390	1260
	2003	1910	1560
	2004	1580	1470
	2005	1670	1810
HW	2001	2320	930
	2002	2550	790
	2003	1840	690
	2004	1770	850
	2005	1590	950

'AQ10' uses the Q_{10} respiration equation and RH uses a rectangular hyperbolic fit. Units are g C m^{-2} year^{-1}.

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