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**Global multi-scale
CO₂ flux**

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Biosphere-atmosphere exchange of CO₂ in relation to climate: a cross-biome analysis across multiple time scales

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Received: 31 March 2009 – Accepted: 3 April 2009 – Published: 14 April 2009

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The biosphere-atmosphere flux of CO₂ responds to climatic variability at time scales from seconds to years and longer. Quantifying the strength of the interaction between the flux and climate variables at multiple frequencies is necessary to begin understanding the climatic controls on the dynamics of the terrestrial carbon cycle. Orthonormal wavelet transformation (OWT) can quantify the interaction between flux and microclimate at multiple frequencies while expressing time series variance in few energetic wavelet coefficients, offering a low-dimensional view of the measured climate-flux interaction. The variability of the net ecosystem exchange of CO₂ (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (RE), and their co-variability with dominant climatic drivers, are explored with a global dataset consisting of 253 eddy covariance research sites. Results demonstrate that the NEE and GEP wavelet spectra are similar amongst plant functional types (PFT) at weekly and shorter time scales, but significant divergence appeared among PFT at the biweekly and longer time scales, at which NEE and GEP are relatively less variable than climate. The RE spectra rarely differ among PFT across time scales. On average, RE spectra had greater low frequency (monthly to interannual) variability than NEE, GEP and climate. The low frequency Fourier coefficients of eight sites with more than eight years of data were compared against CANOAK ecosystem model simulations. Both measurements and theory demonstrate that “multi-annual” spectral peaks in flux may emerge at low (4+ years) time scales. Biological responses to climate and other internal system dynamics provide the likely explanation for observed multi-annual variability, but data records must be lengthened and measurements of ecosystem state must be made, and made available, to disentangle the mechanisms responsible for these patterns.

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1 Introduction

Ecosystems respond to variability in the physical environment directly through their function, and indirectly through alterations to their structure. For example, the diurnal courses of radiation and temperature elicit predictable responses of canopy photosynthesis and ecosystem respiration. Climatic changes, disturbance events, and ecosystem development alter ecosystem structure (Odum, 1969; Scheffer et al., 2001; Chapin et al., 2005), which changes ecosystem functioning. Understanding the consequences of meteorological variability on these physical and biological controls on ecosystem function is required to gain a comprehensive understanding of the role that terrestrial ecosystems play in the global carbon cycle. A major challenge lies in understanding the time scales at which these processes occur across global ecosystems, and integrating this knowledge into ecological models.

Process-based ecosystem models represent an explicit hypothesis about how ecosystem function transfers variability in climatic forcing to an ecological response, namely the flux of mass or energy. These ecosystem transfer properties can now be explored using long-term meteorological and carbon flux measurements from the international FLUXNET project, which consists of eddy covariance tower flux measurements from regional networks (CarboeuropelP, AmeriFlux, Fluxnet-Canada, LBA, Asiaflux, Chinaflux, USCCC, Ozflux, Carboafrika, Koflux, NECC, TCOS-Siberia, (e.g., Aubinet et al., 2000; Baldocchi et al., 2001a; Baldocchi, 2008). The FLUXNET project offers the unprecedented opportunity to relate directly the measured variability in mass and energy flux to the measured meteorological variability at time scales from hours to years, and in some cases over a decade (Grünwald et al., 2007; Urbanski et al., 2007; Granier et al., 2008).

This study investigates global relationships between observed climate and plot-level biosphere-atmosphere fluxes across time scales to address the evidence that variability in the global carbon cycle is dominated by terrestrial ecosystem metabolism (Houghton, 2000; Canadell et al., 2007). We explore how the fluxes from ecosys-

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tems situated in different climatic zones, and with different plant functional types (PFT), respond to climatic variability and thus contribute to observed global oscillations in atmospheric CO₂ concentration.

To help organize a discussion of global ecosystem response to climate, hypotheses are introduced that represent the state of the knowledge. As a logical starting point for developing hypotheses about how the biosphere-atmosphere exchange of CO₂ resonates with climate, we note that the canonical frequencies of flux and meteorological variability can be separated into deterministic and quasi-stochastic classes. Daily and seasonal/annual orbital motions create well-defined, deterministic oscillations of potential solar irradiation to which vegetation has evolved to adapt. Flux measurements contain a strong stochastic component at high (hourly) frequencies due in part to the spatial variability of the flux footprint resulting from the nature of turbulence (Oren et al., 2006; Richardson et al., 2006). Other sources connected to micrometeorological conditions originate from variability in wind (known to be stochastic at such time scales) and cloud formation (whether advected or locally generated by convective processes). The latter is known to impact the photosynthetically active radiation during the day and induce rapid transients in the fluxes at night for strongly stable flows (e.g., Cava et al., 2004). Stochastic mesoscale climatological forcing (e.g. synoptic weather patterns) at time scales on the order of days to weeks, and stochastic low-frequency interannual oscillations such as El Niño (Torrence et al., 1998; Potter et al., 2003) introduce climatic nonstationarity at these scales, to which ecosystems may be expected to respond in a quasi-stochastic manner. By “quasi-stochastic” we mean that ecosystems may respond deterministically to stochastic climatic event and the source of stochasticity is entirely connected with the occurrence of the microclimatic excursion rather than the ecosystem response to it. Quasi-deterministic low frequency oscillations such as the 11-year cycle in solar activity have also been argued to induce variability in plant growth at these time scales (Rigozo et al., 2007), but the relative importance of low frequency deterministic oscillations versus low frequency stochastic events such as ENSO across global ecosystems has yet to be determined.

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We hypothesize that (H1) an interannual spectral gap (a trough in the power spectra) will emerge in global ecosystems as the response of vegetation to climate is less variable than climate itself, “dampening” climatic variability in response to stochastic forcing. If this is the case, it stands to reason that different ecosystems will respond differently to climate such that (H2) flux variability and co-variability with climate, at the time scales of seasonal vegetation development will differ among PFT. Because of these hypothesized differences in response, it follows that (H3) PFT will be a logical way to separate multi-scale ecosystem response to climate, as assumed by global ecosystem models.

To address the hypotheses, we quantify statistical differences among the spectra of net ecosystem exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (RE) using 999 site-years of eddy covariance data from 253 ecosystems across the globe in the FLUXNET database using both orthonormal wavelet transformation (OWT) and Fourier decomposition (Katul et al., 2001; Baldocchi et al., 2001b). After exploring the inherent variability in NEE, GEP and RE across time scales, we quantify: (1) ecosystem spectral transfer (EST), defined here as the ratio between the orthonormal wavelet power spectra of ecosystem response variables, in this case NEE, GEP and RE, and the OWT spectra of different meteorological forcings (e.g. photosynthetic photon flux density (PPFD), air temperature (T_a), vapor pressure deficit (VPD), and precipitation (P); see Fig. 1: Analysis I); (2) The wavelet co-spectra, which can be used to investigate the scale-wise correlations between climate and flux (see Fig. 1: Analysis II); (3) the low-frequency (interannual) climate-flux relationship of the eight FLUXNET sites that currently contain eight or more years of continuous daily data, including comparisons with CANOAK (Baldocchi and Meyers, 1998) model output driven by a long-term continuous meteorological record.

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Analysis (1) assesses the frequencies at which ecosystem response modulates a given meteorological forcing via changes in state variables or functional parameters, and how the frequencies of this modulation shift among climate and ecosystem type. Analysis (2) is intended to unveil if scale-wise correlations between ecosystem responses and climatic variables shift with respect to ecosystem type and climate regime. Analysis (3) identifies low frequency climate and flux variability. Results are discussed in the context of the hypotheses and the implications for multi-scale ecological modeling of the terrestrial carbon cycle (Williams et al., 2009).

2 Methods

2.1 FLUXNET database

Flux and meteorological data from version 2 of the LaThuile FLUXNET database (www.fluxdata.org) was used. Data were collected at individual sites according to network specific protocols (e.g., Aubinet et al., 2000), although deviations in methodology cannot be fully excluded for all sites. Half-hourly flux data were then processed according to the FLUXNET protocols for data filtering for periods of insufficient friction velocity (u_{*c}), filling the data gaps that result from missing measurements, and partitioning measured NEE into GEP and RE (Papale et al., 2006; Reichstein et al., 2005). The version 2 database includes 253 research sites encompassing 7 climate types and 11 vegetation types (Table 1) (Cook et al., 2007; Agarwal et al., 2007). To obtain sufficient sample sizes of different ecosystem types for the statistical analysis, the vegetation classes “savanna” and “woody savanna” were combined to create one class called savanna, and the classes “open shrubland” and “closed shrubland” were combined to create one class called shrub. Data records extended from several months to over a decade. The database currently contains over 17.5 million half-hourly data points for each variable, and over 18 billion total cells of information. The FLUXNET database comprises both half-hourly and daily averaged data products, both of which are used

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in the subsequent analyses.

2.2 Orthonormal Wavelet Transformation (OWT)

A brief, qualitative description of wavelet methodology is presented here; we refer the reader to Torrence et al. (1998) for a basic treatment for geo-scientific applications, and Katul and colleagues (1995; 2001) for a detailed discussion of wavelet analysis for flux applications. Scanlon et al. (2001) and Stoy et al. (2005) present conceptual descriptions of wavelet techniques and further examples of wavelet analysis for biosphere-atmosphere flux research.

Wavelet decomposition differs from standard Fourier techniques in that it employs a finite basis function, called a “mother wavelet”, that is translated (shifted across) and dilated (expanded and contracted) across a signal to quantify, for the case of a time series, signal variance across both time and time scale. An infinite number of wavelet basis functions exist given the admissibility criteria that its integral is zero (Daubechies, 1992). The choice between multiple wavelet basis functions for a given application may appear subjective, but basis functions that are optimal for given time series properties can and should be selected (Torrence and Compo, 1998). For the case of FLUXNET time series the Haar wavelet basis function (a square wave) is the most logical choice given its localization in the temporal domain and consequent ability to control for the effects of the sharp discontinuities created by the inherent gaps (Falge et al., 2001) in eddy covariance time series (Katul et al., 2001). In this way, scale-wise contributions to the variance of the measured flux data can be quantified without considering the contributions of models to gapfill missing flux data, which are characterized by the frequency dynamics of their underlying driving variables.

The wavelet transform can be continuous, but discretizations that avoid redundant information and to return a tractable number of coefficients are advantageous. Orthonormal wavelet transformation (OWT) is a log-spaced discretization that quantifies the total variance of a time series of length 2^N in only N coefficients. Hence, interpreting the multi-scale flux-climate relationship is carried out with orders of magnitude

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less information across time scale than contained by the time series itself across time. For the case of FLUXNET data, the response between climatic drivers and the surface exchange of mass and energy for each measurement site across temporal scales can be expressed in terms of tens of wavelet coefficients that represent variability at different scales in time (the “time scale domain”) rather than tens to hundreds of thousands of data points in the temporal domain (Katul et al., 2001; Braswell et al., 2005; Stoy et al., 2005; Richardson et al., 2007). The wavelet cospectra between driver and flux can also be quantified to explore scale-wise climate-flux correlations (Stoy et al., 2005) (see also Saito et al., 2008).

We note that differences in the spectral estimate between Fourier and wavelet based methods are expected given that the two techniques decompose data using fundamentally different basis functions and algorithms. However, it should also be emphasized there is no “true” spectrum for complex, finite time series; Fourier decomposition assumes that the time series is composed of a combination of sinusoidal curves, which need not be the case. There is no reason why two spectra obtained with different kernels should be identical (Torrence et al., 1998). The only necessary requirement for spectral decomposition is conservation of spectral energy when summed across all frequencies (i.e. Parseval’s Identity, Dunn and Morrison, 2005), which OWT satisfies. This is one reason why spectral scaling exponents inferred from OWT and Fourier methods agree reasonably well and are insensitive to the choice of the basis function when the time series exhibits an extensive scaling law across a wide range of scales (Katul and Parlange, 1994).

To compute OWT coefficients, all half-hourly measurements of NEE, GEP, RE, T_a , VPD, PPFD, P and latent heat flux (LE) in the FLUXNET database were multiplied by their quality control flag (1 for raw data, 0 for missing data) to exclude missing or gapfilled measurements (Stoy et al., 2005). This treatment ensured that data gaps do not contribute to the total series variance after Haar wavelet decomposition. All time series were then normalized to have zero mean (with zeroes in place of gaps) and unit variance for comparison. The time series for each site then underwent a standard

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“zero-padding” (Torrence et al., 1998) by adding zero values to both ends of the time series in order to make the length of each time series equal to a power of 2 for fast wavelet decomposition. The resulting zero-padded series was then again normalized to ensure that the normalized time series have unit variance and that all periods without valid measurements were set to zero. Differing lengths of the flux data records resulted in 15–18 dyadic scale representation per site and data record. The lowest-frequency wavelet coefficient for each normalized time series is poorly constrained and was dropped from the analysis, resulting in a maximum time scale of 217 half hours, or 7.48 years for the 16 year Harvard Forest time series.

For simplicity, when discussing orthonormal wavelet coefficients for all flux time series (NEE, GEP and RE) are abbreviated OWT_{FLUX} and all meteorological time series are abbreviated OWT_{MET} . For the purposes of this investigation, LE is considered alongside the meteorological drivers to investigate the coupling between carbon and water fluxes.

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The ecosystem spectral transfer (EST) can be defined as¹

$$EST_{FLUX,MET} = \log \frac{OWT_{FLUX}}{OWT_{MET}} . \quad (1)$$

The flux signal is said to be “amplified” (“dampened”) compared to the respective climatic input if the $EST_{FLUX,MET}$ is positive (negative) (Fig. 1: Analysis I). We note that concepts and terminology from the signal processing literature, “amplifying”, “dampening”, “modulating”, and “resonating” find a natural application when discussing eddy covariance measurements because the flux and meteorological variables are time-varying signals and ecosystems can be thought to process this signal in a corresponding, time-varying response (Fig. 1). Amplification or dampening need not imply causality in systems, like ecosystems, that respond to a range of factors.

The EST analysis is intended to identify how ecosystems dampen climatic variability at multiple time scales, (H1) if $EST_{FLUX,MET}$ is dampened at low frequencies (long time scales). To investigate how climatic inputs and flux outputs co-resonate to explore

¹When dealing with information transfer between forcing and response functions, the concept of transfer function is usually used though it is primarily applicable to linear and time-invariant systems (LTI). In LTI, linearity means that a linear map describes the relationship between input and output so that if input $x_1(t)$ produces a response $y_1(t)$ and input $x_2(t)$ produces response $y_2(t)$, then an input comprising of $a_1x_1(t)+a_2x_2(t)$ produces a response that can be described by $a_1y_1(t)+a_2y_2(t)$. It should be noted that LTI are not connected to the linearity in $x(t)$ or $y(t)$. The log transformation in Eq. (1) plays a crucial role here if multiplicative processes are to be converted to additive as is the case in ecological applications when relating fluxes to driving variables via multiplicative reduction functions (Jarvis, 1976). The time invariance here means that if the input $x_1(t)$ produces a response $y_1(t)$, then an input $x_1(t-\tau)$ produces an output of $y_1(t-\tau)$ (often, this concept is intimately linked to time reversibility). Such LTI systems can be characterized by a single and unique transfer function. Examples of LTI are numerous – any system that can be described by a linear (and higher order) ordinary differential equation (ODE) with constant coefficients is an LTI (even though the solutions to these ODEs are highly nonlinear).

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H2, we quantified the wavelet covariance (Torrence et al., 1998) for all flux and meteorology combinations, and abbreviate the resulting coefficients $OWT_{FLUX,MET}$ (Fig. 1: Analysis II). It is important to note that $OWT_{NEE,MET}$ and $OWT_{GEP,MET}$ will be negative if the relationship between flux and meteorological variability is positive due to the micrometeorological sign convention where flux from atmosphere to biosphere is denoted as negative.

2.3 Fourier decomposition

OWT returns at most 3 dyadic scales for the case of the longest-running site, Harvard Forest, at interannual and multi-annual time scales, and increased resolution at low frequencies is desirable to address H1 and goal (3). To examine low frequency variations with greater spectral resolution, a standard Fourier decomposition was applied to the FLUXNET daily meteorological and flux data products for the eight sites that contained at least eight years of continuous data. These data represent both measurements and data that were gapfilled using the aforementioned standard FLUXNET protocols. To further investigate the mechanisms of low-frequency variability, we performed a Fourier analysis of variability of GEP and RE predictions from the CANOAK model (Balocchi and Meyers, 1998) driven with 18 years of continuous daily meteorological measurements from Walker Branch, TN, USA.

2.4 Statistical analyses

A mixed model (PROC MIXED in SAS 9.1) was implemented to test for differences among OWT_{FLUX} , $EST_{FLUX,MET}$, and $OWT_{FLUX,MET}$ for different climate and vegetation classes for the 250 of 253 FLUXNET sites with climate and vegetation information. Wavelet variances were log-transformed prior to analysis when necessary to ensure normality of the response variables, noting that EST is computed from log-transformed coefficients (Eq. 1). Coefficients at the 3.74 year and 7.48 year time scales were not included in the statistical analysis because the variable length of the flux data records

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resulted in a smaller sample size at low frequencies (see Fig. 2). Time scale, climate type, and PFT were specified as fixed main effects, and time scale climate and time scale \times vegetation were included as interaction effects. The vegetation \times climate interaction effect was not included because of the large number of unreplicated combinations (Table 1). Observations for each site at different time scales were considered repeated measures, and a first-order autoregressive covariance structure was employed. Overall least-square means were calculated for the main effects climate and vegetation. The Tukey-Kramer multiple comparison test was used to evaluate overall differences among effect levels. We also tested for simple interaction effects among climate and vegetation (“sliced”) per time scale using the PROC MIXED procedure in SAS 9.1. Test statistics that are significant at the 95% confidence level are reported.

When testing for significant differences in Fourier coefficients among sites, we note that the corresponding frequencies may not overlap given the variable length of the data records, and we chose a two-sided t-test for identifying significant differences among low-frequency Fourier coefficients.

3 Results

3.1 Variability in NEE, GEP and RE

Medians and ranges of OWT_{FLUX} for all FLUXNET sites are presented in Fig. 2. Abbreviations (“hourly”, “daily”, “annual”, etc.) are used to approximate the discrete time scales for simplicity; for example, the annual coefficients represent variability at 0.935 years, daily coefficients represent 16 h variability as 24 is not a power of 2, and “multi-day” represents 1.33 day and 2.67 day variability because these time scales are longer than 1 day yet shorter than 1 week (Fig. 2, Table 2). These descriptions present a simple and intuitive means of communicating temporal scale for interpreting results and are used subsequently. It should be noted that sampling every third data point (1.5 h) would have resulted in OWT coefficients at exactly 24 h, but the annual variability would

be poorly resolved given that coefficients at 256 and 512 days would also be returned.

Local reductions in OWT_{FLUX} power spectra (the so-called “spectral gaps”) exist at hourly time scales, and multi-day to bi-monthly time scales. A low frequency spectral gap begins to appear at interannual time scales in OWT_{NEE} and OWT_{GEP} ; less so in OWT_{RE} (Fig. 2). NEE and GEP variability is, on average, relatively lower at these time scales than the corresponding spectral peaks at daily, seasonal and annual time scales. The relative difference in OWT_{RE} amongst sites increases at the longest time scale for which there are replicates (3.74 y), while inter-site differences in OWT_{NEE} and OWT_{GEP} decreases at low frequencies (Fig. 2). In other words, RE variability among sites is becoming more different at interannual time scales, while seasonal and annual variability in NEE and GEP are more different among sites than RE. The single site with sufficient time series length to identify 7.48 y variability, Harvard Forest, has relatively high flux variability in GEP and RE at these “multi-annual” time scales compared to the average 3.74 y interannual variability of other ecosystems.

3.2 Flux variability by climate zone and plant functional type

OWT_{FLUX} (Fig. 2) was separated by climate and vegetation type (Fig. 3). Time scales for which there are significant differences among climate or vegetation types at the 95% confidence level, as determined by the multiple comparison tests, are listed in Table 2 and also demarcated by the horizontal bars in Fig. 3. (We note again that significance at the two lowest frequency time scales, 3.74 and 7.48 years, was not determined due to lack of replicates.)

There were no significant differences in OWT_{NEE} among climate zones at hourly to weekly time scales, and among PFT at hourly (2 h) to bi-weekly time scales. This implies universality in the total relative variability, but not magnitude, of NEE at these time scales. OWT_{GEP} differed among climate types at bi-monthly to annual time scales, and among PFT at high-frequency (hourly) time scales and also monthly to seasonal time scales. High frequency (hourly to daily) OWT_{RE} differed among climate types, but lower frequency differences were only found at the seasonal time scale. PFT-related

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differences in OWT_{RE} emerged at seasonal to interannual frequencies (Table 2, Fig. 3).

3.3 Analysis I: spectra of meteorological drivers and ecosystem responses

The median normalized power spectra of the flux and meteorological drivers varied by orders of magnitude across time scales (Fig. 4), highlighting the temporal dynamics of microclimate at characteristic frequencies and subsequent vegetation/ecosystem response via carbon flux (Baldocchi and Wilson, 2001; Baldocchi et al., 2001b; Katul et al., 2001). Median OWT_{T_a} and OWT_{LE} are notably energetic at seasonal and annual time scales. OWT_P tends to be roughly equal across time scales larger than the isolated storm time scale, approximating white-noise, consistent with other studies (Katul et al., 2007; Mahecha et al., 2008); P is known to possess a composite spectrum with multiple scaling laws across various frequencies (Gilman et al., 1963; Fraedrich and Larnder, 1993; Peters et al., 2002). Interestingly, average interannual variability at the 3.74 y time scale is greater than interannual variability at the 1.87 y time scale for OWT_{GEP} , OWT_{RE} , OWT_{LE} , and the meteorological drivers OWT_P , OWT_{VPD} and OWT_{PPFD} , lending support to the notion that multi-annual spectral flux peaks may emerge in the FLUXNET database (Analysis 3). The magnitude of OWT_{GEP} , OWT_{RE} and OWT_{LE} at Harvard Forest at the 7.48 y time scale is large in comparison to FLUXNET median flux interannual variability at the 1.87 and 3.74 y time scales (Figs. 3 and 4).

The tendency of ecosystems to dampen or amplify the variability of climatic drivers was explored via EST (Figs. 1 and 5). Figure 5 displays the median EST for each flux/meteorological driver comparison. At hourly time scales where flux footprint variability is known to dominate the measurement signal in spatially heterogeneous ecosystems (Oren et al., 2006), the variability of NEE tended to be greater than that of T_a and VPD, but not PPFD. NEE and GEP were on average less variable than PPFD at time scales greater than an hour and shorter than a day, consistent with the observed saturating response of GEP to PPFD. NEE and GEP are damped with respect to T_a and VPD variability at weekly and longer time scales, on average (Fig. 5a and

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b), but variability in RE is on average similar to or greater than T_a and VPD variability at time scales of weeks and longer (Fig. 5c). Median OWT_{NEE} was most similar to OWT_{PPFD} across time scales as evidenced by the near-zero scale-wise $EST_{NEE,PPFD}$ (see also Fig. 4), but at lower (monthly to annual) frequencies, OWT_{GEP} was most similar to OWT_{VPD} (Figs. 4, 5a and b). OWT_{RE} was most similar to OWT_{T_a} across time scales, but was also surprisingly similar to the medial OWT_{LE} spectra. High-frequency (hourly) variability of P is strongly dampened by the flux signal on average, both for the FLUXNET database as a whole (Fig. 5), and also for the dry and subtropical-Mediterranean ecosystems (data not shown) which may be expected to have a greater response to precipitation pulses (Daly and Porporato, 2005; Porporato et al., 2002).

As a whole, $EST_{GEP,MET}$ followed similar scale-wise patterns to $EST_{NEE,MET}$ (Fig. 5b and c), but median $EST_{NEE,MET}$ was dampened to a greater degree, on average, at lower frequencies. Conversely, $EST_{RE,MET}$ was amplified compared climatic variability, on average, at the lower frequencies.

$EST_{FLUX,MET}$ was significantly different among climate type and PFT across a complex array of time scales with distinct patterns, as demonstrated by the horizontal bars in Fig. 5, noting again that the bars in the upper sections of the subplot demarcate significant differences among climate type and the bars in the lower sections of the subplots signify significant differences among PFT. Slicing by climate type reveals significant differences at both short and long time scales in the relationship between all fluxes and climate. Significant differences among PFT emerged at longer (seasonal to annual) time scales in $EST_{NEE,MET}$ and $EST_{GEP,MET}$, less so $EST_{RE,MET}$.

3.4 Analysis II: wavelet cospectra between NEE and climatic drivers

The covariance between flux and climate was dominated by the deterministic daily and seasonal/annual time scales, but the magnitude of this covariance tended to be greater at daily rather than seasonal/annual time scales (Fig. 6). Mean OWT_{NEE,T_a} (i.e. the wavelet covariance between NEE and T_a) at the seasonal and annual time scales for different climate types were often of the same magnitude as those at the daily

time scale, in contrast to $OWT_{NEE,LE}$, $OWT_{NEE,VPD}$, and $OWT_{NEE,PPFD}$, which have a greater magnitude, on average, at daily time scales than seasonal or annual time scales (Fig. 6a). $OWT_{GEP,LE}$ was on average larger at seasonal/annual time scales than at daily time scales, and the median $OWT_{RE,LE}$ was unexpectedly large across
5 monthly to annual frequencies.

Despite the relatively low $OWT_{FLUX,MET}$ magnitude at interannual time scales, in almost all cases these cospectra are greater than a random signal, as determined by a Monte Carlo analysis with 1000 synthetic autoregressive pink noise time series as commonly applied in geoscientific studies (e.g., Allen et al., 1996, see also Richardson
10 et al., 2008, data not shown).

Most of the statistically-significant differences in $OWT_{FLUX,MET}$ among climate type and PFT are clustered around the daily and seasonal/annual spectral peaks, where most of the energy in the cospectra resides (Fig. 6). No significant differences in the interaction effects among cospectra sliced by climate or PFT emerge at the
15 weekly/monthly time scales. There are significant differences at the diurnal time scale when separating by both climate type and PFT for $OWT_{NEE,MET}$ and $OWT_{GEP,MET}$, and significant differences at the seasonal and annual time scales among both climate type and PFT for all $OWT_{NEE,MET}$ and $OWT_{GEP,MET}$ except the PPFD cospectra. There are no PFT-related differences at hourly to seasonal time scales in OWT_{RE,T_a} ; significant
20 climate and PFT-related differences for all $OWT_{RE,MET}$ emerge only at seasonal to annual time scales.

3.5 Analysis III: low frequency variability

GEP and RE variability increased at the lowest Fourier frequency compared to the second-lowest frequency for five of eight long-term research sites with continuous daily
25 flux and meteorological data (listed in Table 3). This increase is statistically significant (paired t-test, $p < 0.05$) for those five sites, and this effect was not observed in the time series of meteorological drivers.

Low frequency flux variability in response to climate was additionally investigated

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with the CANOAK model (Baldocchi and Meyers, 1998) with 18 years of continuous climate measurements from Walker Branch, TN (Fig. 7). CANOAK-modeled photosynthesis and RE spectra demonstrated a clear 7–11 year spectral peak, recalling that GEP and RE were highly energetic at the 7.48 y time scale at Harvard Forest (Figs. 2 and 3) (note also Battle et al., 2000; Rocha et al., 2006; Rigozo et al., 2007).

4 Discussion

4.1 Multi-scale flux variability across global ecosystems

Spectral peaks at daily and seasonal/annual time scales are a general feature of the global NEE time series (Figs. 2 and 3). These peaks have been quantified previously in temperate forested ecosystems (Baldocchi et al., 2001b; Katul et al., 2001; Braswell et al., 2005; Stoy et al., 2005; Moffat et al., 2007; Richardson et al., 2007) and further emphasize the dominant role of deterministic climatic oscillations at diurnal and seasonal/annual time scales in controlling the total variability in measured flux time series. Naturally, resolving such multi-scale variability alone does not necessarily translate to accurate estimation of long-term mean flux, but does give hints as to how global ecosystems respond to climatic variability.

These findings suggest that flux variability is concentrated in few time scales, i.e. the spectra are “unbalanced” (Katul et al., 2007). It has been previously argued that low-dimensional ecosystem models that capture these dominant modes of variability are a logical way forward for modeling flux at multiple time scales (Katul et al., 2001), but accurately modeling the seasonal and annual variability of fluxes has proven elusive for ecosystem models (Hanson et al., 2004; Siqueira et al., 2006), in part because of the shift from physical to biological control at longer time scales (Stoy et al., 2005; Richardson et al., 2007) as also evidenced by the PFT-related flux differences at longer time scales (Fig. 3). For example, a series of drought years can lead to a carry-over effect of reduced carbohydrate reserves for tree growth and a shift in carbon allocation

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in subsequent years, which is not dynamic in ecosystem process models. Such dynamics were detailed at a semi-arid pine site in which NEE was much lower in a third year of drought than the previous years, suggesting a cumulative effect on the biology of the system (Thomas et al., 2009).

5 The statistical analysis of spectral differences was designed to address the experimental hypotheses. It was found that the magnitude of the NEE and GEP spectra are not statistically different among climate zones or PFT until bi-weekly to monthly time scales are reached (Fig. 3). In other words, PFT is not a logical way to separate differences in the variability of flux time series at high frequencies, at least when quantifying
10 the total time series variance across scale rather than the changes in variance across scale and season. These results support H2: PFT-related differences emerge at the time scales of vegetation development in the case of NEE and GEP. Results also partly support H3: that PFT will be a logical way to separate the variability in observed fluxes, at least at the lower (monthly and longer) frequencies that are arguably more important
15 for quantifying the role of terrestrial ecosystems in the global carbon cycle.

Climate and PFT-related differences in the RE spectra do not emerge until seasonal time scales (Fig. 3b). Given the ability of the eddy covariance system to resolve RE, PFT is not a logical way to separate RE variability across most of the time scales investigated here, which does not fully support H3. Differences in RE variability did
20 not emerge at the time scales of vegetation development, which does not support H2. The implications of these analyses are that PFT is a scale-dependent concept when considering the variability of flux in response to climate.

4.2 Ecosystem spectral transfer

Ecosystem CO₂ uptake strongly dampened the variability of most climatic drivers, on average (i.e. average EST_{NEE,MET} and EST_{GEP,MET} are less than zero) at time scales
25 from weeks to years (Fig. 5), but ecosystem CO₂ loss was observed to be more variable than climatic drivers at these lower frequencies (i.e. average EST_{RE,MET}>0). These results partially support H1: ecosystem CO₂ uptake dampens instantaneous low fre-

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quency meteorological variability, but low frequency amplification of climate by RE does not. Rather, climatic variability “excites” the RE spectra on average, which is consistent with the exponential transfer function commonly used to model RE variability at high frequencies and the strong spectral covariance between RE and T_a at low frequencies (Figs. 5c and 6c). Also, significant differences in $EST_{RE,MET}$ emerged among different climate types, rather than PFT, across time scales (Fig. 5c). Together with findings from the previous subsection, these results agree with the notion that RE is determined by the effects of climate and moisture, more so than ecosystem type, on ecosystem C pools with different time scales of input and loss (Parton et al., 1987; Adair et al., 2008) despite the known coupling between GEP and RE (Högberg et al., 2001; Ryan and Law, 2005).

4.3 Cospectral relationships between flux and climate

Spectral peaks in NEE at longer (seasonal/annual) deterministic time scales are less-related to environmental drivers than the diurnal spectral peak (Fig. 6), which demonstrates a decreasing instantaneous influence between climate and NEE at longer time scales globally (Richardson et al., 2007). Hence, it is no surprise that ecological models that use highly resolved PPFD variability (i.e. hourly), and to a lesser extent VPD variability, can explain the high-frequency energetic modes in NEE variability (Siqueira et al., 2006). At longer time scales, explaining flux variability via climatic variables alone is no longer effective (Siqueira et al., 2006; Richardson et al., 2007; Stoy et al., 2008), in part because NEE and GEP tend to damp climatic variability at low frequencies, supporting the homeostatic mechanism explored in H1. These results agree with previous studies that have found a shift from exogenous to endogenous control of NEE in temperate deciduous broadleaf (DBF) and evergreen needleleaf (ENF) forests (Baldocchi et al., 2001b; Stoy et al., 2005; Richardson et al., 2007). Quantifying flux variability at longer time scales requires information on how ecosystems change in response to climatic variability, rather than how they merely respond to climatic variability.

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4.4 Implications for ecological modelling

Significant climate and PFT differences in $EST_{FLUX,MET}$ appeared across more time scales than significant differences in $OWT_{FLUX,MET}$, which are primarily restricted to the deterministic time scales (Figs. 5 and 6). To the extent that changes in EST represent a change in the state variables or parameters that transfer climatic input to ecosystem output, these state variables, parameters, and their variability are often different among PFT at bi-weekly to monthly time scales for NEE and GEP. Few PFT-related differences in $EST_{RE,MET}$ are significant, which again demonstrates that including PFT is less important for modeling multi-scale RE (see also Fig. 3). More ecosystem level ancillary data is required to determine how the shifts in transfer properties result from changes in ecosystem carbon stocks and/or the parameters of photosynthesis and respiration models (Wilson et al., 2001; Palmroth et al., 2005) to further investigate low frequency biological controls on flux (Richardson et al., 2007). An emerging challenge is to model the multi-annual spectral energy of GEP and RE which, when combined, results in a low frequency dampening of carbon sequestration with respect to climatic variability.

The significant variation of the EST and co-spectra across time scale indicates that the representation of ecosystems as simple instantaneous physical transformers, e.g. in simple soil-vegetation-atmosphere models (SVATs) for photosynthesis, or time invariant regression equations for ecosystem respiration, is likely to fail (Carvalho et al., 2008) at longer time scales. This study confirms and generalizes former site-specific studies that have shown that biological variation in space and time is an important control of fluxes and may be empirically represented by changing biological ecosystem parameters that define the properties of the system (Wilson et al., 2001; Reichstein et al., 2003; Hibbard et al., 2005; Owen et al., 2007). In ecosystem process models, such temporal dynamics, which can change the response to climate variables across time-scales, may be represented by state variables (e.g. leaf area index, soil water content) and the appropriate representation of these state variables is pivotal for modeling NEE correctly across time-scales, including pools of soil carbon with slow turnover

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times (Adair et al., 2008). Moreover, whether biophysical and ecophysiological parameters may be kept constant as is often the case in typical terrestrial biosphere models employed at global scale, or if parameters should be made temporally dynamic is a critical issue for modeling the land-surface C cycle (Curiel Yuste et al., 2004; Palmroth et al., 2005; Ryan and Law, 2005; Davidson and Janssens, 2006; Juang et al., 2008; Williams et al., 2009). Modeling or measuring rapid transients in endogenous variables (e.g. green-up of LAI in deciduous forests) may be critical for explaining flux variability over the stochastic weekly-monthly spectral gap in some ecosystems (Stoy et al., 2005). The importance of endogenous variables compared to climate drivers might well be one general reason why remote sensing based approaches that incorporate the biophysical state of the vegetation are comparably successful in quantifying terrestrial productivity, even after completely abandoning the use meteorological drivers (Jung et al., 2008).

A major motivation for the present study is to investigate the multi-scale coupling between climate, hydrology and carbon flux to identify potential improvements in ecosystem C models at the longer time scales at which they often fail (Hanson et al., 2004; Siqueira et al., 2006). The strong seasonal and annual cospectra between $OWT_{GEP,LE}$ suggests that improving the representation of ecosystem hydrology and its coupling to CO₂ uptake is a logical step to improve models of CO₂ flux (Katul et al., 2003) in globally-distributed ecosystems. Interestingly, the mean seasonal/annual $OWT_{GEP,VPD}$ was of greater magnitude than $OWT_{GEP,PPFD}$ (Fig. 5b), further emphasizing the importance of hydrology over radiation in determining the low frequency variability of photosynthesis.

4.5 Interannual and multi-annual flux variability in models and measurements

The results hint that multi-annual spectral peaks may emerge in GEP and RE given that five of eight of the long-term measurement sites displayed an increase in variability at the lowest frequency, a pattern that is not observed in the NEE and climate spectra. The 7.48y variability in GEP and RE at Harvard Forest is greater than cli-

matic variability (Fig. 4) and reflects the increase in flux magnitude over the course of measurements related to the species compositional shift toward red maple coupled with multi-annual recoveries from ecosystem disturbance (Urbanski et al., 2007). Such increases in variability at the low frequencies has been observed before (Stoy et al., 2005; Richardson et al., 2007; Mahecha et al., 2008), but are rarely expounded upon. CANOAK predicts multi-annual spectral peaks for a DBF ecosystem (Fig. 7) despite having a simple temperature-response function for a single soil C pool, but evidence for general multi-annual spectral peaks across biomes in the direct flux measurement record remains circumstantial. Until the length of eddy covariance time series is extended, it remains unclear how vegetation and climate interact to create low-frequency flux oscillations and the relative importance of deterministic versus stochastic events in modulating this variability in global ecosystems (Rigozo et al., 2007; Qian et al., 2008).

4.6 Multi-scale coupling between GEP and RE

Quantifying the coupling between photosynthesis and ecosystem respiration has gained attention given that isotopic and ecosystem manipulation studies have consistently demonstrated a strong daily-to-monthly coupling between CO₂ input and output (Högberg et al., 2001; Barbour et al., 2005; Taneva et al., 2006). Despite the known limitation of the artificial correlation between GEP and RE in eddy covariance measurements (Vickers et al., 2009), some evidence for their coupling across time scales may be gleaned from a conservative investigation of their co-spectral properties.

The magnitude of the instantaneous GEP-RE covariance is large at seasonal to annual time scales; this relationship is on average as strong as the seasonal covariance between CO₂ uptake and water loss (Fig. 6). The GEP-RE covariance is also larger, on average, than the covariance between GEP and most meteorological driver investigated, and is of the same average order of magnitude as $OWT_{GEP,LE}$ and OWT_{GEP,T_a} . GEP has been shown to explain 89% of the annual variance of RE across FLUXNET (Baldocchi, 2008) despite site-by-site differences in the strength of this relationship (Stoy et al., 2008). Formally linking GEP and RE variability in models at lower frequen-

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cies is a logical step for improving model skill given the large low-frequency covariance between these fluxes, noting that the degree to which GEP and RE are coupled at low frequencies versus the degree to which they are controlled by similar environmental drivers across ecosystems remains unclear (Reichstein et al., 2007b). Future studies should investigate forthcoming FLUXNET data products that seek to minimize artificial correlations between GEP and RE (Lasslop et al., 2009).

Interestingly, the average seasonal/annual covariance between RE and LE is as strong, or stronger, than the covariance between RE and T_a . This may partly be explained by the tight coupling of photosynthesis and transpiration, and root respiration during the growing season (Stoy et al., 2007). A strong correlation was observed between tree transpiration (sapflow) and root respiration measured on individual isolated trees at the semi-arid Metolius site, and soil respiration declined with soil water deficit as soil temperature continued to increase (Irvine et al., 2008) (see also Tang et al., 2005). The mechanisms for this relationship in the global database are less clear, and are likely linked through photosynthesis as well as soil moisture dynamics, which were not measured at a sufficient number of research sites to determine differences among climate zone and PFT. Measurements of soil moisture must be made to quantify the interaction between the terrestrial carbon and water cycles. The magnitude of the covariance between climate and flux at the proposed quasi-stochastic weekly to monthly and interannual time scales was on average low (Fig. 6), and did not differ among ecosystem type. The instantaneous relationship between climate and flux globally at these time scales is not coherent among PFT, which does not support H1. Rather, the covariance between GEP, RE and LE is consistently high at the seasonal/annual time scale, as is the covariance between GEP, RE and T_a . This significant variability agrees with recent studies that demonstrate a statistically significant relationship between mean annual temperature and GPP and RE across European (Reichstein et al., 2007b) and Asian (Friedlingstein et al., 2006; Kato and Tang, 2008) ecosystems. In other words, despite the strong and well-characterized relationship between temperature and ecosystem respiration at short time scales (Lloyd and Taylor, 1994) (but see

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Janssens et al., 2001), warm years tend to be correlated with greater annual CO₂ uptake across FLUXNET (Delpierre et al., 2009; Kato and Tang, 2008; Reichstein et al., 2007b) except under instances of drought (Ciais et al., 2005; Reichstein et al., 2007a; Granier et al., 2007), and despite the poor annual T_a-RE relationships that are observed at selected sites (Valentini et al., 2000; Law et al., 2002; Stoy et al., 2008) (but see Reichstein et al., 2007b).

5 Conclusions and future studies

Eddy covariance measurement records are extending to time scales where they can be compared against independent measures of interannual variability and multi-annual variability in the functioning of terrestrial ecosystems (Battle et al., 2000; Rocha et al., 2006; Rigozo et al., 2007). Multiannual eddy covariance measurement records are critical to understand the role played by ecosystems in controlling atmospheric CO₂ concentration (Houghton, 2000) and to contribute to global modeling analyses (Potter et al., 2005) for quantifying synchronous responses to disturbance events and climatic oscillations (Reichstein et al., 2007a; Qian et al., 2008) in an era of increasing climatic variability (Schär et al., 2004; Frich et al., 2002).

The broader implications of this study suggest that, at shorter (hourly to weekly) time scales, the variability of C uptake across global ecosystems respond to climatic inputs in a similar matter as revealed by the spectral analyses. PFT is a scale-dependent concept for ecosystem models. It is a logical way to separate the variability in CO₂ uptake function at monthly to interannual time scales, but variability in ecosystem respiration was not clearly separated by PFT across most time scales (Figs. 3 and 5). The strong diurnal coupling between GPP and PPF_D gave way to stronger covariance between the coupled C gain/water loss (via OWT_{GEP,LE}) and C gain/C loss function of ecosystems at lower frequencies.

Few instantaneous climatic inputs were related to instantaneous ecosystem-level responses at the stochastic weekly to monthly and interannual time scales. CO₂ uptake

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(loss) at low frequencies is dampened (amplified) compared climatic variability, low frequency variability in GEP, but not RE in a manner that is indicative of a homeostatic mechanism for ecosystem carbon gain (Odum, 1969), but it is difficult to disentangle the organismal and ecosystem-level mechanisms that may lead to such homeostasis in global ecosystems without additional biological information (e.g. long-term leaf-level gas exchange, Ellsworth, 1999). The “static” ecosystem assumptions that may give parsimonious model results over short time scales must consider changes in vegetation and ecosystem structure and function at longer time scales to match annual and interannual flux (Siqueira et al., 2006; Richardson et al., 2007). Accumulating evidence from this study and others suggest that low-frequency multi-annual modes of variability may be a common feature in the terrestrial C cycle, but the mechanisms for instantaneous resonance with low-frequency climatic oscillations, and/or lagged recovery from extreme events (Arnone et al., 2008), must be disentangled at the site or regional level with ecosystem models that require enhanced ancillary information for accurate prediction. Given the low immediate flux-climate variability at the quasi-stochastic time scales (Fig. 6), the lagged responses of ecosystems to climate variability must be quantified to comprehensively interpret the multi-scale climate-flux relationship. With regards to multi-site multi-scale lag analyses for nonlinear time series, it should be noted that phase can be quantified using wavelet coherence techniques with basis functions that contain an imaginary component (Grinsted et al., 2004).

Acknowledgements. We would first and foremost like to acknowledge the FLUXNET data providers, and the organizers of the FLUXNET database. This work is an outcome of the La Thuile FLUXNET workshop 2007, which would not have been possible without the financial support provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, and the US Department of Energy. The Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory provided databasing and technical support. The AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, ChinaFlux, Fluxnet-Canada, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and USCCC networks provided data. PCS and ADR conceived of the study and wrote the manuscript with DDB, GGK, MDM, MR and coau-

thors. JS assisted with the statistical analyses. PCS acknowledges funding from the National Environmental Research Council (UK) and the Marie Curie European Incoming International Fellowship (project number 237348, TSURF). DDB is supported by the US National Science Foundation RCN FLUXNET project and by the Department of Energy Terrestrial Carbon Program (DOE/TCP). MR acknowledges support from the EU-FP6 project CIRCE. BEL is supported by the AmeriFlux Research grant supported by DOE/TCP (DE-FG02-04ER63911).

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Table 1. The number of FLUXNET research sites in version D1 of the LaThuille FLUXNET dataset, total number of site years of data, the number of potential hour eddy covariance flux measurements, and resulting number of wavelet coefficients after orthonormal wavelet transformation (OWT), with respect to the climate and vegetation classes investigated here (after Williams et al. (2009)).

	Crop	Shrub +	DBF	EBF	ENF	Grass	MF	Savanna –	Wet	Total	Site-years	Time series length*	OWT coeff.
Temperate	17	0	8	2	12	18	4	0	4	65	255	4470473	932
Temp.-Cont.	7	4	9	1	17	7	8	0	0	53	213	3734300	761
Tropical	1	1	0	9	0	1	0	3	0	15	49	858960	214
Dry	0	1	0	1	1	3	0	4	0	10	27	473280	153
Boreal	0	4	2	0	22	4	2	0	4	38	161	2822782	549
Arctic	0	0	2	0	0	1	0	0	3	6	22	385678	86
Subtrop.-Medit.	5	6	11	5	17	11	2	6	0	63	272	4768551	941
Total	30	16	32	18	69	45	16	13	11	250	999	17514024	3594
Site years	79	50	149	77	340	135	74	58	37	999			
Length*	1384799	876576	2612253	1349902	5961015	2366735	1297342	1016684	648718	17514024			
OWT coeff.	416	225	465	263	1010	636	235	188	156	3594			

* Potential half-hour time series magnitude if measurements were continuous.

+ Closed and open shrublands were combined.

– Savanna and woody savanna were combined.

Crop = cropland/agricultural ecosystems. Shrub = shrubland ecosystems. DBF = Deciduous broadleaf forests. EBF = evergreen broadleaf forests. ENF = evergreen needleleaf forests. MF = mixed forests. Grass=grassland. Wet = wetlands. Temp.-Cont. = Temperate-Continental. Subtrop.-Medit. = Subtropical-Mediterranean.

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Table 2. Results from the mixed model analysis for significant interaction effects between meteorology (MET) by time scale (TS), and plant functional type (PFT) by TS on net ecosystem exchange (NEE) gross ecosystem productivity (GEP) and ecosystem respiration (RE) variability. Time scales for which spectra are significantly different at the 95% confidence level are denoted by the flux term abbreviation.

Time scale (h)*	Time scale	Description	MET×TS	PFT×TS
2 ¹⁴	1.87 years	Interannual	–	NEE, RE
2 ¹³	0.935 years	Annual	NEE, GEP	NEE, RE
2 ¹²	170.67 days	Seasonal	NEE, GEP	NEE, GEP, RE
2 ¹¹	85.33 days	Seasonal	NEE, GEP, RE	NEE, GEP
2 ¹⁰	42.67 days	Bi-Monthly	NEE, GEP	NEE, GEP
2 ⁹	21.33 days	Monthly	NEE	NEE, GEP
2 ⁸	10.67 days	Bi-Weekly	NEE	–
2 ⁷	5.33 days	Weekly	–	–
2 ⁶	2.66 days	Multi-day	–	–
2 ⁵	1.33 days	Multi-day	–	–
2 ⁴	16 hours	Daily	RE	–
2 ³	8 hours	Hourly	RE	–
2 ²	4 hours	Hourly	RE	–
2 ¹	2 hours	Hourly	RE	GEP
2 ^{0*}	1 hour	Hourly	RE	NEE, GEP, RE

* Eddy covariance-measured fluxes are calculated on the half-hourly basis. The highest frequency time scale considered is 21 half hours = 1 hour.

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Table 3. The 8 sites in version 2 of the FLUXNET database with 8 or more years of flux measurements with continuous data availability at the daily time scale. Abbreviations follow Table 1.

Site ID	Site	Climate	Vegetation	Latitude	Longitude
CA-Ca1	CampbellRiver	Temperate	ENF	49.8672	−125.3340
CA-Mer	Mer Bleue	Temp.-Cont.	OSH	45.4094	−75.5186
CA-Oas	SSA Old Aspen	Boreal	DBF	53.6289	−106.1980
DE-Tha	Tharandt	Temperate	ENF	50.9636	13.5669
DK-Sor	Soroe	Temperate	DBF	55.4869	11.6458
ES-ES1	El Saler	SubTrop.-Medit.	ENF	39.3460	−0.3188
RU-Fyo	Fedorovskoje	Temp.-Cont.	ENF	56.4617	32.9239
US-Ho1	Howland Forest (main)	Temp.-Cont.	ENF	45.2041	−68.7403

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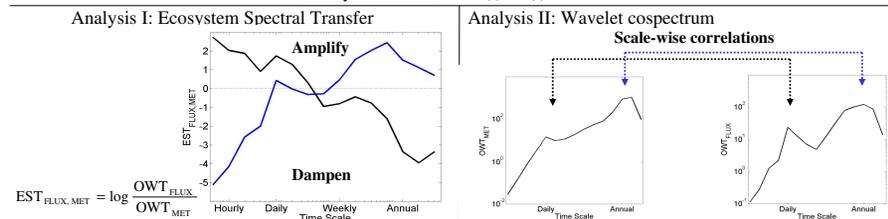
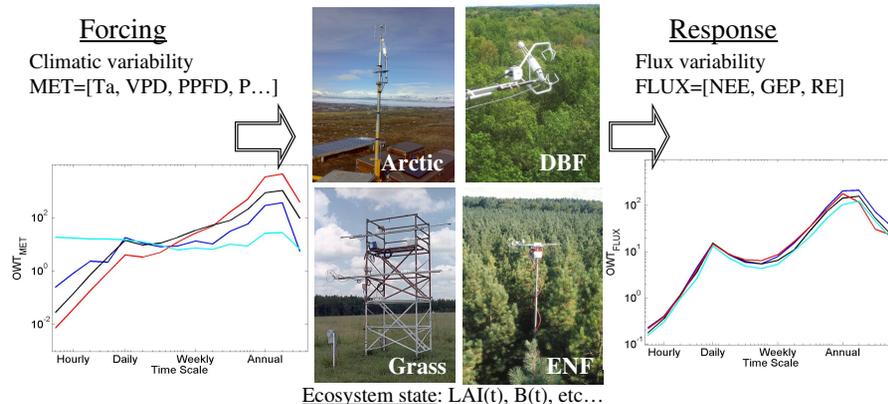


Fig. 1. A conceptual description of the ecosystem transfer process from input (in this case climatic variability, upper left) to response (here the net ecosystem exchange of CO₂, NEE, upper right) as represented by the orthonormal wavelet spectrum of the respective time series (OWT). The response of NEE to climatic variability depends on ecosystem type, Arctic, deciduous broadleaf forest (DBF), grassland and evergreen needleleaf forest (ENF) ecosystems are shown as examples. Response to climatic variability also depends on ecosystem state through, for example, leaf area index (LAI) or biomass (B), both of which vary across time and space. This study introduces the ecosystem spectral transfer function (EST), defined as the ratio between the wavelet spectra of NEE and climatic drivers (Analysis I). A co-spectral analysis to identify scale-wise correlations between climate and flux is performed in Analysis II.

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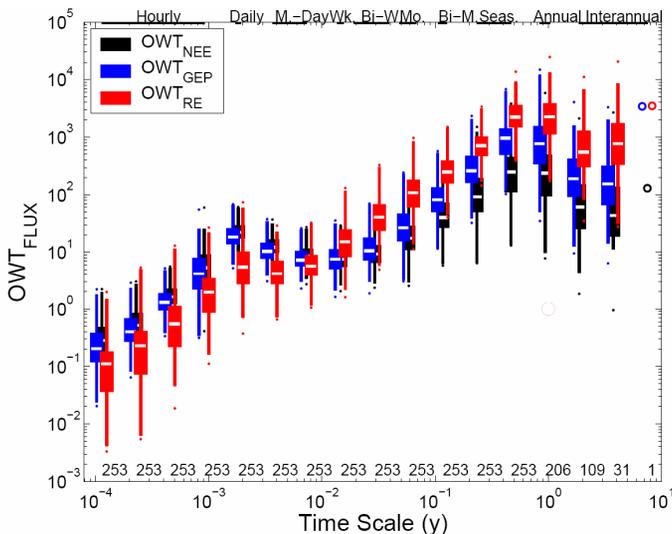


Fig. 2. Orthonormal wavelet power spectra of normalized net ecosystem exchange (OWT_{NEE}), normalized gross ecosystem productivity (OWT_{GEP}) and normalized ecosystem respiration (OWT_{RE}) for the 253 eddy covariance sites in version 2 of the FLUXNET database after transformation using the Haar wavelet basis function. The white bars represent the median of the distribution of wavelet coefficients at each time scale, and the thick vertical bars encompass the interquartile range. Outliers are expressed as dots outside the thin vertical bars, which represent $1.5\times$ the interquartile range. The GEP and RE spectra have been time shifted to avoid overlap. Circles at $7\frac{1}{2}$ years are for the Harvard Forest time series, which began in 1991. The numbers at the bottom of the plot represent the number of sites analyzed at each time scale; some sites have longer data records and therefore a greater number of wavelet coefficients. Text at the top of the figure refers to the expressions and abbreviations for the different time scales used throughout the manuscript. M.-Day = Multi-Day; Wk. = Weekly; Bi-W. = Bi-Weekly; Mo. = Monthly; Bi-M. = Bi-Monthly; Seas. = Seasonal.

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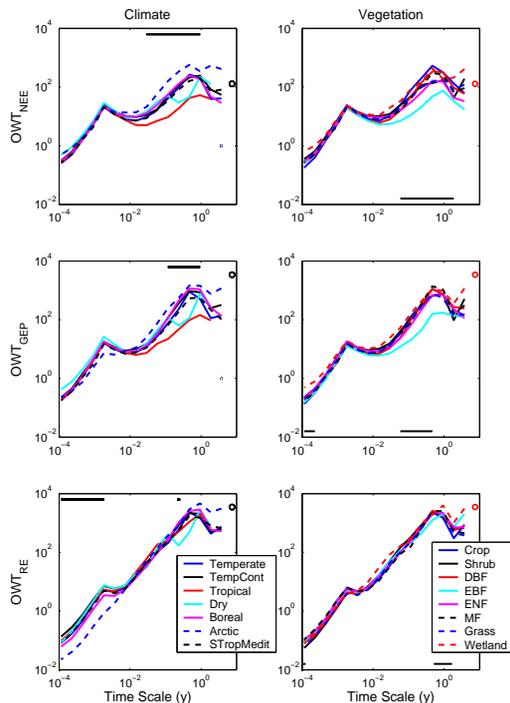


Fig. 3. Mean wavelet spectra of the normalized net ecosystem exchange of CO₂ (OWT_{NEE}), gross ecosystem productivity (OWT_{GEP}), and ecosystem respiration (OWT_{RE}) per climate (left-hand panels) and vegetation type (right-hand panels) for the 250 eddy covariance measurement sites with ecosystem-level information in version 2 of the LaThuille FLUXNET database. Horizontal lines demarcate time scales at which there are significant differences among climate (top of subplot) or vegetation type (bottom of subplot) at the 95% significance level (see Table 3). Significance at the longest time scales (3.74 and 7.48 y) could not be determined among climate types due to lack of replicates. Circles at the 7.48 year time scales represent flux variability at Harvard Forest.

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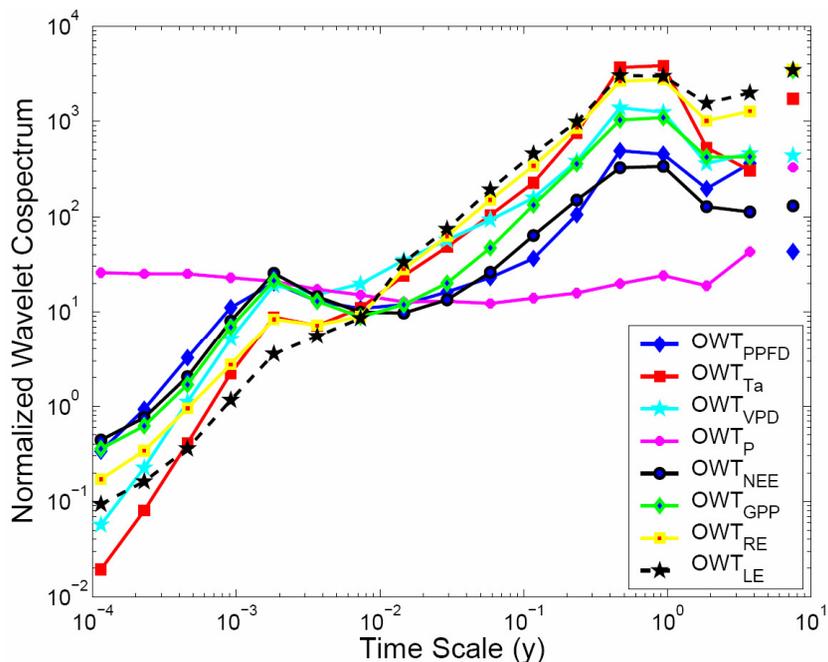



Fig. 4. Median normalized orthonormal wavelet spectra of net ecosystem exchange of CO₂ (OWT_{NEE}), gross ecosystem productivity (OWT_{GEP}), ecosystem respiration (OWT_{RE}), latent heat exchange (OWT_{LE}) and the meteorological drivers air temperature (OWT_{Ta}), photosynthetic photon flux density (OWT_{PPFD}), vapor pressure deficit (OWT_{VPD}) and precipitation (OWT_P). Points at the 7.48 year time scale represent flux variability at a single site, Harvard Forest.

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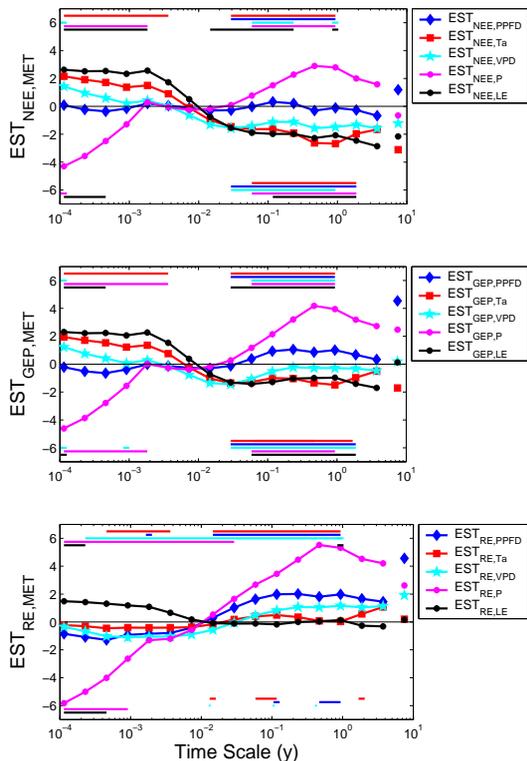


Fig. 5. The mean difference between the log of the meteorological drivers or latent heat exchange and NEE **(a)** (i.e. the ecosystem spectral transfer function, $EST_{NEE,MET}$), GEP **(b)** and RE **(c)** for all sites in version 2 of the LaThuile FLUXNET database. For example, in (a), NEE is more variable than (amplifies) climate variability if values are positive and damps climate variability if values are negative. Horizontal lines demarcate time scales at which there are significant differences among climate (top of subplot) or vegetation type (bottom of subplot) at the 95% significance level after Fig. 3. Points at the 7.48 year time scale represent flux variability at Harvard Forest.

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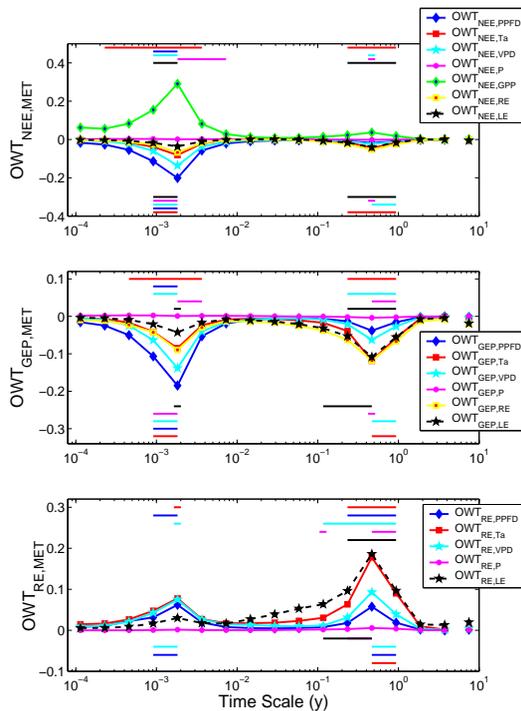


Fig. 6. The median wavelet cospectra between normalized net ecosystem exchange of CO₂ (NEE) and normalized latent heat exchange (LE) and meteorological drivers for all sites in version 2 of the LaThuile FLUXNET database. Negative cospectra indicate correlation between climate and CO₂ uptake given the meteorological convention where C input into the biosphere is denoted as negative. Horizontal lines demarcate time scales at which there are significant differences among climate (top of subplot) or vegetation type (bottom of subplot) at the 95% significance level after Fig. 3. Points at the 7.48 year time scale represent flux variability at Harvard Forest.

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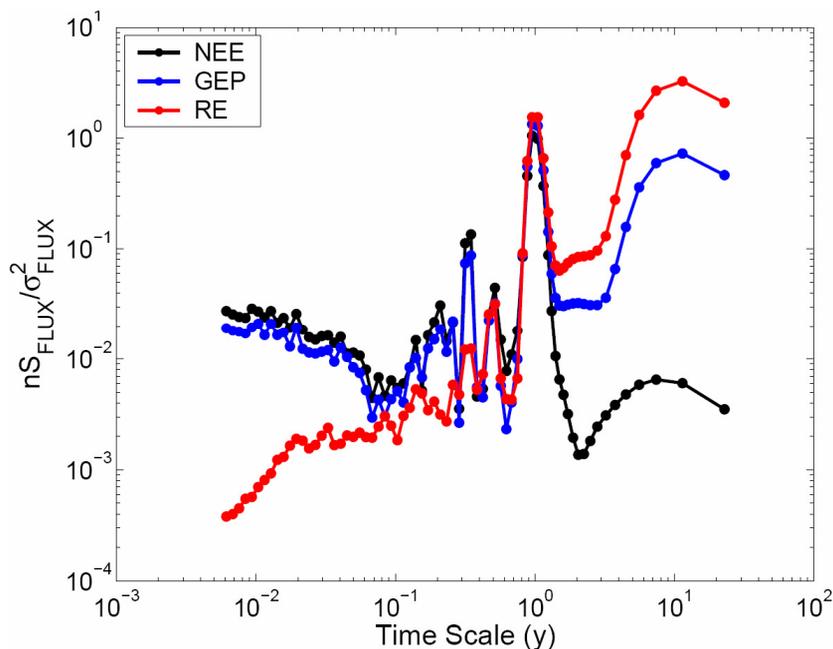


Fig. 7. CANOAK modeled normalized power spectra for NEE, GEP and RE from 18 years of continuous daily-averaged meteorological inputs from Walker Branch, TN, USA.

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