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Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange

ANDREW D. RICHARDSON*[1], DAVID Y. HOLLINGER†, JOHN D. ABER*, SCOTT V. OLLINGER* and BOBBY H. BRASWELL*

**Complex Systems Research Center, University of New Hampshire, Durham, NH 03824, USA, †USDA Forest Service, NE Research Station, Durham, NH 03824, USA*

Abstract

Tower-based eddy covariance measurements of forest-atmosphere carbon dioxide (CO_2) exchange from many sites around the world indicate that there is considerable year-to-year variation in net ecosystem exchange (NEE). Here, we use a statistical modeling approach to partition the interannual variability in NEE (and its component fluxes, ecosystem respiration, R_{eco}, and gross photosynthesis, P_{gross}) into two main effects: variation in environmental drivers (air and soil temperature, solar radiation, vapor pressure deficit, and soil water content) and variation in the biotic response to this environmental forcing (as characterized by the model parameters). The model is applied to a 9-year data set from the Howland AmeriFlux site, a spruce-dominated forest in Maine, USA. Gap-filled flux measurements at this site indicate that the forest has been sequestering, on average, 190 g C m^{-2} yr^{-1}, with a range from 130 to 270 g C m^{-2} yr^{-1}. Our fitted model predicts somewhat more uptake (mean 270 g C m^{-2} yr^{-1}), but interannual variation is similar, and wavelet variance analyses indicate good agreement between tower measurements and model predictions across a wide range of timescales (hours to years). Associated with the interannual variation in NEE are clear differences among years in model parameters for both R_{eco} and P_{gross}. Analysis of model predictions suggests that, at the annual time step, about 40% of the variance in modeled NEE can be attributed to variation in environmental drivers, and 55% to variation in the biotic response to this forcing. As model predictions are aggregated at longer timescales (from individual days to months to calendar year), variation in environmental drivers becomes progressively less important, and variation in the biotic response becomes progressively more important, in determining the modeled flux. There is a strong negative correlation between modeled annual P_{gross} and R_{eco} ($r = -0.93$, $P \leq 0.001$); two possible explanations for this correlation are discussed. The correlation promotes homeostasis of NEE: the interannual variation in modeled NEE is substantially less than that for either P_{gross} or R_{eco}

Keywords: AmeriFlux, ecosystem physiology, eddy covariance, Howland, interannual variability, maximum likelihood, Monte Carlo simulation, net ecosystem exchange, wavelets

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Introduction

In the same way that whole-watershed studies transformed the study of ecosystem ecology in the 1960s and 1970s (e.g. Likens & Bormann, 1995), application of the eddy covariance (EC) approach to the study of ecosystem-scale fluxes of energy, water vapor, and carbon dioxide (CO_2) has again revolutionized the field by enabling the continuous measurement of key ecosystem processes (Baldocchi *et al*., 1988; Baldocchi, 2003). The global network of EC towers in a diverse array of ecosystems (FluxNet and its associated regional networks, such as AmeriFlux and EuroFlux; see Baldocchi

Correspondence: Andrew Richardson, tel. +1 603 868 7654, fax +1 603 868 7604, e-mail: andrew.richardson@unh.edu

[1]Present address: USDA Forest Service, 271 Mast Road, Durham, NH 03824, USA.

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et al., 2001) provides the infrastructure necessary to study these processes across a range of spatial and temporal scales (e.g. Valentini *et al.*, 2000; Janssens *et al.*, 2001; Law *et al.*, 2002). Results from the monitoring network have added significance because of what is seen as a pressing need to better understand the role terrestrial ecosystems play in the global carbon cycle (Baldocchi *et al.*, 1996; Braswell *et al.*, 1997; Schimel *et al.*, 2001; Wofsy & Harriss, 2002).

One of the earliest, and still most significant, results to emerge from multiyear EC studies was an estimate of the magnitude of the year-to-year variation, commonly referred to as interannual variability, in the net ecosystem exchange (NEE) of CO_2. At a temperate deciduous site where NEE ranged between −140 and $-280\,g\,C\,m^{-2}\,yr^{-1}$, above-average uptake in 1 year was attributed to increased photosynthesis, and in another year to decreased respiration (Goulden *et al.*, 1996a). At a boreal coniferous forest, the ecosystem was a carbon source ($+70\,g\,C\,m^{-2}\,yr^{-1}$) in 1 year but a weak carbon sink ($-10\,g\,C\,m^{-2}\,yr^{-1}$) 2 years later; the variation in carbon balance was attributed to respiration, which was controlled by the depth and duration of soil thaw (Goulden *et al.*, 1998). Multisite syntheses indicate that interannual variability in net exchange is a universal characteristic of flux sites around the world (Baldocchi *et al.*, 2001).

Because NEE is a relatively small difference between two much larger sums (ecosystem respiration and gross photosynthesis; Valentini *et al.*, 2000), and because EC data are inherently noisy (Hollinger & Richardson, 2005), there may have been initial concern that the measured interannual variation in NEE had more to do with the shortcomings of the method, rather than actual year-to-year differences in carbon sequestration. However, error and uncertainty analyses (Goulden *et al.*, 1996b; Morgenstern *et al.*, 2004), paired towers (Hollinger *et al.*, 2004; Hollinger & Richardson, 2005), intercomparison with a roving set of reference instrumentation (Baldocchi *et al.*, 2001; D. Y. Hollinger *et al.*, unpublished data), and cross-biome modeling efforts (Schimel *et al.*, 2000; Raich *et al.*, 2002) provide conclusive support for the idea that the measured interannual variation in NEE is real.

Modeling interannual variation in NEE has proven challenging. It is necessary that the basic processes underlying CO_2 uptake (photosynthesis) and release (respiration) both be modeled well, so as to avoid compensating errors. This is also an important consideration if models are to be used for prognostic purposes, (i.e. to make predictions about terrestrial carbon cycle implications of future climatic scenarios). Because the interannual variation in NEE is much smaller than seasonal or spatial variation in photosynthesis and respiration, it therefore represents an extreme test for models, which may otherwise appear to adequately capture temporal or global variation in CO_2 fluxes. For example, Hanson *et al.* (2004) used a range of ecosystem models (including BIOME-BGC, CANOAK, Ecosys, Ealco, LoTEC, and PnET-II) to predict annual NEE and net primary productivity (NPP) of the Oak Ridge AmeriFlux site for the years 1993–2000. Based on their Table 12, there was no significant correlation between the annual predictions of any of the models and the observed interannual variation in NEE (based on 5 years eddy flux data) or NPP (based on 8 years of biometric data). Furthermore, there was only weak agreement among the model predictions of interannual variation in NEE: of the 28 possible paired model comparisons, only six were significantly correlated ($P<0.05$) at the annual time step. More recently, Siqueira *et al.* (2006) used spectral analysis to assess the ability of four models to capture flux variation across a range of time scales and found that the models were 'inconsistent' at the interannual timestep. Although some models appeared to perform well at the interannual scale, Siqueira *et al.* attributed this result to the cancellation of offsetting errors.

Multiyear EC datasets provide the tools to address the causes of interannual variability in NEE. To date, however, most such studies have attributed (either explicitly or implicitly) the interannual variation in NEE entirely to interannual environmental variation, (i.e. variation in climatic drivers such as air or soil temperature, solar radiation, or precipitation). In many cases, this attribution has been anecdotal, as few flux data sets are long enough to permit rigorous statistical analysis (but see Aubinet *et al.*, 2002; Carrara *et al.*, 2003; Hollinger *et al.*, 2004). Lagged correlation analyses have suggested relationships between climate anomalies and subsequent flux anomalies (Barford *et al.*, 2001), but these relationships may differ among ecosystems (Hollinger *et al.*, 2004).

While environmental variation is important, interannual variability in net exchange may also be due to changes in the biotic response to the environmental forcing (Schimel *et al.*, 2001; Wang *et al.*, 2004) of either (or both) of the underlying processes. Such changes could be due to variation either in the basal or maximum rate of a process (e.g. maximum photosynthetic uptake), or in the sensitivity of the process to environmental drivers (e.g. temperature response of respiration), or changes in the size of carbon or nutrient pools.

By combining EC data with simple, physiologically based ecosystem models driven by basic environmental data, researchers have the ability to address relationships between ecosystem processes and the abiotic environment (Baldocchi, 2003). If there was significant

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interannual variation in the biotic response to environmental forcing, then the fitted model parameters would be expected to differ among years. Interannual variability in canopy-level photosynthetic capacity could be due to acclimation to prevailing light regimes, variation in foliar nutrient status (in particular, N content and consequent photosynthetic capacity), or changes in leaf area index (Flanagan *et al*., 2002). Interannual variability in basal respiration could be due to the quantity and quality of the available substrate – for heterotrophic soil respiration, this depends on previous production (especially litterfall from the most recent growing season), but for root respiration, it depends on current production (Janssens *et al*., 2001). Results of Lee *et al*. (1999), Chen *et al*. (1999), Flanagan *et al*. (2002), and Hollinger *et al*. (2004), for example, document (but do not explain the causes of) interannual variation in photosynthetic capacity or respiration rates in a variety of different biomes. The causes of this variation could include direct climatic effects, as well as indirect or lagged (at various time scales) climatic effects, and also independent factors such as disturbance.

To fully understand the interannual variation in NEE, it is therefore necessary to consider not only the interannual variation in environmental drivers but also the variation in the biotic response to these drivers. Hui *et al*. (2003) previously partitioned interannual variation in NEE into environmental driver and biotic response effects using a stepwise, multiple regression model. To assess year-to-year differences in the biotic response to environmental forcing, the linear response to the driving environmental variables was allowed to vary by year. A sum-of-squares approach was then used to partition the overall variance to four factors, which Hui *et al*. (2003) referred to as functional change, interannual climatic variability, seasonal climatic variation, and random error.

In the present study, we begin by developing a parsimonious, physiologically based model to explain, as a function of basic environmental data, 9 years (1996–2004) of half-hourly, ecosystem-level carbon fluxes measured using the EC technique at the Howland (Maine, USA) AmeriFlux site. Analysis of the 1996–2002 Howland data set (Hollinger *et al*., 2004) indicated that the site has been sequestering (mean $\pm$ 1 SD) $174 \pm 46\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; years with above-average C sequestration were characterized by warmer than average spring and fall temperatures, and adequate summer soil moisture.

In our model, potential ecosystem respiration (representing the sum of autotrophic and heterotrophic respiration) and potential gross photosynthesis are each described by a single equation. Actual fluxes equal the potential flux multiplied by a set of environmental scalars that reduce the flux under suboptimal environmental conditions. To account for interannual variation in the biotic response to environmental forcing, four model parameters (controlling the base rate and temperature sensitivity of respiration, and the maximum rate and PPFD sensitivity of photosynthesis) are fit at the annual time step. Then, by running the model with 1 year's environmental driving data and another year's parameter values, we simulate the NEE effects of interannual variation in both environmental drivers and the biotic response to environmental forcing. We then use a sums-of-squares approach to determine the relative importance of environmental driver and biotic response effects in determining interannual flux variability across a range of timescales, from daily to annual flux integrals. The 'variation in biotic response' we refer to is really just the residual variance (at the annual time step) that is not explained by the model with fixed parameters. Much of this presumably arises from inadequacies in the model (oversimplification of processes or pools) and our lack of potentially illuminating data such as canopy nitrogen content. However, by evaluating simple models in this way we may be able to determine, at least at the gross level (between photosynthesis and respiration), the source of this biotic variation.

Data and method

Study site

Nine complete years (1996–2004) of data from the main tower at the Howland Forest AmeriFlux research site (45°12′N, 68°44′W, 60 m a.s.l.), located about 35 miles north of Bangor, ME, USA, were used for the present analysis. This forested site is located within a transition zone between the boreal forest (to the north) and northern hardwood forest (to the south). Forest composition is dominated by *Picea rubens* (41%) and *Tsuga canadensis* (25%), with hardwood species (mainly *Acer rubrum* and *Betula papyrifera*) together accounting for <10% of the total basal area. Site characteristics, instrumentation, and data collection and processing are described in greater detail by Hollinger *et al*. (1999, 2004).

Only valid, measured (i.e. not gapfilled) data were used to fit the model. Night-time (PPFD $<5\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) observations were filtered with a friction velocity threshold of $u^* \geq 0.25\,\mathrm{m\,s^{-1}}$ (Hollinger *et al*., 2004), resulting in annual data coverage between 28% (1997, 2003) and 44% (1999). Daytime coverage was considerably better, ranging from 55% (1996, 1997) to over 80% (2001, 2004). The longest data gap was 19 days, in August 1999. There were only 5 weeks in total (out of 470 weeks in the 9-year data record) with no valid night-time observations, and only 3 weeks in total with no valid daytime observations. Ninety-five percent of

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all weeks had at least 10% night-time coverage, and 98% of all weeks had at least 10% daytime coverage.

Model details

Our objective was to simulate a complete time series of CO_2 fluxes using a parsimonious model that required as inputs only a minimal set of environmental data: solar PPFD (Q), soil temperature (T_{soil}), air temperature (T_{air}), saturation vapor pressure deficit (VPD), and soil water content (SWC).

The measured net flux of CO_2, F_{CO_2} $\mu mol\, CO_2\, m^{-2}\, s^{-1}$), was modeled as the sum of gross photosynthesis (P_{gross}, a negative flux) and ecosystem respiration (R_{eco}, a positive flux)

$$F_{CO_2} = P_{gross} + R_{eco} \tag{1}$$

For each of these component fluxes, the actual flux (R_{eco}, P_{gross}) was calculated as a potential flux ($\dot{R}_{eco}$, $\dot{P}_{gross}$) multiplied by a set of scalar functions, $f[x]$, that reduce the flux under suboptimal environmental conditions (described below, see also Table 1). This approach is similar to that employed previously in other modeling efforts (e.g. PnET; Aber & Federer, 1992; Aber *et al.*, 1996). These scalar functions were specified as sigmoidal functions [Eqn (2)] that are well behaved in that $f[x]$ is constrained to the interval [0,1]. Parameters for the scalar functions were fit globally to all years of data, because the environmental variability in individual years was often insufficient to adequately constrain the parameterization:

$$f[x] = \frac{1}{1 + e^{\theta_1 - \theta_2 x}}. \tag{2}$$

Night-time data were used to fit the Lloyd & Taylor (1994) respiration model [Eqn (3)], which was specified as a function of T_{soil} (°C) because soil respiration accounts for $\approx$60% of ecosystem respiration at Howland (Davidson *et al.*, 2006).

$$\dot{R}_{eco} = R_{ref} \times \exp\left(\frac{E_0}{T_{soil} + 273.15 - T_0}\right) \tag{3}$$

Here, the parameter R_{ref} is a scaling coefficient, the parameter E_0 is similar to an activation energy, and the parameter T_0 determines the temperature minimum at which predicted respiration equals zero. R_{ref} has flux units $\mu mol\, CO_2\, m^{-2}\, s^{-1}$) whereas both E_0 and T_0 are in Kelvin. In a previous study (Richardson & Hollinger, 2005), we found that these three model parameters were so highly correlated with each other that the model was essentially overparameterized and at least one parameter was redundant. We, therefore, elected to fix the value of E_0 at a constant value (−68.3, which was the best-fit value when a single set of parameters was fit to all 9 years of data), but note that we could just as easily have fixed the T_0 parameter without substantially affecting the analysis. Fixing E_0 in this manner helps to better constrain estimates of the R_{ref} and T_0 parameters, reducing parameter uncertainties by roughly fivefold (Richardson & Hollinger, 2005).

Soil drying can inhibit respiration (Carlyle & Ba Than, 1988; Savage & Davidson, 2001), and so the potential ecosystem respiration given in Eqn (3) was multiplied by a scalar function of soil water content [Eqn (2), Table 1], to yield the actual flux, as in Eqn (4)

$$R_{eco} = \dot{R}_{eco} \times f[SWC]. \tag{4}$$

Equation (4) was used to estimate daytime R_{eco}, and P_{gross} was then estimated by Eqn (5)

$$P_{gross} = F_{CO_2} - R_{eco} \tag{5}$$

Potential P_{gross} was modeled [Eqn (6)] as a function of Q ($\mu mol\, m^{-2}\, s^{-1}$ PPFD) using a simple Michaelis–Menten light response model (e.g. Hollinger *et al.*, 2004):

$$\dot{P}_{gross} = A_{max} \times \left(\frac{Q}{Q + K_m}\right). \tag{6}$$

Here, the parameter K_m is the quantum flux ($\mu mol\, m^{-2}\, s^{-1}$ PPFD) at which half-saturation of the light response curve occurs and A_{max} is the light-saturated rate of gross canopy photosynthesis ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$).

In this coniferous forest, the dates at which measurable carbon uptake begins in the spring and ends in the autumn appear to be controlled mostly by soil temperature (Hollinger *et al.*, 1999), and so $f[T_{soil}]$ was used as a proxy for the phenology of carbon uptake (see also Baldocchi *et al.*, 2005). Photosynthesis is also sensitive

Table 1 Environmental scalar parameters (θ_1, θ_2) for sigmoid response functions, $f[x] = 1/(1 + e^{\theta_1 - \theta_2 x})$, used to modify modeled potential fluxes (R_{eco}, ecosystem respiration; P_{gross}, gross photosynthesis) under suboptimal environmental conditions

Flux		θ_1	θ_2
R_{eco}			
	f [SWC]	29.2 (1.9)	256 (16)
P_{gross}			
	f [SWC]	43.1 (2.3)	376 (19)
	f [VPD]	−1.980 (0.020)	−0.7913 (0.0065)
	f [T_{air}]	1.1274 (0.0053)	0.1573 (0.0007)
	f [T_{soil}]	1.4578 (0.0043)	0.7715 (0.0030)

Note: SWC, soil water content; VPD, vapor pressure deficit. Standard errors on parameter estimates are given in parentheses.

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to ambient T_{air} and is reduced by stomatal closure when *VPD* is high or SWC is limiting (Aber & Federer, 1992; Jones, 1992). Thus, the potential P_{gross} was modified by four environmental scalars [Eqn (2)] to yield the actual flux as in Eqn (7):

$$P_{gross} = \dot{P}_{gross} \times f[T_{soil}] \times f[T_{air}] \times f[\mathrm{VPD}] \times \mathrm{f[SWC]}. \quad (7)$$

Parameter estimates for the environmental scalar functions were well constrained by the data (Table 1), and consistent with expectations based on previously published studies and our knowledge of the site.

Model parameterization

We used maximum-likelihood techniques to fit the model parameters; the resulting parameter estimates are those that would be most likely to generate the observed data, given the model and what is known about the random flux measurement error (Press *et al*., 1993). It is well documented that the flux measurement error is better approximated by a double-exponential, rather than Gaussian, distribution, and that the variance of the measurement error is nonconstant (Richardson *et al*., 2006a). Given that the measurement error has these characteristics (which violate two key assumptions of ordinary least squares fitting; see Richardson & Hollinger, 2005), maximum likelihood parameter estimates are obtained by minimizing the mean absolute weighted error [MAWE; Eqn (8)], rather than mean squared error (MSE) (Press *et al*., 1993).

$$MAWE = \frac{1}{N}\sum_{i=1}^{N}\frac{|y_i - y_{pred}|}{\sigma(\delta_i)} \quad (8)$$

Here, the weighting factor, $1/\sigma(\delta_i)$, is the reciprocal of the estimated standard deviation of the random measurement error associated with each half-hourly NEE measurement. As noted by Raupach *et al*. (2005), $1/\sigma(\delta_i)$ provides us with a measure of our confidence in the data: observations in which we have greater confidence receive more weight in the cost function and hence exert a greater influence during the optimization. Based on results from a cross-site synthesis of flux measurement uncertainty (Richardson *et al*., 2006a), we used Eqn (9a) (growing season) and Eqn (9b) (dormant season) as the basis for estimating $\sigma(\delta_i)$.

$$\sigma(\delta_i) = 2.71 + 0.75 \times 10^{-3}Q \quad (\mathrm{JD}\,122 - 295) \quad (9a)$$

$$\sigma(\delta_i) = 1.32 + 0.87 \times 10^{-3}Q \quad (\text{rest of year}). \quad (9b)$$

Best-fit parameters were determined using an iterative algorithm suitable for nonlinear curve fitting (Marquardt method in PROC NLIN, SAS 9.1, SAS Institute, Cary, NC, USA).

Estimation of model parameters required two steps. In the first step, a single set of model parameters was fit to all 9 years of data. There were 15 parameters fit in this manner (R_{ref}, T_0, E_0, A_{max}, and K_m, plus the θ_1 and θ_2 parameters for each of the five environmental scalar functions). In the second step, we fixed the environmental scalar parameters (Table 1), as well as E_0, to the values determined in the first step, but allowed the remaining parameters for $\dot{R}_{eco}$ (R_{ref}, T_0) and $\dot{P}_{gross}$ (A_{max}, K_m) to vary among years, reflecting interannual variation in the biotic response to environmental forcing.

Once the best-fit parameter set (R_{ref}, T_0, A_{max}, and K_m) for each year was determined, Monte Carlo simulations ($n = 500/\mathrm{yr}^{-1}$) were used to obtain the joint probability distributions of the parameter estimates, following the procedures described by Press *et al*. (1993) and summarized in Richardson & Hollinger (2005). These probability distributions give insight into parameter uncertainties and covariances, and permit evaluation of uncertainty in model predictions.

Crossed model runs and posterior analyses

Our objective was to assess the effects of interannual variation in both environmental drivers themselves, as well as the biotic response to environmental forcing (the model parameters), on modeled NEE and its component fluxes, R_{eco} and P_{gross}. To do this, we ran our model by crossing each 'driver year' (each of the 9 years of environmental drivers) with each 'parameter year' (each of the 9 years of model parameter sets), resulting in a 9×9 matrix of model predictions. This 'crossed model' was run 500 times, once for each of the Monte Carlo simulations, effectively yielding a 9×9 matrix with 500 layers.

We used analysis of variance (ANOVA) to partition the variance in crossed model predictions to different factors, with an emphasis on 'driver year' and 'parameter year' effects. With large sample sizes, ANOVA is known to be relatively robust to departures from non-normality and heteroscedasticity, but we note that at the annual time step, ANOVA residuals were homoscedastic and approximately normal. ANOVA is, therefore, an appropriate tool for our objective, which is simply to partition the variance in model predictions, rather than rigorous hypothesis testing. Our approach was as follows: for each 'driver year' × 'parameter year' × 'model run' combination, half-hourly model predictions were summed, first by day of year, and subsequently at longer periods of integration (week, month, season,

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year). At each of these periods of integration, the ANOVA was conducted on the integrated sums (mean–adjusted) of NEE, R_{eco}, and P_{gross}. Analysis was conducted separately by, for example, each week, but then the sums of squares for each model factor were added across all weeks, so that the proportion of the total variance accounted for by each factor could be determined. ANOVA factors were specified as follows: 'driver year,' 'parameter year,' 'driver year' × 'parameter year' interaction, and 'parameter year' × 'model run' interaction. The final term is important because it captures the variance that can be attributed to uncertainty in model parameterization, which results from the fact that the original data are measured with some imprecision [measurement error δ, Eqn (9a and 9b)]. Remaining unexplained variance, which was negligible ($\leq$ 0.05% of the total variance) was accounted for by the ANOVA model error term.

PnET modeling

We also used a process-based canopy physiology model (PnET-DAY; Aber *et al*., 1996) to determine the range of foliar nitrogen concentrations required to capture the modeled interannual variation in P_{gross}. PnET-DAY simulates carbon assimilation for a multilayered forest canopy at a daily time step using standard climatic inputs (temperature, precipitation and PPFD), along with vegetation parameters for canopy light attenuation, phenology, photosynthetic capacity, leaf mass, and turnover rate, and response to temperature, PPFD, and VPD (see Aber *et al*., 1996, for full discussion of model parameters). Our analysis focuses on the effects of variation in foliar N because in the PnET model, maximum photosynthetic capacity scales directly with foliar N, and thus the variation in N required for PnET predictions to align with model predictions may be relevant for understanding interannual variation in the A_{max} parameter in Eqn (6).

Results

Interannual environmental variation

At both the annual and monthly time steps, there were measurable anomalies in surface-atmosphere exchange (gap-filled tower NEE) and three key environmental factors (air temperature, solar radiation, and precipitation) over the 9-year period of study (Fig. 1). Pronounced deviations in annual NEE were seen in 1998 (1 SD above normal, i.e. less uptake), as well as 2000 and 2004 (both 1 SD below normal, i.e. more uptake). Air temperatures were 1 SD warmer than the 9-year average in 1998, 1999, and 2001, but 1 SD cooler in 2000, 2003, and 2004. Solar radiation in 2001 was almost 2 SD above the average. Precipitation was more than 1.5 SD above the average in 1996, but close to 2 SD below the average in 2001.

At the monthly time step, patterns were sometimes different from those at the annual time step (Fig. 1). For example, air temperatures in March 2000, were almost 2 SD above the 9-year average, but from April through September of that year, temperatures were well below average. In 2002, air temperatures were above average during the winter, below average during the spring, above average during the summer, and below average during the autumn; on the whole, the mean annual air temperature was approximately equal to the 9-year average. In 2003, precipitation through July was generally below average, but from August onwards, precipitation was above average.

Model fit, annual sums, and diagnostics

With a separate set of $\dot{R}_{eco}$ and $\dot{P}_{gross}$ model parameters fit to each calendar year of measured flux data, the fitted model explains about 50% of the half-hourly night-time F_{CO_2} variance, and 65% of the daytime variance (Table 2). The root mean squared error (RMSE) is about 65% larger during the day than at night, whereas the mean absolute error (MAE) is twice as large during the day than at night.

At the annual time step, the correlation between tower (gap-filled) NEE and fitted model NEE is strong ($r = 0.88$, $P < 0.01$), although the fitted model tends to predict more NEE than indicated by gap-filled tower measurements (difference of $84 \pm 25\,g\,C\,m^{-2}\,y^{-1}$, mean ± 1 SD; see Table 3). Differences between model and tower are negligible during the day ($16 \pm 14\,g\,C\,m^{-2}\,yr^{-1}$ more uptake predicted by model) but substantial during the night ($68 \pm 14\,g\,C\,m^{-2}\,yr^{-1}$ less release predicted by model) (Table 3). The nocturnal difference can be largely attributed to the fact that the present model is fit using maximum-likelihood approach, whereas gap-filling has previously been conducted using a least-squares approach. In an earlier study (Richardson & Hollinger, 2005), we found that maximum-likelihood fitting of respiration models tended to result in about a 10% reduction in estimated R_{eco} compared with models fit by least squares.

Aggregated to the weekly time step, mean model residuals exhibit some seasonal patterns that indicate model predictions are biased at certain times of the year. Except during the winter, there is a tendency for the mean night-time error to be >0, with the most pronounced bias extending from day 90 to 270, and peaking around days 180 and 240 (Fig. 2a). Mean daytime error is <0 from day 90 to 120, and from day 180 to 260,

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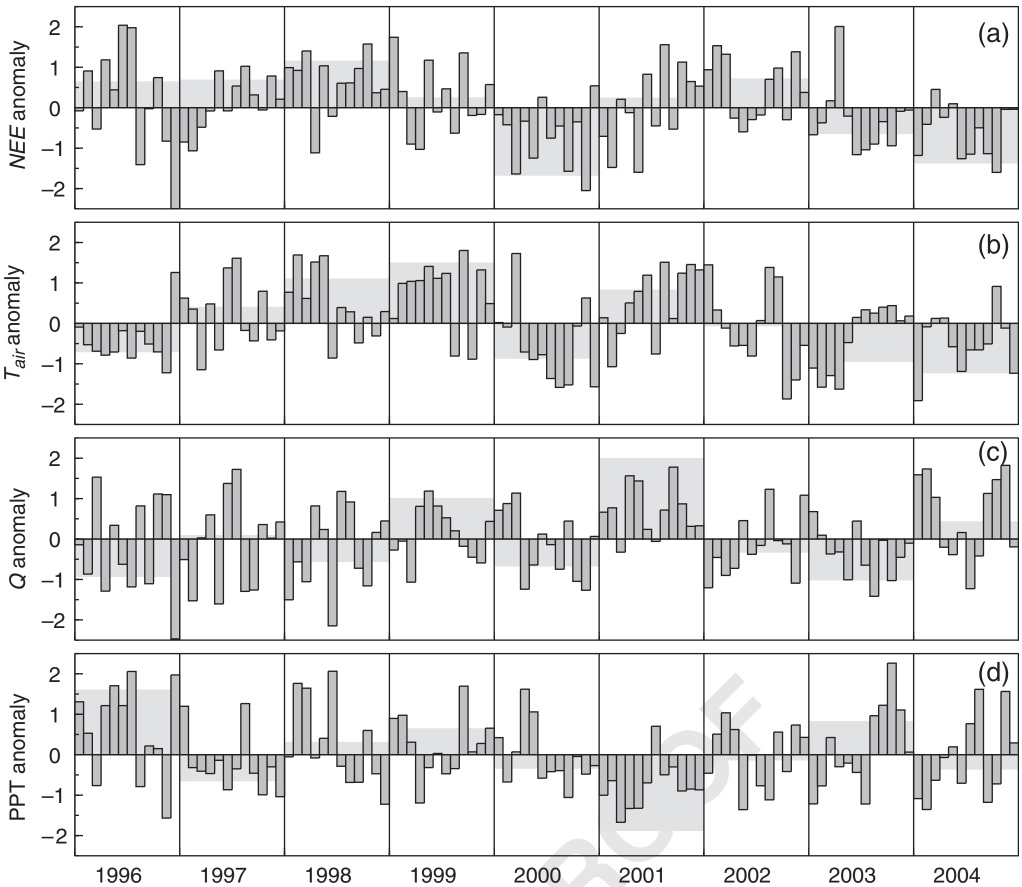

Fig. 1 Monthly (narrow bars, dark shading) and annual (wider bars, lighter shading) anomalies in gap-filled CO_2 fluxes (net ecosystem exchange, NEE), air temperature (T_{air}), solar PPFD (Q), and precipitation (PPT), based on a 9-year record from the Howland Forest AmeriFlux site in central Maine, USA. The y-axis of all four panels is in terms of standard deviations from the mean. Note that a positive NEE anomaly means less negative uptake.

but >0 from day 120 to 180 and from day 270 to 300 (Fig. 2b). These biases could be due to factors or process details not included in the model (e.g. separation of above- and below-ground controls on respiration) or mis-specification of the functional form of one or more components of the model.

Spectral analyses based on wavelet transformations complement traditional analyses of data-model agreement (Katul *et al*., 2001; Braswell *et al*., 2005; see also Siqueira *et al*., 2006), and indicate (Fig. 3) that there is good agreement between model predictions and tower measurements (not gap filled) across a wide range of time scales, from hours to years. Wavelet variance is highest at the strongly forced diurnal and seasonal time scales. Compared with tower measurements, the fitted model somewhat under-estimates the high-frequency variance, which is largely due to measurement uncertainty (flux measurement errors and footprint variation) at the half-hourly time step. However, the variance at longer time scales is captured by the fitted model, as well as (or, for time scales >1 month, better than) by the Howland gap-filling routine. For the analysis performed here, it is especially important that the fitted model adequately capture this low-frequency variance.

Model predictions and Monte Carlo simulations

The fitted model predicts the smallest NEE in 2002 ($234\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) and the largest in 2000 ($320\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$). R_{eco} and P_{gross} are both smallest in 1996, but R_{eco} is largest in 1999, whereas P_{gross} is largest in 2000 (Table 3). Monte Carlo simulations indicate that 95% confidence intervals on the total modeled annual NEE, R_{eco} and P_{gross} are $\pm$ 19–23, $\pm$ 28–36, and $\pm$ 17–22 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively. These confidence intervals are based solely on the random measurement uncertainty, both as it affects the individual measurements, and as it is propagated out through the model parameterization and predictions (e.g. Richardson & Hollinger, 2005), and does not include the additional uncertainty associated with fixed biases (e.g. choice of u* threshold). Because the 95% confidence intervals on

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Table 2 Model error ($\varepsilon_i = y_i - y_{model}$) statistics for simple physiologically based model of forest-atmosphere CO_2 exchange fit to 9 years of data from the Howland AmeriFlux site

	Night-time					Daytime				
Year	Obs.	R^2	RMSE	MAE	MAWE	Obs.	R^2	RMSE	MAE	MAWE
1996	2499	0.49	2.23	1.20	0.59	4910	0.63	3.64	2.33	0.84
1997	2406	0.50	2.24	1.08	0.51	4993	0.65	3.57	2.27	0.81
1998	3051	0.46	2.47	1.24	0.60	6383	0.63	3.85	2.43	0.89
1999	3755	0.45	2.23	1.16	0.59	7035	0.62	3.73	2.32	0.88
2000	3214	0.51	2.13	1.11	0.58	6914	0.65	3.95	2.46	0.92
2001	3301	0.48	2.69	1.40	0.68	7374	0.65	3.79	2.38	0.87
2002	3214	0.55	2.06	1.14	0.54	6544	0.68	3.53	2.26	0.82
2003	2405	0.54	1.91	1.02	0.51	6523	0.70	3.53	2.28	0.83
2004	3149	0.51	1.89	1.00	0.51	7277	0.72	3.26	2.13	0.77

Note: Separate model parameter sets fit to each calendar year of data (see text for details). Night-time periods are defined as PPFD $<5\,\mu mol\,m^{-2}\,s^{-1}$. Obs. refers to the number of valid measurements used for fitting. RMSE is the root mean squared error. MAE is the mean absolute error. MAWE is the mean absolute weighted error, $(1/N)\sum_{i=1}^{N}[|\varepsilon_i|/\sigma(\delta_i)]$, where the weighting factor, $1/\sigma(\delta_i)$, is the estimated standard deviation of the measurement error (see Richardson & Hollinger, 2005, for more details). The maximum-likelihood paradigm used for model fitting minimizes MAWE.

Table 3 Model predictions ($g\,C\,m^{-2}\,y^{-1}$), aggregated to the annual time step, of a physiologically based model of forest-atmosphere CO_2 exchange, fit to data from the Howland AmeriFlux site

		Modeled			Tower		Modeled		
Year	Tower NEE	NEE	R_{eco}	P_{gross}	Night	Day	Night	Day	PnET GCE
1996	−158	-244 ± 11^{bc}	878 ± 18^{a}	-1119 ± 11^{a}	441	−598	367	−611	−1126
1997	−153	-252 ± 11^{bc}	924 ± 17^{a}	-1174 ± 11^{b}	471	−624	387	−639	−1187
1998	−131	-253 ± 10^{bc}	1063 ± 16^{c}	-1316 ± 10^{d}	541	−672	458	−711	−1207
1999	−178	-254 ± 10^{bc}	1078 ± 16^{c}	-1334 ± 9^{d}	523	−701	465	−719	−1260
2000	−271	-321 ± 10^{a}	1057 ± 17^{c}	-1378 ± 10^{e}	503	−774	447	−768	−1127
2001	−175	-295 ± 9^{a}	1071 ± 14^{c}	-1367 ± 9^{e}	540	−716	451	−746	−1216
2002	−154	-235 ± 10^{c}	1002 ± 15^{bc}	-1237 ± 9^{c}	481	−636	425	−659	−1106
2003	−221	-282 ± 10^{ab}	945 ± 17^{ab}	-1227 ± 10^{c}	452	−673	400	−683	−1112
2004	−254	-318 ± 9^{a}	927 ± 15^{a}	-1246 ± 9^{c}	451	−705	387	−706	−1129

Tower NEE column reports gap-filled eddy covariance measurements of net ecosystem exchange (NEE). The modeling approach, and the procedure for separating NEE into its component fluxes (R_{eco}, ecosystem respiration; P_{gross}, gross photosynthesis), is described in the text. Modeled NEE, R_{eco} and P_{gross} annual sums are reported as ± 1 SD, as determined by Monte Carlo simulation; in these three columns, values followed by the same letter indicate years for which 95% confidence intervals on the annual sum are overlapping. Night refers to periods with PPFD $<5\,\mu mol\,m^{-2}\,s^{-1}$. PnET GCE is gross carbon exchange predicted by the PnET model with a fixed canopy N concentration of 1.05%.

the highest and lowest annual sums are clearly non-overlapping, we can conclude that there is significant interannual variation in forest-atmosphere CO_2 exchange (Table 3), as expected. Interestingly, the interannual variation in *NEE* predicted by the fitted model (1 SD = $\pm 32\,g\,C\,m^{-2}\,yr^{-1}$; CV = 11%) is substantial, but is considerably less than the interannual variation in either modeled R_{eco} (1 SD = $\pm 77\,g\,C\,m^{-2}\,yr^{-1}$; CV = 8%) or P_{gross} (1 SD = $\pm 89\,g\,C\,m^{-2}\,yr^{-1}$; CV = 7%).

The Monte Carlo simulations confirm that some of the interannual variation in CO_2 exchange can be attributed to interannual variation in the biotic response to environmental forcing, as the parameter clouds for each year are generally distinct (nonoverlapping) from each other for both the of $\dot{R}_{eco}$ and $\dot{P}_{gross}$ model components (Fig. 4). For $\dot{R}_{eco}$ (Fig. 4a), the best-fit R_{ref} parameter ranges from 54.7 (2004) to 65.2 (2001) $\mu mol\,m^{-2}\,s^{-1}$, whereas T_0 ranges from 257.86 (1998) to 260.23 (1996) K; 95% confidence intervals on these

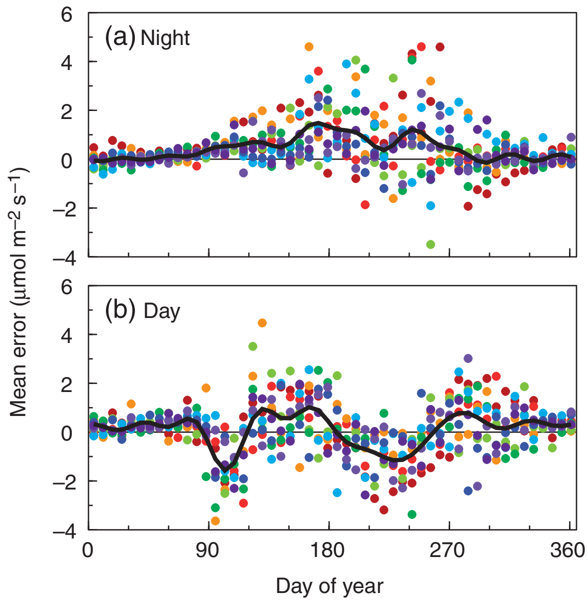

Fig. 2 Model bias (in terms of the mean error, $\bar{\varepsilon}_i = (1/N)\sum(y_i - y_{model})$, calculated by week) for a physiologically based model fit to 9 years of CO_2 flux data from the Howland Forest AmeriFlux site, during (a) night-time, defined as PPFD $<5\,\mu mol\,m^{-2}\,s^{-1}$, and (b) daytime periods. Colors denote different years of data; the smoothed line (black) is based on all 9 years of data.

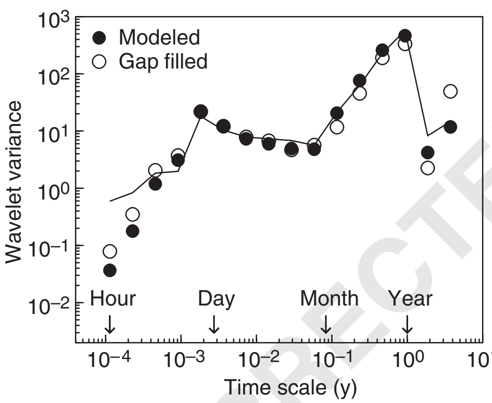

Fig. 3 Spectral analysis, based on wavelet transformation, of tower measurements (nongap-filled, black line), gap-filled (hollow circles), and modeled (filled circles) time series of CO_2 fluxes from the Howland Forest AmeriFlux site. At time scales from hours to years, the agreement between the modeled fluxes and measured fluxes is as good, if not better than, the agreement between gap-filled and measured fluxes.

parameter estimates are $\pm\,3.0$–$5.5\,\mu mol\,m^{-2}\,s^{-1}$ and $\pm\,0.42$–$0.59\,K$, respectively. In all years, R_{ref} and T_0 are strongly correlated with each other ($r \approx 0.85$). As a consequence of these parameter differences, the range of predicted rates of $\dot{R}_{eco}$ becomes progressively larger as T_{soil} increases. For example, at $T_{soil} = 20\,°C$, which is about the maximum observed at Howland, predicted $\dot{R}_{eco}$ with the year 2000 parameters is $8.8\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$, compared with $7.5\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ for the 1996 model parameters; this is a difference of roughly 18% (Fig. 4b).

For $\dot{P}_{gross}$ (Fig. 4c), the best-fit K_m parameter ranges from 368 (2000) to 571 (1997) $\mu mol\,m^{-2}\,s^{-1}$ PPFD, whereas A_{max} ranges from −36.15 (1996) to −40.24 (2001) $\mu mol\,CO_2\,m^{-2}\,s^{-1}$; 95% confidence intervals on these parameter estimates are $\pm\,21$–$49\,\mu mol\,m^{-2}\,s^{-1}$ PPFD and $\pm\,0.74$–$1.26\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$, respectively. In all years, K_m and A_{max} are strongly correlated with each other ($r \approx -0.80$). At $Q = 2000\,\mu mol\,m^{-2}\,s^{-1}$ PPFD, predicted $\dot{P}_{gross}$ for the year 2000 parameters is $-31.8\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$, compared with $-28.1\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ for the year 1996 parameters; this is a difference of about 13% (Fig. 4d). It is important to remember that $\dot{P}_{gross}$ reflects a maximum potential rate of gross uptake under ideal environmental conditions; when the various environmental scalars are taken into account (Eqn (2), Table 1), the maximum P_{gross} predicted by the fitted model ranges from $-21.2\,g\,C\,m^{-2}\,yr^{-1}$ (1996) to $-23.8\,g\,C\,m^{-2}\,y^{-1}$ (2001).

Partitioning the variance in modeled fluxes

By crossing each 'driver year' with each 'parameter year,' we generated environmental drivers × biotic response scenarios for forest NEE that vary at the annual time step by over $100\,g\,C\,m^{-2}\,yr^{-1}$ in their predictions. For example, with year 2004 model parameters, NEE ranges between $-227\,g\,C\,m^{-2}\,yr^{-1}$ (1997 environmental drivers) and $-337\,g\,C\,m^{-2}\,yr^{-1}$ (2001 environmental drivers) (Fig. 5a). Similarly, with year 2004 environmental drivers, NEE ranges between $-247\,g\,C\,m^{-2}\,yr^{-1}$ (1999 model parameters) and $-352\,g\,C\,m^{-2}\,yr^{-1}$ (2000 model parameters) (Fig. 5b).

Analysis of variance conducted on the 9 × 9 matrix of crossed model predictions aggregated to different timescales indicates that as the period of integration is lengthened, the percentage of total variance accounted for by variation in environmental drivers is reduced, and the percentage of total variance accounted for by variation in model parameters (i.e. the biotic response to environmental forcing) is increased (Fig. 6). One interpretation of this result is that although the weather can be highly variable over days and weeks, this variability tends to even out across months and seasons. With this averaging, the interannual variation in model parameters becomes progressively more important. Thus, environmental variation is directly responsible for short- but not long-term variation in CO_2 exchange. Our analysis suggests that NEE is most sensitive to variation in environmental drivers (and least sensitive

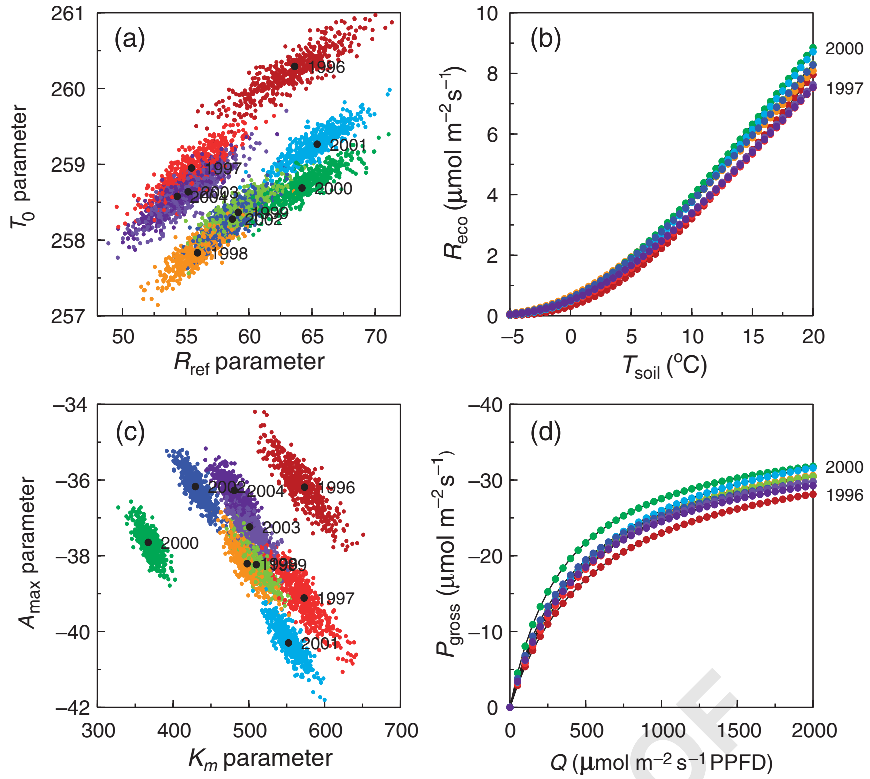

Fig. 4 Model parameters (a, c) and model predictions (b, d) for potential ecosystem respiration ($\dot{R}_{eco}$; (a, b) and gross photosynthesis ($\dot{P}_{gross}$; (c, d), based on 9 years of CO_2 fluxes measured at the Howland AmeriFlux site. Fluxes are 'potential' in that they represent expected fluxes under optimal environmental conditions; environmental scalars (Table 1) reduce potential to actual fluxes under suboptimal conditions. Separate model parameters were fit for each calendar year; clouds of data points illustrate parameter uncertainty, as determined by Monte Carlo simulation ($n = 500/\mathrm{yr}^{-1}$).

to variation in the model parameters), whereas R_{eco} is least sensitive to variation in environmental drivers (and most sensitive to variation in the model parameters). Even at the shortest timescale, variation in environmental drivers accounts for only 60% of the total variation in modeled R_{eco}, whereas the figure is >95% for both NEE and P_{gross} (Fig. 6). This is probably because there tends to be less day-to-day variation in soil temperature compared with either air temperature or PPFD, and so the modeled R_{eco} tends to be relatively stable over time for any given parameter set. In comparison, modeled P_{gross} varies dramatically depending on whether it is a sunny or cloudy day. The 'driver year' × 'parameter year' interaction, 'parameter year' × 'model iteration' interaction, and ANOVA model error term together account for <7% of the total variation in NEE, regardless of the period of integration.

Based on ANOVA of the crossed model annual sums for R_{eco}, P_{gross}, and NEE, we determined the magnitude of the 'driver year' and 'parameter year' effects for each year (Fig. 7). The sign convention is that a positive effect for R_{eco} means increased respiratory losses (more positive R_{eco}), whereas a negative effect for P_{gross} indicates increased canopy uptake (more negative P_{gross}). Relative to the average crossed model prediction, parameter year effects for R_{eco} (Fig. 7a) range from $-100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (1996) to $+94\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2000). Thus, for a climatically 'typical' year, ecosystem respiration could vary by close to $200\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ depending on whether the forest is functioning as it had in 1996 or 2000. Driver year effects for R_{eco} are much smaller, $\pm 40\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ or less, reflecting the result that at the annual time step, R_{eco} is more influenced by variation in model parameters (83%) than the direct effect of variation in environmental drivers (12%) (Fig. 6).

For crossed model annual P_{gross} (Fig. 7b), parameter year effects range from $-151\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2000) to $+123\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (1996), and are more or less comparable in magnitude to those for R_{eco}. By comparison, P_{gross} driver year effects range from $-74\,\mathrm{C\,m^{-2}\,yr^{-1}}$ (2001) to $+67\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (1999) and are roughly 50% larger than those for R_{eco}, reflecting the greater sensitivity of P_{gross} to variation in environmental drivers (Fig. 6). Parameter year effects for P_{gross} are negatively correlated with those for R_{eco} ($r = -0.85$, $P \leq 0.01$). Similarly, driver year effects for P_{gross} are

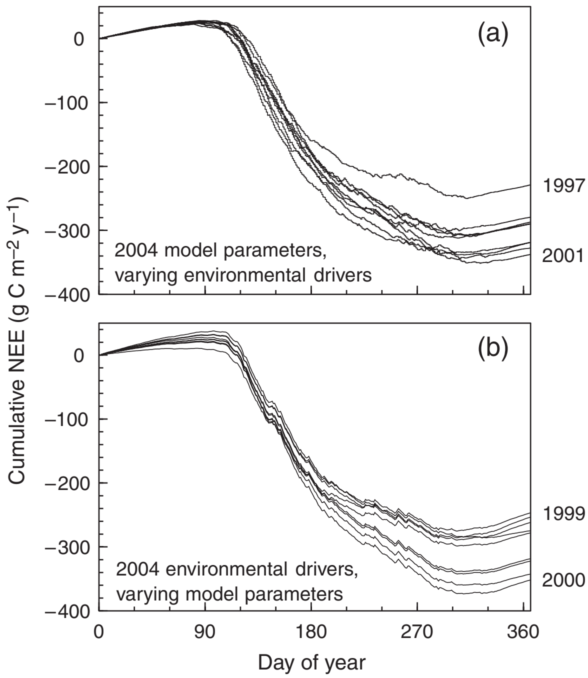

Fig. 5 Modeled cumulative net ecosystem exchange (NEE) at the Howland AmeriFlux site. In (a), the model was run using year 2004 model parameters against 9 years (1996–2004) of environmental driver data. In (b), the same model was run using 9 years (1996–2004) of model parameters against the year 2004 environmental driver data. In both cases, the extreme model prediction years are identified.

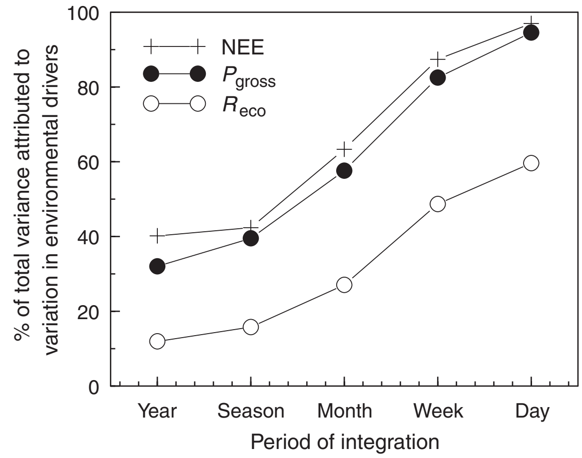

Fig. 6 Role of interannual variation in environmental drivers in determining the modeled ecosystem respiration (R_{eco}), gross photosynthesis (P_{gross}), and net ecosystem exchange (NEE), in relation to the time-scale at which these fluxes are integrated. The variation in model predictions was partitioned to 'driver year' and 'parameter year' effects using a sums-of-squares approach, as described in text.

negatively correlated with those for R_{eco} ($r = -0.78$, $P = 0.01$). These correlations obviously contribute to the very strong negative correlation between modeled P_{gross} and R_{eco} ($r = -0.93$, $P < 0.001$).

Compared with either P_{gross} or R_{eco} variation in environmental drivers (40%) and variation in model parameters (55%) contribute more evenly to the total variation in modeled NEE (Figs 6 and 7c). The magnitudes of the driver year and parameter year effects for annual NEE indicate that this flux is less sensitive (smaller effect sums-of-squares) to variation in environmental drivers than P_{gross}, more sensitive to variation in environmental drivers than R_{eco}, and less sensitive to variation in model parameters than either of the component fluxes. Related to this (as noted above), the interannual variation in NEE is less than half that of either R_{eco} or P_{gross}. Driver year effects for annual P_{gross} (but not R_{eco}) and NEE are positively correlated ($r = 0.87$, $P \leq 0.01$), indicating that a climate-driven increase in P_{gross} is also associated with a climate-driven increase in NEE. There is a weak negative correlation ($r = -0.59$, $P = 0.10$) between driver year and parameter year effects for NEE, suggesting that interannual variation in the biotic response to environmental forcing tends to offset interannual variation in the environmental drivers.

PnET analysis

The PnET-DAY ecosystem model (Aber *et al*., 1996), run for Howland with a fixed foliar N concentration of 1.05%, predicts mean annual gross carbon exchange (GCE, $1163 \pm 55\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) that is in reasonable agreement with the 9-year mean P_{gross} of the fitted model ($1266 \pm 88\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) (Table 3). Note that the reported standard deviations indicate that the PnET model predicts roughly 40% less interannual variation than the fitted model. The linear correlation between PnET and fitted model annual sums is weak ($r = 0.45$, $P = 0.22$), reflecting the fact that the difference between PnET and fitted model predictions is highly variable at the annual time step (mean difference of $103 \pm 80\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$).

PnET predicts that an increase of 0.01% in foliar N, from 1.05% to 1.06%, is associated with an increase in annual GCE of $\approx 9\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Thus, by varying foliar N at the annual time step, from a low of 1.04% in 1996 to a high of 1.34% in 2000, the interannual variation in P_{gross} can be replicated by the PnET model. The required foliar N concentrations are weakly correlated ($r = -0.62$, $P = 0.07$) with the predicted potential P_{gross} at $Q = 2000\,\mathrm{\mu mol\,m^{-2}\,s^{-1}}$. Because foliar N at Howland has been measured only sporadically, we cannot conclude that variation in foliar N was the principal source of interannual variation in gross photosynthesis. We

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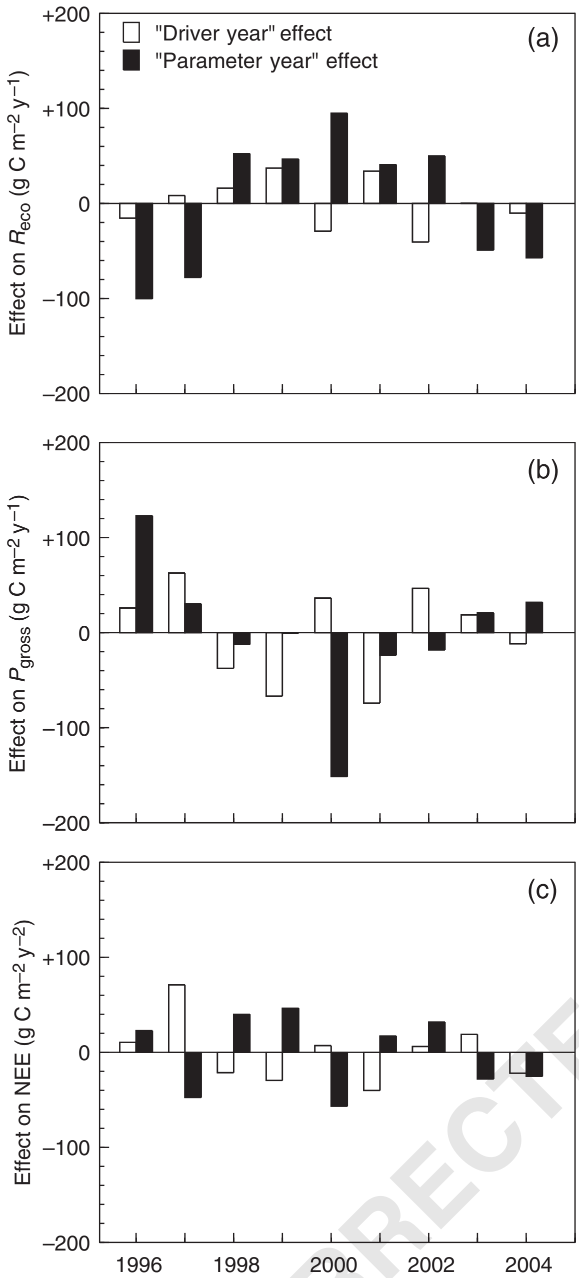

Fig. 7 Effects of interannual variation in environmental drivers (‘driver year’ effects) and model parameters (‘parameter year’ effects) on modeled CO_2 fluxes at the annual time step: (a) ecosystem respiration (R_{eco}), (b) gross photosynthesis (P_{gross}) and (c) net ecosystem exchange (NEE). The sign convention is that a positive effect for R_{eco} increases respiratory losses (more positive R_{eco}), whereas a negative effect for P_{gross} increases canopy uptake (more negative P_{gross}).

note that the range of required foliar N values is consistent with that which has been documented (across sites) for the dominant conifer species at Howland (e.g. Pardo *et al*., 2005), and foliar N of red pine has been seen to vary (across years) between 0.98% and 1.29% at the Harvard Forest (Magill *et al*., 2004). However, the required 30% variation in foliar N at Howland would seem to be unlikely given the multiyear lifespan of the dominant conifers, red spruce, and hemlock. Therefore, while interannual variation in foliar N may contribute to the interannual variation in P_{gross}, there are presumably additional factors involved.

Discussion

Limitations of the model

The simple model used in the present study is far from perfect. Parameterized as it is (for a particular site and particular year) we cannot expect it to perform well at other sites, or if run into the future. A more complex model might perform better in these more generalized applications, although recent work suggests that modeling interannual variation in forest ecosystem C exchange remains a major challenge (Hanson *et al*., 2004, Siqueira *et al*., 2006).

Obvious deficiencies of our model include the fact that model parameters are fixed across the calendar year, despite the fact that both key ecosystem state variables (e.g. leaf area index for P_{gross}) and physiological attributes (e.g. leaf-level A_{max}) can vary seasonally (Hollinger *et al*., 2004; Gove & Hollinger, 2005). Model predictions show some seasonal biases (Fig. 2). Because the data are arbitrarily broken into calendar years, there is a discontinuity in model parameters at the December 31–January 1 boundary. For P_{gross}, the model treats the canopy as a ‘big leaf,’ rather than a multilayered canopy, and does not consider how variation in the ratio of direct : diffuse solar radiation may influence photosynthetic light use efficiency (e.g. Hollinger *et al*., 1994). The model does not explicitly incorporate phenology (Richardson *et al*., 2006b) or stomatal control (Mäkelä *et al*., 1996) components; instead, the environmental scalars for T_{soil} and *VPD* effectively assume these roles. For R_{eco}, we do not distinguish between aboveground, root respiration, and heterotrophic soil respiration, although the contribution of these to R_{eco} may vary seasonally. Soil temperature is assumed to represent the thermal state of the ecosystem as a whole, despite the fact that aboveground components account for $\approx 40\%$ of R_{eco} (Davidson *et al*., 2006). The model has only a single soil carbon pool, which is fixed in size (essentially the R_{ref} parameter) across the entire year. We do not account for seasonally varying litter inputs or ‘hidden’ ecosystem C pools (Hanson *et al*., 2003) such as carbohydrate reserves or the forest floor, and feedbacks between respiration and production are similarly ignored.

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These caveats aside, it is clear that the model does a reasonable job reproducing the measured fluxes across a range of time scales (Table 2, Figs 2 and 3), and it is only through a modeling approach that it is possible to partition the interannual variation into environmental driver and biotic response effects (Fig. 5). Because of equifinality issues (Hollinger & Richardson, 2005), there are strong arguments to be made for keeping models as simple as possible, which is why we chose the model structure used here, with 11 parameters fit globally to all years of data, and just four parameters varying among years.

Direct and indirect effects of climate

Results of the present study confirm the hypothesis that interannual variation in forest-atmosphere CO_2 fluxes can be attributed both to variation in environmental drivers and variation in the biotic response to environmental forcing (Fig. 5). Furthermore, it appears that the strength of these two effects depends on the period of integration (variation in the biotic response becomes progressively more important as the period of integration is lengthened), and varies among R_{eco}, P_{gross}, and NEE (Fig. 6). One way to interpret this result is that over the short term, the ecosystem characteristics represented by the model parameters in P_{gross} and R_{eco} are essentially fixed. However, these processes (and hence parameters) tend to vary over longer time periods (e.g. Gove & Hollinger, 2005). A consequence of this is that in the short-term (hours and days), CO_2 fluxes can be reasonably well characterized using a fixed set of model parameters, as most of the total variance is attributable to variation in key environmental drivers (a sunny day vs. a cloudy day). However, at longer time scales, our ability to accurately model CO_2 fluxes is clearly constrained by our understanding of how (and why) the biotic response to environmental forcing (i.e. the model parameters) might vary over time.

Numerous connections between environmental or climatic conditions and interannual variation in NEE have been previously observed. Solar radiation and temperature effectively drive photosynthesis and respiration; these processes are modulated by secondary factors, such as soil moisture. Other studies have noted the importance of weather anomalies at certain key points in the growing season (Goulden *et al*., 1996a, 1998; Barr *et al*., 2002), and we have seen such effects at Howland (Hollinger *et al*., 2004). There is a strong connection between early spring temperatures and the date of leaf emergence; an earlier spring flush can lengthen the growing season and increase the annual carbon sequestration (Goulden *et al*., 1996a; Chen *et al*., 1999; Hollinger *et al*., 1999; Aubinet *et al*., 2002; Carrara *et al*., 2003). In the subboreal evergreen forest at Howland, warm April temperatures are associated with enhanced CO_2 uptake (Hollinger *et al*., 2004). However, at other sites, the effect of warm springtime temperatures on NEE may be uncertain, because stimulation of soil respiration can offset or possibly negate the increase in photosynthetic uptake (Chen *et al*., 1999; Barr *et al*., 2002; Carrara *et al*., 2003). Interannual variation in precipitation is critical in some ecosystems, especially when the amount of leaf area produced is controlled by moisture availability (Flanagan *et al*., 2002; Schwarz *et al*., 2004), and El Niño-La Niña cycle differences in precipitation and temperature have been linked to differences in annual NEE (Goldstein *et al*., 2000; Griffis *et al*., 2003; Morgenstern *et al*., 2004).

Braswell *et al*. (1997) suggested that the lagged (and thus indirect) effects of climatic anomalies on CO_2 fluxes may be more important than (and even opposite in sign to) the initial direct effects (see also Barford *et al*., 2001). Indirect effects of climate on ecosystem processes may operate at different time scales: physiological acclimation is presumably a relatively rapid process (days to weeks), whereas biogeochemical effects (e.g. altered N cycling rates) may occur over months or years. These indirect effects can be difficult to observe (or establish a cause–effect relationship), except in dramatic instances. For example, really extreme events, such as heat waves, may cause step changes in ecosystem physiology that have long-lasting effects on CO_2 fluxes (Goldstein *et al*., 2000). Although we have shown here how interannual differences in the biotic response to environmental forcing can be quantified (e.g. Figs 4, 6 and 7), explaining the underlying cause of these differences is more problematic and requires a more comprehensive model and additional data. Neither the model parameters themselves, nor aggregate 'parameter year' effects, correlated strongly with current or lagged (either annual or monthly) weather anomalies, precluding a direct attribution of the biotic response to a direct or indirect effect of climatic variation. It is probable that these connections are complex, likely nonlinear, and certainly not unique (i.e. more than one type of climate anomaly could trigger changes in A_{max}). For this type of analysis to be successful, it would probably be necessary to fit model parameters at a finer temporal resolution (perhaps using state-dependent parameter models), because direct and indirect (lagged) effects of climatic anomalies are likely to be obscured in the course of annual aggregation.

PnET modeling indicated that variation in foliar N is a possible, if somewhat unlikely, explanation for the observed interannual variation in P_{gross}. Unfortunately, we do not have field data to validate this hypothesis. We suggest that along with continued tower-based CO_2

flux measurements, regular measurement of some key biotic factors could contribute to a deeper understanding of the underlying causes of interannual variation in R_{eco} and P_{gross}, and hence NEE. These include changes in soil C pools (especially litter inputs), N cycling rates, foliar N, maximum leaf area index, soil respiration, leaf-level gas exchange, and canopy phenology.

P_{gross} *or* R_{eco} *as the source of variation in NEE?*

The interannual variation in R_{eco}, P_{gross} or NEE at a given site is considerably smaller than that which has been observed across sites and biomes (Valentini *et al*., 2000; Baldocchi *et al*., 2001; Law *et al*., 2002). Under none of the different crossed model scenarios, for example, was it possible for the Howland site to turn from a carbon sink into a source. However, analysis presented here suggests that both P_{gross} and R_{eco} show comparable ranges of interannual variation, and the variation in these component fluxes is considerably larger than the variation in NEE (Savage & Davidson, 2001; but cf. Raich *et al*., 2002). This contrasts with what has previously been reported in other systems. For example, Goulden *et al*. (1998) found that gross production was relatively stable across years, whereas it was the interannual variation in R_{eco} that effectively determined whether the forest was a carbon source or sink. Morgenstern *et al*. (2004) reached a similar conclusion studying a seasonally dry temperate rain forest. Although Barr *et al*. (2002) suggested that a corollary of the results of Valentini *et al*. (2000) is that climate effects on *NEE* occur via R_{eco} rather than P_{gross}, their data indicate the exact opposite: in a deciduous boreal forest and a deciduous temperate forest, P_{gross} was found to be more sensitive than R_{eco} to interannual climatic variation. Thus, Barr *et al*. (2002) concluded that variation in P_{gross} largely controls the interannual variation in NEE (see also Griffis *et al*., 2003).

Our fitted model results suggest an interesting negative correlation between annual P_{gross} and R_{eco} ($r = -0.93$, $P < 0.001$). This correlation may be a spurious artifact of the way in which P_{gross} is calculated (i.e. as $F_{CO_2} - R_{eco}$, Eqn (5)). Alternatively, it may represent a genuine physiological relationship. For example, Janssens *et al*. (2001) demonstrated that cross-site differences in soil respiration are better explained by differences in productivity than differences in annual temperature. Two mechanisms would explain this pattern. First, root respiration is probably constrained by the amount of photosynthate allocated to roots, which will depend on productivity. Second, heterotrophic respiration is probably constrained by the availability of readily decomposed substrate (e.g. recently senesced leaves and fine roots), the abundance of which is also directly linked to productivity (Janssens *et al*., 2001). The opposite is also possible, namely that variation in R_{eco} may lead to a subsequent variation in photosynthesis. For example, interannual variation in N mineralization rates could drive variation in foliar N content and hence photosynthetic capacity at the canopy level (Aber & Federer, 1992; Aber *et al*., 1996). Regardless of the cause of the correlation, it promotes homeostasis of NEE: offsetting variation in R_{eco} and P_{gross} results in less interannual variation in NEE than is seen for either R_{eco} or P_{gross} alone. In this regard, Howland results differ sharply from those described above, where either R_{eco} (Goulden *et al*., 1998; Morgenstern *et al*., 2004) or P_{gross} (Barr *et al*., 2002) was found to control the interannual variation in NEE.

Conclusion

Interannual variation in ecosystem metabolism is known to contribute to variation in the annual growth rate of atmospheric CO_2 (Houghton, 2000). Results from our modeling analysis suggest that interannual variation in NEE at the spruce-dominated Howland Forest can be attributed not only to the direct effect of variation in environmental drivers, but also to variation in the biotic response (basal/maximum rates and driver sensitivities) of R_{eco} and P_{gross} to the environmental forcing. For both of these component fluxes, the direct effect of variation in environmental drivers accounts for less than one-third of the variance in the modeled fluxes at the annual time step; for NEE, the figure is still only 40% (Fig. 6). Related to this, Hui *et al*. (2003) used an approach based on weekly means of daily values to partition the overall variation in pine forest NEE and R_{eco} to four factors (interannual functional change, interannual climatic variability, seasonal climatic variation and random error). In that study, 'functional change' was found to account for $\approx$10% of the observed variation. The conclusion from both Hui *et al*. (2003) and the present study is that prognostic models that fail to take the interannual variation in ecosystem function into account will have little chance of accurately predicting CO_2 fluxes at time scales of seasons to years. Better predictions of future atmospheric CO_2 levels will require improved understanding of the underlying causes of interannual variation in the biotic response to environmental forcing.

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