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On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm

MARKUS REICHSTEIN*†, EVA FALGE‡, DENNIS BALDOCCHI§, DARIO PAPALE*, MARC AUBINET¶, PAUL BERBIGIER‖, CHRISTIAN BERNHOFER**, NINA BUCHMANN††‡‡, TAGIR GILMANOV§§, ANDRÉ GRANIER¶¶, THOMAS GRÜNWALD**, KATKA HAVRÁNKOVÁ‖‖, HANNU ILVESNIEMI***, DALIBOR JANOUS‖‖, ALEXANDER KNOHL††§, TUOMAS LAURILA†††, ANNALEA LOHILA†††, DENIS LOUSTAU‡‡‡, GIORGIO MATTEUCCI§§§, TILDEN MEYERS¶¶¶, FRANCO MIGLIETTA‖‖‖, JEAN-MARC OURCIVAL****, JUKKA PUMPANEN††††, SERGE RAMBAL****, EYAL ROTENBERG‡‡‡‡, MARIA SANZ§§§§, JOHN TENHUNEN¶¶¶¶, GÜNTHER SEUFERT§§§, FRANCESCO VACCARI‖‖‖, TIMO VESALA‖‖‖‖, DAN YAKIR‡‡‡‡ and RICCARDO VALENTINI*

**Department of Forest Science and Environment, University of Tuscia, 01100 Viterbo, Italy, †Potsdam Institute for Climate Impact Research, Telgrafenberg C4, 14473 Potsdam, Germany, ‡Department of Plant Ecology, University of Bayreuth, D-95440 Bayreuth, Germany, §Department of Environmental Science, Policy and Management, Ecosystem Science Division, University of California, 151 Hilgard Hall #3110, Berkeley, CA 94720-3110, USA, ¶Unité de Physique, Faculté des Sciences Agronomiques de Gembloux, B-50 30 Gembloux, Belgium, ‖INRA–EPHYSE, BP 81, F33883 Villenave d'Ornon Cedex, France, **Technische Universität Dresden, IHM-Meteorologie, Pienner Strasse 9, 01737 Tharandt, Germany, ††Max Planck Institute for Biogeochemistry, PO Box 100164, 07701 Jena, Germany, ‡‡Institute of Plant Sciences, ETH Zürich, Universitätsstrasse 2, 8092 Zürich, Switzerland, §§Department of Biology/Microbiology AgH 310, Box 2207B South Dakota State University Brookings, SD 57007-2142, USA, ¶¶INRA, Unité d'Ecophysiologie Forestière, F-54280 Champenoux, France, ‖‖Laboratory of Ecological Physiology of Forest Trees, Institute of Landscape Ecology, Academy of Sciences of the Czech Republic, Porici 3B, Brno 603 00, Czech Republic, ***Finnish Forest Research Institute, Jokiniemenkuja 1, FIN-01300 Vantaa, Finland, †††Finnish Meteorological Institute, PO Box 503, FIN-00101 Helsinki, Finland, ‡‡‡INRA-Ecophysiologie, Domaine de l'Hermitage-Pierroton, 69, route d'Arcachon, 33610 Cestas, France, §§§JRC, Institute for Environment and Sustainability, Via Enrico Fermi, T.P. 051, 21020 Ispra (VA), Italy, ¶¶¶NOAA/Atmospheric Turbulence and Diffusion, PO Box 2456 Oak Ridge, TN 37830, USA, ‖‖‖IBIMET, P.le delle Cascine, 18, 50144 Firenze, Italy, ****DREAM Unit, Centre d'Ecologie Fonctionelle et Evolutive, CNRS, 1919 route de Mende, Montpellier, France, ††††Department of Forest Ecology, PO Box 27, University of Helsinki, FIN-00014 Helsinki, Finland, ‡‡‡‡Department of Environmental Sciences and Energy Research, Weizmann Institute of Science, PO Box 26, Rehovot 76100, Israel, §§§§CEAM, Parque Tecnológico, c/Charles H. Darwin 14, 46980 Paterna (Valencia), Spain, ¶¶¶¶Department of Plant Ecology, University of Bayreuth, D-95440 Bayreuth, Germany, ‖‖‖‖Department of Physical Sciences, University of Helsinki, FIN-00014 Helsinki, Finland*

Abstract

This paper discusses the advantages and disadvantages of the different methods that separate net ecosystem exchange (NEE) into its major components, gross ecosystem carbon uptake (GEP) and ecosystem respiration (R_{eco}). In particular, we analyse the effect of the extrapolation of night-time values of ecosystem respiration into the daytime; this is usually done with a temperature response function that is derived from long-term data sets. For this analysis, we used 16 one-year-long data sets of carbon dioxide exchange measurements from European and US-American eddy covariance networks. These sites span from the boreal to Mediterranean climates, and include deciduous and evergreen forest, scrubland and crop ecosystems.

We show that the temperature sensitivity of R_{eco}, derived from long-term (annual) data sets, does not reflect the short-term temperature sensitivity that is effective when extrapolating from night- to daytime. Specifically, in summer active ecosystems the long-

Correspondence: Markus Reichstein, Department of Forest Science and Environment, University of Tuscia, 01100 Viterbo, Italy, fax +39 0761 357389, e-mail: reichstein@unitus.it

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term temperature sensitivity exceeds the short-term sensitivity. Thus, in those ecosystems, the application of a long-term temperature sensitivity to the extrapolation of respiration from night to day leads to a systematic overestimation of ecosystem respiration from half-hourly to annual time-scales, which can reach >25% for an annual budget and which consequently affects estimates of GEP. Conversely, in summer passive (Mediterranean) ecosystems, the long-term temperature sensitivity is lower than the short-term temperature sensitivity resulting in underestimation of annual sums of respiration.

We introduce a new generic algorithm that derives a short-term temperature sensitivity of R_{eco} from eddy covariance data that applies this to the extrapolation from night- to daytime, and that further performs a filling of data gaps that exploits both, the covariance between fluxes and meteorological drivers and the temporal structure of the fluxes. While this algorithm should give less biased estimates of GEP and R_{eco}, we discuss the remaining biases and recommend that eddy covariance measurements are still backed by ancillary flux measurements that can reduce the uncertainties inherent in the eddy covariance data.

Key words: carbon balance, computational methods, ecosystem respiration, eddy covariance, gross carbon uptake, temperature sensitivity of respiration

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Introduction

The eddy covariance method has become the main method for sampling ecosystem carbon, water and energy fluxes from hourly to interannual time scales (Baldocchi *et al.*, 2001a) and now serves as a backbone for bottom-up estimates of continental carbon balance components (Papale & Valentini, 2002; Reichstein *et al.*, 2003a). Furthermore, eddy covariance data is increasingly used for ecosystem model calibration and validation (e.g. Baldocchi, 1997; Law *et al.*, 2001b; Hanan *et al.*, 2002; Reichstein *et al.*, 2002b, 2003b; Hanson *et al.*, 2004). In the context of the latter, it is useful to separate or partition the observed net ecosystem exchange (NEE) through a 'flux-partitioning algorithm' into gross ecosystem production (GEP) and ecosystem respiration (R_{eco}), since this provides a better diagnostic about which processes (assimilatory or respiratory) are misrepresented in the model (Falge *et al.*, 2002a; Reichstein *et al.*, 2002b). For instance, if a model overestimates both R_{eco} and GEP by a similar amount, this model error would not be detected via comparison of modelled and observed NEE that is the difference between R_{eco} and GEP. Furthermore, partitioning of the NEE flux is needed to better understand how interannual and between-site variability of NEE is caused (Valentini *et al.*, 2000). Apart from the flux-partitioning, it is necessary to fill data gaps that occur under unfavourable meteorological conditions and during instrument failure ('gap-filling') for estimating long-term budgets. While gap-filling essentially is an interpolation of data and has received a lot of systematic attention (Falge *et al.*, 2001a, b; Hui *et al.*, 2003), most flux-partitioning methods are an extrapolation of data from night- to daytime and have only been compared in a less systematic manner (Falge *et al.*, 2002b). In particular, one problem has not received the necessary attention: for the extrapolation of night-time ecosystem respiration data, usually a temperature dependency is used that is derived from an annual data set. However, it is expected that the seasonal apparent temperature sensitivity does not reflect the actual short-term (hour-to-hour) temperature sensitivity, since the former is confounded by other factors that covary with temperature, e.g. soil moisture, growth effects, rain pulses and decomposition dynamics (e.g. Davidson *et al.*, 1998; Reichstein *et al.*, 2002a; Xu & Baldocchi, 2004). For instance, in a summer-active ecosystem like a summer-green deciduous forest or a summer crop ecosystem the apparent seasonal temperature sensitivity should be higher than the short-term temperature sensitivity, since the high respiration fluxes in summer are caused not only by high temperature but also by higher overall activity (leaves and fine-roots are present and active, growth is occurring, etc.). The opposite would be hypothesized for (relative) summer-passive (e.g. Mediterranean), ecosystems. Any systematic error in the temperature sensitivity introduces a systematic error in the daytime estimate of R_{eco} and consequently GEP, and hence in annual sums of these quantities.

Thus, the objective of this paper is to review and discuss existing flux-partitioning algorithms, and then to analyse the effect of short-term vs. long-term temperature sensitivity on the estimation of daytime R_{eco} and thus GEP.

Short review of statistical methods for separation of NEE into assimilation and ecosystem respiration

The final goal of any eddy covariance NEE flux partitioning algorithm is to estimate R_{eco} and gross carbon uptake (GEP) from the NEE according to the definition equation NEE = R_{eco}–GEP. These flux-partitioning algorithms can be classified in those that use only (filtered) night-time data for the estimation of ecosystem respiration and those that exploit daytime data or both day- and night-time data using light-response curves (Table 1). These two general approaches have been compared by Falge *et al*. (2002a), resulting in generally good agreement between the two methods, except in ecosystems where large soil carbon pools exist. Under those conditions, the light-curves derived from daytime data may not well represent respiratory processes during night-time. Moreover, regressions of light-response curves sometimes tend to yield unstable parameters (E. Falge, unpublished). While the standard light-response curve method only allows the estimation of the daily average respiration without estimation of a temperature-dependent diurnal course (Gilmanov *et al*., 2003), have developed a regression model, where GEP and R_{eco} are described in one equation, and where R_{eco} is explicitly dependent on air or soil temperature. Once regression parameters are fitted, GEP and R_{eco} can be computed separately on a half-hourly time step. While this is an elegant approach, it suffers from three problems:

1. The equifinality of the model (i.e. similar model predictions (of NEE)), can be obtained as long as R_{eco} and GEP are tweaked in opposite directions. In particular, the estimation of the temperature response of R_{eco} is confounded by the response of GEP to VPD, which can lead to a bias in the estimation of R_{eco}. Clearly, if an afternoon drop of NEE can be caused by a VPD related drop of GEP or by a temperature related increase in R_{eco}. If a regression model only ascribes the effect of R_{eco} to the drop of NEE, this consequently leads to an overestimation of R_{eco}.
2. With this method, both R_{eco} and GEP are modelled and based on certain assumptions (e.g. hyperbolic light response of GEP). If the flux-partitioned data is then used to evaluate models, one is essentially comparing two models, which can lead to circular arguments (e.g. a model with the same hyperbolic assumption will be more likely validated than other models).
3. CO_2 fluxes near sunrise and sunset are very transient, involve nonstationarity problems and often storage changes occur.

The VPD specific problem in (1) can be tackled by including a VPD response of GEP to the regression model, but only at the cost of an even more strongly over-parameterized model. Problem (2) is quite fundamental and virtually excludes using this method when the aim of the flux-partitioning is model evaluation. Problem (3) is handled by accounting for storage even if it is only measured imperfectly (e.g. if storage and turbulent fluxes have different source areas).

These weaknesses of this algorithm maybe why in most studies the flux-partitioning starts with the estimation of R_{eco} from night-time data (Hollinger *et al*., 1998; Law *et al*., 1999; Janssens *et al*., 2001; Reichstein *et al*., 2002a, b; Falge *et al*., 2002b; Rambal *et al*., 2003). As shown in Table 1, these methods mainly differ in the way how R_{eco} is modelled (apart from the diversity of methods to determine the valid night-time fluxes, which is not the scope of this paper; cf. Foken & Wichura, 1996; Aubinet *et al*., 2000). The simplest algorithm represents R_{eco} as one single function of temperature for the whole year, which is acceptable only in a few – if in any – ecosystems, since usually other factors influence the rate of respiration at a reference temperature (R_{ref}). This effect of other factors has either been incorporated explicitly by assimilation of the relevant factors into the function or implicitly by introducing temporally varying functions of temperature, where R_{ref} can vary with time. In all cases, however, the temperature sensitivity of R_{eco} has been kept constant over the year and has been derived from relatively long data series that potentially introduce confounding seasonal effects into the temperature response of R_{eco}. However, the estimate of a correct temperature sensitivity of R_{eco} is crucial since R_{eco} is extrapolated from night- to daytime and any under- or overestimation of the temperature sensitivity will lead to an over- or underestimation of daytime R_{eco}, respectively (cf. Fig. 1). In the current study, we develop a flux-partitioning algorithm that first estimates the temperature sensitivity from short-term periods, and then applies this short-term temperature sensitivity to extrapolate the ecosystem respiration from night- to daytime. In this case, one can introduce seasonally varying temperature sensitivity or apply site-specific constant temperature sensitivity (Table 1).

Methods

Eddy covariance data

The starting point of this analysis are half-hourly eddy covariance CO_2 fluxes from sites and vegetation types listed in Table 2, mainly European boreal to Mediterranean forest, shrubland and crop sites. To allow for a

Table 1 Classification of currently available statistical flux-partitioning algorithms of eddy covariance net CO_2 flux data

Algorithm	Advantages	Disadvantages
(A) Using only night-time data	Flux data is directly used, i.e. direct estimation of R_{eco}	Filtering of bad night-time data necessary, extrapolation to daytime necessary; near and above the polar circle few or no night-time data in summer, respectively
1. Representation of R_{eco} by one single function of temperature (Hollinger *et al.*, 1994)	Simplicity	Only applicable where no other factors than temperature influence R_{eco} significantly, not generic
2. Representation of R_{eco} by one single function of temperature and other factors (Reichstein *et al.*, 2002a; Rambal *et al.*, 2003)	Simplicity, not only temperature as factor considered; allows for seasonally varying temperature sensitivity	Results in selection of site specific factors that determine R_{eco}, not generic
3. Representation of R_{eco} by temporally varying functions of temperature (R_{ref} varying, one single temperature sensitivity derived from annual data set (Falge *et al.*, 2002a; Law *et al.*, 2002)	Accounts for temporally varying respiration rates at reference temperature, caused by any factor	Long-term temperature sensitivity from annual data set may not reflect short-term response, introduction of systematic error when extrapolating to daytime
4. Representation of R_{eco} by temporally varying functions of temperature (R_{ref}varying, one single temperature sensitivity derived from short-term data set (this study)	Accounts for temporally varying respiration rates at reference temperature, caused by any factor, 'correct' temperature response avoids introduction of systematic error when extrapolating to daytime	Seasonally varying temperature sensitivity not accounted for
5. Representation of R_{eco} by temporally varying functions of temperature (both R_{ref} and temperature sensitivity varying) (this study)	Accounts for temporally varying respiration rates at reference temperature, caused by any factor, seasonally varying temperature sensitivity is accounted for	Often noisiness of eddy covariance data does not allow derivation of temperature sensitivity for large periods of the year with statistical significance, i.e. limited practical applicability
(B) R_{eco} derived from light-response curves (including daytime data)	Reduces influence of night-time data, may capture the effect of photo-inhibition of mitochondrial leaf respiration, if this exists (see Discussion)	Depends on specific light-response curve model; light-response curve can be confounded by other factors, e.g. air humidity, problem of equifinality of different solutions (resulting in high standard errors); R_{eco} estimate susceptible to storage flux problems, since those occur in the morning and evening during low-light conditions
1. R_{eco} as y-intercept from light-response curve of GEP (Falge *et al.*, 2002a)	Day-to-day variation of R_{eco} reflected	Only daily R_{eco} can be derived
2. R_{eco} and GEP are simultaneously modelled as parts of one fixed model equation (Gilmanov *et al.*, 2003)	Uses all data (night- and daytime)	Resulting GEP is from a model and thus constrained by model assumptions (disallows comparison with other models), temperature sensitivity maybe confounded by response of GEP to environmental factors, that are hard to separate; e.g. is afternoon drop in NEE caused by R_{eco} as $f(T)$ or by high VPD, or even by plant-internal hydraulic constraints?)

(continued)

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Table 1 (Contd)

Algorithm	Advantages	Disadvantages
3. R_{eco} and GPP are simultaneously modelled as parts of one model equation with state dependent parameters (Data-based mechanistic modelling approach)	Uses all data (night- and daytime); very flexible approach; parameters can evolve with time and state	Statistical assumptions, e.g. non-correlated residuals, and robustness against violations may be problematic; maybe affected by confounding factors similar to B2.
4. R_{eco} and GPP are derived via *a posteriori* analysis of an artificial neural network conditioned with all data. (cf. Papale & Valentini, 2002 for gap-filling; flux-partitioning not explored)	Uses all data (night- and daytime); very flexible approach; influence of different input data can be evaluated for best description of the data set	Extrapolation problem, because zero radiation has to be assumed estimating R_{eco} from neural network during the day; potentially confounded by other factors similar to B2.

NEE, net ecosystem CO_2 exchange; VPD, vapour pressure deficit; GEP, gross ecosystem production.

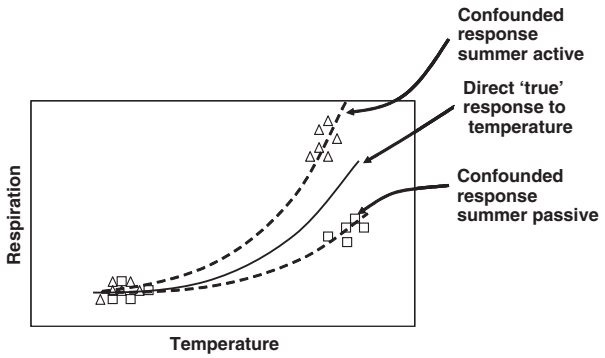

Fig. 1 Schematic representation of the confounding effects introduced into a temperature dependence of ecosystem respiration derived from annual data. Triangles and squares are hypothetical data for summer active and summer passive ecosystems, respectively. The true middle curve is the sensitivity of respiration to short-term variations, the other two are based on long-term data input as confounded by other seasonally varying factors, resulting in an overestimation of the temperature sensitivity in summer active and underestimation in summer passive ecosystems.

better representation of crop sites, two US-American soybean and corn field data sets have been added. Only original data (not gap-filled) was used in this analysis, and all night-time data with nonturbulent conditions were dismissed based on a u^*-threshold criterion (Aubinet *et al.*, 2000). The u^*-threshold was derived specifically for each site using a 95% threshold criterion similar to Reichstein *et al.* (2002a): for the u^*-filtering, the data set is split into six temperature classes of sample size (according to quantiles) and for each temperature class, the set is split into 20 u^*-classes. The threshold is defined as the u^*-class where the night-time flux reaches more than 95% of the average flux at the higher u^*-classes. The threshold is only accepted if for the temperature class, temperature and u^* are not or only weakly correlated ($|r| < 0.4$). The final threshold is defined as the median of the thresholds of the (up to) six temperature classes. This procedure is applied to the subsets of four 3-month periods to account for seasonal variation of vegetation structure. For each period, the u^*-threshold is reported, but the whole data set is filtered according to the highest threshold found (conservative approach). In cases where no u^*-threshold could be found, it is set to $0.4\,m\,s^{-1}$. A minimum threshold is set to $0.1\,m\,s^{-1}$. Night-time data was selected according to a global radiation threshold of $20\,W\,m^{-2}$, cross-checked against sunrise and sunset data derived from the local time and standard sun-geometrical routines, and defined as R_{eco}.

Table 2 List of sites included into this study

Site name (sorted by latitude)	Latitude	Longitude	Vegetation type	Climate type	Reference
Hyytiälä	61.85	24.29	ENF	Boreal	Rannik *et al*. (2002)
Jokioinen	60.90	23.52	CR-C3	Boreal	Lohila *et al*. (2004)
Hainich	51.08	10.45	DBF	Temperate	Knohl *et al*. (2003)
Tharandt	50.96	13.57	ENF	Temperate	Bernhofer *et al*. (2003)
Vielsalm	50.31	6.00	MF	Temperate	Aubinet *et al*. (2001)
BillyKriz	49.50	18.54	ENF	Temperate	Bernhofer *et al*. (2003)
Hesse	48.67	7.06	DBF	Temperate	Granier *et al*. (2000)
Bray	44.72	0.77	ENF	Warm-temperate	Berbigier *et al*. (2001)
Nonantola	44.69	11.09	DBF	Mediterranean	Nardino *et al*. (2002)
Puechabon	43.74	3.60	EBF	Mediterranean	Rambal *et al*. (2003)
SanRossore	43.73	10.29	ENF	Mediterranean	Tirone (2003)
Pianosa	42.59	10.08	OSH	Mediterranean	Georgiadis *et al*. (2002)
Bondville soybean*	40.01	−88.29	CR-C3	Temperate	Meyers (2001)
Bondville corn*	40.01	−88.29	CR-C4	Temperate	Meyers (2001)
ElSaler	39.34	−0.32	ENF	Mediterranean	Sanz *et al*. (2004)
Yatir	31.35	35.05	ENF	Mediterranean	Grünzweig *et al*. (2003)

*Geographically, this is one site. It is separated for the temporally varying vegetation type as a result of crop rotation between soybean and corn.
ENF, evergreen needle leaf forest; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; MF, mixed forest; OSH, open scrubland; CR-C3, cropland with C3 photosynthetic pathway; CR-C4, cropland with C4 photosynthetic pathway.

Estimation of temperature sensitivity from seasonal data

For the estimation of the temperature sensitivity from seasonal data ($E_{0,\mathrm{long}}$), all the available R_{eco} data are simply related to either air or soil temperature (T) using the exponential regression model (Lloyd & Taylor, 1994):

$$R_{\mathrm{eco}} = R_{\mathrm{ref}} \mathrm{e}^{E_0(1/(T_{\mathrm{ref}}-T_0)-1/(T-T_0))}. \quad (1)$$

While the regression parameter T_0 is kept constant at −46.02 °C as in Lloyd & Taylor (1994), the activation energy kind of parameter (E_0), what essentially determines the temperature sensitivity is a free parameter. The reference temperature (T_{ref}) is set to 10 °C as in the original model. T_0 was fixed, since otherwise the regression model was over-parameterized, as detected by parameter correlations of larger than 0.95.

Estimation of temperature sensitivity from short-term data

The short-term temperature sensitivity parameter ($E_{0,\mathrm{short}}$) was estimated with exactly the same regression model as the long-term temperature sensitivity (Eqn (1)). Only, for this estimation the data set is divided into short subperiods, where the regression is performed for each subperiod separately. For all sites, subperiods (*windows*) of 15 days were applied, where window $x+1$ is shifted 5 days with respect to window x (i.e. 10 days overlap). In a prescreening, for each period it is checked whether more than six data points are available and whether the temperature range is more than 5 °C, since only under these conditions reasonable regressions of R_{eco} vs. temperature are expected. The window size of 15 days has been selected to be sufficiently short to avoid strong confounding seasonal effects and to be long enough to provide enough data and an adequate temperature range for the regression. Moreover, a 15-day window was also supported by a secondary maximum in the frequency spectrum of air temperature (after the diurnal peal, not shown), and by earlier results showing a spectral gap at 15 days in flux data (Baldocchi *et al*., 2001b). At the Hytiälä and the Jokioinen sites, that – within their respective vegetation classes – exhibited the largest difference between short- and long-term sensitivity, we studied the effect of the window size on the E_0 parameter estimation by applying window sizes of 7, 15, 30, 60, 120 and 240 days.

We present results obtained using air temperature, because at some sites soil temperatures were not available. Soil temperatures were measured at different depth and often more variance of ecosystem respiration was explained by air temperature. [NB: This result is rather empirical and does not imply a mechanistic interpretation that air temperature is the main driver for ecosystem respiration. It may reflect that measurements of soil temperatures at 5–10 cm depth are already

too deep since a lot of respiration evolves from surface soil compartments, e.g. litter].

For each period, the regression parameters and statistics are stored and evaluated after regressions for all periods have been performed. Only those periods where the relative standard error of the estimates of the parameter $E_{0,\text{short}}$ is less than 50% and where estimates are within an accepted range 0–450 K) are accepted. While theoretically, a seasonal course of the $E_{0,\text{short}}$ parameter can be determined from this procedure, for many periods and sites the estimation error of $E_{0,\text{short}}$ was quite large, resulting in nonsignificant changes of the $E_{0,\text{short}}$ and disallowing the construction of a sensible seasonal course of the E_0 parameter. Hence, a $E_{0,\text{short}}$ parameter representative for the whole year was estimated in two ways: (1) The $E_{0,\text{short}}$ estimates from those three periods that yielded the lowest standard errors are averaged and (2) All $E_{0,\text{short}}$ estimates were averaged with the inverse of the standard error as weighing factor. These $E_{0,\text{short}}$ values are thought to constitute the best estimate of the short-term temperature sensitivity of R_{eco} that can be obtained from the data and has been used for the whole data set.

Estimation of day- and night-time ecosystem respiration

After the temperature sensitivities have been estimated, the temperature independent level of respiration (i.e. the R_{ref} parameter), has to be estimated. Since this parameter is definitely temporally varying in an ecosystem, it was estimated for consecutive 4-day periods by nonlinear regression using the Lloyd & Taylor (1994) model, fixing all parameters except R_{ref}. This estimation was performed once using the long-term temperature sensitivity ($E_{0,\text{long}}$) and once using the short-term temperature sensitivity ($E_{0,\text{short}}$). The R_{ref} estimates were assigned to that point in time, which represents the 'centre of gravity' of the data. For instance, if only R_{eco} data was available during the fourth night of the period from 18:00 to 06:00 hours, the R_{ref} is assigned to 18:00 hours of the fourth night. After the R_{ref} parameters were estimated for each period, they were linearly interpolated between the estimates. This procedure results in a dense time series of the Lloyd & Taylor (1994) parameters R_{ref} and $E_{0,\text{short}}$, the latter being constant.

Consequently, for each point in time, an estimate of R_{eco} can be provided according to

$$R_{\text{eco}}(t) = R_{\text{ref}}(t)\mathrm{e}^{E_0(1/(T_{\text{ref}}-T_0)-(1/T_{\text{soil}}(t)-T_0))}, \qquad (2)$$

that is the same as Eqn (1), but with time-dependent parameters and variables indicated by the symbol t in parentheses. Examples of the time-course for those quantities in Eqn (2) are shown in Fig. 2 for the Hesse beech forest site. Depending on whether E_0 (and derived R_{ref}) from the long- or short-term estimate is placed into the equation, R_{eco} represents an estimate of ecosystem respiration using the long- or short-term sensitivity of respiration.

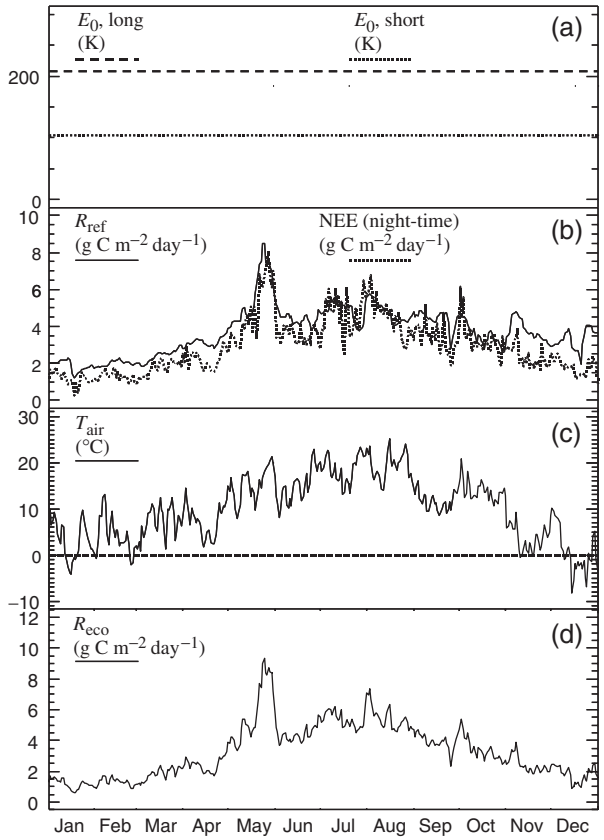

Fig. 2 Time series of the derived Lloyd and Taylor (1994) parameters (cf. Eqn (1)), (a) E_0, and (b) R_{ref}, together with the observed night-time net ecosystem exchange (NEE), (c) air temperature and (d) derived ecosystem respiration for the Hesse site in 2001. The data set has been aggregated to daily values.

The regression analyses were performed using ordinary least squares regression that maximizes the likelihood of the parameter values under the assumption of normally distributed residuals. The distribution of the residuals (i.e. observed night-time flux minus modelled R_{eco}), was inspected for each site and was always almost symmetrical, but narrower than a Gaussian, implying only a minor violation of this assumption.

Soil respiration data

For an independent comparison continuous soil chamber respiration data was analysed. At two sites a sufficient amount of continuous soil respiration data was available (Hyytiälä & Tharandt). Measurements on

both sites were taken with open-dynamics chambers, at Hyytiälä with a system described in Pumpanen *et al.* (2001), at Tharandt with a system developed by Subke *et al.* (2003). For each observed diurnal cycle the average and the range (amplitude) of observed soil CO_2 effluxes was computed and compared with the modelled ecosystem respiration.

Gap-filling

The data was gap-filled using a combination and an enhancement of the Falge *et al.* (2001b) methods as described in the Appendix A.

Results and discussion

As exemplified graphically for the Hesse site the (temperature independent) rate of ecosystem respiration at reference conditions (R_{ref}) varies seasonally more than three-fold (Fig. 2b). Such seasonal changes have been often found earlier for soil respiration (e.g. Davidson *et al.*, 1998; Law *et al.*, 1999; Law *et al.*, 2001a; Xu & Qi, 2001; Subke *et al.*, 2003) and R_{eco} (e.g. Janssens *et al.*, 2001; Falge *et al.*, 2002a; Reichstein *et al.*, 2002a; Xu & Baldocchi, 2004), and can be generally explained by plant phenological (*sensu lato*) patterns, soil moisture, decomposition and/or soil microbial growth dynamics. The strong increase in May 2001 and subsequent decrease of R_{ref} is a signal contained in the night-time data and may be related to fast growth-processes during that period. Figure 3 illustrates the strong and nonlinear statistical positive correlation between temperature and R_{ref} at the Hesse site. At the same time, this fact builds the motivation for this study, since the seasonal covariation of the reference respiration rate with temperature unavoidably results in confounded estimates of the temperature sensitivity of respiration, if long-term data is used, as most recently pointed out by Curiel Yuste *et al.* (2004). In the case of summer active ecosystems, the seasonal covariation of temperature with general biological activity is expected to result in an overestimation of the direct short-term temperature sensitivity of respiration. In summer passive ecosystems (summer dry), like Yatir, R_{ref} is negatively correlated with temperature (Fig. 3), so that an underestimation of the direct short-term temperature sensitivity is expected. This consideration is largely confirmed in the empirical analysis performed here (Fig. 4): at a majority of Mediterranean sites, the long-term E_0 is significantly lower than the short-term E_0 (negative ΔE_0) and interestingly the two Mediterranean sites with a slightly (nonsignificant) positive ΔE_0 are the ones with groundwater influence (San Rossore, El Saler). At temperate and boreal forest sites long-term

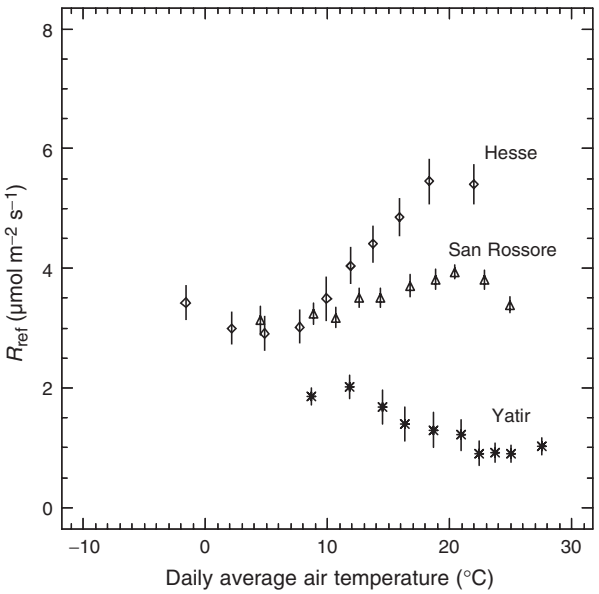

Fig. 3 Statistical relationship between the daily average air temperature and the estimate of the ecosystem respiration under reference conditions (R_{ref}) for the Hesse (◇), San Rossore (△) and Yatir (✱) sites in 2001. Averages for 10%-tile temperature classes ± 1 SE are shown. Polynomial terms up to 3rd degree are highly significant ($P < 0.01$) in all relationships.

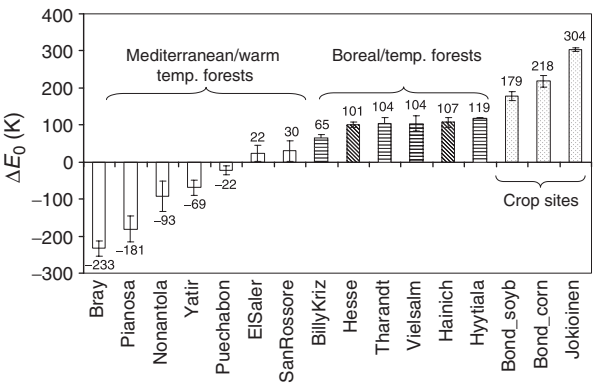

Fig. 4 Difference between long- and short-term temperature sensitivity (ΔE_0) for each site. Unfilled, horizontally, diagonally patterned and dotted bars represent Mediterranean sites, boreal/temperate evergreen forest, temperate deciduous forest and crop sites, respectively. Error bars indicate ± 1 standard error of the short-term E_0 estimate. ΔE_0 values are indicated adjacent to the bars. Positive ΔE_0 means that apparent long-term temperature sensitivity ($E_{0,long}$) is increased by confounding seasonal factors and vice versa.

E_0 was mostly around 100 K higher than the short-term E_0, as expected from the fact that these are summer-active ecosystems. Finally, the bias in E_0 is largest for the crop sites, whose activity is most confined to the summer months with high temperature and reaches up to 304 K in the boreal spring barley site Jokioinen. Here,

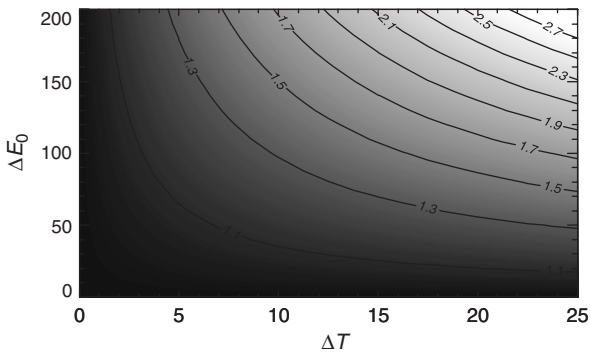

Fig. 5 Theoretical relative bias (RBIAS) of the instantaneous R_{eco} estimation depending on the error of the temperature sensitivity (ΔE_0) and the temperature difference between night- and daytime (ΔT) as contour plot. The figures are a graphical representation of the function $RBIAS(\Delta E_0, \Delta T) = e^{(E_0+\Delta E_0)(1/(T_{ref}-T_0)-1/(T_{night}+\Delta T-T_0))}/e^{(E_0)(1/(T_{ref}-T_0)-1(T_{night}+\Delta T-T_0)}$. T_{night} was set to 10 °C, $T_0 = -46.02$ °C, $E_0 = 150\,K^{-1}$.

the long-term E_0 was 445 K (Table 3), corresponding to an effective Q_{10} of more than 4 in the temperature range 5–15 °C.

The magnitude with which such a bias in the temperature sensitivity affects instantaneous daytime estimates of R_{eco} of course depends on the temperature difference between night- and daytime and can be calculated. Figure 5 shows the theoretical bias of an instantaneous flux as a function of the bias of E_0 and the difference between night- and daytime temperature. Under extreme conditions, the error in the instantaneous flux can be nearly threefold, but under most conditions (temperature difference between 5 and 15 °C, ΔE_0 between 50 and 150 K), theoretical errors of instantaneous R_{eco} estimates are in the range of 10–80%. At the Hesse site for example ($\Delta E_0 = 101$ K) in July the difference between the two different R_{eco} estimates usually reaches around 30% during the early afternoon, when the highest temperatures are reached (Fig. 6). This behavior follows directly from the mathematical properties of the Lloyd and Taylor model, where the relative sensitivity of R_{eco} on the parameters can be expressed as (see Appendix B for derivation)

$$\frac{dR_{eco}}{R_{eco}} = \frac{dR_{ref}}{R_{ref}} + dE_0\left(\frac{T - T_{ref}}{(T_{ref} - T_0)(T - T_0)}\right). \quad (3)$$

Thus, if the temperature T is close to T_{ref}, the error is largely determined by the error in R_{ref}, and the temperature sensitivity does not play a big role. If on the contrary $T - T_{ref}$ is large (e.g. high daytime temperatures), the error in the R_{eco} estimate is more and more dominated by the error term dE_0 and an overestimation of E_0 leads to an overestimation of R_{eco}.

It is obvious that an overestimation of R_{eco} must also result in an overestimation of GEP, since GEP = R_{eco}−NEE. Yet, when annual sums are considered, the bias should be attenuated, because night-time data is nearly unaffected and also winter-time data with lower diurnal temperature amplitudes is less susceptible to a bias in the E_0 estimate. These points are empirically evident in Fig. 7, where the overestimation for the derived annual GEP estimate for temperate and boreal forests is reduced to between 4% and 8%. For most of the Mediterranean sites, the GEP is underestimated slightly, which is consistent with the lower long-term E_0 in those sites (cf. Fig. 4). The magnitude of the bias at Mediterranean sites is smaller, since during the period of the highest temperature amplitudes in summer ecosystem respiration is lowest due to the drought effect and thus the summer bias does not contribute as much to the annual bias as in the temperate ecosystems. Conversely, in the agro-ecosystems the long-term E_0 tended to yield the highest overestimation of annual GEP reaching up to 26% for the boreal, continental Jokioinen spring barley site (Fig. 7).

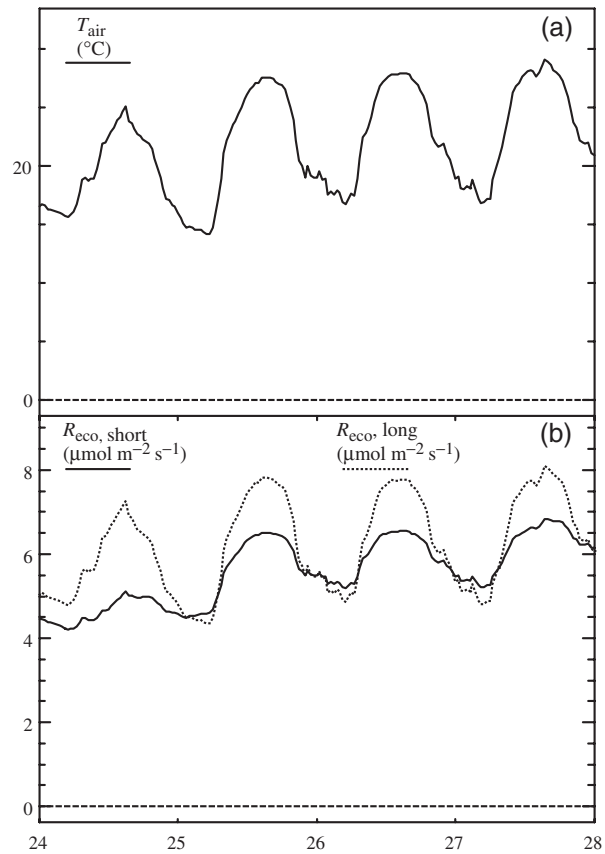

Fig. 6 Four-day time series of (a) air temperature and (b) estimates of ecosystem respiration using short-term ($E_{0,short}$) and long-term ($E_{0,long}$) temperature sensitivities for the Hesse site in July 2001.

The current study on ecosystem respiration confirms recent results concerning soil respiration that seasonal

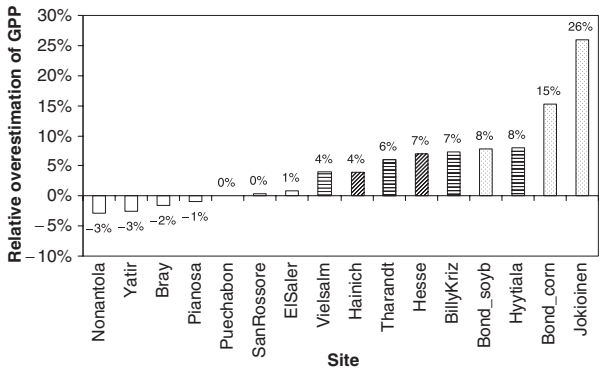

Fig. 7 Bias in the annual estimate of gross carbon uptake (GEP) introduced by using a long-term temperature sensitivity ($E_{0,\mathrm{long}}$) for extrapolating ecosystem respiration from night- to daytime in the flux-partitioning. Bars are patterned as in Fig. 4. The percent overestimation for each site is indicated next to the columns.

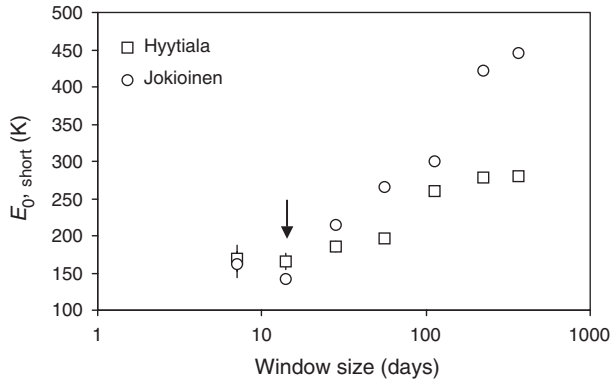

Fig. 8 Empirical dependency of the $E_{0,\mathrm{short}}$ parameter on the window size used the determine the temperature response of R_{eco} from night-time net ecosystem exchange (NEE) data at the Hyytiälä and Jokioinen sites. The arrows points to the 15-day window chosen in this study for all sites. NB: The x-axis is logarithmic.

estimates of the temperature sensitivity can be severely confounded and biased by other factors that seasonally covary. Consequently, a significant bias is introduced into estimates of R_{eco} and GEP at both, short- and long-time scales, when confounded long-term (apparent) temperature sensitivity is used instead of the direct, short-term response to temperature that drives the diurnal respiration dynamics. A big problem is that the magnitude of the introduced bias systematically varies among sites (summer vs. winter active, forests vs. crops, cf. Fig. 7), so that even comparisons of R_{eco} or GEP between different ecosystem types are hampered and might lead to incorrect conclusions about how continental and environmental gradients affect R_{eco} and GEP. From this analysis, we conclude that studies that analysed GPP and R_{eco} in a standard way using the long-term sensitivity will have tended to overestimate R_{eco} and GPP in the high latitudes and slightly underestimated those quantities for southern Europe. Hence, without this bias a slight decline of GEP towards higher latitudes is expected, and a weaker trend of R_{eco} than suggested by Valentini *et al*. (2000), but an analysis of a consolidated CABROEUROFLUX data set should be performed to clarify this. Moreover, since the bias is dependent on the diurnal temperature amplitude (cf. Fig. 5) – the higher the temperature amplitude the larger the bias – it also changes seasonally and affects conclusions about seasonality of R_{eco} and GEP. This seasonal bias is also critical for model evaluations that are often performed at the seasonal time-scale.

The algorithm developed in this study relies on the assumption that a 15-day window largely avoids seasonally confounding effects and at the same time yields enough data points for parameter estimation. We showed the effect of the window size at the two sites (within their vegetation class) that were more strongly affected by the confounding effect (largest ΔE_0). From this analysis, it appears that with window sizes of 1 month or more, significant confounding seasonal effects can be introduced in the estimation of E_0 (Fig. 8), but that the effect is site dependent. At Hyytiälä, a window size of 1 month may still be acceptable, while in Jokioinen, a difference of more than 50 K in the E_0 parameter is introduced. While there is plausible evidence to assume that the long-term temperature sensitivity ($E_{0,\mathrm{long}}$) is confounded by seasonally covarying factors (Reichstein *et al*., 2002a; Curiel Yuste *et al*., 2004), and thus is not appropriate for extrapolating from night to day, an independent assessment can only be tried by comparison with full diurnal cycles of soil respiration measured by soil chambers. As was illustrated in Fig. 6, the different estimates of E_0 (long, short-term) primarily yield different diurnal amplitudes of the predicted ecosystem respiration that can be compared with amplitudes of continuous soil respiration measurements. Such comparison was possible at two sites with ample soil respiration data (R_{soil}) availability and is depicted in Fig. 9, where for Hyytiälä and Tharandt the diurnal range of ecosystem respiration modelled from $E_{0,\mathrm{long}}$ exceeded the observed range of soil respiration by a factor of two. The diurnal range of R_{eco} modelled with $E_{0,\mathrm{short}}$, on the contrary, seems to be higher (at least at low fluxes) than the observed amplitude of R_{soil}. Part of this overestimation will originate from the fact, that observed data includes a random error (noise of measurement) that inflates the observed range. This effect seems to be supported

Table 3 Estimates of the temperature sensitivity parameter E_0 using long- and short-term (15 days) data analysis for each site

	Long-term E_0		Short-term E_0 (average of best three estimates)		Short-term E_0 (all estimates)	
Site name (sorted by latitude)	Estimate	Standard error	Estimate	Standard error	Average, weighted*	Standard deviation
Hyytiälä	284	2.4	165	1.5	174	78
Jokioinen	445	2.2	141	4.2	161	67
Hainich	227	1.4	120	13.0	127	51
Tharandt	237	1.3	133	16.8	141	63
Vielsalm	196	6.0	92	19.8	133	71
BillyKriz	183	1.8	119	8.3	141	63
Hesse	205	0.7	104	7.7	104	71
Bray	40.2	7.7	274	21.4	263	80
Nonantola	125	11.9	218.3	40.9	212	93
Puechabon	131	3.6	153	12.2	163	71
SanRossore	155	2.9	125	27.9	144	66
Pianosa	0†	n.d.	181	36.1	194	35
Bondville soybean	343	1.2	184	12.3	215	75
Bondville corn	437	1.6	218	15.3	237	92
ElSaler	196	2.4	174	21.7	194	93
Yatir	0†	n.d.	70	21.0	101	79

*All E_0 with a standard error lower than 50% were averaged with the inverse of the individual standard errors being the weights.
†Zero was set as lower boundary for the parameter estimation ($E_0 = 0$ implies no response to temperature).

by the very similar intercepts of the regression observed range vs. modelled range (0.36–0.38 $\mu mol\, m^{-2} s^{-1}$ for Tharandt; and 0.45–0.47 $\mu mol\, m^{-2} s^{-1}$ for Hyytiälä), since the intercept would be interpreted as the range of the observed diurnal course when the modelled diurnal amplitude is zero. In fact, as we evaluated with a Monte-Carlo simulation, a noise of 0.1 $\mu mol\, m^{-2} s^{-1}$ in the observed data introduces an artificial range of 0.39 $\mu mol\, m^{-2} s^{-1}$ if 24 samples are taken per day. Hence, the short-term E_0 indeed seems to yield more realistic ranges. On the other hand, the comparison is difficult: one might expect, that R_{eco} exhibits a larger amplitude than R_{soil} since R_{eco} is larger than R_{soil} and partly exposed (above-ground biomass) to larger temperature fluctuations than R_{soil}, although e.g. cooling of leaves through transpiration might also dampen the latter effect. Also, a comparison of the absolute fluxes (R_{eco} vs. R_{soil}) does not indicate that R_{eco} is much larger than R_{soil} (in Tharandt: ca. 30%, in Hyytiälä ca. 10% higher; $r^2 = 0.5$–0.8; for an extensive discussion on how differences between R_{eco} and R_{soil} can emerge see (e.g. Lavigne *et al.*, 1997; Law *et al.*, 1999). In spite of these difficulties with interpretation it is unlikely however, that the R_{eco} amplitude is more than twice as high as the observed R_{soil} amplitude, yielding empirical evidence that the long-term temperature sensitivity ($E_{0,long}$) does introduce a bias in the estimate of R_{eco}. The relatively low regression coefficients between the observed and modelled diurnal ranges are caused by the large spatial variability and because the diurnal courses are not well described exclusively using air temperature as driving force. Because of slow thermal conduction at the Hyytiälä site, often maximum fluxes are reached in the evening, when the air temperature has already dropped (cf. also Pumpanen *et al.*, 2003). This stresses the importance of selecting the 'right' temperature for modelling the diurnal course of ecosystem respiration. Approaches using multiple compartments should theoretically yield better results, but here again the problem of parameter identification with over-parameterized models arises.

To sum up, the algorithm introduced here was able to find a short-term temperature response of R_{eco} at all studied sites and is a significant step forward towards less biased estimates of R_{eco} and GEP. Nevertheless, important limitations should be noted: It is not guaranteed to work at all sites since whether one can find a reliable short-term relationship between R_{eco} and temperature depends on the noisiness of the eddy data and the range of temperatures encompassed during the short period. At sites with very stable temperatures and noisy eddy covariance data, it might be possible that within a year no short period can be found where a temperature–R_{eco} relationship can be established at all. Seasonal changes in the temperature sensitivity that

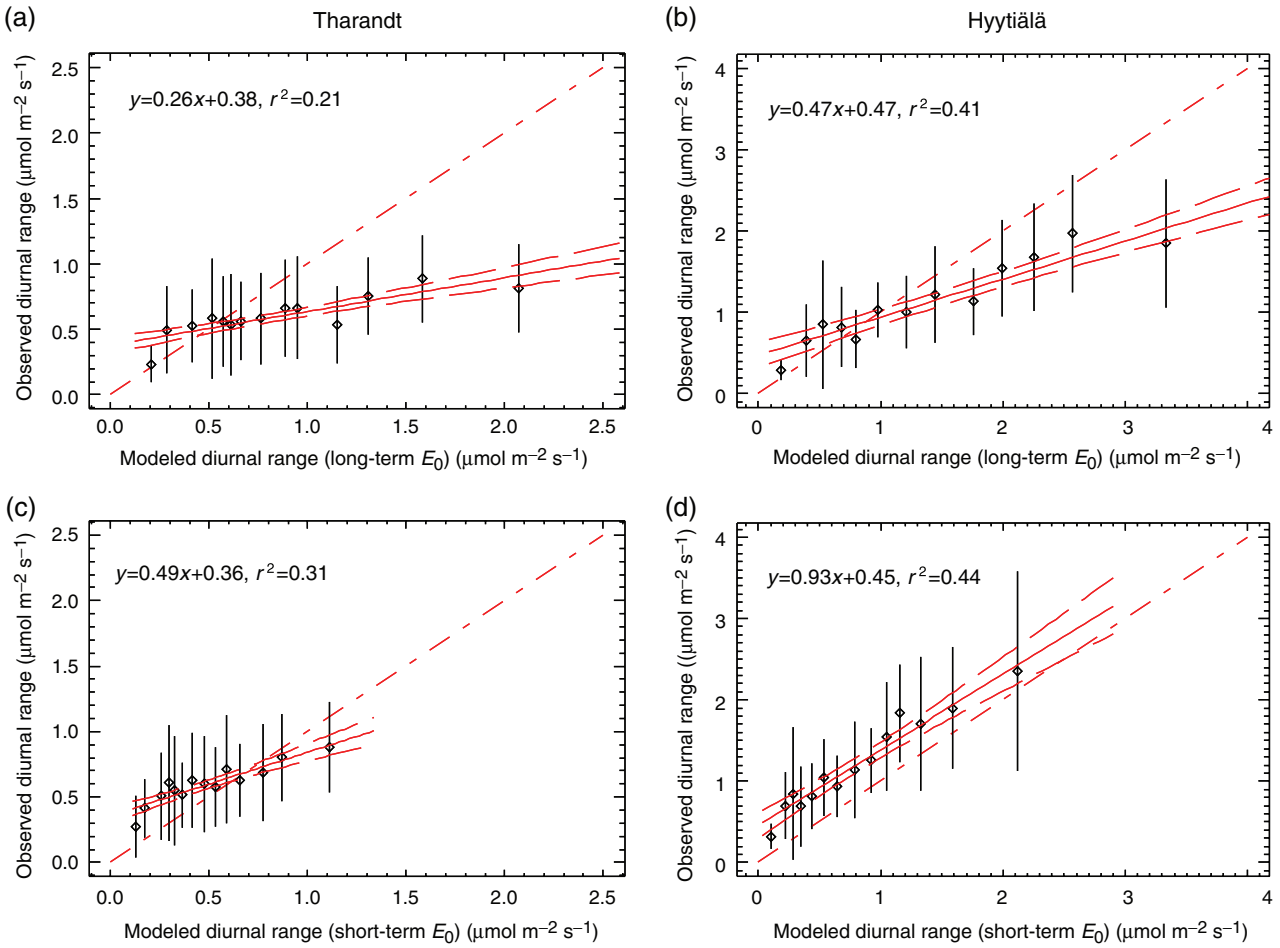

Fig. 9 Statistical comparison of observed diurnal (24 h) ranges of soil respiration (y-axis) with predicted diurnal ranges of ecosystem respiration (x-axis). In (a and b) the modelled ecosystem respiration using the long-term temperature sensitivity (E_0) is shown, in (c and d) using the short-term temperature sensitivity. Data are grouped along the x-axis into 14 classes of equal size, the mean (symbol) and standard deviation for each class are presented. Dash–dotted line is the 1 : 1-line. A linear regression with 95% confidence bands is indicated. All linear relationships are highly significant ($P<0.01$).

have been hypothesized are hard to detect from eddy covariance data, since in many cases not enough short-term periods with a good correlation between temperature and R_{eco} were found to make up a seasonality. It will be worthwhile testing if more advanced statistical techniques like state-dependent parameter estimation (Jarvis *et al.*, 2004) are better able to extract seasonal structure in the temperature sensitivity ecosystem respiration. Moreover, it cannot be excluded that even with the method presented here still other factors are confounding the relationship between T and R_{eco}. In particular, if leaf dark respiration is light-inhibited during the day (Kok, 1948), daytime ecosystem respiration would be overestimated when extrapolating from night-time data. However, recent findings using stable-isotope methodology show that under most conditions the light-inhibition of leaf dark respiration is only apparent and a result of CO_2 refixation in the leaf (Loreto *et al.*, 2001; Pinelli & Loreto, 2003). In this situation, there is no diurnal bias introduced into the daytime R_{eco} and GPP estimate. Rewetting events that cause short-term dynamics of soil moisture would also introduce a confounding effect, but it is likely that such a period is thrown out by the algorithm due to high standard error of the parameters. However, one crucial problem particularly for correctly modelling the diurnal course of R_{eco} and GPP is the identification of the compartments and associated temperatures that drive the diurnal dynamics of R_{eco} (air, litter, soil temperature). Hence, we suggest that the flux-partitioning would be helped a lot with independent estimates of the short-term sensitivity of respiration to temperature of the ecosystem's main respiring components with chamber methods.

Conclusion

For understanding the effect of spatial and environmental gradients on ecosystem NEE from eddy covariance data, it is essential to acquire estimates of its main components, R_{eco} and gross primary production (GEP), through a so-called flux-partitioning algorithm. A number of methods are available for this task but with all methods biased estimates of GEP and R_{eco} are likely, because of the effect of confounding factors. We have shown that by using a temperature–R_{eco} relationship from annual data (that is confounded, e.g. by growth dynamics, and soil drought effects), can introduce a significant bias into R_{eco} and GEP estimates from hourly to annual time-scales. Thus, we introduce and recommend using an algorithm that defines a short-term temperature sensitivity of ecosystem respiration, and thus, largely avoids the bias introduced by confounding factors in seasonal data. Particularly in cases where no reliable short-term relationship between temperature (or another more relevant diurnally varying factor) and R_{eco} can be found from eddy covariance data, such a relationship should be established via observing the main respiring components with chamber methods.

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Appendix A: Gap-filling methodology

The gap-filling of the eddy covariance and meteorological data is performed through methods that are similar to Falge *et al*. (2001a, b), but that consider both the covariation of fluxes with meteorological variables and the temporal auto-correlation of the fluxes: in this new algorithm, three different conditions are identified: (1) Only the data of direct interest are missing, but all meteorological data are available, (2) Also air temperature or VPD is missing, but radiation is available, and (3) Also radiation data is missing. In case (1), the missing value is replaced by the average value under similar meteorological conditions within a time-window of ± 7 days. Similar meteorological conditions are present when R_g, T_{air} and VPD do not deviate by more than $50\,W\,m^{-2}$, 2.5 °C, and 5.0 hPa, respectively. If no similar meteorological conditions are present within the time window, the averaging window is increased to ± 14 days. In case (2) the same approach is taken, but similar meteorological conditions can only be defined via R_g deviation less than $50\,W\,m^{-2}$ and the window size is first not further increased. In case (3) the missing value is replaced by the average value at the same time of the day (± 1 h), i.e. by the mean diurnal course. In this case, the window size starts with ± 0.5 days, i.e. similar to a linear interpolation from available data at adjacent hours. If after these steps the values could not be filled, the procedure is repeated with increased window sizes until the value can be filled. Figure A1 summarizes the algorithm. Both, the method, the window size, and the number and the standard deviation of values averaged is recorded then, so that for individual purposes, appropriate data can be selected and e.g. uncertainties can be estimated. For convenience, the filled data is further classified into three tentative categories (A, B, C) based on the method (1, 2, or 3) and the window size used (Fig. A1). The classification is based on the notion, that the estimation of the missing data improves with the knowledge on meteorological conditions and with the use of the temporal auto-correlation of the variable that favours smaller time-windows.

Appendix B: Derivation of Eqn (3)

Differentiating the equation by Lloyd & Taylor (1994)

$$R_{eco} = R_{ref} e^{E_0((1/T_{ref}-T_0)-(1/T-T_0))}. \tag{B1}$$

Using the multiplicative and chain rules yields:

$$dR_{eco} = dR_{ref}\frac{\partial R_{eco}}{\partial R_{ref}} + dE_0\frac{\partial R_{eco}}{\partial E_0} \tag{B2}$$

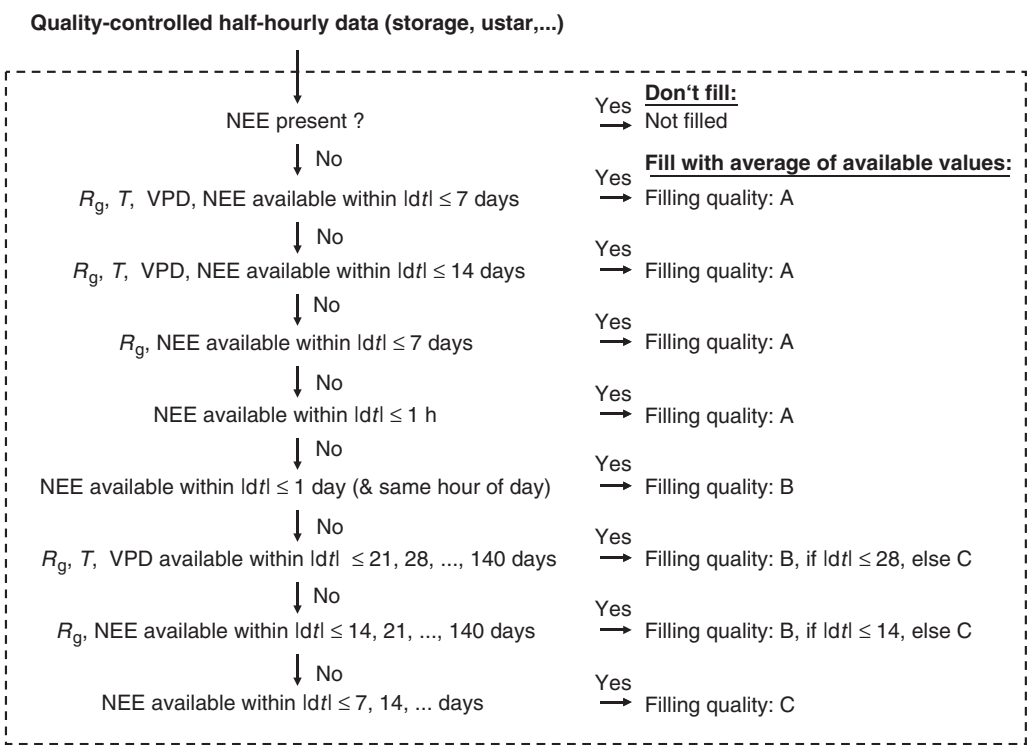

Fig. A1 Flow diagram of the gap-filling algorithm used in this study. Abbreviations: NEE, net ecosystem CO_2 exchange; R_g, global radiation; T, air temperature; VPD, vapour pressure deficit; $|dt|$, absolute difference in time. Filling qualities: A, high; B, medium; C, low.

with

$$\frac{\partial R_{\mathrm{eco}}}{\partial R_{\mathrm{ref}}} = \mathrm{e}^{E_0((1/T_{\mathrm{ref}}-T_0)-(1/T-T_0))} = \frac{R_{\mathrm{eco}}}{R_{\mathrm{ref}}} \tag{B3a}$$

and

$$\begin{aligned}\frac{\partial R_{\mathrm{eco}}}{\partial E_0} &= R_{\mathrm{ref}}\mathrm{e}^{E_0(1/T_{\mathrm{ref}}-T_0-(1/T-T_0))} \\ &\quad\times\left(\frac{1}{T_{\mathrm{ref}}-T_0}-\frac{1}{T-T_0}\right) \\ &= R_{\mathrm{eco}}\left(\frac{1}{T_{\mathrm{ref}}-T_0}-\frac{1}{T-T_0}\right).\end{aligned} \tag{B3b}$$

Dividing Eqn (B2) by R_{eco} to obtain the (relative) sensitivity of R_{eco} and inserting Eqns (B3a), (B3b) yield:

$$\frac{dR_{\mathrm{eco}}}{R_{\mathrm{eco}}} = \frac{dR_{\mathrm{ref}}}{R_{\mathrm{ref}}} + \mathrm{d}E_0\left(\frac{1}{T_{\mathrm{ref}}-T_0}-\frac{1}{T-T_0}\right) \tag{B4}$$

which is Eqn (3).