# Biotic and climatic controls on interannual variability in carbon fluxes across terrestrial ecosystems

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## ABSTRACT

Interannual variability (IAV, represented by standard deviation) in net ecosystem exchange of $CO_2$ (NEE) is mainly driven by climatic drivers and biotic variations (i.e., the changes in photosynthetic and respiratory responses to climate), the effects of which are referred to as climatic (CE) and biotic effects (BE), respectively. Evaluating the relative contributions of CE and BE to the IAV in carbon (C) fluxes and understanding their controlling mechanisms are critical in projecting ecosystem changes in the future climate. In this study, we applied statistical methods with flux data from 65 sites located in the Northern Hemisphere to address this issue. Our results showed that the relative contribution of BE (CnBE) and CE (CnCE) to the IAV in NEE was $57\% \pm 14\%$ and $43\% \pm 14\%$, respectively. The discrepancy in the CnBE among sites could be largely explained by water balance index (WBI). Across water-stressed ecosystems, the CnBE decreased with increasing aridity (slope = 0.18% mm$^{-1}$). In addition, the CnBE tended to increase and the uncertainty reduced as timespan of available data increased from 5 to 15 years. Inter-site variation of the IAV in NEE mainly resulted from the IAV in BE (72%) compared to that in CE (37%). Interestingly, positive correlations between BE and CE occurred in grasslands and dry ecosystems ($r > 0.45$, $P < 0.05$) but not in other ecosystems. These results highlighted the importance of BE in determining the IAV in NEE and the ability of ecosystems to regulate C fluxes under climate change might decline when the ecosystems experience more severe water stress in the future.

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## 1. Introduction

Atmospheric $CO_2$ concentration has been dramatically increased since the Industrial Revolution, which has caused a

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corresponding rise of 0.85 °C in global air temperature from 1880 to 2012 (IPCC, 2013). The interannual fluctuation of atmospheric $CO_2$ concentration is primarily attributed to the interannual variability (IAV) in net ecosystem exchange of $CO_2$ (NEE) between the atmosphere and global terrestrial ecosystems (Le Quéré et al., 2009). The IAV in NEE is a phenomenon observed at almost all eddy-flux sites around the world (Baldocchi, 2008). The factors driving the IAV in NEE include (1) climate, (2) physiological processes, (3) phenology, (4) ecosystem structure, (5) nutrient cycling in ecosystems, and (6) disturbance (Hui et al., 2003; Marcolla et al., 2011; Polley et al., 2008; Richardson et al., 2007). Among these, the changes in climatic variables and physiological processes can directly affect the IAV in NEE. In this study, we defined the direct effects of climatic drivers as the climatic effects (CE) and the effects of ecological and physiological changes (i.e., the changes in photosynthetic and respiratory responses to climate) on the IAV in carbon (C) fluxes caused by either climate or other factors ((3)–(6) above-mentioned) as the biotic effects (BE). As a result, the IAV in NEE can be considered as the combined consequence of CE and BE on NEE.

Quantifying the magnitude of CE and BE and their relative contributions to the IAV is essential to understand the mechanisms underlying the IAV in NEE and to forecast the potential response of ecosystem C cycling to future climate change. Previous studies have shown that the importance of BE could be larger than (Delpierre et al., 2012; Polley et al., 2008; Wu et al., 2012), equivalent to (Hui et al., 2003; Richardson et al., 2007), or less than (Delpierre et al., 2012; Polley et al., 2008; Teklemariam et al., 2010) that of CE at the interannual scale. However, whether such discrepancy was related to disturbances (Polley et al., 2008), vegetation types (Adkinson et al., 2011; Wu et al., 2012), or other factors is not well quantified. In addition, weak or strong negative correlations between CE and BE have been found (Richardson et al., 2007; Shao et al., 2014), which reflects the responses of ecosystem C cycling to climatic variations. Exploring whether such a negative correlation is common among ecosystems will be helpful in clarifying the debate on the positive feedback between C cycling and climatic change (Cox et al., 2000; Friedlingstein et al., 2006; Luo et al., 2009).

At the regional and global scales, the spatial differences of the IAV in NEE might be influenced by ecosystem characteristics (e.g., climate, nutrient, and plant community). Modeling studies suggested that those areas with El Niño-Southern Oscillation (ENSO) and in tropical regions had the relatively larger IAV in NEE (Gurney et al., 2008; Jung et al., 2011), while a synthesis of FLUXNET data showed a latitudinal trend of the IAV in NEE at deciduous broadleaf forests (DBF), in which temperature was the main controlling factor (Yuan et al., 2009). A comparative study in two similar grasslands in Hungary suggested that soil type significantly affected the IAV in NEE by modifying the relationships between precipitation and C fluxes (Pintér et al., 2008). Adkinson et al. (2011) found that nutrient conditions and plant functional types also affected the IAV in NEE between two fens in Canada. However, to our knowledge, no study has investigated the relative importance of CE and BE to the inter-site differences of the IAV in NEE.

To address these issues, it is necessary to quantify the magnitude of CE and BE and their relative importance to the IAV in NEE. Delpierre et al. (2012) defined the relative importance of biotic and climatic variables in a model as the relative contributions of BE and CE to the IAV, respectively. Unfortunately, this approach is not always appropriate because biotic drivers are usually difficult to obtain. Hui et al. (2003) and Richardson et al. (2007) attributed the CE and BE to the changes in the model outputs caused by changed values of variables and parameters, respectively. However, model-data mismatching (Hui et al., 2003; Polley et al., 2008; Teklemariam et al., 2010) and site-specific relationships between climatic variables and C fluxes (Richardson et al., 2007) caused the great difficulty in multi-site comparisons. Therefore, a more flexible method should be developed to compare multi-site results.

In this study, we applied an additive model (a non-parametric regression method) and a model averaging technique (based on Akaike weights) to simulate the relationships between climatic variables and C fluxes. The observed IAV in NEE was then partitioned into BE and CE. Consequently, we were able to examine the relative importance of BE and CE to the IAV in NEE within an ecosystem and to the differences of IAV among ecosystems, and the relationships between BE and CE. Our primary objectives were to distinguish the main factors influencing the relative importance of BE (or CE) to the IAV in NEE, and to evaluate the potential responses of ecosystem C cycling to climatic variations.

## 2. Materials and methods

### 2.1. Data sources and sites information

Our study was based on 481 site-years of data from 65 eddy covariance measurement sites, which belong to AmeriFlux (public.ornl.gov/ameriflux/index.html), CarboEurope (www.carboeurope.org), and ChianFLUX (www.chinaflux.org) from 1992 to 2010 (Fig. 1). The original data includes half-hour $CO_2$ flux (Fc), friction velocity ($u^*$), photosynthetically active radiation
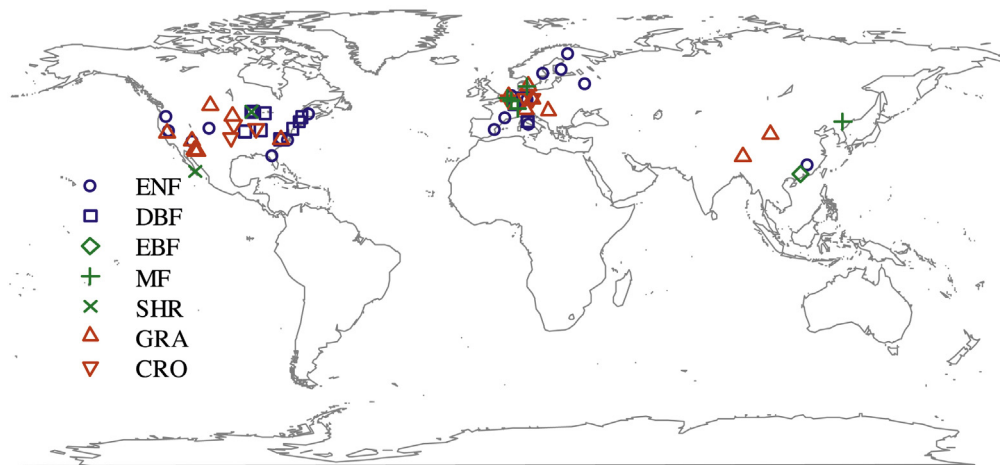


**Fig. 1.** Study sites distribution map. The abbreviations of ecosystem types are the same as those in Table 1. Our study contained 22 evergreen needleleaf forests (ENF), 12 deciduous broadleaf forests (DBF), 1 evergreen broadleaf forest (EBF), 5 mixed forests (MF), 16 grasslands (GRA), 7 croplands (CRO) and 2 shrublands (SHR) from North America, Europe and China.

(PAR) or global radiation (Rg), air temperature (Ta), soil temperature (Ts), precipitation (PPT), relative humidity (RH), vapor pressure deficit (VPD), and latent heat flux (LE). To examine the interannual variability (IAV) in C fluxes, only data covering ≥5 years were selected and the longest time was 15 years. The latitudes range from 23°N to 67°N, longitudes are from 122°W to 128°E, and altitudes vary from sea level to over 4000 m. The ecosystem types include evergreen needleleaf forest (ENF), DBF, evergreen broadleaf forest (EBF), mixed forest (MF), shrubland (SHR), grassland (GRA), and cropland (CRO). Climatic conditions had large inter-site variation. Mean annual temperature (MAT) ranged from −0.8 to 23.4 °C, and annual precipitation was 137–1481 mm (Table S1).

## 2.2. Preprocessing and gap-filling

Spike screening and nighttime filtering were applied at first because of the requirement of data quality. The methods applied to detect and screen spikes in Fc included two processes: double-differenced time series and then the median of absolute deviation as a spiker estimator (Papale et al., 2006). The nighttime Fc was rejected when the corresponding $u^*$ was lower than the threshold value, which was determined for each year of each site with a 99% threshold criterion on night-time data (Reichstein et al., 2005; Papale et al., 2006). After spike screening and nighttime filtering, the valid flux data were $60 \pm 13\%$ of the total observations for all sites.

To minimize the uncertainty derived from assigning different model structures for the study sites, the artificial neural network (ANN) model with a feed-forward back propagation algorithm and sigmoid transfer functions (Papale and Valentini, 2003; Melesse and Hanley, 2005; Moffat et al., 2007) was applied to fill the gaps and partition net ecosystem exchange of $CO_2$ (NEE) into gross primary productivity (GPP) and ecosystem respiration (RE). The ANN model was trained and validated separately for each year's daytime and nighttime data. The nighttime model, which only used nighttime data for the input and output layers, was used to simulate nighttime RE and fill the gaps. The input variables of the model were Ts, RH and four seasonal indices (seasonal fuzzy sets, representing the four seasons, Papale and Valentini, 2003) and the output variable is RE (nighttime Fc). Six nodes (the units in ANN) were set in the hidden layer. The data set was randomly divided into two parts, 70% as the training dataset and 30% as the test dataset. The process was repeated by 20 times. The median of 20 simulated RE values was used to fill the nighttime RE gaps and simulate daytime RE. The difference between daytime RE and NEE (daytime Fc) was daytime GPP and the output variable of daytime model. The input variables of the daytime model were PAR, Ta, RH and the four seasonal indices. The hidden layer contained six nodes. The training and validation procedures were also repeated by 20 times and the median of the simulated GPP was used to fill the GPP gaps. Finally, the NEE was defined as RE–GPP. After gap-filling, the valid data were up to $84 \pm 7\%$ of the total observations.

## 2.3. Differentiating the biotic and climatic effects

After the gap-filling, the carbon (C) fluxes (NEE, GPP and RE) and the corresponding climatic variables were aggregated into the daily scale. A water balance index (WBI), which represents drought condition or hydrologic stress, was defined as ET–PPT, where ET is evapotranspiration calculated from LE (Yuan et al., 2009) and PPT is precipitation. In order to differentiate the biotic (BE) and climatic effects (CE) on the IAV in C fluxes, three model scenarios were defined for each site (Marcolla et al., 2011): variable model and climate (VMVC), constant model and variable climate (CMVC), and constant model and climate (CMCC).

Under the VMVC scenario, we first applied an additive model based on a spline smoother (Faraway, 2006; Zuur et al., 2007, Text S1) to simulate the relationships between daily C fluxes and climatic variables for each year. For each C flux, six climatic variables (PAR, Ta, Ts, PPT, VPD, WBI) were considered as potential explanatory variables,

$$\text{Flux} = s(\text{PAR}) + s(\text{Ta}) + s(\text{Ts}) + s(\text{PPT}) + s(\text{VPD}) + s(\text{WBI}) \quad (1)$$

where the $s()$ is the spline smoother of a specific variable, which can be linear or nonlinear depending on the degree of freedom (df). In order to avoid over-parameterization, the second-order Akaike information criterion (AIC$_c$, Burnham and Anderson, 2002) was used to determine the df of smoothers. The AIC$_c$ is calculated as:

$$\text{AIC}_c = -2 \times \log(\text{Likelihood}) + 2k\left(\frac{n}{n-k-1}\right) \quad (2)$$

where $k$ is the number of parameters, $n$ is the length of data and Likelihood is the likelihood function. The candidate models included all the possible combination of the potential variables. Therefore, there were $2^6$ candidate models. For every candidate model, the Akaike weight was calculated as shown below (Burnham and Anderson, 2002).

$$w_i = \frac{\exp(-1/2\Delta_i)}{\sum\limits_{r=1}^{64} \exp(-1/2\Delta_r)} \quad (3)$$

where $\Delta_i$ is the difference between the AIC$_c$ of the $i$th model and the minimum AIC$_c$ of all the 64 models. Model-averaged outputs with Akaike weights were considered as the modeled fluxes. This approach was applied to every year's data, separately, and the results were expressed as NEE$_{VMVC}$, GPP$_{VMVC}$ and RE$_{VMVC}$, respectively.

Under the CMVC scenario, the model averaging procedure with an additive model was applied for all years' data rather than separate year's data at each site. The additive model under this scenario was used to simulate the outputs of the VMVC scenario rather than the original observed data in order to exclude the influence of random errors. The model-averaged outputs under CMVC scenario were expressed as NEE$_{CMVC}$, GPP$_{CMVC}$ and RE$_{CMVC}$, respectively. Finally, under the CMCC scenario, the multiple-year average daily climatic variables were explanatory variables, and the outputs of the CMVC scenario were response variables. The outputs were expressed as NEE$_{CMCC}$, GPP$_{CMCC}$, and RE$_{CMCC}$.

According to the outputs of these three scenarios, we obtained the BE and CE on the IAV in C fluxes at the daily scale (Text S2). For example, the BE on the IAV in NEE (BE$_{NEE}$) was calculated as: NEE$_{VMVC}$−NEE$_{CMVC}$, because the differences between the VMVC and CMVC scenarios were caused only by changes in the models. The CE on the IAV in NEE (CE$_{NEE}$) was derived from: NEE$_{CMVC}$−NEE$_{CMCC}$, because the differences between the CMVC and CMCC scenarios were only caused by changes in climatic variables. The annual scale values were obtained by aggregating the daily values across the whole year.

## 2.4. Statistical analysis

In this study, we used the standard deviation (SD) to represent the IAV of variables, and the correlation coefficient ($r$) to describe the relationship between two variables. Since the majority (>77%) of the IAV in C fluxes resulted from annual BE and CE (Fig. S1a–c), we used the following equation to partition the BE and CE on the IAV in C fluxes.

$$\text{Var(C flux)} \approx \text{Var(BE + CE)} = \text{Var(BE)} + \text{Var(CE)} + 2\text{Cov(BE, CE)} \quad (4)$$
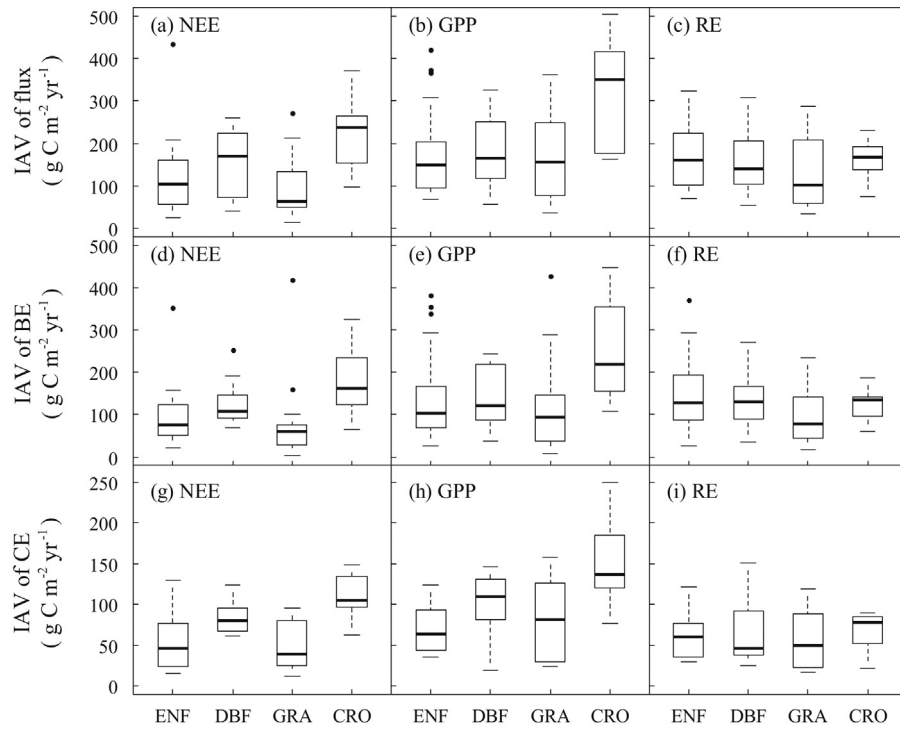
**Fig. 2.** Interannual variability (IAV) of C fluxes (a, b, c), biotic effects (BE, d, e, f) and climatic effects (CE, g, h, i) for evergreen needleleaf forest (ENF), deciduous broadleaf forest (DBF), grassland (GRA), and cropland (CRO). NEE, net ecosystem exchange of $CO_2$; GPP, gross primary productivity, RE, ecosystem respiration.

where C fluxes refer to the observed NEE, GPP, or RE; Var() is the variance; and Cov() is the covariance. Since both BE and CE contribute to the covariance, the relative magnitude of Var(BE) and Var(CE) determines the relative importance of BE and CE. So we defined the relative contribution of BE (CnBE) to the IAV in C fluxes as (Text S2):

$$CnBE = \frac{SD(BE)}{SD(BE) + SD(CE)} \tag{5}$$

where SD() is the square root of Var(). Because the partitioning of the IAV in NEE is not linear, the contributions of BE and CE to the IAV can be only expressed in relative values. More specifically, as the CnBE increases over 50%, the importance of the BE is relative to CE increases, and vice versa. The uncertainties in the CnBE were estimated by the bootstrapping method. The calendar years were resampled by 1000 times with the original sample size. Each time, the CnBE was calculated from the corresponding BE and CE in the resampled years. The 95% confidence interval was the range between 2.5 and 97.5% percentiles of the 1000 CnBE

values. To investigate the effects of timespan of available data on the uncertainties in CnBE, the bootstrapping with a sample size from 5 to 20 years was conducted for each site, and the corresponding uncertainties were calculated.

To examine which effect (i.e., climatic vs. biotic) was more responsible for the differences of the IAV in C fluxes among ecosystems, two correlation coefficients were compared. One was the correlation coefficient between SD(Flux) and SD(BE), which represented the relationship between the IAV of C fluxes and that of BE. The other was the correlation coefficient between SD(Flux) and SD(CE), which represented the relationship between the IAV of C fluxes and that of CE. The two correlation coefficients were dependent because they shared the variable SD(Flux). Therefore, the difference between them was tested by Williams's test (Williams, 1959). If the former correlation coefficient was larger than the latter, the BE was more important to the inter-site differences of the IAV.

All analysis approaches were applied in R version 2.15.2 (R Core Team, 2012). The nnet function from the nnet package was used to

**Table 1**

Correlation coefficients ($r$) between the statistics for C fluxes and climate characteristics for separate ecosystem types. Mean(), average; sd(), standard deviation.

| ENF | Ta | PPT | DBF | Ta | PPT | GRA | Ta | PPT | CRO | Ta | PPT |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean(NEE) | −0.58** | −0.56** | Mean(NEE) | −0.42 | −0.29 | mean(NEE) | 0.23 | 0.28 | Mean(NEE) | 0.09 | −0.32 |
| sd(NEE) | 0.45* | 0.45* | sd(NEE) | 0.11 | 0.23 | sd(NEE) | −0.09 | 0.25 | sd(NEE) | −0.48 | 0.22 |
| sd($BE_{NEE}$) | 0.40 | 0.50* | sd($BE_{NEE}$) | 0.11 | 0.41 | sd($BE_{NEE}$) | 0.10 | 0.31 | sd($BE_{NEE}$) | −0.29 | 0.59 |
| sd($CE_{NEE}$) | 0.51* | 0.46* | sd($CE_{NEE}$) | 0.21 | −0.00 | sd($CE_{NEE}$) | −0.03 | 0.53* | sd($CE_{NEE}$) | −0.72 | 0.72 |
| mean(GPP) | 0.68** | 0.75** | Mean(GPP) | 0.36 | 0.41 | mean(GPP) | −0.08 | 0.83** | Mean(GPP) | −0.58 | 0.40 |
| sd(GPP) | 0.32 | 0.19 | sd(GPP) | −0.09 | 0.35 | sd(GPP) | −0.12 | 0.75** | sd(GPP) | −0.31 | 0.32 |
| sd($BE_{GPP}$) | 0.38 | 0.31 | sd($BE_{GPP}$) | 0.26 | 0.48 | sd($BE_{GPP}$) | 0.01 | 0.60* | sd($BE_{GPP}$) | −0.20 | 0.55 |
| sd($CE_{GPP}$) | 0.24 | 0.07 | sd($CE_{GPP}$) | 0.16 | 0.03 | sd($CE_{GPP}$) | 0.25 | 0.72** | sd($CE_{GPP}$) | −0.15 | 0.94** |
| mean(RE) | 0.46* | 0.55** | Mean(RE) | −0.19 | 0.03 | mean(RE) | −0.06 | 0.83** | Mean(RE) | −0.77* | 0.34 |
| sd(RE) | 0.31 | 0.42 | sd(RE) | −0.21 | 0.28 | sd(RE) | −0.01 | 0.73** | sd(RE) | −0.42 | 0.47 |
| sd($BE_{RE}$) | 0.27 | 0.46* | sd($BE_{RE}$) | −0.27 | 0.22 | sd($BE_{RE}$) | 0.02 | 0.69** | sd($BE_{RE}$) | −0.41 | 0.75 |
| sd($CE_{RE}$) | 0.26 | 0.14 | sd($CE_{RE}$) | −0.21 | −0.07 | sd($CE_{RE}$) | 0.09 | 0.75** | sd($CE_{RE}$) | 0.27 | 0.66 |

* Significant at $P < 0.05$;
** Significant at $P < 0.01$. ENF, evergreen needleleaf forest; DBF, deciduous broadleaf forest; GRA, grassland; CRO, cropland. Ta, air temperature; PPT, precipitation. NEE, net ecosystem exchange; GPP, gross primary productivity; RE, ecosystem respiration. BE, biotic effect; CE, climatic effect.
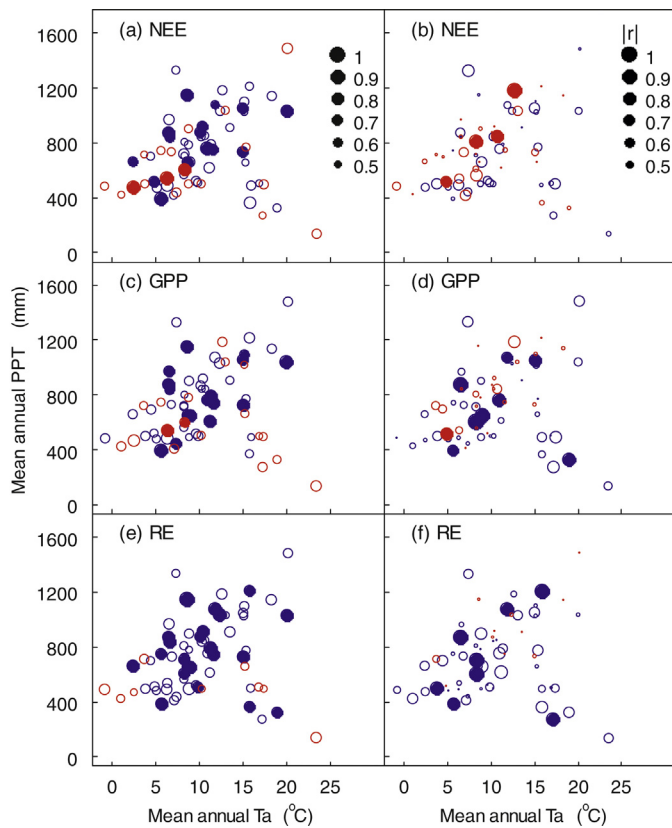
**Fig. 3.** The relative contribution of BE (or CE) to the IAV of C flux (CnBEs, a, c, e), and the correlation ($r$) between BE and CE (b, d, f) at the ecosystem scale in the Ta-PPT climatic domain. For a, c, and e, blue circles indicate CnBE, red circles indicate 1-CnBE, and filled circles indicate the value is larger than 0.5 at the significance level of $P < 0.05$. For b, d, and f, blue circles indicate $r > 0$, and red circles indicate $r < 0$, filled circles indicate that the $r$ is different from zero at the significance level of $P < 0.05$. The size of the circles represents the magnitude of the values, and the references is shown by black filled circles at the top right in a, and b. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** The relationships between CnBEs and mean climatic conditions (Ta and WBI) across all sites. WBI, water balance index, is calculated as evapotranspiration minus precipitation.

train the ANN models, the gam function from mgcv package was used to conduct additive modeling, and the r.test function from psych package was used for Williams's test.

## 3. Results

### 3.1. The IAV in C fluxes, biotic (BE) and climatic effects (CE)

The IAV in C fluxes, BE and CE showed large variation among ecosystems, but there was no significant difference among biomes (Fig. 2). The IAV in NEE, $BE_{NEE}$, and $CE_{NEE}$ was 13-434, 4-419 and 12-125 g C m$^{-2}$ yr$^{-1}$, respectively (Fig. 2a,d,g). Precipitation strongly drove the inter-site variation of the IAV in GPP, the BE on the IAV in GPP ($BE_{GPP}$), the CE on the IAV in GPP ($CE_{GPP}$), RE, the BE on the IAV in RE ($BE_{RE}$), and the CE on the IAV in NEE ($CE_{RE}$) among grasslands ($0.36 < r^2 < 0.56$, $P < 0.05$, Table 1). Among the evergreen needleleaf forests (ENFs), both temperature and precipitation were weakly correlated to the IAV in NEE and $CE_{NEE}$ ($0.20 < r^2 < 0.26$, $P < 0.05$, Table 1). For deciduous broadleaf forests (DBF) and croplands, neither temperature nor precipitation could explain the inter-site variation in the IAV, except for the IAV in $CE_{GPP}$ in croplands, which was significantly correlated with precipitation ($r^2 = 0.88$, $P < 0.01$, Table 1).

### 3.2. Relative importance of BE and CE at the ecosystem level

On average, the relative contributions of BE to the IAV in NEE ($CnBE_{NEE}$), GPP ($CnBE_{GPP}$) and RE ($CnBE_{RE}$) at the ecosystem level
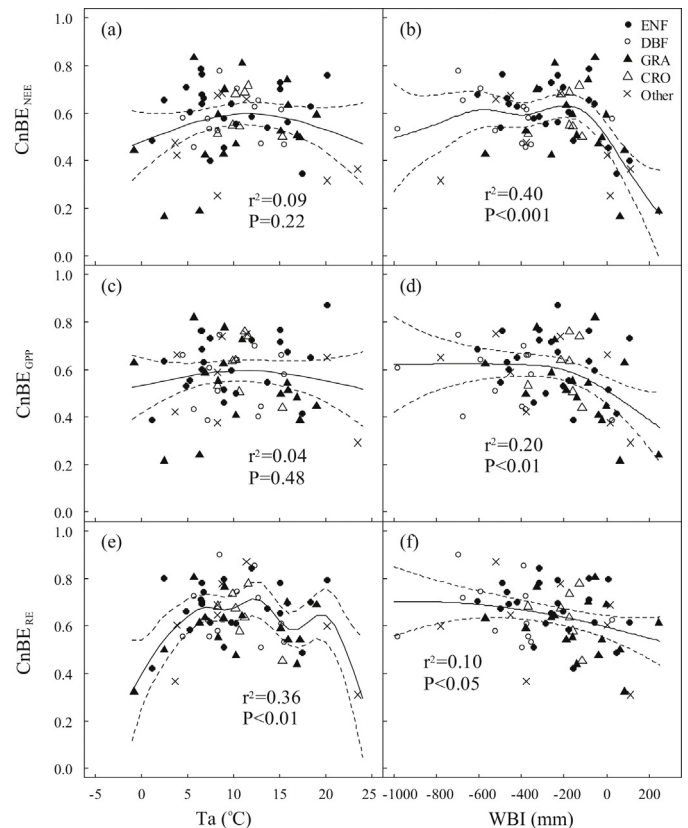
were $57 \pm 14\%$, $58 \pm 14\%$, and $64 \pm 13\%$, respectively, across all study sites. Although BE was not always more important than CE, the CnBE, especially the $CnBE_{RE}$, tended to be larger than 0.5 (Fig. 3a,c,e).

The inter-site difference of CnBE was related to the extent of the climatic stresses. Among the 19 sites with a WBI (water balance

**Table 2**
Correlation coefficients ($r$) between the standard deviation (SD) and the mean of carbon fluxes, the $r$ between the SD of carbon fluxes and the SD of biotic effects (BE), and between the SD of carbon fluxes and the SD of climatic effects (CE), and the comparison of the two kinds of $r$. ENF, evergreen needleleaf forest; DBF, deciduous broadleaf forest; GRA, grassland; CRO, cropland.

| Ecosystem | Flux | mean(C flux) | SD(BE) | SD(CE) | P-value | $n^*$ | $n$ |
|---|---|---|---|---|---|---|---|
| ENF | SD(NEE) | −0.52[*] | 0.94[**] | 0.84[**] | 0.049 | 22 | 22 |
| | SD(GPP) | 0.43[*] | 0.95[**] | 0.52[*] | <0.001 | 8 | 22 |
| | SD(RE) | 0.45[*] | 0.92[**] | 0.74[**] | 0.025 | 18 | 22 |
| DBF | SD(NEE) | 0.36 | 0.65[*] | 0.52 | 0.68 | 215 | 12 |
| | SD(GPP) | 0.21 | 0.89[**] | 0.48 | 0.041 | 12 | 12 |
| | SD(RE) | 0.55 | 0.87[**] | 0.56 | 0.12 | 18 | 12 |
| | | 0.55 | | | | | |
| | | 0.55 | | | | | |
| GRA | SD(NEE) | −0.0097 | 0.84[**] | 0.51[*] | 0.049 | 16 | 16 |
| | SD(GPP) | 0.86[**] | 0.90[**] | 0.78[**] | 0.20 | 33 | 16 |
| | SD(RE) | 0.84[**] | 0.92[**] | 0.86[**] | 0.33 | 55 | 16 |
| CRO | SD(NEE) | −0.37 | 0.82[*] | 0.46 | 0.23 | 14 | 7 |
| | SD(GPP) | 0.47 | 0.82[*] | 0.33 | 0.16 | 11 | 7 |
| | SD(RE) | 0.67 | 0.77[*] | 0.45 | 0.39 | 24 | 7 |

[*] Significant at $P < 0.05$.
[**] significant at $P < 0.01$. P-values are calculated using Williams's test. If P is lower than 0.05 there is a significant difference between the two kinds of $r$. If the actual site number ($n$) exceeds the critical site number ($n^*$), the P value would be lower than 0.05 according to Williams's test.
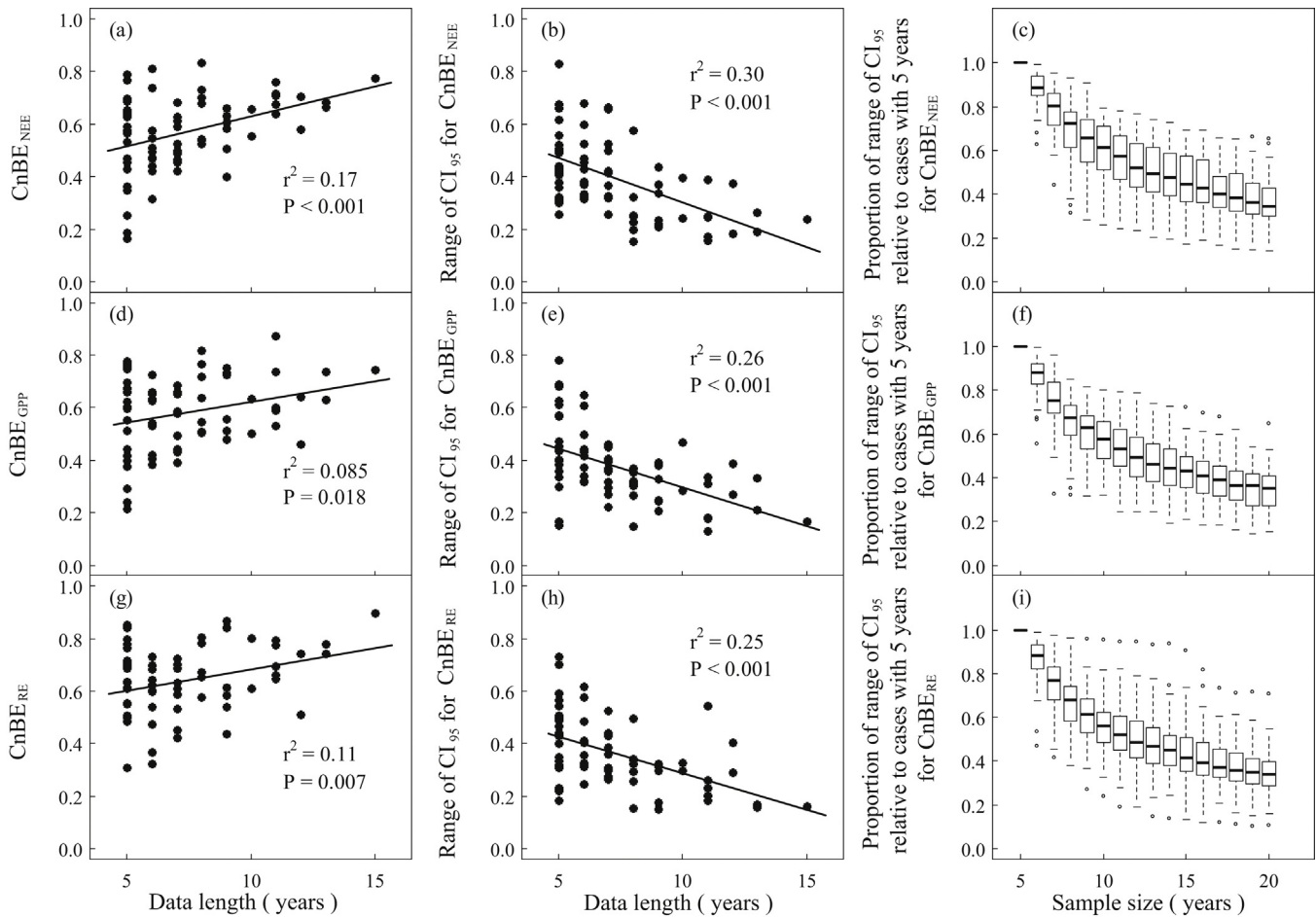
**Fig. 5.** The relationship between the data length and the estimation (a, d, g) and uncertainty (b, e, h) of CnBE, and the reductions in the proportion of uncertainty using a larger sample size relative to the uncertainty when using a sample size of 5 years (c, f, i).

index as an indicator of hydrologic stress) $> -100 \, \text{mm yr}^{-1}$, CnBE$_{NEE}$ significantly decreased with increasing WBI ($r^2 = 0.60$, $P < 0.001$, Fig. 4b). However, the impact of water stress on CnBE$_{GPP}$ and CnBE$_{RE}$ was not obvious (Fig. 4d,f). The temperature did not significantly affect CnBE$_{NEE}$ or CnBE$_{GPP}$ (Fig. 4a,c). When MAT was lower than 7 °C across the 18 sites, the CnBE$_{RE}$ was positively correlated with the temperature ($r^2 = 0.49$, $P < 0.01$). In addition, vegetation type, stand age, vegetation height, and disturbance regime did not significantly affect the spatial variation of CnBE (Fig. S2).

Data length (i.e., the timespan of the available data) was another factor influencing the magnitude and uncertainty of CnBE (Fig. 5). The sites with longer data tended to have a larger CnBE and less uncertainty (Fig. 5a,b,d,e,g,h). The bootstrapping results with different sample size (5–20 years) showed that, relative to the 5-years data, the 10- and 15-years data significantly reduced the uncertainty by 40% and 60%, respectively (Fig. 5c,f,i).

### 3.3. Relative importance of BE and CE in the inter-site differences of IAV

Overall, the differences of the IAV in NEE among ecosystems can be attributed more to BE than CE. The IAV in BE explained 72%, 83%, and 81% of the variations of IAV in NEE, GPP and RE, respectively (Fig. 6b,f,j), while the IAV in CE only explained 37%, 38%, and 44%, respectively (Fig. 3c,g,k). Williams's test showed that these differences were significantly for NEE ($t_{64} = 3.88$, $P < 0.001$), GPP ($t_{64} = 5.54$, $P < 0.001$) and RE ($t_{64} = 4.47$, $P < 0.001$), respectively.

The BE was also more important than CE in determining the inter-site differences of the IAV in C fluxes at the biomes scale

(Table 2). In ENF, compared to the IAV in CE, the IAV in BE explained 18%, 63%, and 30% more inter-site variance of the IAV in NEE, GPP, and RE, respectively (Table 2). In DBF, the differences were 15%, 56%, and 44% for IAV in NEE, GPP, and RE, respectively (Table 2), although the latter two were non-significant. In grasslands, the BE$_{NEE}$ was 45% more important than CE$_{NEE}$ to the inter-site variance of the IAV in NEE (Table 2). For croplands, the differences were also large (46%, 56%, and 39% for NEE, GPP and RE, respectively), although the results were not significant due to the small sample size (Table 2).

### 3.4. Relationships between BE and CE

Negative correlations between BE$_{NEE}$ and CE$_{NEE}$ were found at four sites (Fig. 3b), and that between BE$_{GPP}$ and CE$_{GPP}$ was only at one site (Fig. 3d). Significant and positive correlations between BE$_{GPP}$ and CE$_{GPP}$ and between BE$_{RE}$ and CE$_{RE}$ were found at eight sites, respectively (Fig. 3d,f). On the biome scale, BE and CE were independent in DBFs and croplands, while a very weak relationship (all $r^2$ about 0.1, $P < 0.001$) was found in ENFs (Fig. 7). For grasslands, there was a stronger correlation between BE$_{GPP}$ and CE$_{GPP}$ ($r^2 = 0.27$, $P < 0.001$, Fig. 7g), and between BE$_{RE}$ and CE$_{RE}$ ($r^2 = 0.30$, $P < 0.001$, Fig. 7k). In addition, water condition played a critical role in regulating the relationship between BE and CE. The BE and CE were independent for the ecosystems with a WBI less than $-500 \, \text{mm}$ (Fig. 8a). The relationship was weak for the ecosystems with WBI between $-500$ and $0 \, \text{mm}$ ($r < 0.3$, Fig. 8b,c), and stronger for the drought ecosystems (WBI $> 0$, $r > 0.45$; Fig. 8d,e).
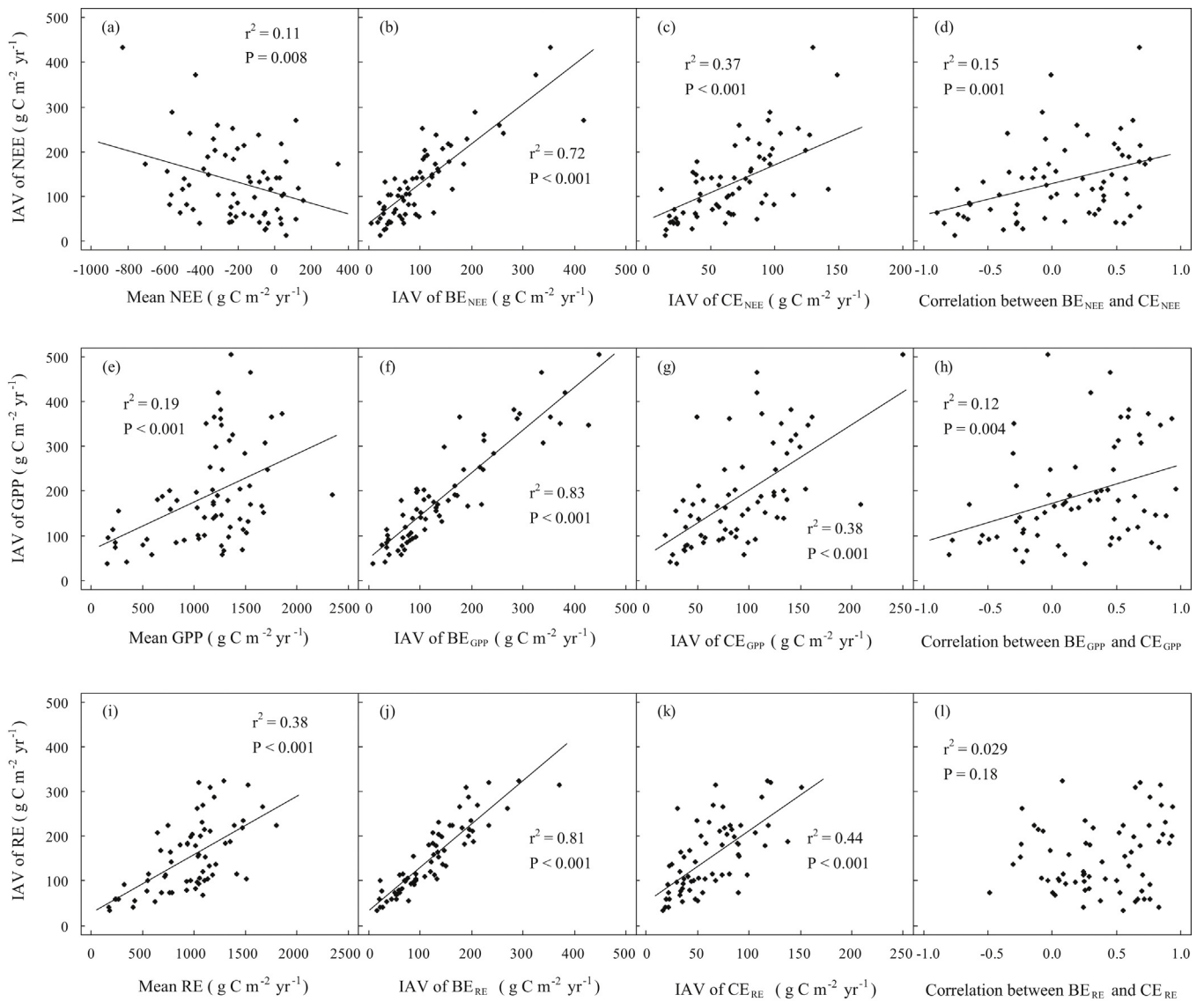
**Fig. 6.** The relationships between the IAV in C flux and the mean annual flux (a, e, i), the IAV in BE (b, e, j), the IAV in CE (c, f, k), and r between BE and CE (d, g, l) across all study sites.

## 4. Discussion

### 4.1. Relative contribution of BE to the IAV in C fluxes at the ecosystem scale

The IAV in NEE is usually driven by climatic (Barr et al., 2007; Wen et al., 2010; Jongen et al., 2011) and biotic drivers (Aeschlimann et al., 2005; Dragoni et al., 2011; Xiao et al., 2011) in terrestrial ecosystems. However, only a few studies have examined the relative contribution of BE (CnBE) and CE to the IAV in NEE, which varied largely among different ecosystems (Richardson et al., 2007; Teklemariam et al., 2010; Wu et al., 2012). In this study, we applied an additive model and a model averaging technique to partition the IAV in C fluxes into BE and CE. Our results showed that climatic stresses (e.g., low temperature and water stress) significantly decreased CnBE (Fig. 4), largely resulting from the inhibition of plant and microbial activity that increased with stress intensity while physiological acclimation or genetic adaptation to stresses declined (Levitt, 1980; Schulze et al., 2005).

Climatic stresses can make ecosystems develop multiple mechanisms to acclimate or adapt. At the individual level, plant biomass is allocated to leaves, stems, and roots to minimize the multiple environmental limitations (Poorter et al., 2012). Under prolonged cold weather and drought stress, the plants are forced to invest more biomass in roots (Poorter et al., 2012), which constrains the allocation pattern and decreases the CnBE. At the community level, both intra- and inter-specific variations in plant traits are important sources of ecosystem functioning stability (Loreau and de Mazancourt, 2013), which might be restricted by long-term climatic stresses because only those species with particular similar traits can survive in severe environments. At the ecosystem level, with the increase of water stress, the apparent water use efficiency (WUE) gradually approaches to the intrinsic WUE, which can be retained in prolonged drought conditions across all biomes, resulting in a convergent WUE and a small CnBE (Huxman et al., 2004; Ponce-Campos et al., 2013).

Climatic stresses affected photosynthesis and respiration differentially (Shi et al., 2014). In general, GPP was more sensitive to drought than RE (Schwalm et al., 2010). Our results showed that water stress decreased the $CnBE_{GPP}$ more than $CnBE_{RE}$ among sites with a mean annual WBI > −100 mm (Fig. 4d,f), probably because photosynthesis was primarily driven by available water
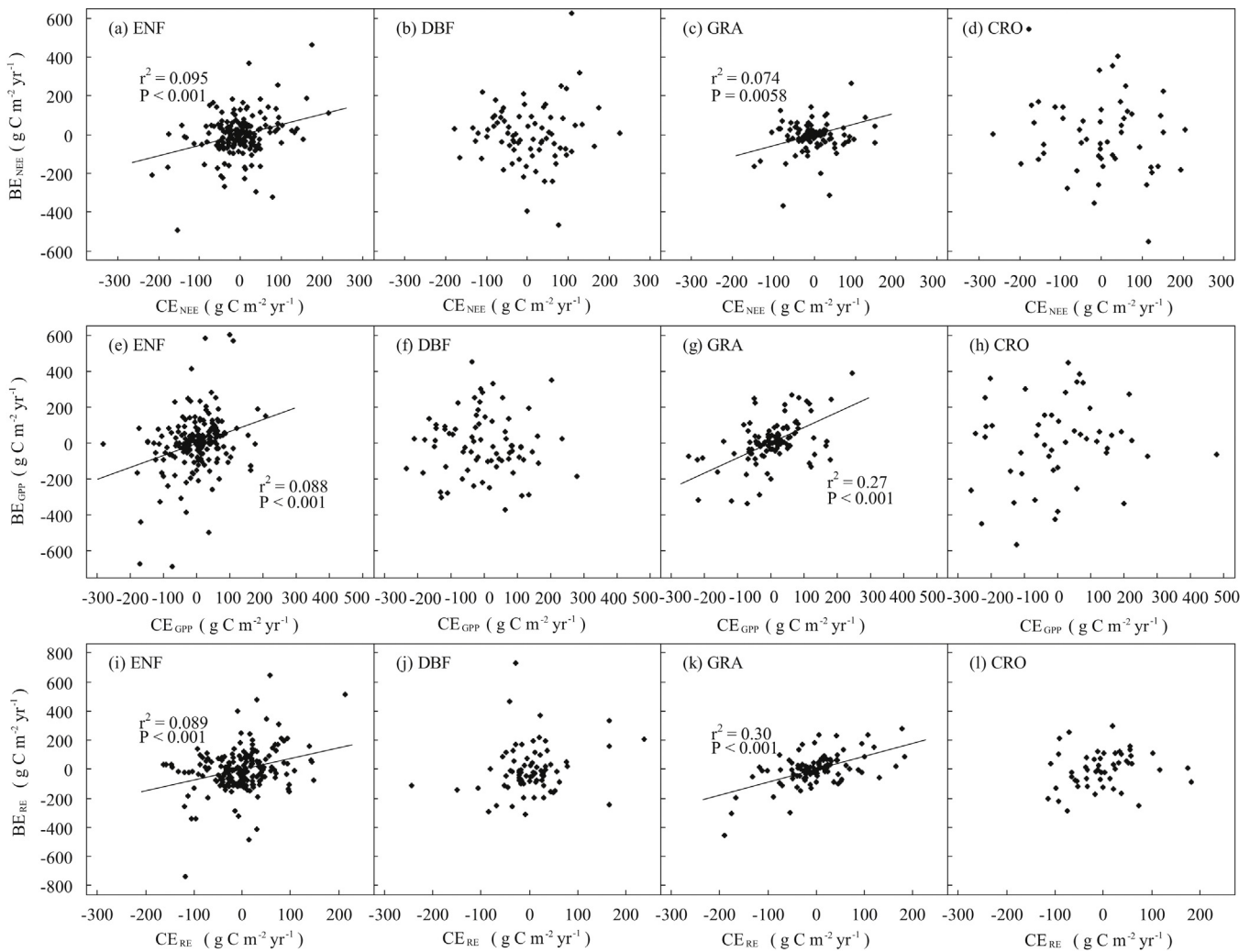
**Fig. 7.** The relationship between BE and CE for ENF (a, e, i), DBF (b, f, j), GRA (c, g, k) and CRO (d, h, l). Every point represents the value at one year.

while heterotrophic respiration was a C pool-controlled process at the situation of long-term drought (Shi et al., 2014). In addition, although the thermal acclimation of photosynthesis and respiration was found widely at both species and ecosystem scales, the different responses of these two processes to low temperature have not been well studied (Atkin and Tjoelker, 2003; Way and Yamori, 2014; Niu et al., 2012). However, we found that among the 18 sites where the MAT was <7 °C, lower temperature decreased the $CnBE_{RE}$ but not $CnBE_{GPP}$ (Fig. 4c,e), likely stemming from that the cold-tolerant species were able to maintain photosynthesis at low temperature via photoacclimation in order to balance the energy flow (Ensminger et al., 2006), while soil microbes were inactive.

Although the climatic drivers were often found to drive the IAV in NEE, some studies suggested that biotic drivers might be a more critical force. For example, Janssens et al. (2001) suggested that substrate supply was more important than temperature in affecting RE across European forests. Dios et al. (2012) pointed out that the endogenous processes drove a large part of the variation in NEE even at the daily scale. Consistent with these results, we found that, among the 36 sites with a WBI < −100 mm and MAT > 7 °C, 32 sites had a $CnBE_{NEE}$ larger than 0.5 (Fig. 4a). This might be because ecosystems under the climate optimum often reached their photosynthetic and respiratory potentials, resulting in the larger contribution of BE (compared to CE) to the IAV in NEE. However, the biotic properties of ecosystems (e.g., stand age, plant

height) had no clear influence on $CnBE_{NEE}$ (Fig. S2a–c), although they might theoretically impact the sensitivity of ecosystems to climatic variations. For example, ecosystem type was suggested as a factor related to the $CnBE_{NEE}$ with the largest value in grassland, followed by deciduous forest, evergreen forest, and peatland (Hui et al., 2003; Polley et al., 2008; Richardson et al., 2007; Teklemariam et al., 2010; Wu et al., 2012). Young stands might tend to have larger $CnBE_{NEE}$ due to their rapid growth. However, our results did not confirm these expectations, even when we excluded the confounding factors by the multiple regression method.

Disturbance and management practice were expected to weaken the relationship between C fluxes and climatic variables, resulting in a larger CnBE. However, no clear pattern was found in our study (Fig. S2d). To factor out the confounding effects, we examined some adjacent ecosystems with similar climate and vegetation but with different disturbances. Although the $CnBE_{NEE}$ of a managed forest (0.63) was larger than that of a neighboring unmanaged forest (0.47) at Arizona, USA, the opposite result was also found in a previous study on two grasslands (one grazed and one ungrazed) in North Dakota, USA (Polley et al., 2008). Moreover, different disturbance regimes seemed to influence the CnBE differentially. For three adjacent forests in Maine, USA, the one with selective logging had a larger $CnBE_{NEE}$ (0.77), whereas the natural one and a forest with N addition had similarly lower CnBE (0.66 and 0.64, respectively). It is thus difficult to draw a clear conclusion on the explicit role of disturbance because of the insufficient dataset.
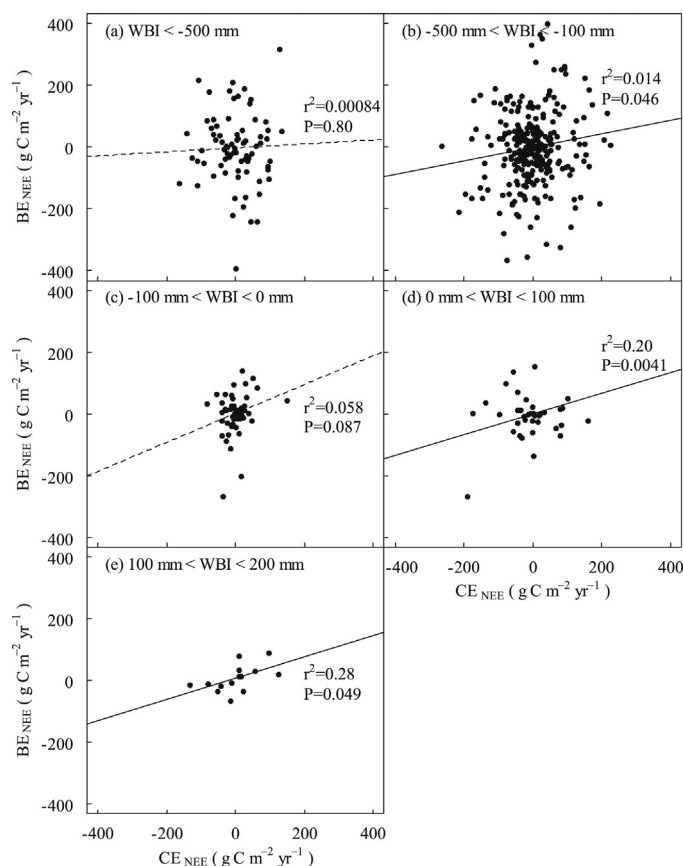
**Fig. 8.** The relationship between *BE* and *CE* for the ecosystems with WBI < −500 mm, −500 mm < WBI < −100 mm, −100 mm < WBI < 0 mm, 0 mm < WBI < 100 mm, and WBI > 100 mm, respectively.

### 4.2. BE was more important to the inter-site differences of the IAV in C fluxes than CE

Both BE and CE are critical to the inter-site variations of the IAV in C fluxes (Ammann et al., 2009; Baldocchi et al., 2010; Jung et al., 2011). However, our results showed that the IAV in BE represented the IAV in C fluxes very well, whereas that in CE largely underestimated them (Fig. 6b,c,f,g,j,k). This is probably because the inter-site pattern is largely determined by the long-term climatic and biotic conditions of ecosystems, which were characterized by BE rather than CE. In addition, the time lag in C cycling processes may also be important to the IAV in C fluxes. For example, Marcolla et al. (2011) pointed out that, without the BE, the actual delay between GPP and RE could not be represented since the $CE_{GPP}$ and $CE_{RE}$ both synchronized with climatic variation, while the scenario with BE only represented the magnitude of IAV well. The difference of this lag between and within biomes can result from the different bottle-neck processes of photosynthesis production, stand age, plant height, root depth, physiology, and growth stage (Kuzyakov and Gavrichkova, 2010), and therefore, resulted in different IAVs in BE and C fluxes. Other modelling studies also highlighted the importance of biotic drivers, such as leaf area index and soil C/N ratio, to spatial patterns of C fluxes (Migliavacca et al., 2011; Ngao et al., 2012).

The importance of BE in the IAV in C fluxes suggested that, even within the biomes (e.g., ENFs, Table 2), although CE contributed to a large part of IAV in C fluxes, the BE should not be ignored. For the ecosystems without water stress, the BE undoubtedly controlled the inter-site variation of IAV since it was the main source of IAV in C fluxes in these ecosystems. In dry ecosystems, although the CnBE

declined with the increase of water stress, the positive correlation between BE and CE in these ecosystems still caused a tight relationship between the IAV in BE and C fluxes (Fig. 8). Consequently, the IAV in BE was a good indicator of the IAV in C fluxes regardless of the water conditions or vegetation types (Fig. 6; Table 2). Therefore, considering the spatial variations of BE will practically improve the model performance, which can be represented by different biotic drivers or model parameter values.

In grasslands, the CE explained the inter-site differences of the IAV in GPP and RE well, but not NEE (Table 2). This might be due to the different features of CE and BE. For CE, we assumed that ecosystem responses to climatic variation did not change interannually. Therefore, tight coupling between GPP and RE in grasslands damped the relationship between climate and $CE_{NEE}$. However, the interannual changes in photosynthetic and respiratory responses were not in-phase, probably due to the different acclimation abilities of these two processes. Overall, the BE well explained the inter-site differences of IAV not only in GPP and RE, but also in NEE for all biomes (Table 2). Therefore, incorporating the BE into process models properly might be a general strategy to scale the IAV in NEE from the ecosystem to the regional level.

### 4.3. Biotic responses of C cycling to climatic variations

The correlation between BE and CE can reveal the biotic responses of C cycling to climatic variations. The sign of the correlation coefficient depends on the relationships between climatic and biotic drivers (Ricciuto et al., 2008; Krishnan et al., 2006; Tjoelker et al., 2001). The relative contributions of these relationships determine the ultimate correlation between BE and CE in an ecosystem. Our results showed that the BE was independent of CE in most sites (Fig. 4b,d,f), which may result from multiple controlling drivers and different responses of plant species to the changing climate in an ecosystem. Studies on photosynthetic adjustment to temperature at the species level suggested that photosynthetic adjustments could be constructive (acclimation) or detractive (Way and Yamori, 2014). The acclimation of respiration to temperature has usually been characterized by the relationship between $Q_{10}$ and temperature, which has been confronted with contrary evidences (Mahecha et al., 2010; Tjoelker et al., 2001). Similarly, diverse drought-tolerant or resistant traits of different species have also been found in forests and grasslands (Craine et al., 2013; Poorter and Markesteijn, 2008).

A previous study found a strong negative correlation between BE and CE in a subtropical plantation, which might be due to the single dominant controller (water condition) and drought resistant property of the dominant species in this relatively simple community composition (Shao et al., 2014). However, we found a positive correlation between BE and CE in dry ecosystems (Fig. 8). This might be because of the differential impacts of short- and long-term stresses (Mendivelso et al., 2014). In the above mentioned plantation, the annual precipitation was high (about 1500 mm) with a summer drought, which allowed the plant physiological traits to recover after the stress period (van der Molen et al., 2011). In addition, dry ecosystems in this study were characterized by long-term water deficit, which might have different effects from the short-term drought. For example, Mendivelso et al. (2014) found that tree species in a dry forest can be tolerant to short-term drought but not long-term water stress due to their failure to access deep soil water.

At the community level, although the species composition might shift according to the water condition (Craine et al., 2013), the photosynthetic rate might inevitably be constrained by water stress due to the high cost of maintaining photosynthesis. To take an extreme instance, drought can even cause the mortality of plants due to hydraulic failure and carbon starvation, and thus reduced the

ecosystem productivity (McDowell et al., 2008; Niu et al., 2014). The direct effect of water stress is usually accompanied by reduction of leaf area index, maximum photosynthetic rate, and respiratory substrate, and the changes in plant morphology and microbe community, which might further reduce the ecosystem physiological rates (Bahn et al., 2008; van der Molen et al., 2011).

At the biome scale, BE was independent with CE in DBFs, and very weakly correlated to CE in ENFs, while the two effects were correlated with each other more strongly in grasslands (Fig. 7). The difference might derive from both the climate and vegetation characteristics of the ecosystems. Grasslands are usually located in arid and semiarid areas (Woodward and Lomas, 2004), resulting in the positive correlation between BE and CE, as discussed above. In addition, the shallow root systems prevented the grasses from taking up the deep soil water (Jackson et al., 1996). Trees can better buffer the drought effects due to their deeper roots, larger amount of water storage, and associated mycorrhizal fungi (van der Molen et al., 2011). The ecophysiological changes seen in croplands were largely related to managements (i.e., irrigation, fertilization, rotation), which may be independent of the climatic variations.

### 4.4. Uncertainty, model limitations, and implications

Our results highlighted the importance of BE in determining the IAV in C fluxes, which was largely affected by the degree of drought stress. However, the observed C fluxes and the partitioning approach might cause biases in the estimated BE or CE in a few sources. First, systematic and random errors may introduce some uncertainty (Mauder et al., 2013), but the standardized data-processing approaches used have reduced the systematic error to typically 5–10% and the aggregated random error on an annual scale was generally about 5% (Baldocchi, 2008). The approach of partitioning the IAV in NEE into BE and CE is thus relatively reliable according to the comparison between $BE_{NEE}$ (or $CE_{NEE}$) and $BE_{RE} - BE_{GPP}$ (or $CE_{RE} - CE_{GPP}$; Fig. S1d,e). Second, the estimated CnBE tended to increase with the timespan of the available data (Fig. 5a,d,g), which might be caused by the sampling effect, because the potential ecophysiological changes may be easier to be captured by longer observations in ecosystems. Meanwhile, the uncertainty of CnBE in an ecosystem reduced with the longer data (Fig. 5b,c,e,f,h,i). The significant difference between the importance of BE and CE to the inter-site variation of the IAV in C fluxes was easily monitored with more sites (Table 2). Our results suggested that the data should be longer than 10 years when the CnBE was estimated, and at least 20 sites were required to investigate the spatial patterns.

Our approach effectively estimated the relative contribution of BE to the IAV in C fluxes, but the exact biotic drivers can only be examined with the corresponding biological data, which were often lacking. In addition, the study sites were all located in the Northern Hemisphere and the dominant biomes were ENF, DBF, grassland, and cropland (Fig. 1; Table S1). Whether the situations in the Southern Hemisphere and other typical biomes (tropical rain forest, tundra, and wetland) are consistent with our results still remains unclear.

The CnBE quantifies the importance of ecosystem responses to the IAV in C fluxes relative to climatic variations. The importance of BE highlighted in this study suggested that the sources of BE are crucial in understanding and predicting the ecosystem functioning in the future. Theoretically, the changes in BE within an ecosystem mainly result from three aspects. The first is the internal changes of ecosystems (e.g., plant growth and community succession) when there are no effects of climatic variations or disturbances. The second is the ecophysiological acclimation of ecosystems to climatic variations. The third includes the natural or human disturbances such as fire, hurricanes, grazing, logging, fertilization, irrigation,

and crop rotation. To partition the effects of these drivers, it is necessary to set up pairs of eddy-flux towers and conduct long-term observations on vegetation. For example, locating eddy-flux towers in neighboring ecosystems with similar climate and vegetation but different disturbance regimes might reveal the effects of disturbance (Dore et al., 2008; Polley et al., 2008). It is more difficult to manipulate the ecosystems to discover the influence of internal changes and ecophysiological acclimation. However, tracing the growth stage of plants and the community composition may provide valuable information.

The predicted ecosystem C fluxes in the future largely rely on the ability of models to capture the underlying mechanisms. However, current state-of-the-art C-cycle models failed to generate the interannual pattern of NEE (Keenan et al., 2012). According to our results, a lack of BE in the model might be one of the causes because these models usually use constant parameters and varied climate to simulate C fluxes. Therefore, the CnBE may be a useful indicator of the potential bias of current process models. The simulated C fluxes in ecosystems with lower CnBE might be more accurate than those with higher CnBE. In the light of the fact that the majority of study sites had a CnBE larger than 50%, it is very important to consider the long-term effects of biotic drivers in models for projecting the ecosystem responses to future climate change. However, this requirement faces some challenges. For example, the biological data relating to the IAV in NEE are not always available at eddy-flux sites, which need to pay more attention to observing biological processes related to C cycling. Parameterizing and evaluating models based on the data from a short temporal scale (e.g., half-hour and daily) inevitably overestimated the importance of climatic variations, resulting in the difficulty of detecting the BE that might be low-frequent signals compared to climatic variations and observational noises. Therefore, evaluating the model performance at multiple scales might be a critical procedure for bridging the gaps between the observed and simulated IAV in NEE.

Large changes in the CnBE indicate that ecosystems experience dramatic shifts in structure and/or functioning. Our results showed that climatic stresses decreased the CnBE. In the context of global change, the extreme climate events will occur more frequently, especially severe drought in many parts of the world (Dai, 2013). Therefore, the global terrestrial ecosystems will reduce their ability to regulate C fluxes due to the environmental change. More importantly, the functional change may be irreversible once the effects of climate change cross a certain threshold. For example, severe drought can trigger the mortality of trees, cause the pathogen and pest outbreaks, and increase fire risk, all of which might have a profound influence on C cycling (Reichstein et al., 2013; Zhang et al., 2015). The effects of these processes are difficult to eliminate even though the conditions recover quickly. This situation implies that terrestrial ecosystems may not have the ability to mitigate any further global warming, although they have contributed greatly to the global C sink over the most recent half century (Le Quéré et al., 2009).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2015.02.007.

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