Primary research article

Relative importance of climatic variables, soil properties and plant traits to spatial variability in net CO₂ exchange across global forests and grasslands

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ABSTRACT

Compared to the well-known drivers of spatial variability in gross primary productivity (GPP), the relative importance of climatic variables, soil properties and plant traits to the spatial variability in net ecosystem exchange of CO₂ between terrestrial ecosystem and atmosphere (NEE) is poorly understood. We used principal component regression to analyze data from 147 eddy flux sites to disentangle effects of climatic variables, soil properties and plant traits on the spatial variation in annual NEE and its components (GPP and ecosystem respiration (RE)) across global forests and grasslands. Our results showed that the largest unique contribution (proportion of variance only explained by one class of variables) to NEE variance came from climatic variables for forests (24%-30%) and soil properties for grasslands (41%-54%). Specifically, mean annual precipitation and potential evapotranspiration were the most important climatic variables driving forest NEE, whereas available

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soil water capacity, clay content and cation exchange capacity mainly influenced grassland NEE. Plant traits showed a small unique contribution to NEE in both forests and grasslands. However, leaf phosphorus content strongly interacted with soil total nitrogen density and clay content, and these combined factors represented a major contribution for grassland NEE. For GPP and RE, the majority of spatial variance was attributed to the common contribution of climate, soil and plant traits (50% - 62%, proportion of variance explained by more than one class of variables), rather than their unique contributions. Interestingly, those factors with only minor influences on GPP and RE variability (e.g., soil properties) have significant contributions to the spatial variability in NEE. Such emerging factors and the interactions between climatic variables, soil properties and plant traits are not well represented in current terrestrial biosphere models, which should be considered in future model improvement to accurately predict the spatial pattern of carbon cycling across forests and grasslands globally.

1. Introduction

Terrestrial ecosystems absorb about 30% of the carbon dioxide (CO_2) released by fossil fuel emissions and land use change, having great impact on climate change mitigation (Denman et al., 2007; Friedlingstein et al., 2019). The ability of the terrestrial ecosystem to absorb CO_2 is determined by the net CO_2 exchange between land and the atmosphere (NEE), which is the balance between gross primary productivity (GPP, absorption of CO_2 by ecosystem) and ecosystem respiration (RE, the release of CO_2 by ecosystem) (Chapin et al., 2006). Growing evidence from globally distributed eddy-covariance sites has shown large spatial variability in NEE globally, ranging from a carbon (C) sink of 1000 g C m^{-2} year^{-1} to a carbon source of 1300 g C m^{-2} year^{-1} (Baldocchi, 2008). Understanding the underlying drivers of the large spatial variability in NEE is important for predicting the global carbon budget under climate change (Lovenduski and Bonan, 2017; Bonan and Doney, 2018).

The spatial variability in NEE can, for example, be driven by climatic variables, soil properties and plant traits (Hirata et al., 2008; Fernández-Martínez et al., 2014a, 2014b; Chen et al., 2019). However, the relative importance of these three factors is still controversial. Peichl et al. (2013) found that the climate was the most important factor determining NEE across nine grasslands, whereas Chen et al. (2015; 2019) showed that the enhanced vegetation index (EVI) and leaf area index (LAI) were more important than climate across both Northern Hemisphere and global terrestrial ecosystems. Fernández-Martínez et al. (2014a) suggested that 19% of the variance in NEE across global forests was explained by nutrient availability, much larger than that explained by mean annual temperature (MAT) (9%) or stand age (5%). Some researchers suggest that water availability has a larger effect on NEE than temperature for Europe and the Northern Hemisphere (Reichstein et al., 2007; Chen et al., 2015), while others show the opposite pattern across North American forests (Yuan et al., 2009) and Asian ecosystems (Chen et al., 2013).

These inconsistent results could be for several reasons. First, different biomes might exhibit differential spatial patterns. Globally, the forests and grasslands together cover 54% of the total terrestrial area (Chen et al. 2015), with their GPP values up to 53.71± 4.83 Pg C yr^{-1} and 11.00 ± 0.31 Pg C yr^{-1}, respectively (Ma et al., 2015; Liang et al., 2017). Grasslands mainly exist in arid and semiarid regions, and they have shallow roots and labile herbaceous tissue (Mason and Zanner, 2005; Díaz et al., 2016). Forests, on the other hand, occupy more humid areas, have deep roots and produce recalcitrant woody tissues (Boyle 2005; Díaz et al., 2016). As a result of these morphological differences, forests and grasslands have different sensitivities towards environmental fluctuations (Shi et al., 2014; Song et al., 2014; Gao et al., 2019), and thereby climatic variables, soil properties and plant traits give a differential contribution to spatial variability in NEE. Most studies have focused on differential impact of climate on carbon fluxes between forests and grasslands (Reichstein et al., 2007; Yuan et al., 2009; Anderson-Teixeira et al., 2011; Shi et al., 2014), with little focused on effects of soil properties and plant traits, and their relative importance on NEE.

Second, the different conclusions can also result from the perspective on whether the factors important to GPP and RE will also be critical to NEE. Some studies suggested that the spatial NEE variability was mainly caused by factors important to either GPP or RE, such as temperature and precipitation (Valentini et al., 2000; Chen et al., 2013; Ahlström et al., 2015). Other studies pointed out that the factors critical to GPP or RE were not always the exact driver of spatial variability in NEE (Luyssaert et al., 2007; Anderson-Teixeira et al., 2011; Xu et al., 2016; Han et al. 2020). This is because NEE is a small signal compared to the two large opposing fluxes of GPP and RE, which means the parallel effects of a certain driver on GPP and RE may weaken its influence on NEE. Only using such drivers to simulate NEE might be one of the reasons that current global biogeochemical models maybe not able to precisely map the terrestrial NEE.

Reliable estimates of the relative importance of climatic variables, soil properties and plant traits require methods adequately relating these factors to carbon fluxes. However, few studies considered all the three classes of drivers, and those focused on one or two classes showed that the predictive power of them to the spatial variability in NEE was relatively low (10.1%-36.0%, Reichstein et al., 2007; Chen et al., 2013, 2015; Fernández-Martínez et al., 2014a; Chen et al. 2019). A possible reason is that the linear models used in these studies may underestimate the associations between carbon fluxes and driving factors if the underlying relationships were nonlinear (Wang et al., 2016; Zhang et al., 2016). Another difficulty is the collinearity among explanatory variables, which may mask the relative importance of each variable. To overcome these difficulties and obtain reliable estimations of the relative importance of climatic variables, soil properties and plant traits to spatial variability in NEE, we applied principal component regression (PCR) integrated principal component analysis (PCA) and generalized additive models (GAMs) to analyze a global dataset of multi-year averaged NEE data from 147 eddy covariance flux sites. Specifically, our objectives were (1) to estimate the relative contributions of climatic variables, soil properties and plant traits to the spatial variability in NEE, GPP and RE across global forests and grasslands, and (2) to reveal the different mechanisms underlying the spatial pattern of NEE of global forests and grasslands. Our results can inform biogeochemical models aimed at describing the spatial distribution of the CO_2 net exchange of terrestrial ecosystems.

2. Materials and methods

2.1. Data sources

2.1.1. Flux-tower-based carbon fluxes

The site-wise and multi-year averaged NEE, GPP and RE ($\geq$ 4 years, from 2000 to 2014) was acquired from the Fluxnet 2015 database (Tier1, https://fluxnet.fluxdata.org, Pastorello et al., 2020), Ameriflux (https://ameriflux.lbl.gov), Ozflux (http://ozflux.org.au/) and published data. In total, there were 980 site-years from 147 sites, including 74 forests, 44 grasslands, 5 shrublands, 7 wetlands and 17 croplands (Fig. 1; Table S1). We aimed to examine differencies in the driving factors of spatial variability in NEE among different biomes, and to quantify the relative importance of climatic variables, soil properties and plant traits. As the number of sites for shrublands, wetlands and

croplands were relatively small, we primarily focused on the forests and grasslands. The flux sites were combined into four datasets: All sites (a total of 147 sites) and forests and grasslands (FG; 118 sites), forests (74 sites) and grasslands (44 sites). The ecosystems other than forests and grasslands were included in dataset 'All sites' in order to investigate the ability of plant traits to explain the spatial variability in carbon fluxes regardless of the biome type.

2.1.2. Climatic variables

The climatic variables included incoming shortwave radiation (SW), mean annual temperature (MAT), mean annual precipitation (MAP), mean annual potential evapotranspiration (PET), and number of frost days (Frs), which were extracted from global data maps according to the geographic coordinates (Table 1). The global maps of monthly MAT, MAP, PET and Frs (2001 - 2014) were from the Centre for Environmental Data Analysis (version CRU TS 4.00, https://catalogue.ceda.ac.uk), and averaged into annual means. SW data (2007 - 2014) was from the NASA Earth Observatory (https://neo.sci.gsfc.nasa.gov/view.php?data setId=CERES_SWFLUX_M).

2.1.3. Soil properties

Soil properties included clay content (Clay), bulk density (BD), soil organic carbon (SOC), total nitrogen (TN), ratio of soil carbon and nitrogen (C:N), cation exchange capacity (CEC), soil pH and available water capacity (AWC, Table 1). BD, TN, AWC and C:N ratio were from Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS, Global Soil Data Task Group, 2000). Clay, SOC, CEC and pH were from the Harmonized World Soil Database (version 1.2, Fischer et al., 2008). All soil properties were averaged over a soil depth of 0-1.0 m.

2.1.4. Plant traits

Plant traits included leaf area index (LAI), plant height (H), specific leaf area (SLA), leaf nitrogen content (LN) and leaf phosphorus content (LP) (Table 1). Plant height was from Simard et al. (2011). Monthly gridded LAI was from NASA's Earth Observatory Team (MOD15 product), which were averaged into annual means. SLA, LN and LP were from the TRY database (Kattge et al., 2020), the largest global dataset of plant traits. Because of the important roles played by dominant species in regulating ecosystem functions (Grime, 1998; Lavorel and Garnier, 2002; Finegan et al., 2015), the dominant species-based traits were used to indicate the ecosystem-level plant traits (see details in Method S1).

2.2. Quantifying the relative contributions of climatic variables, soil properties and plant traits

The unique (proportion of variance that can be uniquely explained by a single predictor) and common contributions (proportion of variance that is explained by two or more different variables) of climatic variables, soil properties and plant traits to the spatial variability in carbon fluxes (NEE, GPP and RE) were determined by a deviance decomposition method based on principal component regression (PCR, Abdi and Williams, 2010). We chose to use this PCR approach because it minimizes the influence of multicollinearity and has the ability to feasibly account for the nonlinear relationships (Abdi and Williams, 2010; Faraway, 2016). The PCR consisted of two stages. In the first stage, principal component analysis was used to extract the principal components of the explanatory variables (Abdi and Williams, 2010). In the second stage, generalized additive models (GAM) was used to describe the relationships between principal components and carbon fluxes. We used GAM rather than a specified functional form in prior to deal with the potential nonlinear patterns, due to the complexity of the spatial relationships between carbon fluxes and their driving factors across global terrestrial ecosystems (Chen et al., 2013; Kondo et al., 2017; Chen et al., 2019; Tang et al., 2020). However, we acknowledge that the nonparametric methods such as GAM may suffer over-fitting problems and exhibit unrealistic relationships. To minimize this problem, we limited the potential degree of freedom (df) of the GAMs (see details below).

Specifically, we set seven model scenarios containing each class of explanatory variables and their potential combinations (Method S2). For each model scenario, to obtain the model which best explain the spatial variance in the carbon flux (NEE, GPP or RE), we applied a model selection technique. First, a series of candidate GAMs, with the principal components (PCs) being explanatory variables and carbon fluxes (NEE, GPP or RE) being response variable, were set:

$$Carbon flux = s(PC1, k = 3) + s(PC2, k = 3) + \ldots + s(PCi, k = 3) \qquad (1)$$

where the $s()$ is the spline smoother of a specific PC. All possible combinations up to eight PCs were allowed in the GAM. The curvature of smoother pattern depends on the df. To minimize the overfitting problem, we set the largest possible df to 3 for each smoother. Furthermore, if the resulting df was close to 1, we used the linear relationship in the GAM, to make the model structure as simple as possible.

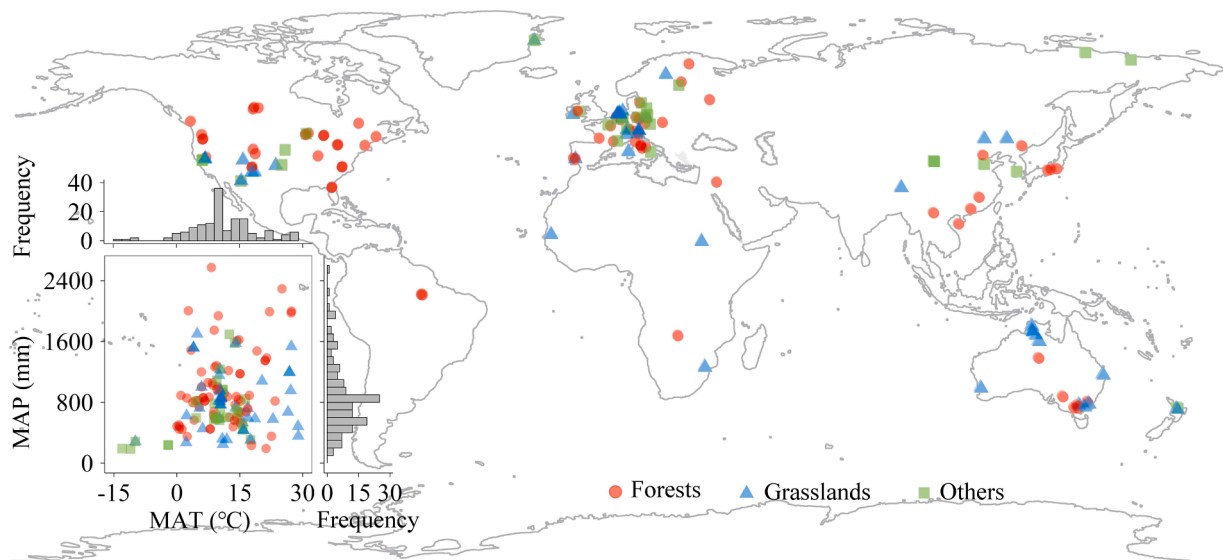The best model for each scenario was determined by model selection

Fig. 1. Flux sites included in this study. We used 74 forest and 44 grassland ecosystems. In addition, there were 29 other ecosystems, including 5 shrublands, 7 wetlands and 17 croplands sites. MAT, mean annual temperature; MAP, mean annual precipitation.

Table 1

The climatic variables, soil properties and plant traits used in this study. CEDA, Centre for Environmental Data Analysis; IGBP-DIS, Global Gridded Surfaces of Selected Soil Characteristics; HWSD, Harmonized World Soil Database.

Explanatory variables	Abbreviation	Unit	Year	Soil depth	Resolution	Data source
Climatic variables						
Mean annual temperature	MAT	°C	2001-2014		0.5°	CEDA (CRU TS 4.00)
Mean annual precipitation	MAP	mm	2001-2014		0.5°	CEDA (CRU TS 4.00)
Incoming shortwave radiation	SW	W m^{-2}	2001-2007		0.25°	NASA Earth Observatory
Mean annual potential evapotranspiration	PET	mm	2001-2014		0.5°	CEDA (CRU TS 4.00)
Number of frost days	Frs	days yr^{-1}	2001-2014		0.5°	CEDA (CRU TS 4.00)
Soil properties						
Clay content	Clay	%mass	0-100 cm	6%-46% 30 arc-second	HWSD (version 1.2)
Bulk density	BD	g cm^{-3}		0-100 cm	0.0833333°	IGBP-DIS
Soil organic carbon	SOC	%mass		0-100 cm	6%-46% 30 arc-second	HWSD (version 1.2)
Total nitrogen density	TN	g m^{-2}		0-100 cm	0.0833333°	IGBP-DIS
Available water capacity	AWC	mm		0-100 cm	0.0833333°	IGBP-DIS
Ratio of soil carbon and nitrogen	C:N	-		0-100 cm	0.0833333°	IGBP-DIS, calculated as total soil carbon density divided by TN
Soil pH	pH	-		0-100 cm	6%-46% 30 arc-second	HWSD (version 1.2)
Cation exchange capacity	CEC	mmol kg^{-1}		0-100 cm	6%-46% 30 arc-second	HWSD (version 1.2)
Plant traits						
Leaf area index	LAI	-	2000-2014		0.1°	NASA Earth Observatory
Specific leaf area	SLA	cm^2 g^{-1}			-	TRY database
Leaf nitrogen (N) content per leaf dry mass	LN	%			-	TRY database
Leaf phosphorus (P) content per leaf dry mass	LP	%			-	TRY database
Plant height	H	m			-	Simard et al., 2010

procedure based on Akaike information criterion (AIC) and Bayesian information criterion (BIC). It has been a long debate about the applications of AIC and BIC for model selection. Generally, AIC is more suitable in situations where sample size of data is relatively small compared to the complexity of true underlying processes (in which case the true model is usually not included in the candidate model set), while BIC is more suitable in situations when the sample size largely exceeds the complexity of true processes (in which case the true model can be in the candidate model set, Aho et al., 2014). Considering the potential differences of underlying mechanisms among different biomes (Archibald et al., 2009; Ahlström et al., 2015; Wood et al., 2012; Johnston et al., 2021), we used both AIC and BIC as the model selection criteria. If the results based on these two criteria were similar, our conclusions could be regarded as robust. In detail, the best model was the model with the largest deviance explained (DE) among models whose IC (AIC or BIC) values were between the minimum IC (IC$_{min}$) and IC$_{min}$ + 2, since the models with ΔAIC or ΔBIC less than 2 being considered not significantly different from the best model (Burnham and Anderson, 2002; Kass and Raftery, 1995). Once all the seven best models were obtained (one for each scenario), the unique and common contributions of climatic variables, soil properties and plant traits were quantified according to the DEs of the seven best models (Method S2).

In addition to the relative contribution of the three classes of variables, we also quantified the unique contribution of each original variable by using a similar procedure. For each variable i, a principal component analysis of the remaining 17 variables was conducted and the derived PCs were used as the potential explanatory variables of the GAMs. Model selection for the remaining 17 variables based on ICs and

DE, was used to obtain a best model (N1) excluding the variable i, whose DE was then indicated as DE$_{18-i}$. Then the variable i was added to the above best model (N2), and the corresponding DE was DE$_i$. The unique contribution of i was calculated as the difference between DE$_i$ and DE$_{18-i}$. When the unique contribution of a given factor was higher than the average value, its impact on NEE was shown based on N2.

2.3. Detecting the interactive effects among climatic variables, soil properties and plant traits

We also detected the interactive effects among climatic variables, soil properties and plant traits on spatial variability in carbon fluxes (NEE, GPP and RE). All possible two- and three-way interactive effects were detected based on the GAMs. For a certain interactive term, we constructed two GAMs to predict NEE, one with (M1) and another without (M2) the interactive term. The corresponding ICs (AICs or BICs) were IC$_1$ (AIC$_1$ or BIC$_1$) and IC$_2$ (AIC$_2$ or BIC$_2$), respectively. If IC$_2$ – IC$_1$ > 2, we considered the interactive effect statistically significant (Kass and Raftery, 1995; Burnham and Anderson, 2004).

The relative importance of each interactive effect was calculated as the weight (w_j, Akaike weight and posterior model probability for AIC and BIC, respectively) of the model containing this effect (Burnham and Anderson, 2004):

$$w_j = \frac{\exp\left(-\frac{1}{2}\Delta_j\right)}{\sum \exp\left(-\frac{1}{2}\Delta_j\right)} \tag{2}$$

where Δ_j is the difference between IC_1 of the M1 model with interaction j (AIC_{1j} or BIC_{1j}) and the minimum IC of all the M1 models IC_{min} (AIC_{min} or BIC_{min}). The relative importance of interactive effects were detected according to w_j. Only when the w_j was greater than 10.0% were the interactive effects of factors on NEE displayed.

2.4. Statistical analysis

The t-test was used to test the difference in NEE between forests and grasslands. Levene's test was applied to compare the spatial variance in NEE between forests and grasslands. All analyses were implemented in R version 4.0.2 (R Core Team, 2019). PCA, GAM and Levene's test were conducted by functions *prcomp, gam* (in *mgcv* package, Wood and Wood, 2015) and *leveneTest* (in *car* package, Fox et al., 2007), respectively.

3. Results

3.1. Spatial variability in NEE

Annual NEE greatly varied across the global terrestrial ecosystems (-226 $\pm$ 304 g C m^{-2} yr^{-1}, mean $\pm$ SD), with most ecosystems (118 of 147 sites) being carbon sinks (i.e., negative NEE). Both the magnitude and spatial variability of NEE in forests (-312 $\pm$ 363 g C m^{-2} yr^{-1}) were larger than those in grasslands (-103 $\pm$180 g C m^{-2} yr^{-1}) ($t_{113.02} =$ -4.16, $P < 0.001$; $F_{1,116} = 8.33, P < 0.001$). For both forests and grasslands, the spatial variability in NEE was driven by the covariance of GPP and RE, rather than the variance in GPP or RE (Fig. S1).

3.2. Relative contributions of climatic variables, soil properties and plant traits to spatial variability of NEE

Climatic variables, soil properties and plant traits influenced annual NEE differently (Fig. 2; Table S2). For NEE, GAMs including all three classes of variables explained 39.4%-40.2%, 53.7%-56.5% and 80.0%-
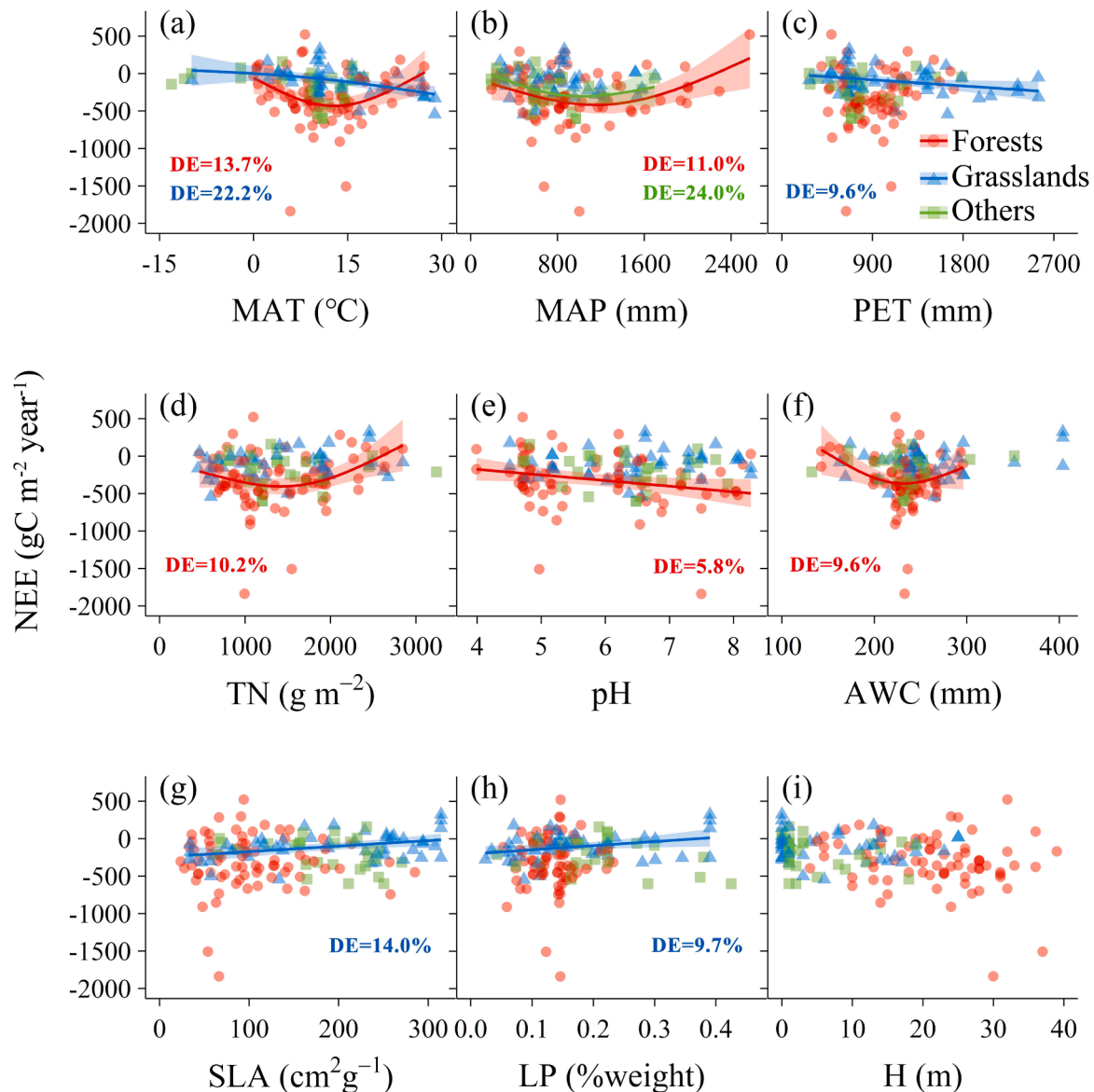

Fig. 2. Relationships between NEE and driving factors across forests, grasslands and other ecosystems. Only the significant relationships are shown ($P < 0.05$). The regression lines are based on the generalized additive models (GAMs). MAT, mean annual temperature; MAP, mean annual precipitation; PET, mean annual potential evapotranspiration; TN, soil total nitrogen density; AWC, available water capacity; SLA, specific leaf area; LP, leaf phosphorus content; H, plant height.

81.0% of the spatial variability across all sites, forests and grasslands, respectively (Fig. 3; Table S3). For GPP and RE, however, the climatic variables, soil properties or plant traits alone explained a large proportion (24.5%-71.4%) of the spatial variability (Table S3). In the dataset FG, models distinguishing biome type better explained the spatial variability in NEE than models not considering the biome type (Table S3).

The general pattern of the unique and common contributions of climate, soil properties and plant traits were similar between the results based on AIC and those based on BIC, except for a few differences in the exact values. For forests, both the results based on AIC and BIC showed that climatic variables had the highest unique contribution to the spatial variability in NEE (23.8%-30.4%). The common contributions of two or three classes of explanatory variables were less than the unique contributions of these variables (Figs. 4a and S4a). Interestingly, for grasslands, the soil properties were the most important factors (41.4%-53.5%). The common contribution of all the three classes of variables was negative (-13.7%–9.4%, Figs. 4d and S4d). The negative common contribution meant there were interactive effects on spatial variaibility in carbon fluxes from two or three classes of factors, because the

combined two or three classes of factors explained more variance than the separate classes did (Figs. 4a, d and S4a, d).

With respect to the spatial variability in GPP and RE, the unique contributions of climatic variables were higher than those of soil properties and plant traits across both forests and grasslands (Figs. 4b, c, e, f and Figs. S4b, c, e, f). Moreover, the common contributions explained 49.7% - 62.0% of the total variance in GPP or RE, much larger than the unique contributions. The unique contribution of plant traits to carbon fluxes for all sites was larger than that in FG, when not considering the biome type. However, the unique contribution of plant traits largely decreased when forests were distinguished from grasslands (Figs. S2 and S3).

3.3. Effects of individual variables on the spatial variability in NEE

The importance of individual variables showed negligible differences between AIC and BIC results, and did not change the general pattern. For forests, mean annual precipitation (MAP) and mean annual potential evapotranspiration (PET) were the most important climatic variables driving the spatial variability in NEE (Figs. 5a and S5a). NEE first
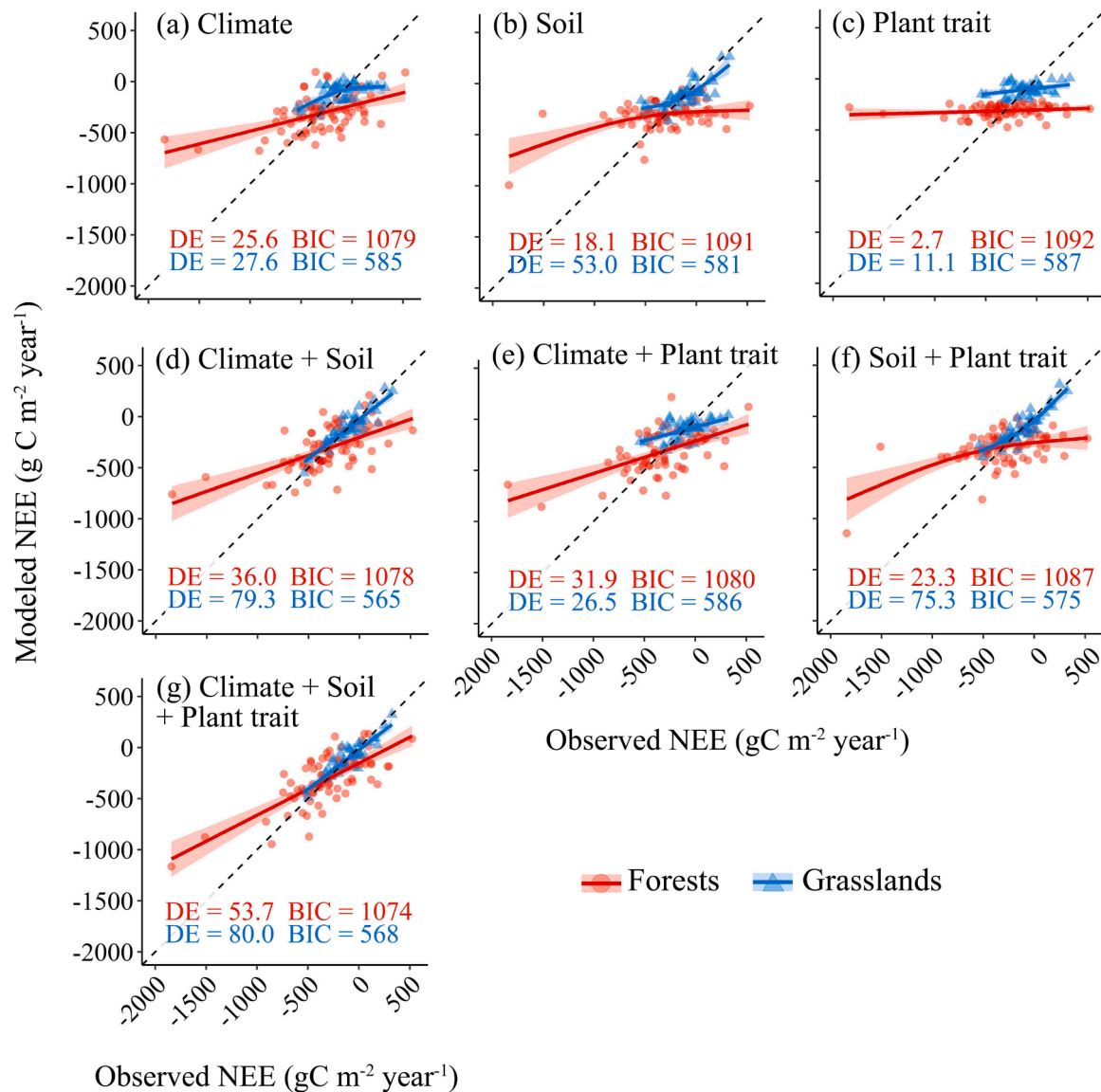

Fig. 3. The relationship between modeled and observed NEE under different model scenarios with differential combinations of explanatory variables. The regression lines are based on the principal component regression integrated principal component analysis with generalized additive models. The dashed lines are the 1:1 lines. DE is deviance explained and BIC is the Bayesian information criterion.
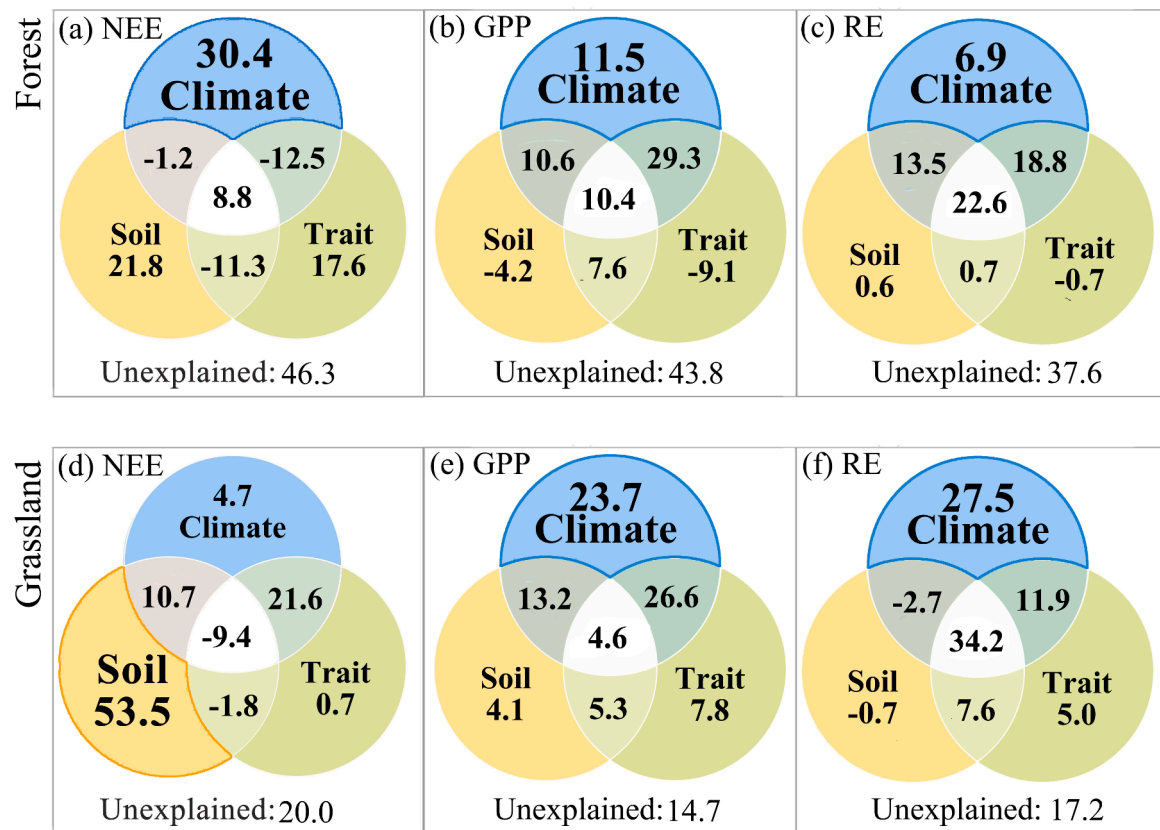
Fig. 4. Contributions (%) of climatic variables, soil properties and plant traits to spatial variation in carbon fluxes (NEE, GPP and RE) across forests (a, b, c) and grasslands (d, e, f). These results are from the best models based on BIC. The corresponding results based on AIC are shown in Fig. S2.
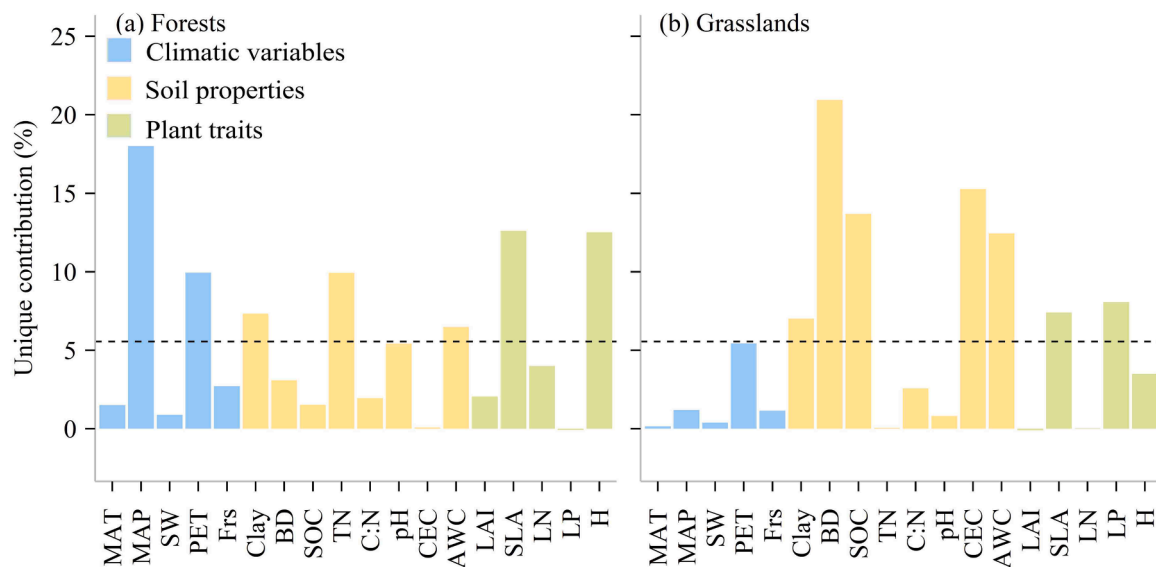

Fig. 5. Unique contributions of climatic variables, soil properties and plant traits to spatial variability in NEE across forests (a) and grasslands (b). The horizontal dashed line indicates the average unique contribution. MAT, mean annual temperature; MAP, mean annual precipitation; SW, incoming shortwave radiation; PET, mean annual evapotranspiration; Frs, number of frost days; Clay, clay content; BD, bulk density; SOC, soil organic carbon; TN, total nitrogen density; C:N, ratio of soil carbon and nitrogen; pH, soil pH; CEC, cation exchange capacity; AWC, available water capacity; LAI, leaf area index; SLA, specific leaf area; LN, leaf nitrogen content; LP, leaf phosphorus content; H, plant height. These results are based on BIC, whereas those based on AIC are shown in Fig. S5.

decreased, but thereafter increased with increases in MAP and PET (Figs. 6a and b; Figs. S6a and b). Of the soil properties, clay content had a negative relationship with NEE while available water capacity showed a nonlinear influence with lowest NEE at intermediate levels (Figs. 6c and e; Figs. S6c and d). Within plant traits, the NEE first increased and then

decreased with increasing specific leaf area (SLA), whereas it monotonically decreased with the increasing plant height (Figs. 6f and g; Figs. S6e and f), indicating a higher carbon sink.

For grasslands, both AIC and BIC results showed that soil properties had much higher unique contributions to the spatial variability in NEE
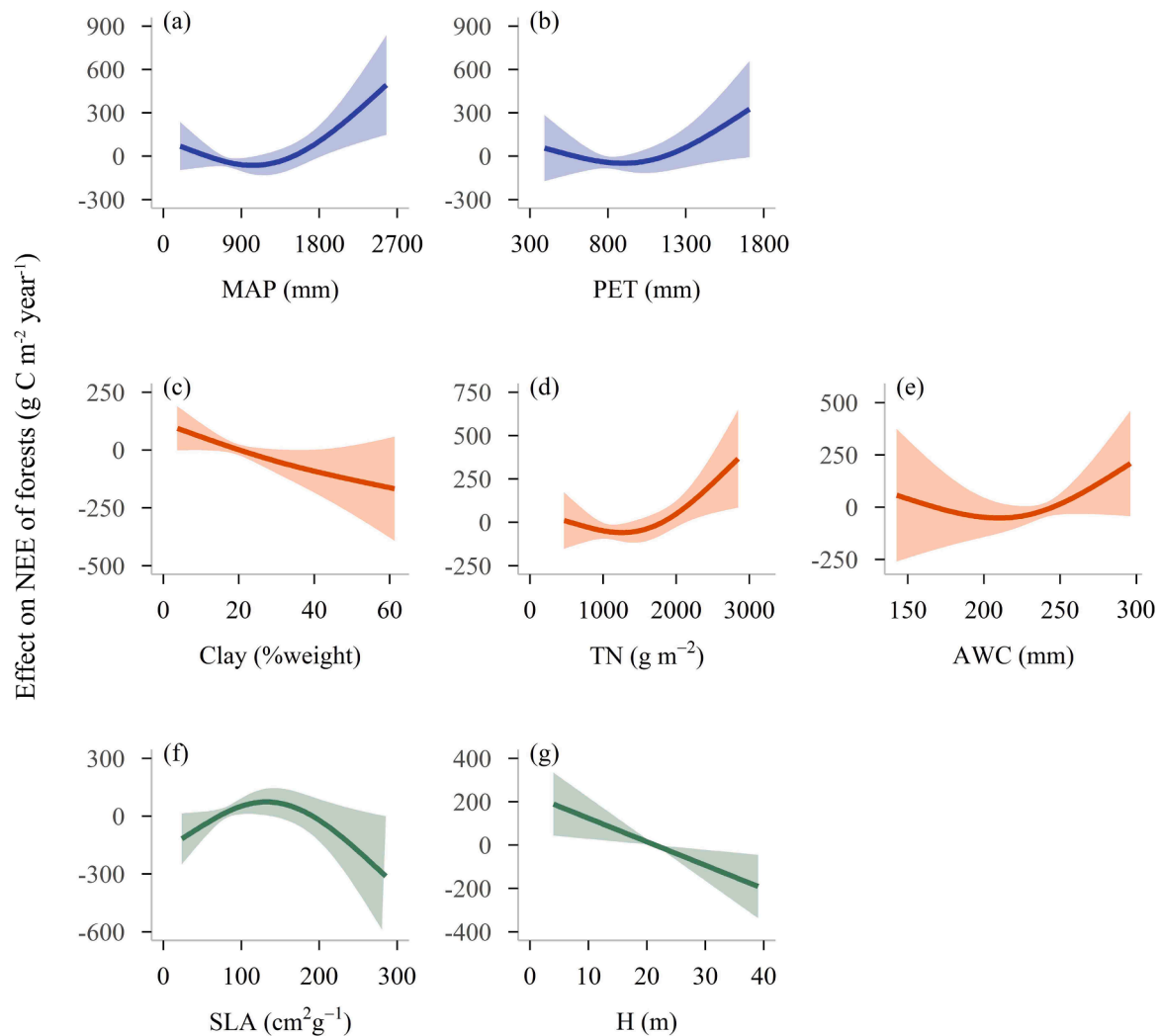
Fig. 6. Impact of important factors on NEE across forests. Shaded areas indicate the 95% confidence interval of regression lines. A NEE increase means less carbon uptake or more carbon loss. MAP, mean annual precipitation; PET, mean annual potential evapotranspiration; Clay, clay content; TN, soil total nitrogen density; AWC, available water capacity; SLA, specific leaf area; H, plant height. Blue lines display the effect of climatic variables on NEE, red lines the effect of soil properties, green lines the effect of plant traits. These results are based on BIC, whereas those based on AIC are shown in Fig. S6.

than climatic variables or plant traits did (Figs. 5b and S5b). Within the soil properties, clay content (Clay) had positive effects while bulk density (BD), cation exchange capacity (CEC) and available water capacity had negative effects on NEE (Figs. 7a, b, d, e and S7c, d, f, g). For plant traits, leaf phosphorus content (LP) decreased NEE whereas the SLA had little influence (Figs. 7f and g; Figs. S7h and i). The AIC results indicated that PET and number of frost days (Frs) were important climatic variables for NEE but BIC results suggested that none of the climatic variables was important (Fig. 5b vs Fig. S5b).

3.4. Interactive effects among explanatory variables

The two- and three-way interactive effects among climatic variables, soil properties and plant traits were examined. For forests, a few differences between the results based on AIC and those based on BIC were observed. The interactions between soil C:N ratio, soil pH and leaf area index (C:N-pH and C:N-pH-LAI) were the most important according to BIC, while those between mean annual temperature, soil C:N ratio and soil pH (MAT-C:N-pH) were the most important according to AIC (Tables 2 and S4). Specifically, the effect of C:N ratio on NEE was stronger for forests with higher MAT, LAI and pH (Figs. 8a and c; Figs. S8a and b).

Across grasslands, the results based on AIC were consistent with those based on BIC, showing that the interactive effects within soil

properties (i.e., those among soil clay content, soil total nitrogen density and cation exchange capacity, Clay-TN-CEC) were the most important, followed by the interactive effects between soil properties and plant traits (i.e. the interaction of clay, total nitrogen density of soil and leaf phosphorus content, Clay-TN-LP, Table 2 and Table S4). Specifically, the effect of total nitrogen density of soil on NEE was stronger in grasslands with lower soil clay and higher CEC (Figs. 8d, f). The effect of Clay on NEE was weaker in grasslands with higher leaf phosphorus content (Fig. 8e). Both for forests and grasslands, the interactions important to NEE showed little influence on the spatial variability in GPP or RE (Table 2 and Table S4).

4. Discussion

4.1. Relative importance of climate, soil properties and plant traits to spatial variability in NEE

Current carbon cycle models have limited ability to spatially represent NEE distribution in terrestrial ecosystems (Cox, 2001; Arora, 2003; Lawrence et al. 2019). One reason is that there is still confusion about the main drivers of NEE (Fernández-Martínez et al., 2014a; Michaletz et al., 2018; Chen et al., 2019; Luo et al., 2019; Ji et al., 2020; Tang et al., 2020). In this study, we applied a principal component regression (PCR)
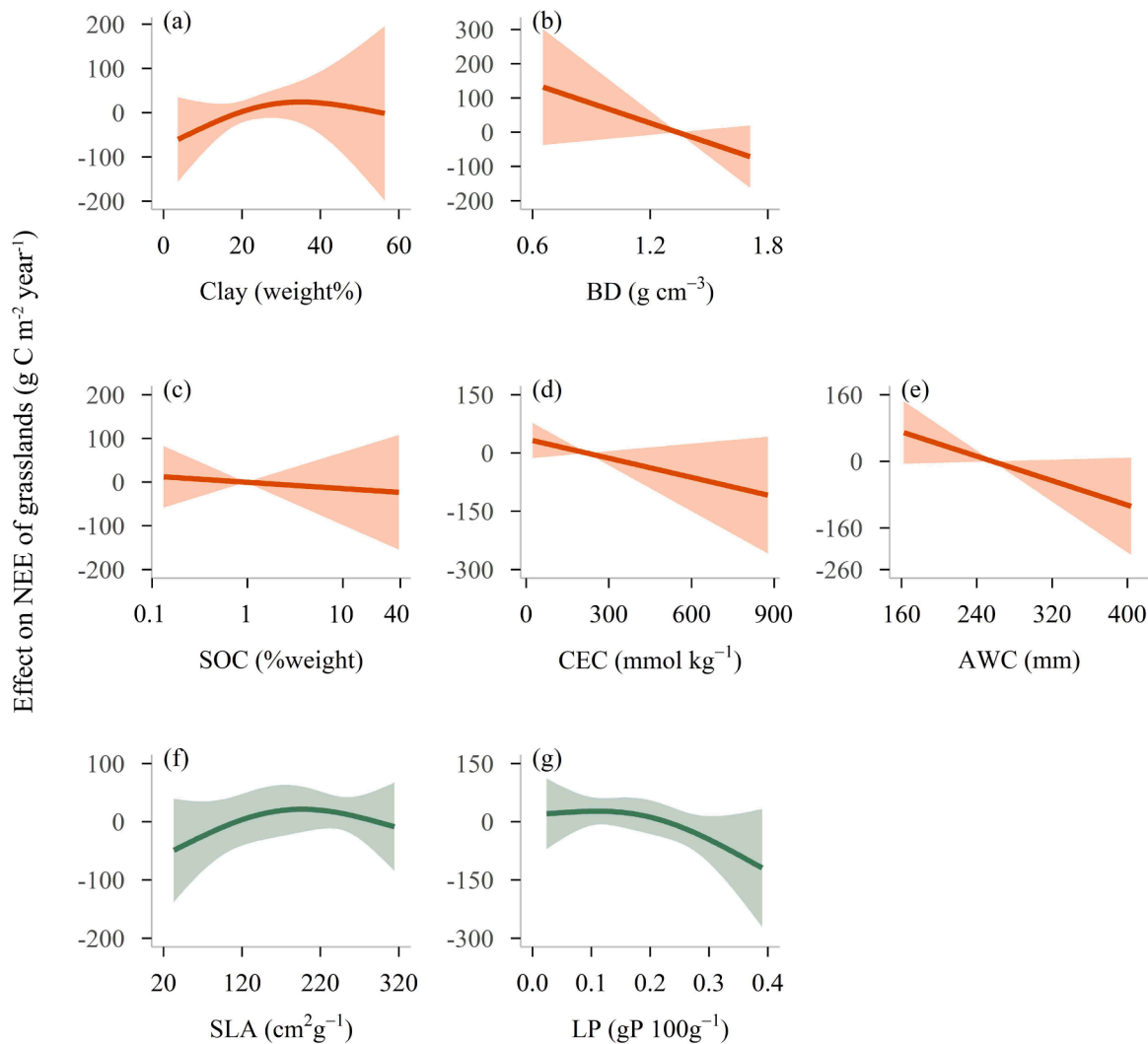
Fig. 7. Impact of important factors on NEE of grasslands. Shaded areas indicate the 95% confidence interval of regression lines. An NEE increase means less carbon uptake or more carbon loss. Clay, clay content; BD, bulk density; SOC, soil organic carbon; CEC, cation exchange capacity; AWC, available water capacity; SLA, specific leaf area; LP, leaf phosphorus content. Blue lines display the effect of climatic variables on NEE, red lines the effect of soil properties, green lines the effect of plant traits. These results are based on BIC, whereas those based on AIC are shown in Fig. S7.

Table 2

The top five most important interactions with the spatial variability in NEE of forests and grasslands ranked in all detected two and three-way interactions of climatic variables, soil properties and plant traits. w_j is the importance weight of the specific interaction to all interactions for the spatial variability in NEE. $w_{j,BIC}$ and $w_{j,AIC}$ refer to w_j for BIC and AIC, respectively.

Biome types	Interactions	$w_{j,BIC}$			$w_{j,AIC}$		
		NEE	GPP	RE	NEE	GPP	RE
Forests	C:N-pH	0.52	<0.01	<0.01	<0.01	<0.01	<0.01
	C:N-pH-LAI	0.15	<0.01	<0.01	0.08	<0.01	<0.01
	MAT-C:N-pH	0.06	<0.01	<0.01	0.72	0.01	<0.01
	MAT-Frs	0.04	<0.01	<0.01	<0.01	<0.01	<0.01
	MAP-C:N-pH	0.03	<0.01	<0.01	0.04	<0.01	<0.01
Grasslands	Clay-TN-CEC	0.43	<0.01	<0.01	0.65	<0.01	<0.01
	Clay-TN-LP	0.18	<0.01	<0.01	0.13	<0.01	<0.01
	Clay-BD-CEC	0.08	<0.01	<0.01	0.05	<0.01	<0.01
	Clay-C:N-AWC	0.07	<0.01	<0.01	0.05	<0.01	<0.01
	Clay-CEC-AWC	0.07	<0.01	<0.01	0.03	<0.01	<0.01

MAT, mean annual temperature; MAP, mean annual precipitation; SW, incoming shortwave radiation; PET, mean annual potential evapotranspiration; Frs, number of frost days; Clay, soil clay content; BD, bulk density; SOC, soil organic carbon; TN, total nitrogen density; C:N, ratio of soil carbon and nitrogen; pH, soil pH; CEC, cation exchange capacity; AWC, available water capacity; LAI, leaf area index; SLA, specific leaf area; LN, leaf nitrogen content; LP, leaf phosphorus content; H, plant height.

method, which integrated principal component analysis (PCA) and generalized additive models (GAMs), to analyze the effects of climatic variables, soil properties, and plant traits on carbon fluxes (NEE, GPP and RE) across 147 eddy-flux sites globally. We found that the spatial variability in NEE was mainly driven by climatic variables across forests and by soil properties across grasslands regardless of the model selection
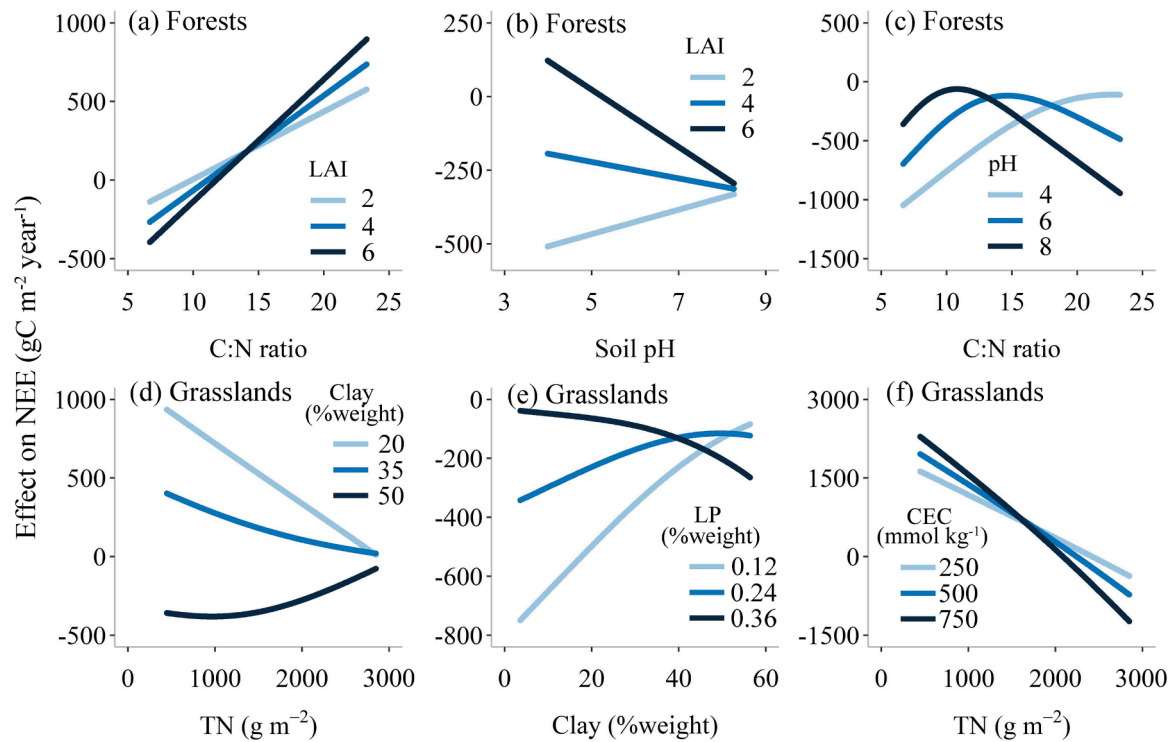
Fig. 8. Interactive effects of climatic variables, soil properties and plant traits on NEE across forests (a-c) and grasslands (d-f). Interactions between soil C:N ratio, soil pH and leaf area index (C:N-pH and C:N-pH-LAI) are the most important interactive effect on NEE of forests. Interactions between soil clay content, soil total nitrogen density, soil cation exchange capacity and leaf phosphorus content (Clay-TN-C:N, Clay-TN-LP) are the most important interactive effect on NEE of grasslands. These results are based on BIC selected best models, whereas the corresponding unique contributions based on AIC selected best models are shown in Fig. S8.

criteria (Figs. 4 and S4).

The importance of climatic variables to forest NEE has been well documented (Yi et al., 2010; Yu et al., 2013). However, by applying general linear models (GLM) to a global forest dataset, Fernández-Martínez et al. (2014a) showed that nutrient availability exerted a stronger control on NEE than climatic variables. The discrepancy between Fernández-Martínez et al. (2014a) and our results might be due to the differences in classification of factors and statistical approaches. For example, Fernández-Martínez et al. (2014a) also used the plant traits (leaf nitrogen and phosphorus contents), in addition to soil nutrient content as the indicators of nutrient availability, whose contributions could highly overlap with those of climate (Figs. 4a and S4a), potentially overstating the explanatory power of climate and nutrient availability. Du (2015) pointed out that the outliers of very young forests (<5 years) in the linear model used in Fernández-Martínez et al. (2014a) may have biased the importance of nutrient availability. In our study, nonlinear relationships between climatic variables and NEE were observed (Figs. 6a and b; Figs. S6a and b). Furthermore, Chen et al. (2019) suggested that leaf area index (LAI) might have a larger effect on spatial variability in NEE than climate. However, our results showed the opposite pattern (Figs. 5a and S5a). As Chen et al. (2019) did not differentiate forests from grasslands, it was unclear if their conclusion was robust within forest ecosystems.

Few studies have investigated the relative importance of climatic variables, soil properties and plant traits to spatial variability in NEE across grasslands. Some studies have shown a larger contribution of climatic variables than soil properties to the temporal variability in grasslands (Peichl et al., 2013; Zhang et al., 2017; Liang et al., 2020). However, such results are difficult to extend to large spatial scales because of the spatial heterogeneity of soil properties (Stark, 1994; Ryel et al., 1996), which might cause the uncertainty in predicting carbon sequestration of grasslands.

4.2. Unique contribution of each explanatory variable to spatial variability in NEE

Among the climatic variables, the water conditions (MAP and PET) were the most important drivers of the spatial pattern in NEE across forests (Figs. 5a and S5a). Specifically, NEE first declined (increase in C uptake) and then increased (increase in C loss) with MAP (Figs. 6a and S6a). This might be because the positive effect of MAP on GPP decreased with increasing water availability, while that of RE did not change (Chen et al., 2013; Li et al., 2013) or decreased to a lesser extent (Liu et al., 2018), causing a nonlinear change of NEE with MAP. However, for grasslands, the effect of climate on spatial variability in NEE need to be further confirmed due to uncertainties in the results (Figs. 5b vs S5b).

Soil provides most of nutrients and water for plant growth, and mediates the decomposition of organic matter, which can influence the NEE. The effects of available water capacity on NEE observed in both forests and grasslands mainly reflected the influence of water availability. The NEE decreased with soil clay content in forests but increased in grasslands (Figs. 6c and 7a; Figs. S6c and S7c) because forests have a larger proportion of particulate organic matter, consisting of small pores that are not accessible to microbes (van Lutzow et al., 2006; Guidi et al., 2015; Cotrufo et al., 2019). Physical protection mechanisms are stronger in soils with higher clay content and thus reduce soil respiration. The proportion of particulate organic matter being much lower in grasslands (Cotrufo et al., 2019) made the protective effect of clay on soil organic carbon (SOC) not as important as in forests. As a result, the higher substrate in soils with higher clay content accelerated the decomposition of organic carbon and increased the NEE (Fig. 7a).

In grasslands, NEE also decreased with cation exchange capacity (CEC) and bulk density (Figs. 7b and d; Figs. S7d and f), probably because metal cations such as Ca^{2+} and Fe^{3+} strengthened the bonds between the mineral matrix and the organic matter (Six et al., 2004; Kögel-Knabner et al., 2008). High bulk density leads to lower soil porosity and oxygen concentration, thus suppressing the activities of

roots and microbes, and reducing decomposition rates (Yang et al., 2019). Moreover, high CEC is also an indication of higher availability of essential elements (Mg^{2+}, K^+ and Ca^{2+}) for plant growth (Tränkner et al., 2018; Wang et al., 2019). The effects of CEC and bulk density on NEE were not observed in forests because the surface organic soil layer and particulate organic matter in forest soils are more susceptible to climate and disturbance than in grasslands (Guidi et al., 2015; Cotrufo et al., 2019).

Among plant traits, the specific leaf area (SLA) and plant height were important drivers of NEE in forests (Figs. 5a and S5a). Many studies have found that plant growth rate, ecosystem productivity and litter decomposition increase with SLA (Santiago and Wright, 2007; Cornwell et al., 2008; Liu et al., 2018). Small SLA values are usually found in cold and arid ecosystems with relatively short period for carbon sequestration (Schulze et al., 2006; Rosbakh et al., 2015). As the carbon uptake period increases, the relative contribution of RE decreased while that of GPP increased, resulting in the nonlinear relationship between NEE and SLA. Tree height is directly related to the biomass and stand age (Feldpausch et al., 2012; Tilly et al., 2015; Pugh et al. 2019), which in turn can strongly affect ecosystem productivity (Chu et al., 2016). As a result, NEE decreased with tree height (Figs. 6g and S6f). NEE in grasslands was regulated by leaf phosphorus content. Phosphorus is an essential element of phospholipids (Hammond and White, 2007) and energy-carrying molecules (e.g., ATP and NADPH), which are critical to GPP at the ecosystem level (Walker et al., 2014; Taiz and Zeiger, 2010). A recent study suggests that the plant conservation of phosphorus is more important in grasslands than forests (Du et al., 2020), which might be the reason why leaf phosphorus content had a stronger relationship with carbon fluxes in grasslands than in forests (Figs. 5 and S5).

4.3. Interactive effects among climatic variables, soil properties and plant traits

Many researchers have suggested that interactions between climatic variables can considerably affect the ecosystem carbon cycle (Chen et al., 2013; Chen et al., 2019). Similarly, other interactive effects among climatic variables and non-climate factors (e.g. soil moisture, leaf traits, nutrient availability and evolutionary factors) have also been reported to be important in carbon-related processes (Wang et al., 2014; Fernández-Martínez et al., 2014b; Michaletz et al., 2016; Reich et al., 2018; Shao et al., 2019). However, we found that, for spatial variability in NEE, the interactions between climatic variables and non-climatic factors, and those among non-climate factors, were more important than those within climatic variables (Table 2 and Table S4). These results suggested that the interactions related to soil properties (such as C: N and soil pH) might play a more important role in driving the spatial variability in NEE than those of climatic variables and plant traits do.

Specifically, the interactive effects among soil clay content, total nitrogen density and CEC (Clay-TN-CEC), and those among soil clay content, total nitrogen density and leaf phosphorus content were identified in grasslands (Clay-TN-LP, Table 2 and Table S4). The effect of total nitrogen density on NEE was weaker in higher soil clay (Fig. 8d and S8d). In grasslands, NO_3^- can easily be lost from the ecosystem as a result of leaching (Brust, 2019). High clay may reduce the NH_4^+ use by plants and microbes, partly by absorption (Hazelton and Murphy, 2007) and partly due to the smaller soil pores decreasing the accessibility of SOC to microbes (Wei et al., 2014). The effect of clay on NEE was weaker in grasslands with higher leaf phosphorus content (Fig. 8e and S8e). Ecosystems with high soil phosphorus content are generally located at high latitudes (Chadwick et al., 1999; Reich and Oleksyn, 2004), where the temperature can be more influential on decomposition rate than substrate availability (Davidson and Janssens, 2006), therefore weakening the contribution of clay content to soil respiration. The effect of soil total nitrogen density on NEE was stronger at high CEC (Fig. 8f and S8f), because high CEC means high capacity of nutrient holding elements, which may alleviate the co-limitation of K^+, Ca^{2+} and Mg^{2+} on plant

growth and ecosystem productivity (Wells and Wood, 2007).

4.4. Implications for future research and model improvement

Our study quantified the relative importance of climatic variables, soil properties and plant traits to the spatial variability in NEE across forests and grasslands. Although recent carbon cycle models adopt trait-based approaches to account for the effects of plant morphological, physiological and phenological features on ecosystem function (Lamarque et al., 2014; Fry et al., 2019), our results showed that plant traits generally had lower unique contributions to the spatial variability in NEE, GPP and RE than climatic variables and soil properties (Figs. 4 and S2-4). This finding is consistent with empirical models showing that climate alone can be a better predictor of ecosystem function than detailed process-based land surface models (Haughton et al., 2018). However, a large proportion of variability could be explained by the common contributions of plant traits with climatic variables and soil properties (Fig. 5). Accommodation of vegetation under long-term environmental filtering may lead to covariation of climate, soil and plant traits across the landscape. If the vegetation type shifts under future climate change (Svenning and Sandel, 2013; Franklin et al., 2020), plant traits may have independent effects on carbon fluxes, the importance of which may be further amplified by the potential interactions among plants traits, climatic variables and soil properties (Fig. 8, Hu et al., 2020; Reichstein et al., 2014).

In order to simplify model structure, terrestrial biosphere models usually explicitly consider the dominant drivers and ignore drivers with small impacts on GPP and RE (Cox, 2001; Arora, 2003; Lawrence et al., 2019). However, we found that the factors important to GPP and RE were not necessarily the same as for NEE. For example, soil properties had very small effects on GPP and RE across both forests and grasslands, but induced large effects on NEE (Figs. 4 and S4). Similar patterns were also found for the interactive effect of soil clay content, total nitrogen density and CEC in grasslands (Table 2 and Table S4). These emergent factors, as well as the interactions between climate, soil and plant traits are not well represented in current terrestrial biosphere models.

Effects of some factors (e.g., forest age, fire) on spatial variability of NEE (Pugh et al., 2019; Beringer et al., 2015) might be important but could not be investigated in this study due to insufficient data. With the expansion of the global eddy flux network (e.g. Fluxnet: https://fluxnet.fluxdata.org), further research integrating more accurate global observations, such as plant traits (e.g., the ongoing yearly information of plant traits at site level, ICOS, https://www.icos-cp.eu/) and natural or human disturbance (e.g., fire, insect attacks and harvesting) could help to disentangle the underlying mechanisms, and accurately predict the spatial pattern of carbon cycling across global forests and grasslands.

Another source of uncertainty might be the result of the interannual variability in carbon fluxes, which may confound the spatial patterns. Fortunately, the absolute magnitude of interannual variability in NEE ($0\sim30$ gC m^{-2} year^{-1}, Piao et al., 2020) was far smaller than the spatial variability (-2400$\sim$600 gC m^{-2} year^{-1}, Pastorello et al., 2020) based on eddy flux data. Some studies suggested that both the temporal and spatial patterns of carbon fluxes were strongly influenced by climate and nutrient availability (Ahlström et al., 2015; Wieder et al., 2015; O'Sullivan et al., 2019; Figs. 5 and S5). However, the importance of soil physicochemical properties (e.g., Clay, BD, CEC) for spatial variability in NEE (Figs. 5b and S5b) has been rarely studied for the temporal variability in carbon fluxes. Greater attention should be paid to soil properties to accurately predict the spatio-temporal variability in carbon fluxes of terrestrial ecosystems.

5. Conclusions

The large spatial variability in NEE across terrestrial ecosystems is driven by climatic variables, soil properties and plant traits, but the relative importance of these drivers is under debate. We took advantage

of 147 eddy-flux sites across the globe and investigated the effects of climatic variables, soil properties and plant traits to spatial variability in NEE of forests and grasslands. Our results showed that the spatial variability in NEE was mainly driven by climatic variables across forests and by soil properties across grasslands. Plant traits had much lower unique contribution than the other two classes of variables, but the leaf phosphorus content strongly interacted with soil total nitrogen density and clay content in grasslands. There were also interactive effects of soil clay content, total nitrogen density and CEC on NEE in grasslands. These driving factors (i.e., the soil properties and the interactive effect among climatic variables, soil properties and plant traits) for NEE should be integrated into land surface models to better inform the spatial pattern in NEE across terrestrial ecosystems.

Declaration of Competing Interest

The authors declare no competing financial interests.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108506.

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