Climate control of terrestrial carbon exchange

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Understanding the relationships between climate and carbon uptake by terrestrial ecosystems is critical to predicting future levels of atmospheric carbon dioxide because of the potential accelerating effects of positive climate-carbon cycle feedbacks[1, 2]. However, knowledge of even the broad relationships between climate and terrestrial CO_2 exchange with the atmosphere on yearly to decadal scales remains highly uncertain[3, 4, 5]. Here we present data describing net ecosystem exchange of carbon (NEE) and climate factors as measured using the eddy covariance method[6] at 132 unique sites over 6 continents with a total of 583 site-years. With respect to controlling factors we find two distinct groupings of sites: (1) a temperature-limited group where NEE has an exponential relationship with mean annual temperature; and (2) a dryness-limited group where NEE has an inverse exponential relationship with the dryness index[7]. A strong latitudinal dependence emerges, with 92% of the temperature-limited sites located above 42°N, and 77% of the dryness-limited sites located below 42°N. The sensitivity of NEE to mean annual temperature breaks down at a threshold value of ~16°C, above which no further increase of CO_2 uptake with temperature was observed and dryness influence overrules temperature influence. Our findings suggest that (1) net ecosystem carbon exchange is highly limited by mean annual temperature at mid- and high-latitudes, and (2) net ecosystem carbon exchange is highly limited by dryness at low latitudes.

Determining the relationships between terrestrial carbon exchange and climate is fundamentally important because climate-carbon cycle feedback could significantly accelerate (or decelerate) future climate warming[1, 2]. Globally, the observed growth rate anomaly of atmospheric CO_2 concentration is correlated with the multivariate El Nino-Southern Oscillation index[8]. Inversion modelling[9] and biome-based analyses of climate anomalies[10] suggest that the oceanic carbon reservoir is a minor player in this variability. Instead, variations in the atmospheric CO_2 growth rate result largely from the impact of climate on terrestrial carbon sequestration, including regional impacts of extreme climate conditions such as heat waves and droughts[3].

On much smaller spatial scales, large amounts of data have been collected continuously over the last two decades using the eddy-covariance technique to measure directly the net ecosystem exchange of CO_2 (NEE) between the biosphere and the atmosphere[6]. Although a typical eddy covariance footprint is relatively small (*ca.* $1km^2$), NEE variability at these sites is often representative of variability over much larger spatial scales as a result of the spatial coherence of climate anomalies[3]. These temporal variations in NEE, the imbalance between photosynthesis (fixation of atmospheric carbon dioxide into organic carbon) and ecosystem respiration (plant and microbial respiration converting organic carbon into atmospheric carbon dioxide), are caused predominately by climatic drivers on the daily and seasonal time scales[11]. Although several synthesizing analyses have been conducted across eddy-flux tower sites, the role that climatic drivers make to NEE variability across multiple sites on annual or longer time scales is still not clear[4, 11,12].

Climate indices have been used extensively to categorize ecosystems. The Holdridge life zone is differentiated by a combination of mean annual temperature, mean annual precipitation, and the ratio of mean annual potential evapotranspiration to mean annual precipitation[13]. Major biogeographical zones are classified by mean annual net radiation and a dryness index[7]. Spatial variations in annual biosphere-atmosphere CO_2 exchange at the landscape scale are due to underlying ecosystem attributes, but at regional and larger scales are clearly sensitive to climatic variations, although the exact combination of factors causing this variability is poorly understood[14]. Determining the environmental controls on NEE is complicated because NEE is the difference between photosynthesis and ecosystem respiration, and climate variations may affect these individual components in different ways. Spatial variability in respiration is strongly correlated with temperature and precipitation[15], and gross primary productivity has been shown to be subject to climate-based limiting factors: temperature, precipitation and/or radiation, depending on the region[16]. Although non-climate factors such as nutrient availability and disturbance history also are strong drivers of NEE magnitudes at individual sites[14, 17], we hypothesize that climatic factors are the dominant factor in NEE variability globally as represented within FLUXNET.

The present analysis is based on 583 site-years of eddy covariance data measured from 132 sites throughout the world from 1992 to 2008 (supplementary Table 1). The latitudes vary from 37°S to 71°N, longitudes are broadly covered, and elevation ranges from -2 m to 3288 m (supplementary Figure 1). The climatic zones of the sites include polar tundra, maritime temperate, continental temperate, humid subtropical, Mediterranean, arid, semi-arid, tropical monsoon, and tropical wet-and-dry climates. The vegetation types include grassland, cropland, evergreen needle-leaf forest, deciduous broad-leaf forest, mixed forest, permanent wetland, open shrubland, closed shrubland, savanna, evergreen broad-leaf forest, and tundra. Stand age ranges from young seedlings to 500 years old[18]. Sites from all ecosystem types with at least one year of complete NEE and meteorological data are included. Cropland sites are included visually in the figures, but are not factored into the statistical analysis because potential climate impacts may be heavily distorted by irrigation and fertilization practices. NEE and meteorological data used in this analysis are taken from standardized files archived in the FLUXNET-LaThuile database which includes data from the AmeriFlux, Fluxnet-Canada, CARBOEUROPE, ChinaFlux, OzFlux, CarboAfrica, and AsiaFlux networks. These data have been quality controlled and gap-filled by consistent methods[19, 20, 21]. Meteorological variables used include air temperature, net radiation and precipitation. We have developed a new method to gap-fill the half-hourly meteorological data to produce reliable annual averages (see Methods). In many cases, the site principal investigators have submitted revised annual

NEE estimates based on more detailed, site-specific reanalyses. The data were used in this analysis only in those years when temperature, precipitation, net radiation, and NEE all meet the gap-filling criteria (see Methods).

Eddy flux measurements are inherently uncertain due to: (1) the advection errors caused by complex terrain[22, 23] and complicated canopy structure [24]; (2) imbalance errors in the energy budget[25, 26], and (3) the stochastic nature of turbulence [27, 28, 29]. These errors have been studied intensively and remain to be quantified exactly for all sites[12]. Annual errors in NEE typically range between 0.3 and 1 t C ha^{-1} yr^{-1} (ref. 19). The total error is certainly below the value of 2 t C ha^{-1} yr^{-1} tested conservatively by a Monte-Carlo analysis[12].

An empirical method (see Methods) was used to segregate sites into two groups (supplementary Table 1): (1) Those in which variations in NEE are best explained by mean annual temperature; and (2) those in which variations in NEE are best explained by a dryness index.

In the temperature-limited group, 65% of spatial variations in NEE can be explained by mean annual temperature (Figure 1a). The following empirical exponential relationship best fits the temperature response of NEE:

$$NEE = NEE_{T_0} e^{\alpha_T T} \tag{1}$$

Where $NEE_{T_0} = -0.41$ t C ha^{-1} yr^{-1} at $T = 0^{\circ}\mathrm{C}$ and $\alpha_T = 0.195\ {}^{\circ}\mathrm{C}^{-1}$, and *T* is mean annual temperature. Statistical analysis demonstrated that there is no significant correlation between the residuals of the empirical prediction (1) and the dryness index (see supplementary Figure 2a). We speculate that this residual NEE is primarily driven by non-climate factors such as stand age, disturbance history, species composition, or canopy leaf area index, reflecting local variation in nutrient and water availability[14].

In the dryness-limited group, 77 % of spatial variation in NEE can be accounted for by a dryness index (Figure 1b). An empirical dryness response function of NEE is given:

$$NEE = NEE_{D_0} e^{-\alpha_D D} \qquad (2)$$

where $\alpha_D = 1.579$, $NEE_{D_0} = -18.10$ t C ha^{-1} yr^{-1} at $D = 0$ (under the condition of unlimited water supply), dryness D is defined as $R_n / (\lambda P)$, where R_n is mean annual net radiation MJ m^{-2} yr^{-1}, P is mean annual precipitation mm yr^{-1}, and λ (=2.5 MJ kg^{-1}) is the enthalpy of vaporization[7]. R_n / λ is approximately equal to annual potential evaporation[7]. Statistical analysis also demonstrated that there is no significant correlation between the residual of the empirical prediction (2) to temperature (see supplementary Figure 2b). Mean annual NEE is underestimated by the empirical model (2) for the subgroup of the forest sites and overestimated for the subgroup of the non-forest sites in the dryness-limited group (Figure 1b). The correlations between the NEEs of subgroups (forest and non-forest sites separately) and dryness are better than that between forest and non-forests taken together and dryness. The NEE of subgroups can be more accurately predicted by the empirical model (2) with their own model parameters: (1) forest subgroup, $\alpha_D^f = 1.382$, $NEE_{D_0}^f = -19.34$ t C ha^{-1} yr^{-1} (the thin red curve in Figure 1b); (2) non-forest subgroup, $\alpha_D^o = 1.692$, $NEE_{D_0}^o = -15.42$ t C ha^{-1} yr^{-1} (the thin blue curve in Figure 1b). In the temperature limited group however, there is no significant bias between the two sub groups (forested and non-forested sites) and the predictions based on the entire temperature limited group.

The empirical subdivision of groups also corresponds to latitudinal zonation: most sites of the dryness-limited group were located in the zones of subtropical climate (77% are located below 42°N), while most sites of the temperature-limited group were located in the zones of temperate and boreal climate (92% are located above 42°N). Our findings suggest that NEE at mid-to-high latitudes is controlled largely by the mean annual temperature, while at low latitudes, it is controlled largely by dryness. This conclusion is further verified by the very poor correlation between the entire dataset and mean annual temperature (r^2=0.24, supplementary Figure 3a), and between the entire dataset and dryness (r^2=0.08, supplementary Figure 3b) respectively. The controlling function of temperature for terrestrial carbon exchanges breaks down as mean annual temperature approaches 16°C. All sites with mean annual temperature above 16°C are in the dryness group (Figure 1).

Links between terrestrial CO_2 exchanges and climate controls are clearly demonstrated by many site-years of data from the eddy flux tower networks (AmeriFlux, Fluxnet-Canada, CARBOEUROPE, ChinaFlux, OzFlux, AsiaFlux, CarboAfrica, and FLUXNET). Our findings are essential to understand how future climate change affects terrestrial CO_2 exchanges with the atmosphere in the 21st century. In the IPCC 2007 report, projected warming in the 21st century is expected to be greatest over land and at high northern latitudes, while projected decreases in precipitation are likely in most subtropical land regions[30]. Our results suggest that the most likely future climate change scenarios would strongly intensify terrestrial CO_2 uptake in high latitudes and weaken CO_2 uptake in low latitudes. We also conclude that forest and woodland ecosystems are better adapted to water limitation, which is a strong argument to preserve forests as efficient carbon sinks to mitigate further climate change.

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Meteorological data gap filling

Producing reliable estimates of site-average temperature, radiation and precipitation requires comprehensive gap-filling techniques because of the sporadic data collection outages that occur at eddy covariance sites. Without gap filling, the distribution of these gaps can bias long-term averages (e.g., if there are more gaps in summer, the site's mean temperature will have a low bias). Although gap-filled meteorological data are available from the FLUXNET database, these are problematic because they do not account for missing precipitation data. We developed an algorithm to locate the nearest flux tower or climate station in the National Climatic Data Center (NCDC in Asheville North Carolina) database to provide daily temperature and precipitation data. If data from a nearby tower were available, these were used to fill missing meteorological data. When alternate towers were not available within a 30km radius, daily NCDC data from the nearest station were downscaled to hourly or half-hourly resolution and used to fill the gaps. Temperature data were downscaled by using the daily maximum and minimum information to construct a sine wave with the appropriate amplitude (assuming daily maximum at 15 LST and daily minimum at 3 LST), and precipitation data were downscaled by dividing daily totals by the number of daily time steps (24 or 48 depending on the site). Differences in annual averages between the eddy covariance site and the climate stations were adjusted using linear regression so that the inclusion of station data did not alter long-term temperature or precipitation averages.

Net radiation data were not available from NCDC. If no alternate tower was available, gaps in these data were filled with the diurnal average values for the given hour and day of year. Diurnal averages were calculated for each hour or half-hour and day of the year using all available years and a 20-day moving window. Similarly, if NCDC temperature and precipitation data were not available to fill data gaps, diurnal average values of the site were also used.

The accuracy of our empirical findings are limited by eddy flux measurements in the following aspects: (1) the flux sites probably do not represent true random samples of biome types; a number of biomes, like tropical rain forests and savannas, are underrepresented; and (2) potential biases in the eddy covariance method as a result of advection errors, energy imbalance errors, and errors associated with the data integration approach.

Segregation method

We used a second order polynomial regression with Microsoft Excel to segregate the entire data set into temperature-limited group (TG) and dryness-limited group (DG). Main steps are summarized below. (1) *Establish initial subgroups*. First, we choose10 sites as an initial temperature-limited group and 10 sites as an initial dryness-limited group by guess. We then perform a regression between NEE and temperature in the temperature group, and between NEE and dryness in the dryness group using a second order polynomial. The initial subgroups are considered to be established when each regression $r^2 > 0.60$. If an initial subgroup's regression $r^2 < 0.60$, we replace outlier sites with new sites until the regression $r^2 > 0.60$. These subgroup members (10 in TG and 10 in DG) are checked again at the end of the segregation process. (2) *Determine the grouping of a new site (TG or DG) by comparing the new regression r^2 when including the new site with the previous r^2*. The new site is added to such a group in which the increase in r^2 is largest (or in which the decrease is smallest) (3) *Use the same rule as stated in (2) to test if the initial subgroup members (10 in TG and 10 in DG) belong to their respective initial groups, respectively.*

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Supplementary Table 1 Main site characteristics, climatic index, and carbon flux of terrestrial ecosystems observed in this analysis.

<TBLROW>

Site Code	Latitude (°N)	Longitude (°E)	Elevation (m)	Vegetation type	T (°C)	Dryness	C-flux (t C ha^{-1} yr^{-1})	Years of gap-filled data
TEMPERATURE-LIMITED GROUP								
AT-NEU	47.12	11.32	970	GRA	6.5	0.67	-0.10	2001-2008
AU-WAC	-37.43	145.19	545	EBF	10.1	0.80	-3.76	2006
BE-LON	50.55	4.74	167	CRO	10.7	1.05	-3.83	2005-2007
CA-CA1	49.87	-125.33	300	ENF	8.7	0.73	-3.59	1998-2006
CA-CA3	49.53	-124.90	165	ENF	8.8	0.53	0.63	2001-2006
CA-GRO	48.22	-82.16	300	MF	3.4	1.30	-0.83	2004-2006
CA-MAN	55.88	-98.48	259	ENF	-1.2	1.91	0.09	1994-2006
CA-MER	45.41	-75.52	70	WET	6.2	1.05	-0.53	1999-2006
CA-NS1	55.88	-98.48	260	ENF	0.4	1.83	-0.94	2004
CA-NS2	55.91	-98.52	260	ENF	0.9	1.70	-1.91	2002, 2004
CA-NS3	55.91	-98.38	260	ENF	-2.4	1.71	-0.89	2002-2004
CA-NS4	55.91	-98.38	260	ENF	-2.1	1.56	0.05	2003-2004
CA-NS5	55.86	-98.49	260	ENF	-1.8	1.69	-1.25	2002, 2004
CA-NS6	55.92	-98.96	276	OSH	-0.4	1.51	-0.23	2002-2004
CA-NS7	56.64	-99.95	273	OSH	-1.7	1.41	0.29	2003-2004
CA-OAS	53.63	-106.20	530	DBF	2.3	1.67	-1.61	1997-2006
CA-OBS	53.99	-105.12	628	ENF	1.7	1.85	-0.55	2000-2006
CA-OJP	53.92	-104.69	579	ENF	1.5	1.69	-0.25	2000-2006
CA-QCU	49.27	-74.04	392	ENF	1.3	0.81	1.41	2002-2006
CA-QFO	49.69	-74.34	382	ENF	1.1	0.97	-0.33	2004-2006
CA-SJ1	53.91	-104.66	580	ENF	0.7	2.08	-0.73	2004-2005
CA-SJ2	53.94	-104.65	580	ENF	0.4	1.08	1.48	2003-2006
CA-SJ3	53.88	-104.64	488	ENF	2.2	2.06	0.31	2005

CA-TP1	42.66	-80.56	265	ENF	8.7	0.82	-0.38	2003-2007
CA-TP3	42.71	-80.35	184	ENF	8.8	1.10	-4.42	2003-2007
CA-TP4	42.71	-80.36	184	ENF	8.6	1.08	-1.36	2003-2007
CA-WP1	54.95	-112.47	540	MF	1.9	1.85	-2.21	2004-2007
CH-OE1	47.29	7.73	450	GRA	9.6	0.65	-3.72	2002-2007
CH-OE2	47.29	7.73	452	CRO	10.0	0.59	-3.25	2004-2005,2007
CN-CHA	42.40	128.10	761	MF	4.8	1.90	-2.50	2003-2004
DE-BAY	50.14	11.87	775	ENF	6.2	0.64	0.44	1997-1999
DE-GEB	51.10	10.91	161	CRO	9.7	1.21	-2.81	2004-2006
DE-GRI	50.95	13.51	385	GRA	8.0	0.97	-2.83	2005-2006
DE-HAI	51.08	10.45	430	DBF	8.3	0.89	-2.94	2000-2007
DE-WET	50.45	11.46	785	ENF	6.5	0.87	-1.32	2002-2007
DK-LVA	55.68	12.08	15	GRA	9.3	0.77	-2.57	2006-2007
DK-SOR	55.49	11.65	40	DBF	8.3	0.75	-0.63	1997-2006
FI-HYY	61.85	24.29	181	ENF	4.3	1.41	-2.09	1997-1999, 2001-2004,2006
FI-KAA	69.14	27.30	155	WET	-1.1	0.64	-0.20	2000-2007
FI-SII	61.83	24.19	162	WET	4.0	1.35	-0.51	2005
FI-SOD	67.36	26.64	180	ENF	-0.7	0.80	0.62	2000-2001,2003-2007
FR-FON	48.48	2.78	90	DBF	11.5	0.84	-3.80	2006
FR-GRI	48.84	1.95	125	CRO	11.2	1.30	-2.36	2005-2006
FR-HES	48.67	7.06	300	DBF	10.0	0.97	-3.71	1997-1999, 2001-2007
FR-LQ1	45.64	2.74	1040	GRA	7.7	0.32	-1.51	2004-2006
FR-LQ2	45.64	2.74	1040	GRA	7.7	0.32	-1.86	2004-2006
FR-PUE	43.74	3.60	270	EBF	13.7	1.23	-2.60	2001-2007
HU-HH2	46.96	16.65	248	GRA	8.9	1.10	-2.20	1999-2000,2007
IE-DRI	51.99	-8.75	187	GRA	9.6	0.51	-1.85	2003
IT-CPZ	41.71	12.38	68	EBF	14.9	1.68	-5.60	1997,2001-2006
IT-MBO	46.02	11.05	1550	GRA	5.6	0.97	-0.47	2003
IT-NON	44.69	11.09	25	DBF	13.8	1.04	-5.04	2001-2003,2006
IT-PT1	45.20	9.06	60	DBF	14.3	1.82	-4.86	2003
IT-REN	46.59	11.43	1730	ENF	4.80	1.20	-2.00	1999,2001-2007
IT-RO2	42.39	11.92	224	DBF	14.9	1.42	-7.52	2002-2006
IT-SRO	43.73	10.28	4	ENF	14.2	1.59	-4.76	1999-2007

JP-TAK	36.15	137.42	1420	DBF	6.5	0.47	-2.28	1994-2004
NL-CA1	51.97	4.93	0.7	GRA	10.9	0.97	-4.40	2003-2004,2006-2007
NL-HOR	52.03	5.07	-2.2	GRA	11.0	1.11	-3.29	2004-2005
NL-LAN	51.95	4.90	-1	CRO	11.3	1.06	-4.88	2005
NL-LOO	52.17	5.74	25	ENF	10.3	1.00	-3.07	1997-2007
PT-ESP	38.64	-8.60	95	EBF	16.0	2.17	-5.76	2002-2004, 2006-2007
SE-ABI	68.36	18.79	TBD	DBF	0.1	0.42	-1.30	2005
SE-DEG	64.18	19.55	270	WET	2.6	0.45	-0.53	2001-2002, 2004-2005
SE-FLA	64.11	19.46	226	ENF	2.7	1.27	-0.57	1997-1998.2001-2002
SE-NOR	60.09	17.48	43	EBF	6.3	1.07	0.96	1996-1997,1999,2003,2005
UK-HAM	51.12	-0.86	80	DBF	10.5	0.59	-5.88	2004
US-ATQ	70.47	-157.41	15	WET	-10.6	4.87	-0.45	2003-2006
US-BAR	44.06	-71.29	272	DBF	7.5	0.76	-3.71	2004-2006
US-BN1	63.92	-145.38	518	ENF	0.2	1.99	-1.4	2002-2004
US-BN3	63.92	-145.74	469	MF	0.2	1.99	-0.09	2002-2003
US-BO1	40.01	-88.29	219	CRO	11.4	1.25	-2.99	1997-2006
US-FPE	48.31	-105.10	634	GRA	5.8	1.41	0.32	2000-2006
US-HA1	42.54	-72.17	340	DBF	7.9	0.78	-2.53	1992-2007
US-HO1	45.20	-68.74	60	ENF	6.6	1.17	-1.88	1996-2004
US-IB2	41.84	-88.24	227	GRA	10.5	2.14	-3.97	2005
US-ME2	44.45	-121.56	1253	ENF	7.6	2.91	-4.71	2002-2008
US-ME3	44.32	-121.61	1005	ENF	8.5	2.76	-1.76	2004-2005
US-ME4	44.44	-121.57	1183	ENF	7.9	2.77	-2.06	2001-2002
US-PFA	45.95	-90.27	470	MF	5.0	1.24	-1.02	1997-2000,2003
US-SYV	46.24	-89.35	540	MF	4.2	1.01	-1.16	2002-2003,2005
US-UMB	45.56	-84.71	234	DBF	5.5	1.19	-1.51	1999-2003
US-WBW	35.96	-84.29	283	DBF	14.9	0.95	-9.06	1995-1998
US-WCR	45.81	-90.08	520	DBF	5.3	1.21	-0.90	1999-2006
US-WRC	45.82	-121.95	371	ENF	8.9	0.54	-0.79	1999-2002,2004
DRYNESS-LIMITED GROUP								
AU-HOW	-12.49	131.15	38	WSA	26.2	0.93	-3.60	2001-2005
AU-TUM	-35.66	148.15	1200	EBF	9.5	1.26	-3.37	2002-2007

BE-VIE	50.31	6.00	450	MF	8.2	1.10	-5.17	1997-2006
BR-MA2	-2.61	-60.21	120	EBF	25.9	0.77	-3.87	1999-2002
CA-LET	49.71	-112.94	960	GRA	6.4	2.12	-1.30	1999-2006
CN-ANH	33.00	117.00	TBD	DBF	17.5	0.48	-9.79	2005-2006
CN-DO1	31.52	121.96	2-5	WET	15.6	0.58	-6.23	2005
CN-DO2	31.58	121.90	2-5	WET	15.6	0.70	-4.37	2005
CN-DO3	31.52	121.97	2-5	WET	15.7	0.77	-5.12	2005
CN-HAM	37.37	101.18	3250	GRA	-1.5	2.48	-0.49	2003-2005
CN-QYZ	26.74	115.07	100	MF	18.6	1.30	-3.07	2003-2004
CZ-BK1	49.50	18.54	908	ENF	8.3	0.64	-7.09	2004-2006
DE-THA	50.96	13.57	380	ENF	8.8	0.94	-6.00	1997-2007
ES-LMA	39.94	-5.77	260	SAV	16.2	1.46	-1.28	2004-2006
FR-LBR	44.72	-0.77	61	ENF	14.0	1.29	-4.12	1997-1998
HU-BUG	46.69	19.60	140	GRA	10.0	1.63	-0.74	2003-2007
IT-AMP	41.90	13.61	884	GRA	9.5	1.20	-1.28	2003-2006
IT-COL	41.85	13.59	1550	DBF	7.4	0.96	-5.87	1997-1998,2000-2001,2005
IT-RO1	42.41	11.93	234	DBF	15.4	1.38	-3.04	2001-2006
PT-MI1	38.54	-8.00	250	EBF	15.9	2.46	-0.89	2003-2005
PT-MI2	38.48	-8.02	190	GRA	14.4	1.63	-0.93	2005-2007
UK-EBU	55.87	-3.21	190	GRA	9.1	0.42	-6.73	2004
UK-GRI	56.61	-3.80	340	ENF	7.4	0.86	-6.12	1997-1998,2000-2001
US-AUD	31.59	-110.51	1469	GRA	16.1	1.94	0.97	2003-2005
US-BLO	38.90	-120.63	1315	ENF	11.2	0.99	-5.76	2000-2006
US-DK2	35.97	-79.10	168	DBF	15.1	1.07	-4.44	2001-2005
US-DK3	35.98	-79.09	163	ENF	14.7	1.10	-4.54	2001-2005
US-FMF	35.14	-111.73	2160	ENF	10.0	2.07	0.51	2007
US-FUF	35.09	-111.76	2180	ENF	9.2	2.04	-0.58	2007
US-GLE	41.36	-106.24	3190	ENF	0.1	0.97	-3.9	2005-2008
US-GOO	34.25	-89.87	87	GRA	16.3	0.95	-2.13	2003-2006
US-IVO	68.49	-155.75	570	WET	-9.4	1.38	-0.22	2004-2006
US-KS2	28.61	-80.67	3	CSH	22.1	1.31	-3.60	2002,2004-2006
US-MLT	42.5	-113.41	1370	GRA	8.8	2.90	-0.26	2005
US-MMS	39.32	-86.41	275	DBF	12.4	1.05	-4.23	1999-2005

US-MOZ	38.74	-92.20	219	DBF	13.5	1.47	-3.40	2005-2006
US-NC2	35.80	-76.67	12	ENF	15.8	0.94	-5.91	2005-2008
US-NR1	40.03	-105.55	3050	ENF	2.5	1.86	-0.49	1999-2000,2002-2003
US-OHO	41.55	-83.84	230	DBF	10.4	1.42	-2.67	2004-2008
US-SO2	33.37	-116.62	1394	CSH	14.4	1.97	-0.54	2004-2005
US-SO3	33.38	-116.62	1429	CSH	14.5	2.03	-0.89	2005-2006
US-SP1	29.74	-82.22	50	ENF	20.3	1.34	-1.99	2001, 2003, 2005-2006
US-SP3	29.75	-82.16	50	ENF	20.1	1.03	-6.40	2001-2004
US-TON	38.43	-120.97	177	WSA	16.3	2.11	-1.71	2002-2006
US-VAR	38.41	-120.95	129	GRA	15.9	1.60	-0.58	2001-2006
ZA-KRU	-25.02	31.5	300	SAV	21.8	2.72	0.25	2001-2005
ZM-MON	-15.43	23.25	1053	SAV	22.0	1.42	-0.01	2007

Style tag for all material within a table, with the exception of the title and any footnotes.

<TBLFN> The vegetation is coded according to the IGBP classification: CRO, croplands; CSH, closed shrublands; DBF, deciduous broad-leaf forests; EBF, evergreen broad-leaf forests; ENF, evergreen needle-leaf forests; GRA, grassland; MF, mixed forests; OSH, open shrublands; SAV, savannas; WET, permanent wetlands; WSA, woody savannas.

<BX> Style tag for box heading and body text within a box.

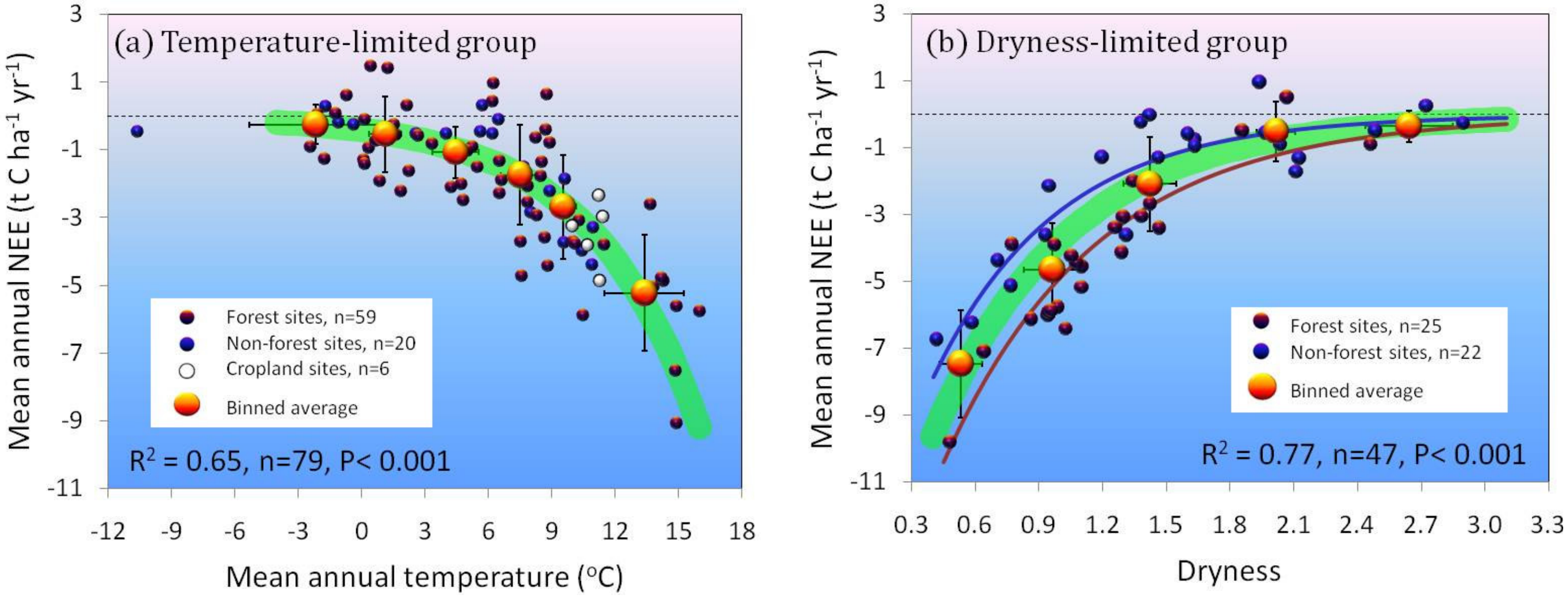
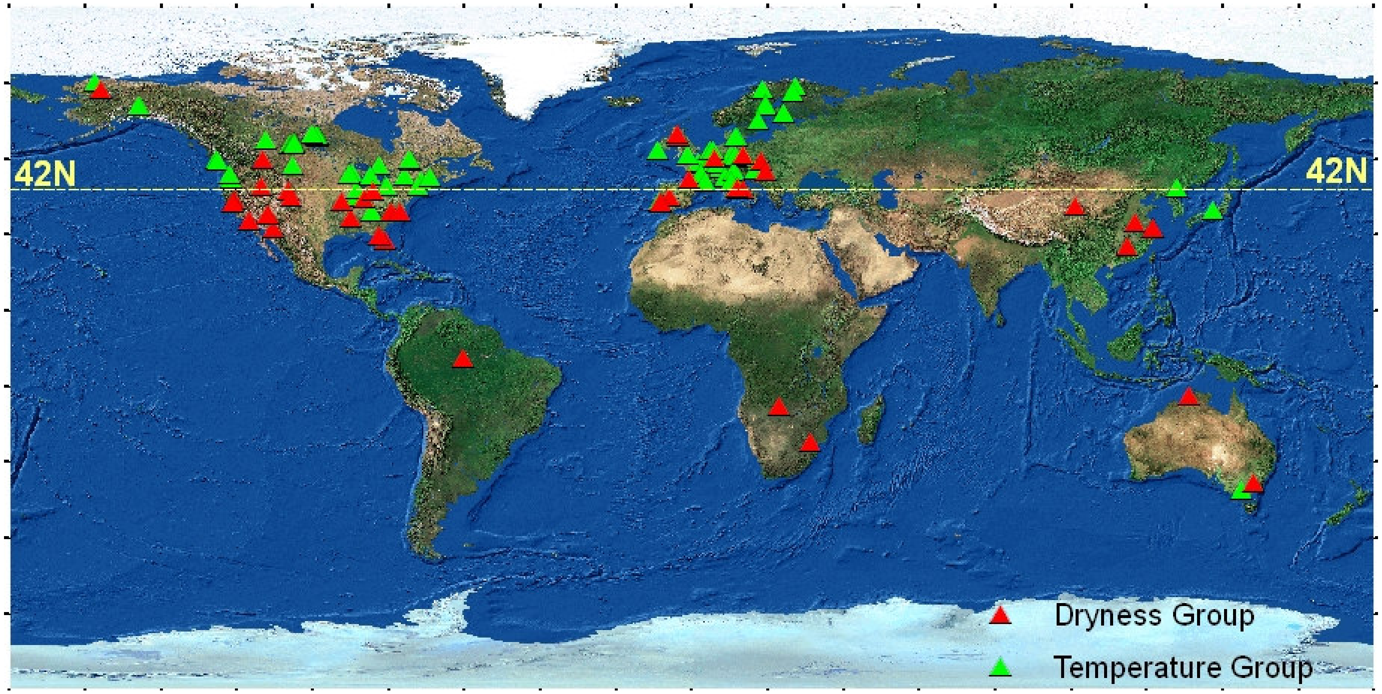
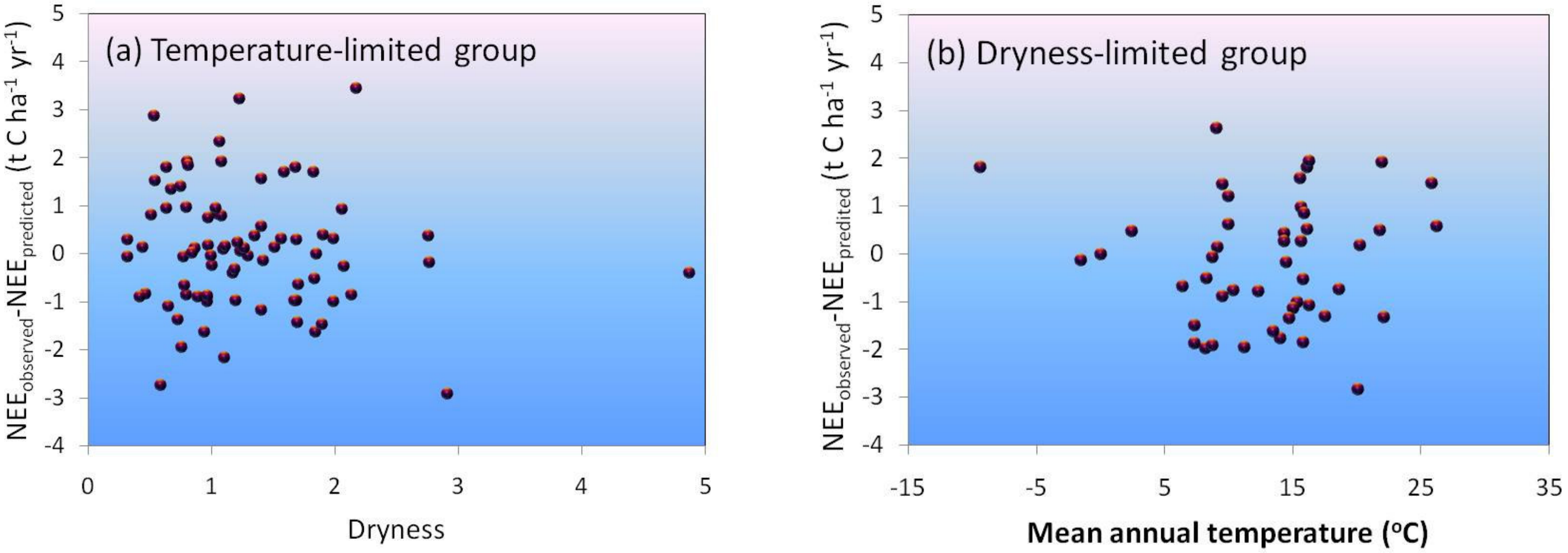

(a) Temperature-limited group
Mean annual NEE (t C ha^{-1} yr^{-1})
3
1
-1
-3
-5
-7
-9
-11
Forest sites, n=59
Non-forest sites, n=20
Cropland sites, n=6
Binned average
R^2 = 0.65, n=79, P< 0.001
-12
-9
-6
-3
0
3
6
9
12
15
18
Mean annual temperature (°C)
(b) Dryness-limited group
Mean annual NEE (t C ha^{-1} yr^{-1})
3
1
-1
-3
-5
-7
-9
-11
Forest sites, n=25
Non-forest sites, n=22
Binned average
R^2 = 0.77, n=47, P< 0.001
0.3
0.6
0.9
1.2
1.5
1.8
2.1
2.4
2.7
3.0
3.3
Dryness

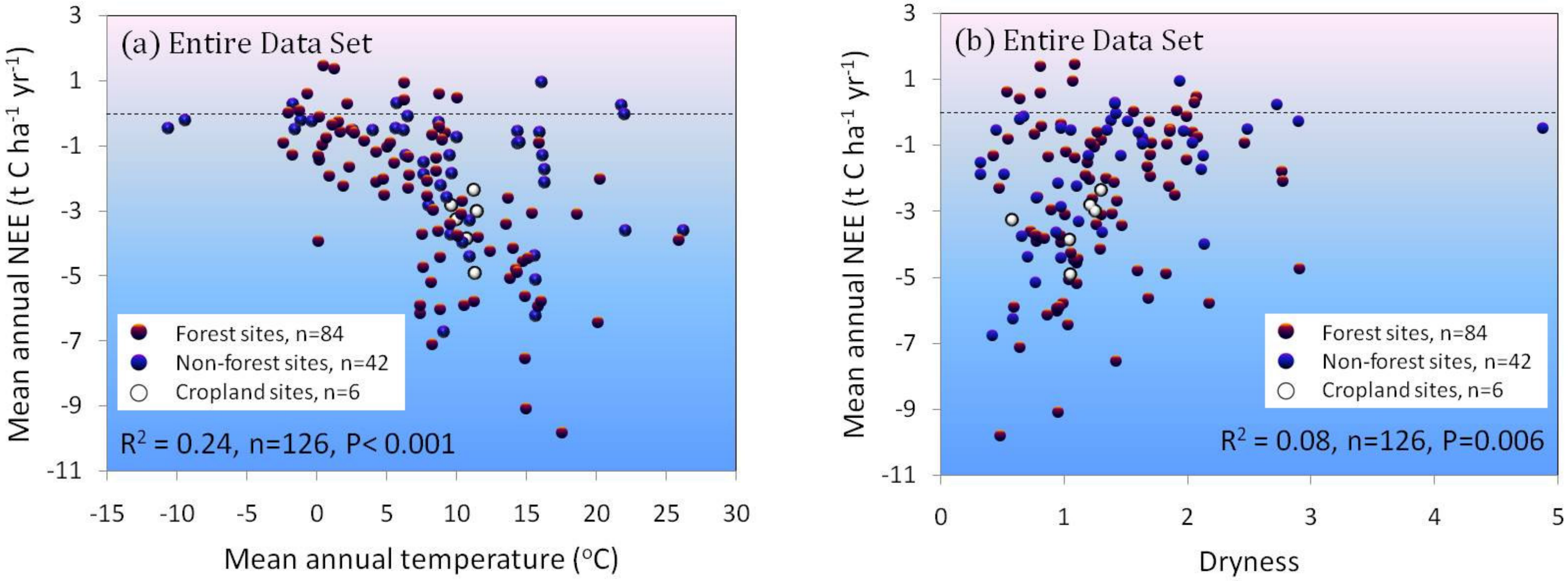
Figure 1. Climatic controls of the site-average net ecosystem exchange (NEE) across the FLUXNET sites (see supplementary Table 1): (a) temperature limited group; and (b) dryness limited group. The negative NEE values indicate that atmospheric carbon is assimilated by terrestrial ecosystems, while the positive NEE values indicate that terrestrial organic carbon is converted into atmospheric carbon. Small filled circles are site-average NEE, the large filled circles with standard deviation bars are binned-averaged values, in which the cropland sites (irrigated and fertilized) were excluded. The equations (1) and (2) were derived from the binned-averaged values. The thick green lines represent model predictions. The thin red line in (b) represents model prediction for the sub-group of forest sites in the dryness-limited group, while thin blue line in (b) represents model prediction for the sub-group of non-forest sites in the dryness-limited group.



Supplementary Figure 1. The geographical distribution of the eddy flux tower sites involved in this analysis.



Supplementary Figure 2: (a) The residual of the temperature based empirical prediction for the temperature-limited group (1) versus dryness; (b) The residual of the dryness based empirical prediction for the dryness-limited group (2) versus temperature for the dryness-limited group. The cropland sites (irrigated and fertilized) were excluded from this residual analysis.



Supplementary Figure 3. Correlation of the site-average net ecosystem exchange (NEE) for all sites used in Figure 1 with: (a) mean annual temperature; (b) dryness as independent variables respectively. The cropland sites were excluded in the statistical analysis as in Figure 1.