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Controls on winter ecosystem respiration in temperate and boreal ecosystems

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Abstract. Winter CO_2 fluxes represent an important component of the annual carbon budget in northern ecosystems. Understanding winter respiration processes and their responses to climate change is also central to our ability to assess terrestrial carbon cycle and climate feedbacks in the future. However, the factors influencing the spatial and temporal patterns of winter ecosystem respiration (R_{eco}) of northern ecosystems are poorly understood. For this reason, we analyzed eddy covariance flux data from 57 ecosystem sites ranging from ∼35° N to ∼70° N. Deciduous forests were characterized by the highest winter R_{eco} rates ($0.90 \pm 0.39\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$), when winter is defined as the period during which daily air temperature remains below 0 °C. By contrast, arctic wetlands had the lowest winter R_{eco} rates ($0.02 \pm 0.02\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$). Mixed forests, evergreen needle-leaved forests, grasslands, croplands and boreal wetlands were characterized by intermediate winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) of 0.70(±0.33), 0.60(±0.38), 0.62(±0.43), 0.49(±0.22) and 0.27(±0.08), respectively. Our cross site analysis showed that winter air (T_{air}) and soil (T_{soil}) temperature played a dominating role in determining the spatial patterns of winter R_{eco} in both forest and managed ecosystems (grasslands and croplands). Besides temperature, the seasonal amplitude of the leaf area index (LAI), inferred from satellite observation, or growing season gross primary productivity, which we use here as a proxy for the amount of recent carbon available for R_{eco} in the subsequent winter, played a marginal role in winter CO_2 emissions from forest ecosystems. We found that winter R_{eco} sensitivity to temperature variation across space (Q_S) was higher than the one over time (interannual, Q_T). This can be expected because Q_S not only accounts for climate gradients across sites but also for (positively correlated) the spatial variability of substrate quantity. Thus, if the models estimate future warming impacts on R_{eco} based on Q_S rather than Q_T, this could overestimate the impact of temperature changes.

1 Introduction

The processes controlling the winter carbon cycle of northern ecosystems, which is mainly ecosystem respiration (R_{eco}), have received much less attention than processes active during the growing season. The longstanding view of marginal wintertime biological activity (e.g. Coyne and Kelley, 1971; Steudler et al., 1989) proposes that winter respiration is very small compared to growing season respiration. Recent field studies suggest a different picture by demonstrating the larger than expected wintertime respiration rates in Arctic tundra, bog, and mountain ecosystems (e.g. Oechel et al., 1997; Fahnestock et al., 1998; Grogan and Chapin, 1999; Panikov and Dedysh, 2000; Aurela et al., 2002; Monson et al., 2006; Bergeron et al., 2007). These studies suggest that winter R_{eco} should not be ignored when attempting to quantify and understand the annual carbon balance of terrestrial ecosystems (Hobbie et al., 2000; Grogan and Jonasson, 2005; Johansson et al., 2006). However, due to the large carbon storage and heterogeneity of northern ecosystems, winter R_{eco} remains incompletely understood given the limited spatial representativeness of individual-site studies.

In general, mid and high-latitude ecosystems contain large amounts of soil carbon (Post et al., 1982; Tarnocai et al., 2009), which implies that these ecosystems could provide a significant positive feedback to climate change if warming stimulates soil carbon decomposition and CO_2 release to the atmosphere (Friedlingstein et al., 2006). The increased high-latitude warming projected by climate models includes winter warming (Serreze et al., 2000; Giorgi et al., 2001) and has already been observed over the past 30 yr (IPCC, 2007). The response of the soil organic carbon (SOC) balance to warming differs widely among coupled climate-carbon models (Friedlingstein et al., 2006). This is because the net balance in these models depends on two fluxes of opposite directions: the litter input that may increase under warming if vegetation net primary productivity increases, and the soil carbon microbial decomposition rate that also responds positively to warming (e.g. Jones et al., 2005). Therefore, it is important to disentangle how temperature and vegetation productivity separately affect winter respiration. Previous studies (e.g. Clein and Schimel, 1995; Hobbie, 1996; Mikan et al., 2002; Grogan et al., 2001; Grogan and Jonasson, 2005) were concentrated on the site-level or landscape-level. For example, Grogan and Jonasson (2005) found that both the amount of substrate available for respiration and soil temperature (T_{soil}) determine landscape-level variation of winter R_{eco} of birch forest and heath tundra. These studies are valuable for understanding site-specific or landscape-level processes, but their results cannot be readily extrapolated across sites and climate gradients to infer regional sensitivities.

Eddy covariance measurements of CO_2 fluxes have been collected continuously, together with climate variables, at many sites in temperate, boreal and arctic ecosystems, and are available in the FLUXNET database (Baldocchi et al., 2001; Baldocchi, 2008). These data represent a valuable source of information for the analysis of the spatial and temporal variability of winter R_{eco}. In this study, we focus on Northern Hemisphere sites from ∼35° N to ∼70° N, covering a climate gradient of 24 °C of mean annual temperature. In the first part, we investigate the importance of winter R_{eco} and its contribution to annual R_{eco} for different ecosystem types. The results are based on five different definitions of the winter season, having different temporal and thermal thresholds. In the second part, we analyze the temperature dependency of winter daily R_{eco} at each site, using an Arrhenius type model. We also consider a total of 218 site-years that have been aggregated to quantify the sensitivity of anomalies of winter R_{eco} to temperature on the temporal (interannual) scale. This sensitivity to temperature variation over time is hypothesized to be lower than the one across space given that the latter not only accounts for direct climate effects, but also site productivity (Mahecha et al., 2010; Wang et al., 2010). Finally, in an attempt to improve our understanding of spatial controls on winter R_{eco}, we examine the relationships between winter R_{eco}, climate variables and productivity-related variables across sites.

2 Materials and methods

2.1 Data sources

2.1.1 Eddy covariance flux data

The eddy covariance data used in this study are extracted from the La Thuile FLUXNET synthesis database which contains 965 site years processed according to standardized protocols (Papale et al., 2006) (http://www.fluxdata.org). The processing of this dataset is based on friction velocity ($u*$) filter and despiking of half hourly flux data, which would be expected to reduce the bias of flux measurements during the calm night and winter stable stratification period. Daily cumulative values of Net Ecosystem Exchange (NEE, $\mathrm{g\,C\,m^{-2}\,day^{-1}}$) are retrieved from the half hourly values included in the database, where a positive NEE represents a carbon release and a negative NEE a carbon uptake. The NEE time series can be partitioned into gross primary productivity (GPP) and ecosystem respiration (R_{eco}). The flux-partitioning algorithm, which is implemented in La Thuile FLUXNET database, uses short-term temperature sensitivities to extrapolate night-time respiration to daytime. This approach avoids significantly biased estimates of R_{eco} that can be obtained using long-term temperature sensitivities affected by confounding factors such as growth dynamics (Reichstein et al., 2005). T_{air}, T_{soil} and soil moisture in upper layer (between 2 and 10 cm depth), precipitation, GPP and ancillary observations of maximum LAI from site measurements were also used in this study.

Of the 200 sites located north of 35° N, we identified a subset of sites meeting the following criteria:

- having at least two years of T_{air}, upper T_{soil}, precipitation, NEE, GPP and R_{eco} data;
- having a winter duration (according to definition D_AT0: T_{air} below 0 °C, Sect. 2.2) longer than 15 days;
- having more than 70 % of data coverage, both at the annual scale and during the winter period defined by D_AT0.

This resulted in a total of 57 sites, and 218 site years of data being selected, covering evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF), mixed forests (MF), boreal wetlands (BWET), arctic wetlands (AWET), croplands (CRO) and grasslands (GRA) (the number of site years are 78, 54, 17, 11, 5, 20 and 33, respectively) (Table 1).

Nearly one third (20) of the selected 57 sites employed open-path infrared gas analyzers (IRGA) for measuring CO_2 concentrations (Table 1), which are known to underestimate CO_2 emissions in cold conditions due to self-heating of the open-path IRGAs (Burba et al., 2006; Hirata et al., 2007; Lafleur and Humphreys, 2007). The effects of self-heating can be corrected for in post-processing (Burba et al., 2008), however while some studies found these corrections to improve the correspondence with concurrent closed-path CO_2 flux measurements (Burba et al., 2006, 2008; Grelle and Burba, 2007; Järvi et al., 2009), others did not (Wohlfahrt et al., 2008a; Haslwanter et al., 2009). The reasons for these mixed results are unclear at present; they may be partly attributed to differences in environmental conditions (Haslwanter et al., 2009), partly to the deployment of the open-path analyser. For example, the correction after Burba et al. (2008) applies to a vertical setup only, while many researchers prefer to tilt their open-path IRGAs in order to speed up drying of the lower window after wetting. Given these uncertainties, we decided not to correct open-path CO_2 flux measurements for the effect of self-heating in the present study. In an attempt to quantify how much this may bias our results we compared the parameters of Eq. (1) optimised for sites with open- and closed-path IRGAs separately. Both parameters (E_0,R_{ecoref}) were found to be not statistically significantly different (e.g. $E_{0:}$ open- vs. closed-path: 85.6 vs. 83.0 $\mathrm{kJ\,mol^{-1}}$; R_{ecoref}: open- vs. closed-path: 0.9 vs. 1.1 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ when investigating T_{air}-R_{eco} relationship based on winter definition D_AT0), suggesting that any bias due to the IRGA design is small in the present study.

2.1.2 LAI dataset

Information on the leaf area index (LAI) was retrieved for each investigated site from MODIS-Aqua satellite data downloaded from the ORNL-DAAC MODIS – Collection-5 LAI data (MYD15A2) (https://daac.ornl.gov). These LAI data, which are only available after the year 2000, have a spatial resolution of 1 km and a temporal resolution of 8-days. They also include quality control (QC) information about cloud and data processing conditions. Only LAI data without significant cloud contamination described in the LAI user's guide (http://landweb.nascom.nasa.gov) within an area of 1 × 1 km centered on each site were retained for each 8-day period to obtain the maximum and minimum LAI values for each site year. The seasonal amplitude (ΔLAI) is defined as the difference between maximum and minimum of LAI and can be considered as a proxy for recent carbon inputs to soil, i.e. substrate available for sustaining winter R_{eco}. In-situ ΔLAI can not be retrieved since the majority of minimum LAI measurements are not reported in La Thuile ancillary dataset. It should be noted that in-situ LAI substitution with MODIS-LAI at 1 km resolution can introduce uncertainty, whose magnitude is dependent on the size of the eddy covariance tower footprint and the landscape heterogeneity

Table 1. General characterization of study sites used in this study.

Site	Type	Lat.	Lon.	Index	Ann. Precip. (mm)	Ann. Temp. (°C)	WLEN (D_AT0) (SD) (d)	ΔLAI (SD) ($m^2 m^{-2}$)	R_{eco} (D_AT0) (SD) ($g C m^{-2} d^{-1}$)	R_{eco} (D_TM) (SD) ($g C m^{-2} d^{-1}$)	Available years	Reference
AT-Neu*	GRA	47.1	11.3	1	852	6.5	116(16)	5.8(0.4)	1.24(0.12)	1.06(0.24)	2002–2005	Wohlfahrt et al. (2008b)
BE-Vie	MF	50.3	6.0	2	1065	7.4	71(35)	5.4(0.2)	1.02(0.16)	1.10(0.16)	1996–2002	Aubinet et al. (2001)
CA-Ca1	ENF	49.9	−125.3	3	1369	9.9	54	5.6	1.33	1.48	2001	Humphreys et al. (2006)
CA-Ca2*	ENF	49.9	−125.3	4	1474	9.9	39(31)	4.4(0.7)	0.82(0.13)	1.24(0.22)	2001, 2004	Humphreys et al. (2006)
CA-Let	GRA	49.7	−112.9	5	398	5.4	138(13)	1.1(0.5)	0.22(0.08)	0.17(0.06)	1998–2004	Flanagan et al. (2002); Flanagan and Johnson (2005)
CA-Mer	BWET	45.4	−75.5	6	891	6.1	128(22)	5.5(0.3)	0.32(0.03)	0.29(0.04)	1998–2004	Lafleur et al. (2003)
CA-Oas	DBF	53.6	−106.2	7	429	0.3	169(17)	6.0(0.2)	0.50(0.06)	0.33(0.07)	1997–2003	Black et al. (2000)
CA-Obs	ENF	54.0	−105.1	8	406	0.8	185(15)	3.9(0.2)	0.47(0.04)	0.27(0.04)	1999–2004	–
CA-Ojp	ENF	53.9	−104.7	9	431	0.1	176(13)	3.0(0.4)	0.24(0.02)	0.12(0.03)	1999–2004	Kljun et al. (2006)
CA-Qcu*	ENF	49.3	−74.0	10	950	0.1	175(15)	2.2(0.2)	0.22(0.06)	0.13(0.01)	2001–2005	Giasson et al. (2006)
CA-Qfo	ENF	49.7	−74.3	11	962	−0.4	172(19)	4.0(0.2)	0.44(0.07)	0.28(0.06)	2003–2005	Bergeron et al. (2007)
CA-SJ1*	ENF	53.9	−104.7	12	430	0.1	181(15)	2.3(0.2)	0.14(0.05)	0.08(0.04)	2001–2004	–
CA-SJ2	ENF	53.9	−104.6	13	430	0.1	197	1.3(0.5)	0.09(0.00)	0.02(0.01)	2003–2004	–
CA-TP4*	ENF	42.7	−80.4	14	936	8.7	107(8)	5.8(0.1)	0.66(0.06)	0.67(0.02)	2003–2004	Arain and Restrepo-Coupe (2005)
CA-WP1*	MF	55.0	−112.5	15	461	1.1	159(7)	3.9(0.3)	0.22(0.02)	0.12(0.00)	2003–2004	Syed et al. (2006); Flanagan and Syed (2011)
CH-Oe1*	GRA	47.3	7.7	16	945	9.1	85(28)	2.4(0.4)	0.83(0.24)	0.87(0.24)	2002–2005	Ammann et al. (2007)
CN-HaM*	GRA	37.4	101.2	17	577	−0.8	182	4.7	0.08	0.02	2002	Kato et al. (2006)
CZ-BK1	ENF	49.5	18.5	18	1026	4.7	112(19)	5.8(0.6)	0.54(0.07)	0.57(0.06)	2004–2005	–
DE-Bay	ENF	50.1	11.9	19	1159	5.2	127(32)		1.22(0.21)	1.20(0.13)	1997–1998	–
DE-Geb*	CRO	51.1	10.9	20	444	8.7	87(7)	5.7(0.6)	0.57(0.27)	0.59(0.28)	2004–2005	Kutsch et al. (2010b)
DE-Hai	DBF	51.1	10.5	21	780	7.2	74(22)	6.2(0.3)	1.01(0.12)	1.06(0.15)	2001–2004	Knohl et al. (2003); Kutsch et al. (2010a)
DE-Meh	GRA	51.3	10.7	22	695	7.8	96(20)	5.1(0.7)	0.54(0.06)	0.57(0.09)	2003–2005	–
DE-Tha	ENF	51.0	13.6	23	643	8.1	85(21)	5.7(0.5)	0.94(0.18)	1.00(0.10)	1996–2002	Grunwald and Bernhofer (2007)
DK-Sor	DBF	55.5	11.6	24	573	8.0	71(35)	5.8(0.2)	1.44(0.25)	1.62(0.22)	1996–1998 2000–2001	Pilegaard et al. (2003)
FI-Hyy	ENF	61.8	24.3	25	620	2.2	153(21)	5.9(0.6)	0.55(0.11)	0.47(0.14)	1996–1998, 2000–2002,	Suni et al. (2003b)
FI-Kaa	BWET	69.1	27.3	26	454	−1.4	191(13)	1.5(0.1)	0.18(0.06)	0.15(0.06)	2000, 2003–2005	Aurela et al. (2002)
FI-Sod	ENF	67.4	26.6	27	525	−1.1	183(14)	2.2(0.2)	0.42(0.09)	0.32(0.18)	2000–2001, 2003–2005	Suni et al. (2003a)

within the footprint. Besides this, the satellite product might give large errors for evergreen needleleaf forests during the winter season, for example, the in-situ LAI at RU-Fyo site (spruce evergreen forest) was around 3.0 ($m^2 m^{-2}$) but the MODIS-derived LAI value is almost near zero. When comparing maximum LAI, we found that the coefficient of determination (r^2) between satellite and in-situ measurements was 0.48 (root mean square = 1.67, $n = 52$, data not shown). Given the uncertainties in satellite-derived ΔLAI, mean daily gross primary productivity during the growing season (May–October) (GPP_gs) at site level was also used as a proxy for recent carbon inputs to the soil.

2.2 Winter season definition

In this study, we focus on carbon cycling during the freezing period of the year, which has been rarely explored in previous meta-data analyses (e.g. Yuan et al., 2009; Migliavacca et al., 2011). The winter seasons defined below are thus referenced to the freezing period of the year. Four winter season definitions were tested to estimate the effect of this arbitrary choice: D_AT0, D_AT-2, D_AT-5 and D_AT-10 are defined as the period during which the 10-day smoothed daily T_{air} remained below 0 °C, −2 °C, −5 °C and −10 °C for at least five consecutive days, which allowed for year-to-year variability in winter length since these definitions are based on each site year. We also include the established climatological winter (D_TM), which is defined as the three cold months December, January and February, hence implying the same winter onset and duration at each site.

2.3 Definitions of winter R_{eco} ratios and winter R_{eco} temperature dependency

2.3.1 Winter R_{eco} ratios definition

We investigated two types of winter R_{eco} ratios, one (RWCR) is defined as the ratio of winter cumulative R_{eco} ($g C m^{-2}$) to annual cumulative R_{eco} ($g C m^{-2}$) and the other (RWRR) is calculated as the ratio of mean winter R_{eco} rates ($g C m^{-2} d^{-1}$) to mean annual R_{eco} rates ($g C m^{-2} d^{-1}$). Both of the ratios are expressed in percentage (%). RWRR is used to represent winter average metabolism relative to the annual level. Although RWCR only differs from RWRR by the inclusion of winter duration, providing RWCR for each ecosystem can indicate the role of winter season in the annual

Table 1. Continued.

Site	Type	Lat.	Lon.	Index	Ann. Precip. (mm)	Ann. Temp. (°C)	WLEN (D_AT0) (SD) (d)	ΔLAI (SD) ($m^2\,m^{-2}$)	R_{eco} (D_AT0) (SD) ($g\,C\,m^{-2}\,d^{-1}$)	R_{eco} (D_TM) (SD) ($g\,C\,m^{-2}\,d^{-1}$)	Available years	Reference
FR-Hes	DBF	48.7	7.1	28	793	9.2	57(31)	5.8(0.5)	1.00(0.22)	1.17(0.24)	1997–1998, 2001–2003	Granier et al. (2000)
HU-Bug*	GRA	46.7	19.6	29	555	10.5	92(3)	1.5(0.1)	0.42(0.14)	0.45(0.14)	2002–2005	–
IT-Amp*	GRA	41.9	13.6	30	945	10.6	93(23)	2.0(0.2)	1.10(0.64)	0.97(0.24)	2002–2004	Gilmanov et al. (2007)
IT-Col	DBF	41.8	13.6	31	971	7.3	83(53)	6.3(0.4)	0.72(0.00)	0.75(0.15)	1996, 2000	–
IT-MBo*	GRA	46.0	11.0	32	1185	5.4	141(29)	5.8(0.4)	0.91(0.12)	0.84(0.20)	2003–2005	Marcolla and Cescatti (2005); Gianelle et al. (2009)
IT-Ren	ENF	46.6	11.4	33	965	6.2	150(19)	5.4(0.2)	0.38(0.07)	0.31(0.13)	2001–2005	Montagnani et al. (2009)
JP-Tak	DBF	36.1	137.4	34	1024	6.5	123(16)	6.2(0.1)	0.58(0.17)	0.53(0.17)	2000–2003	–
JP-Tom*	MF	42.7	141.5	35	1156	6.7	114(14)	6.0(0.3)	0.51(0.02)	0.46(0.05)	2001–2002	–
NL-Loo	ENF	52.2	5.7	36	786	9.4	63(34)	5.7(0.5)	1.54(0.74)	2.06(0.43)	1996, 1998, 2002	Dolman et al. (2002)
RU-Fyo	ENF	56.5	32.9	37	671	4.4	143(19)	5.9(0.4)	0.91(0.19)	0.78(0.27)	1998–2004	Milyukova et al. (2002)
US-Atq*	AWET	70.5	−157.4	38	93	−12.3	254(14)	0.9(0.1)	0.02(0.01)	0.00(0.00)	2003–2005	–
US-Bkg*	GRA	44.3	−96.8	39	586	6.0	124(5)	1.8(0.1)	0.15(0.07)	0.13(0.09)	2004–2005	Gilmanov et al. (2005)
US-Bo1*	CRO	40.0	−88.3	40	991	11.0	96(18)	4.5(0.4)	0.22(0.07)	0.40(0.26)	1996–1998, 2001–2002	Meyers and Hollinger (2004)
US-Bo2*	CRO	40.0	−88.3	41	991	11.0	84(14)	4.5(0.4)	0.50(0.50)	0.53(0.49)	2004–2005	Meyers and Hollinger (2004)
US-Ha1	DBF	42.5	−72.2	42	1071	6.6	110(16)	–	1.43(0.44)	1.34(0.43)	1991–1992, 1994–1997	Urbanski et al. (2007)
US-Ho1	ENF	45.2	−68.7	43	1070	5.3	130(16)	5.5(0.2)	0.62(0.13)	0.52(0.13)	1996–2002	Hollinger et al. (2004)
US-IB2*	GRA	41.8	−88.2	44	930	9.0	103(15)	1.7(0.3)	0.38(0.04)	0.37(0.13)	2004–2005	–
US-Ivo	AWET	68.5	−155.8	45	304	−8.3	239(26)	2.0(0.1)	0.03(0.03)	0.03(0.02)	2003–2004	–
US-LPH	DBF	42.5	−72.2	46	1071	6.7	119(11)	6.1(0.2)	0.81(0.19)	0.75(0.21)	2002–2004	Borken et al. (2006)
US-MMS*	DBF	39.3	−86.4	47	1032	10.9	77(12)	5.9(0.1)	0.87(0.12)	0.91(0.18)	2000–2004	Schmid et al. (2000)
US-MOz*	DBF	38.7	−92.2	48	878	13.5	64(26)	6.4(0.2)	0.76(0.38)	0.91(0.21)	2004–2005	Gu et al. (2006)
US-NR1	ENF	40.0	−105.5	49	595	0.4	169(41)	4.3(0.2)	0.77(0.19)	0.64(0.27)	1999, 2002	Monson et al. (2002)
US-Ne1	CRO	41.2	−96.5	50	790	10.1	92(10)	2.3(0.3)	0.61(0.03)	0.62(0.03)	2001–2004	Verma et al. (2005)
US-Ne2	CRO	41.2	−96.5	51	789	10.1	95(9)	2.1(0.2)	0.58(0.11)	0.59(0.12)	2002–2004	Verma et al. (2005)
US-Ne3	CRO	41.2	−96.4	52	784	10.1	94(8)	2.2(0.4)	0.59(0.10)	0.55(0.06)	2001–2004	Verma et al. (2005)
US-PFa	MF	45.9	−90.3	53	823	4.3	141(1)		0.55(0.08)	0.53(0.12)	1996–1998	Ricciuto et al. (2008)
US-Syv	MF	46.2	−89.3	54	826	3.8	148(20)	6.3(0.2)	0.52(0.32)	0.42(0.36)	2002, 2004–2005	Desai et al. (2005)
US-UMB	DBF	45.6	−84.7	55	803	5.8	121(21)	6.4(0.2)	0.77(0.09)	0.77(0.05)	1999–2002	Gough et al. (2008)
US-WCr	DBF	45.8	−90.1	56	787	4.0	140(17)	6.0(0.2)	0.58(0.19)	0.45(0.17)	1999–2002, 2004–2005	Cook et al. (2004)
US-Wrc	ENF	45.8	−122.0	57	2452	9.5	70	5.7	1.08	0.82	2000	–

Type: DBF: deciduous broadleaf forests; ENF: evergreen needleleaf forests; GRA: grasslands; CRO: croplands; BWET and AWET are boreal and arctic wetlands, respectively; MF (mixed forests).
* denotes the sites that use open-path gas analyzer.
Lat. and Lon. are latitude and longitude, respectively.
Annual precip. and Annual temp. represent annual total precipitation and mean annual temperature, respectively.
WLEN is the winter length (unit: day).
ΔLAI: the average difference between maximum and minimum of MODIS LAI ($m^2\,m^{-2}$) from corresponding available years, and the MODIS LAI data is only available after year 2000.
R_{eco} is mean winter R_{eco} rates ($g\,C\,m^{-2}\,d^{-1}$) for D_AT0 (air temperature $<0\,°C$) and D_TM (December–February) over available years, respectively.
SD is standard deviation.

carbon budget. One-way variance analysis (ANOVA) was employed to examine whether winter R_{eco} ratios (or winter R_{eco}) were different among ecosystem types. Before ANOVA, the data sets were tested for normality using one-sample Kolmogorov-Smirnov test (K-S test). Both of the statistical analyses were performed using SPSS statistical package (SPSS windows, version 17.0, SPSS Inc.).

2.3.2 Winter R_{eco} sensitivity to temperature variation over time

Owing to the short length of R_{eco} and temperature records, temporal correlations between winter R_{eco} and predictor temperature are not applicable for studying the interannual (temporal) sensitivity of R_{eco} to temperature in detail at each site. Instead, we calculated mean winter R_{eco} rates ($g\,C\,m^{-2}\,d^{-1}$) and mean winter temperature anomalies at each site year, which was achieved by removing the multi-year mean winter R_{eco} rates and mean winter temperature from their respective mean annual values. A least squares regression was then performed between all site-year anomalies of mean winter R_{eco} rates and mean winter temperature in order to quantify the response of winter R_{eco} to interannual variations in temperature (or Q_T, winter R_{eco} sensitivity to temperature variation over time; $g\,C\,m^{-2}\,d^{-1}\,°C^{-1}$). For each winter season definition and each vegetation type using winter definition D_AT0, Q_T is calculated and its uncertainty is estimated using a bootstrapping algorithm (random resampling with replacement) with 500 draws.

2.3.3 Arrhenius equation to describe the temperature dependency of R_{eco}

The temperature dependency of winter R_{eco} within- and across-sites was analyzed using an Arrhenius type equation (Lloyd and Taylor, 1994):

$$R_{\mathrm{eco}} = R_{\mathrm{ecoref}}\ \exp(\frac{E_0}{R}(\frac{1}{T_{\mathrm{ref}}} - \frac{1}{T})) \tag{1}$$

where R_{ecoref} ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) represents a reference respiration rate at the reference temperature (T_{ref}, 273.15 K) related both to the amount of substrate available for decomposers, and its quality (Lloyd and Taylor, 1994). E_0 ($\mathrm{kJ\,mol^{-1}}$) is the activation energy parameter and represents the R_{eco} sensitivity to temperature, R the universal gas constant and T is temperature (K). Model parameters (E_0, R_{ecoref}) were estimated using the Levenberg-Marquardt method, implemented in the IDL library (Interactive Data Language 8.0), a non-linear regression analysis that optimizes model parameters finding the minimum of a defined cost function. The cost function used here is the sum of squared residuals. The standard errors of model parameters (E_0, R_{ecoref}) were estimated using a bootstrapping algorithm (random resampling with replacement) with 500 draws.

In order to obtain site-year-specific parameters (E_0, R_{ecoref}), half-hourly nighttime NEE over the defined winter season (Sect. 2.2) was regressed against the corresponding nighttime T_{air} and T_{soil} based on Eq. (1). This is done given that daytime R_{eco} is derived from NEE based on the temperature sensitivity of nighttime NEE in the La Thuile dataset (Reichstein et al., 2005). It should be noted that other analyses in this study are based on daily R_{eco} values. The parameters (E_0, R_{ecoref}) from the site years were then averaged to get site-specific values based on the criterion that both the relative error of site-year-specific E_0 and R_{ecoref} is less than 50 % and E_0 estimates were within an acceptable range (0–450 $\mathrm{kJ\,mol^{-1}}$).

Across sites, we investigate two different temperature dependencies of winter R_{eco} across space using Eq. (1). The first one uses a fixed value of R_{ecoref} across sites in Eq. (1). The second one allows R_{ecoref} to vary across sites, relying on the assumption that R_{ecoref} might have different values for different substrates (Ågren, 2000). To achieve this, mean winter temperature was regressed against mean winter R_{eco} rates divided by site-specific R_{ecoref}, which is provided by above-mentioned within-site analysis. This analysis is conducted towards all winter definitions and all vegetation types using winter definition D_AT0.

Across sites, Eq. (1) was also reformulated by adding the dependency of R_{ecoref} on ΔLAI ($\mathrm{m^2\,m^{-2}}$) or GPP_gs ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) in forest ecosystems. Winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) can thus be expressed by:

$$R_{\mathrm{eco}} = (A_{\mathrm{air}}S + B_{\mathrm{air}})\exp\left[\frac{E_{0\_\mathrm{air}}}{R}\left(\frac{1}{T_{\mathrm{ref}}} - \frac{1}{(T_{\mathrm{air}} + T_{\mathrm{ref}})}\right)\right] \tag{2}$$

$$R_{\mathrm{eco}}=(A_{\mathrm{soil}}S+B_{\mathrm{soil}})\exp\left[\frac{E_{0\_\mathrm{soil}}}{R}\left(\frac{1}{T_{\mathrm{ref}}}-\frac{1}{(T_{\mathrm{soil}}+T_{\mathrm{ref}})}\right)\right] \tag{3}$$

where S stands for substrate and represents either ΔLAI ($\mathrm{m^2\,m^{-2}}$) or GPP_gs ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$). E_{0_air}, E_{0_soil}, A_{air}, A_{soil}, B_{air} and B_{soil} are fitted parameters. To test the effect of soil carbon stock, besides ΔLAI (or GPP_gs), soil carbon stock is also linearly added in the same way as ΔLAI (or GPP_gs) into Eqs. (2) and (3). The model accuracy was then assessed by a cross-validation technique: one site at a time was excluded using the remaining subset for training and the excluded for validation and the model was fitted against the training set and then applied to calculate the modeled value for the validation set.

3 Results and discussion

3.1 Winter R_{eco} and its ratio to annual R_{eco} among ecosystem types

Figure 1 shows the frequency distribution of winter cumulative R_{eco} and RWCR based on the two winter definitions D_AT0 and D_TM. These histograms contain data from all site-years. The winter cumulative R_{eco} ($\mathrm{g\,C\,m^{-2}}$) for D_TM and D_AT0 ranges from 0.5 to 201.5 (median, 25th and 75th percentiles: 51.2, 24.1 and 78.0) and from 2.3 to 229.2 (64.8, 37.8 and 90.9), respectively. The RWCR (%) varies from 0.01 to 18.2 (5.3, 3.8 and 7.7) and from 0.7 to 22.5 (8.4, 5.9 and 10.4) for D_TM and D_AT0, respectively.

Table 2 provides the statistics of mean winter R_{eco} rates and winter cumulative R_{eco} for different ecosystem types using winter definition D_AT0 and D_TM. The values for other winter definitions (D_AT-2, D_AT-5 and D_AT-10) are shown in Table A1 in the Appendix. As shown in Table 2, deciduous broadleaf forests have the highest winter R_{eco} and arctic wetlands have the lowest. Both boreal and arctic wetlands have a smaller winter R_{eco} (mean rates and cumulative) when using the definition D_TM (90 days) compared to definition D_AT0 (151 and 248 days). This can be expected due to the fact that microbial activity decreases rapidly as T_{soil} descends towards −5 °C (Clein and Schimel, 1995) and arctic wetlands exhibit the lowest T_{soil} (e.g. D_AT0: US-Ivo: −4.9 °C and US-Atq: −11.3 °C). Besides the low temperature constraint, anaerobic conditions pose another constraint on microbial respiration because of oxygen limitation. For example, boreal wetlands with relatively high T_{soil} (CA-Mer: −0.3 °C and FI-Kaa: −1.1 °C) has lower mean respiration rate compared to other ecosystem types except arctic wetlands. Both mean winter R_{eco} rates and winter cumulative R_{eco} are expected to decrease when the winter definition was changed from D_AT-2 to D_AT-10 (Table A1). Consistent with D_AT0 and D_TM, the highest and lowest mean winter R_{eco} rates (winter cumulative R_{eco}) were always found in deciduous broadleaf forests and arctic wetlands if using other winter definitions (Table A1).

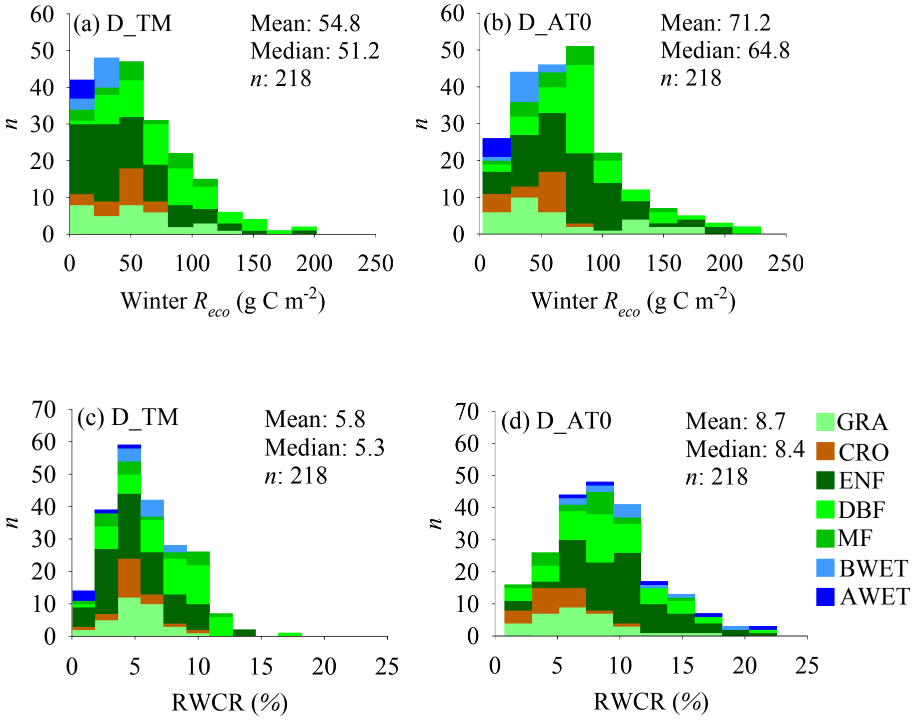

Fig. 1. Frequency histograms of winter cumulative R_{eco} and the ratio of winter cumulative R_{eco} to annual cumulative R_{eco} (RWCR) (%) according to winter definition D_TM (December–February) and D_AT0 (air temperature $<0\,^{\circ}$C) across all of the site-years. n is the number of site years.

The RWCR (%) varies among ecosystem types (Table 2). Using definition D_AT0, the highest RWCR values are found in both arctic and boreal wetlands and the lowest values in grasslands and croplands (Table 2). In contrast, when using the D_TM definition with a much shorter winter duration in high latitudes, both arctic and boreal wetlands have a lower RWCR (Table 2). Compared to the RWCR, the RWRR (%) is less varied among different ecosystem types but shows a higher relative value for ecosystems with large permanent biomass such as forests, indicating the contribution of autotrophic respiration. Arctic wetlands have much lower RWRR in D_TM than D_AT0, which can be related to the possibility that the microbial activity is much more constrained by very low temperatures in D_TM (T_{soil}: $-15.9\,^{\circ}$C) than D_AT0 (T_{soil}: $-11.3\,^{\circ}$C). Similar to the RWCR, both croplands and grasslands have the relatively lower RWRR values (Table 2), which may be related to management practices that remove the plant residuals fuelling winter respiration.

Except winter definition D_TM, the RWCR increases with latitude (e.g. D_AT0: $r=0.33$, $p<0.05$, $n=57$) since winter is often longer at higher-latitude sites (e.g. D_AT0: $r=0.51$, $p<0.01$). This pattern can be also found if grasslands and croplands are separated from forests (data not shown). The increase of the RWCR with latitude is not found in D_TM due to its constant winter duration. These results imply that winter R_{eco} in colder regions carries a higher relative contribution to annual cumulative R_{eco}, due to its longer duration, than at warmer sites and thus further stresses the importance of winter R_{eco} for the carbon balance of alpine, arctic and boreal ecosystems (e.g. Oechel et al., 1997; Fahnestock et al., 1998; Bergeron et al., 2007; Wohlfahrt et al., 2008b). In this respect, we suggest that the established climatological winter season (December through February) should not be chosen to represent the role of winter time for annual carbon balances of seasonally cold sites. Due to sparse data for cold regions in global FLUXNET, the RWCR (4.9–13.2 %) using D_AT0 is on average lower in this study than in previous works (15–50 %) by Zimov et al. (1996) and Fahnestock et al. (1998), focused on arctic ecosystems.

3.2 Temperature sensitivity of winter R_{eco}

3.2.1 Temperature sensitivity of winter R_{eco} at the site level

Under the winter definition D_AT0, across sites, values of the reference respiration rate R_{ecoref} (g C m^{-2} d^{-1}) and activation energy E_0 (kJ mol^{-1}) range from 0.17 to 1.74 and from 5.1 to 50.8, respectively, when T_{air} is used as the predictor, and from 0.17 to 1.43 and from 26.5 to 192.6 when T_{soil} is used. Across sites, R_{ecoref} was found to increase with ΔLAI

Table 2. Summary statistics of mean winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$), winter cumulative R_{eco} ($\mathrm{g\,C\,m^{-2}}$). RWRR values (%) and RWCR values (%) with winter definitions D_AT0 (air temperature <0 °C) and D_TM (December–February) across ecosystem types.

Vegetation type	D_AT0						D_TM				
	Num	Winter Length Mean (SD) d	Winter cumulative R_{eco} Mean (SD) ($\mathrm{g\,C\,m^{-2}}$)	RWCR Mean (SD) (%)	Mean Winter R_{eco} rates Mean (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	RWRR Mean (SD) (%)	Num	Winter cumulative R_{eco} Mean (SD) ($\mathrm{g\,C\,m^{-2}}$)	RWCR Mean (SD) (%)	Mean Winter R_{eco} rates Mean (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	RWRR Mean (SD) (%)
DBF	54	$106^{ab}(42)$	$89.0^{b}(44.7)$	$8.9^{abc}(4.0)$	$0.90^{c}(0.39)$	$31.7^{b}(11.6)$	54	$85.1^{c}(42.7)$	$7.8^{b}(3.1)$	$0.95^{c}(0.47)$	$31.6^{b}(12.7)$
ENF	78	$144^{ab}(45)$	$76.3^{b}(40.4)$	$9.9^{bc}(3.9)$	$0.60^{bc}(0.38)$	$26.0^{ab}(8.4)$	78	$65.4^{bc}(53.6)$	$6.2^{b}(3.4)$	$0.73^{bc}(0.60)$	$25.0^{b}(13.9)$
MF	17	$113^{ab}(44)$	$68.4^{b}(33.4)$	$7.3^{ab}(3.1)$	$0.70^{bc}(0.33)$	$26.0^{ab}(10.4)$	17	$67.5^{bc}(35.8)$	$6.7^{b}(3.3)$	$0.75^{bc}(0.41)$	$27.1^{b}(13.5)$
GRA	33	$114^{ab}(29)$	$67.6^{b}(50.1)$	$6.8^{ab}(3.4)$	$0.62^{ab}(0.43)$	$22.4^{ab}(9.3)$	33	$50.0^{abc}(34.7)$	$4.9^{ab}(2.1)$	$0.56^{abc}(0.39)$	$20.5^{b}(8.5)$
CRO	20	$93^{a}(12)$	$45.3^{ab}(20.8)$	$4.9^{a}(1.9)$	$0.49^{abc}(0.22)$	$19.4^{ab}(7.5)$	20	$46.1^{abc}(19.7)$	$5.0^{ab}(1.9)$	$0.51^{abc}(0.22)$	$20.3^{ab}(7.9)$
BWET	11	$151^{b}(37)$	$38.6^{ab}(11.5)$	$10.8^{bc}(3.7)$	$0.27^{ab}(0.08)$	$25.8^{a}(4.3)$	11	$21.6^{ab}(7.6)$	$5.7^{b}(1.1)$	$0.24^{ab}(0.08)$	$23.1^{b}(4.7)$
AWET	5	$248^{c}(18)$	$6.0^{a}(4.4)$	$13.2^{c}(6.4)$	$0.02^{a}(0.02)$	$19.5^{a}(9.4)$	5	$1.1^{a}(1.6)$	$1.7^{a}(1.7)$	$0.01^{a}(0.02)$	$6.8^{a}(7.1)$

ENF, DBF, MF, GRA, CRO, BWET and AWET represent evergreen needle leaf forests, deciduous broadleaf forests, mixed forests, grasslands, croplands, boreal wetlands and arctic wetlands, respectively.

RWCR and RWRR is the ratio of winter cumulative R_{eco} ($\mathrm{g\,C\,m^{-2}}$) to annual cumulative R_{eco} ($\mathrm{g\,C\,m^{-2}}$) and the ratio of mean winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) to mean annual R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$), respectively.

SD is standard deviation. Mean (±1 SD) within a column followed by different letters (a, b and c) were significantly different ($p < 0.05$).

Data normality was tested using one-sample Kolmogorov-Smirnov (K-S test) without the Dallal-Wilkinson-Lilliefor correction and the distribution of the data pooled from all of the site years is not significant from the normal distribution except winter R_{eco} rates in D_TM ($p = 0.013$, $n = 218$). However, if K-S test with correction is used, the data in all of the cases did not conform to the normal distribution. We should thus take cautions about the existence of the risk of violation of assumptions of ANOVA.

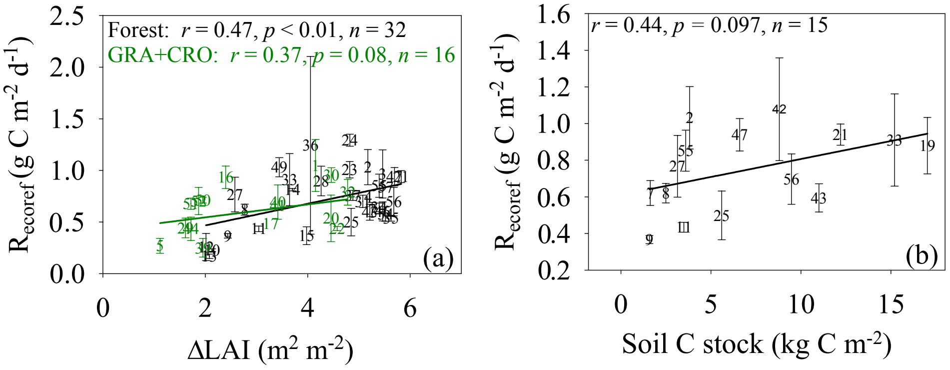

Fig. 2. The relationship between reference winter respiration (R_{ecoref}) calculated from the Arrhenius function and ΔLAI ($\mathrm{m^2\,m^{-2}}$) **(a)** and total soil carbon stock ($\mathrm{kg\,C\,m^{-2}}$) **(b)** across sites. The site-specific R_{ecoref} is averaged from its site years, and its error bar is the standard deviation of R_{ecoref} over the site-years. All values are calculated according to winter definition D_AT0.

(Fig. 2a) (or GPP_gs, data not shown) both in the forests and in grasslands and croplands. These results indicate that substrate availability, for which ΔLAI and GPP_gs are taken as proxies, exerts a significant positive control on R_{ecoref} across sites, and thus supports the conclusions of Grogan and Jonasson (2005) who found that R_{ecoref} was significantly reduced after removing plant and litter in a birch and heath tundra. We also found that R_{ecoref} is marginally correlated with total soil carbon stock in forest ecosystems (Fig. 2b). We did not perform the same analysis for grasslands and croplands due to their limited number of samples ($n = 5$). Based on the forest ecosystems our results support previous studies (Grogan et al., 2001; Nobrega and Grogan, 2007), which suggested that winter soil respiration is more derived from easier decomposable carbon (e.g. litter) than bulk soil organic matter (SOC). This can be expected due to the fact that total soil carbon stock reflects the fraction of slow and passive compounds, which do not contribute much to R_{eco}. However, SOC, which is buried beneath the active layer in frozen soils, has found to be labile and could be respired in case of permafrost thawing (Dutta et al., 2006; Nowinski et al., 2010). The decomposition of this old but labile SOC is of concern for future warming (on decadal scale), although this process is masked by the faster C cycling of fresh litter (on seasonal to interannual scale).

Our analysis shows that the arctic permafrost site US-Atq has the lowest E_0 in all winter definitions (e.g. D_AT0: 26.5 $\mathrm{kJ\,mol^{-1}}$). This can be attributed to the fact that substrate availability for microbial respiration (Ostroumov and Siegert, 1996; Mikan et al., 2002) can be significantly

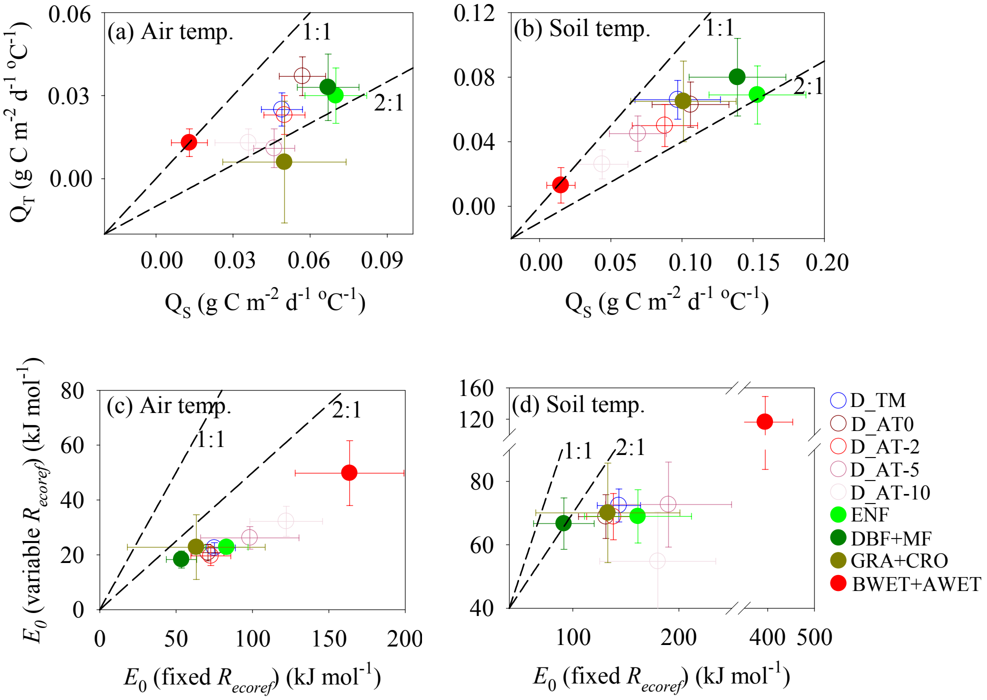

Fig. 3. The winter R_{eco} sensitivity to temperature variation across space and the one over time is compared across different winter definitions and vegetation types, using both air **(a)** and soil **(b)** temperature, and two different types of winter R_{eco} sensitivity to temperature variation across space calculated from the Arrhenius function are also compared using both air **(c)** and soil **(d)** temperature. The values from vegetation type are calculated according to winter definition D_AT0.

reduced if the soil reaches a critical freezing temperature (e.g. D_AT0: US-Atq: −11.3 °C) in which microorganisms can be in a state of anabiosis (e.g. −10 °C in Vorobyova et al., 1997). In contrast, another arctic permafrost site (US-Ivo) had a comparably high activation energy (e.g. D_AT0: 66.3 kJ mol^{-1}) presumably due to higher T_{soil} (e.g. D_AT0: −4.9 °C). Our understanding of winter R_{eco} controls in arctic permafrost regions is still very poor since only two permafrost sites are included in this study. This calls for further studies of different permafrost (e.g. continuous, discontinuous, and sporadic etc., Jorgenson et al., 2001; Zhang, 2005), vegetation types (e.g. Eugster et al., 2005) and in particular the different responses to freezing of oxic and anoxic systems underlain by permafrost.

3.2.2 Winter R_{eco} sensitivity to temperature variation over time

Our analysis shows that winter R_{eco} anomalies positively correlated with winter T_{soil} anomalies, which explained more variability (e.g. D_AT0: $r = 0.40$, $p < 0.01$, $n = 218$; D_TM: $r = 0.37$, $p < 0.01$, $n = 218$, data not shown) than T_{air} (e.g. D_AT0: $r = 0.30$, $p < 0.01$, $n = 218$; D_TM: $r = 0.22$, $p < 0.01$, $n = 218$, data not shown). This is also found when using other winter definitions (data not shown). The explained variance by the temperature is very low, but this analysis might suggest that T_{soil} was superior to T_{air} in explaining anomalies in winter R_{eco} likely because of the influence of snow cover which acts as a thermal insulator controlling soil microbial activity (Zhang, 2005). This is consistent with the results of a six-year record of eddy covariance measurements at the Niwot Ridge Ameriflux site in the Rocky Mountains, where Monson et al. (2006) showed that interannual variability of net carbon exchange is less controlled by T_{air} anomalies than by T_{soil} anomalies, which in turn were controlled by snow depth. To verify this observation with our dataset, daily snow water equivalent from AMSR-E/Aqua (Kelly et al., 2004) was used but no significant relationship between anomalies of snow water equivalent and winter R_{eco} could be found (data not shown). This could be expected since the snow characteristics at site level can not be truly reflected by a remote sensing product at a spatial resolution of 25 × 25 km^2. In addition, we found no significant relationship, with r always close to zero, between winter R_{eco} and winter precipitation anomalies (e.g. D_AT0: $p = 0.49$; D_TM: $p = 0.71$) and no correlation with ΔLAI anomalies (e.g. D_AT0: $p = 0.44$; D_TM: $p = 0.82$) and GPP_gs (e.g. D_AT0: $p = 0.34$; D_TM: $p = 0.69$). This was also found if forest ecosystems and managed ecosystems (grasslands and croplands) were considered separately (data not shown).

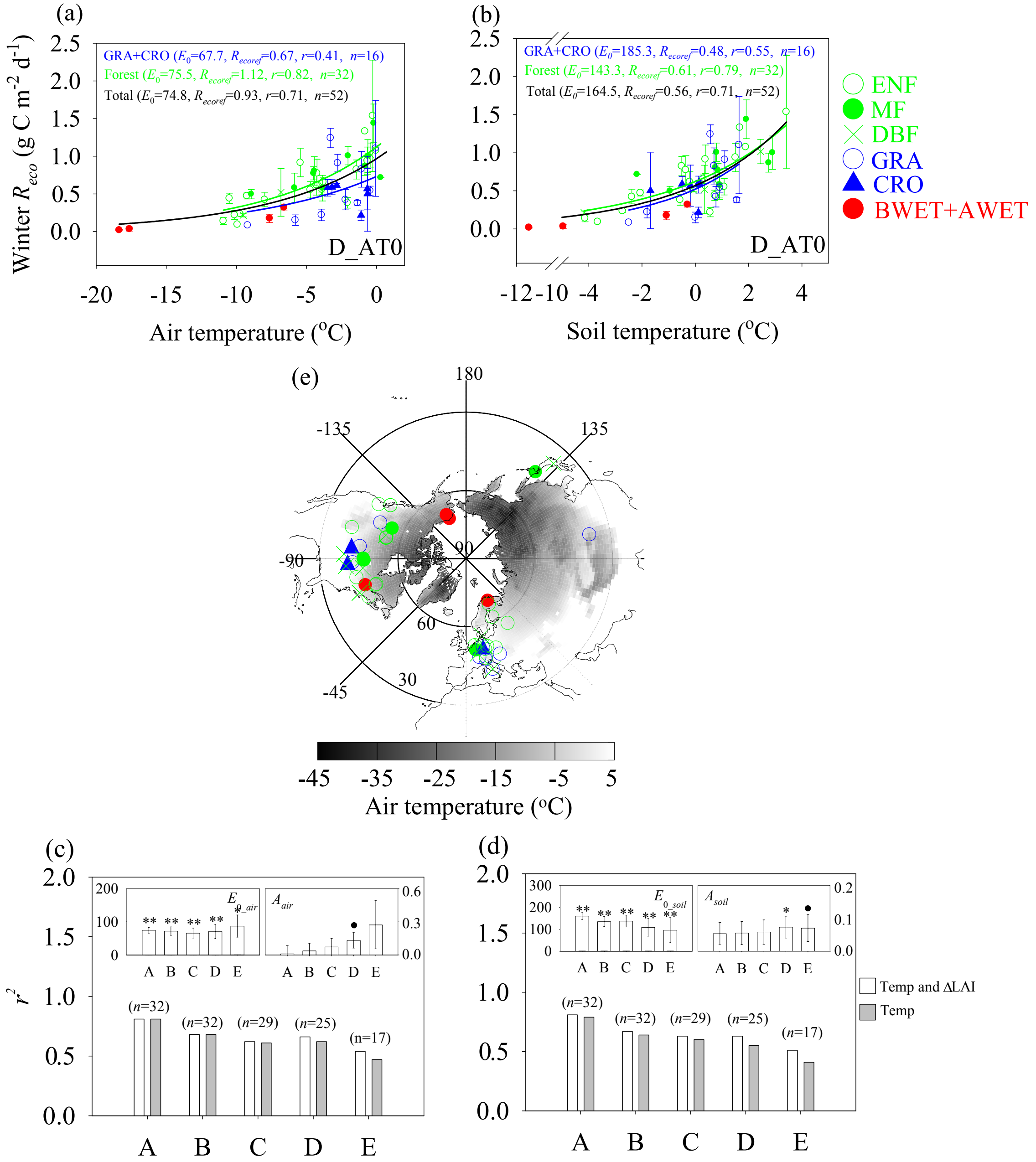

Fig. 4. Relationships between winter air temperature **(a)**, soil temperature **(b)** and R_{eco} using winter definition D_AT0. The coefficient of determination (r^2) between the Arrhenius models with and without ΔLAI is compared using air temperature **(c)** and soil temperature **(d)** respectively in the forest ecosystems. A, B, C, D, and E in both **(c)** and **(d)** denote winter definitions D_TM, D_AT0, D_AT-2, D_AT-5 and D_AT-10, respectively. The spatial distribution of eddy covariance sites is displayed in **(e)**. Winter air temperature from 1 December to 28 February is used as the background in **(e)**. Significance levels are indicated as **, * and • representing $p < 0.01$, 0.05 and 0.1, respectively.

3.2.3 The comparison between winter R_{eco} sensitivity to temperature variation across space and over time

Our analysis shows that the winter R_{eco} sensitivity to variation of T_{air} or T_{soil} across space (Q_S; $\mathrm{g\,C\,m^{-2}\,d^{-1}\,{}^{\circ}C^{-1}}$), defined as the slope of a linear regression between mean winter R_{eco} rates and mean winter T_{air} or T_{soil} across all sites is higher than Q_T (winter R_{eco} sensitivity to temperature variation over time) among different winter definitions (Fig. 3a and b). In addition, we categorized the sites by vegetation types for the winter definition D_AT0, and the difference between these two temperature sensitivities can also be found in all ecosystem types except boreal and arctic wetlands (Fig. 3a and b). No difference for the wetland (boreal and arctic wetlands) category may be due to the low number of the samples in wetland ($n = 4$). The same differences between the two temperature sensitivities can also be obtained if sites are categorized by vegetation types according to other winter definitions (data not shown).

The differences between these two winter R_{eco} temperature sensitivities are due to the fact that Q_T is mainly driven by direct climate effects, but Q_S not only accounts for gradients of climate affecting decomposition, but also reflects gradients in ecosystem state (e.g. soil C pools) in space (Hibbard et al., 2005) or the degree of adaptation of microorganisms to low temperatures. To test this hypothesis, we regressed mean winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) divided by site-specific R_{ecoref} provided by the within-site analysis (Sect. 3.2.1) against mean winter T_{air} or T_{soil} using the Arrhenius function. As shown in Fig. 3c and d, activation energies (E_0, $\mathrm{kJ\,mol^{-1}}$) were much smaller when using site-specific R_{ecoref} in all winter definitions and all vegetation types based on winter definition D_AT0. This is consistent with the findings of recent studies (Mahecha et al., 2010; Wang et al., 2010), which showed that the temperature sensitivity (Q_{10}) became much smaller after removing the influence of confounding effects imposed by substrate availability. Furthermore, from a multiple regression analysis conducted between mean winter R_{eco} rates and both mean winter temperature and ΔLAI (or GPP_gs) across sites, we found that Q_S became smaller if ΔLAI (or GPP_gs) was included (data not shown). For example, for winter defined as D_AT0, Q_S (SD) calculated as a function of T_{soil} changed from 0.11(0.03) to 0.08(0.03) after ΔLAI was included as an additional predictor. However, the Q_S after including ΔLAI (D_AT0: 0.08 ± 0.03) remains larger than its corresponding Q_T (D_AT0: 0.05 ± 0.01), which can be expected due to the possibility that ΔLAI only partly accounts for inter-site variation in substrate availability (Sect. 3.2.1). This might imply that Q_S can become closer to Q_T if spatial gradients in substrates can be mostly taken into account.

The temperature sensitivity of respiration is a key parameter controlling carbon-climate feedbacks in coupled models (Friedlingstein et al., 2006). A fixed value of temperature sensitivity, obtained from meta-analysis of spatial data (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994) is often incorporated in these models (e.g. Cox et al., 2000; Friedlingstein et al., 2006). If Q_S rather than Q_T is used for winter R_{eco}, then, the current generation of models will likely overestimate the effect of future warming on soil C pools. However, great care should be taken into this extrapolation when using Q_T obtained from soil temperature. On the one hand, in La Thuile dataset, the soil temperature measurement depth is not uniform across sites (the range is from 2 to 10 cm). On the other hand, the active layer where winter R_{eco} occurs might be shallow and its depth might not necessarily coincide with the one for which soil temperature was provided in the dataset. These two factors might contribute to the biased estimate of actual temperature response of winter R_{eco} (e.g. Reichstein and Beer, 2008; Subke and Bahn, 2010).

3.3 Environmental and biotical controls on winter R_{eco} across sites

Since grasslands and croplands are heavily affected by human management on a short-term (e.g. seasonal and annual) basis, we conducted two separate cross site analyses, one for forests and the other for both grasslands and croplands. Wetland sites were not included in the analysis since the number of the samples suited for our winter R_{eco} study in La Thuile dataset is too small ($n = 4$).

Under all winter definitions, winter R_{eco} is found to increase exponentially with increasing T_{air} and T_{soil} (Fig. 4a and b) across sites. On the basis of the aforementioned results (Sect. 3.2.1), a linear dependence of the reference respiration on ΔLAI or GPP_gs was included (Eqs. 2 and 3). We only explored ΔLAI or GPP_gs effects in the forest ecosystems since ΔLAI or GPP_gs may be weak indicators of recent carbon inputs to the soil in grasslands and croplands (Fig. 2a), where much of the produced carbon is exported from the sites.

As shown in Fig. 4c and d, when integrated over five different winter definitions, the coefficients of determination for Eqs. (2) and (3) range from 0.54 to 0.82 and from 0.51 to 0.81, while the root mean square errors are within the range of 0.17–0.22 and 0.17–0.22 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$, respectively (data not shown). A cross validation of the regression models in Eqs. (2) and (3) shows that 50–79 % and 48–76 % of winter R_{eco} variance can be explained by Eqs. (2) and (3). Both equations empirically describe the spatial variability of winter R_{eco} and thus have predictive power to extrapolate winter R_{eco} to the continental scale. Given that temperature is the dominant controlling factor of winter R_{eco} across sites and co-varies with other potential drivers, we regressed the residuals of Eqs. (2) and (3) against the total precipitation during winter period (winter precipitation) to determine if this alternative driver could explain additional variance. There was no significant correlation between the residuals and winter precipitation using all winter definitions (e.g. D_AT0: Eq. (2): $r = 0.00$, $p = 0.632$; Eq. (3): $r = 0.01$, $p = 0.901$, data not shown). The lack of a significant correlation between winter precipitation and winter R_{eco} may be explained as follows. First, precipitation effects on respiration can be manifested through its influences on soil moisture (e.g. Migliavacca et al., 2011). Since most of the sites in this study are expected to be covered by snow thanks to a freezing or below freezing temperature-threshold based winter definition, precipitation is expected to influence soil moisture to a lesser extent. For example, at site AT-Neu where upper soil moisture data were available, soil moisture (%) is almost constant (50.5 ± 2.0) during the period from day 322 of year 2002 to day 108 of year 2003, which is within the range of winter definition D_AT0. In this respect, the role of winter precipitation in regulating R_{eco} is not as evident as in the growing season (e.g. Migliavacca et al., 2011). Second, winter snowfall (solid precipitation) is one of many variables controlling snow depth, which was found to regulate T_{soil} and microbial respiration under the snow pack when using T_{air} as a predictor of winter R_{eco} (e.g. Groffman et al., 2001, Grogan and Jonasson, 2006; Monson et al., 2006; Nobrega and Grogan, 2007). Snow depth is not simply related to winter snowfall since it is influenced by local factors such as topography (e.g. Liston, 2004), wind speed (e.g. Li and Pomeroy, 1997), vegetation structure (e.g. Li and Pomeroy, 1997; Rutter et al., 2009), sublimation and melting. This justifies neglecting precipitation in our temperature response model (Eqs. 2 and 3).

Our results also showed that the inclusion of ΔLAI can only make a marginal improvement in winter R_{eco} prediction of forest ecosystems (Fig. 4c and d), which was also observed if both total soil carbon stock and ΔLAI or GPP_gs was included (data not shown). This may be related to the fact that aboveground respiration from tree biomass can still accounts for a significant fraction of winter R_{eco} (e.g. the reported values are below 10 % or even higher than 50 %, Monson et al., 2005; Davidson and Janssens, 2006), thus reducing the fraction of heterotrophic respiration on winter R_{eco} using the substrates such as litter. It would also suggest that both recent aboveground carbon inputs (approximated by ΔLAI or GPP_gs) and soil carbon stock can not fully account for substrate availability (Fig. 2a and b), and belowground carbon inputs such as the senescence of fine roots and the supply of dissolved organic carbon or nitrogen (e.g. Edwards et al., 2006; Larsen et al., 2007) might play a role. Most notably, the substrates for winter soil respiration can be provided by the dead biomass of mycorrhizal fungi and other rhizospheric microbial cells that die at the autumn-winter transition period following the nighttime soil freezing.

4 Conclusions

The availability of meteorological and eddy covariance flux data across different ecosystems opens a new opportunity to quantify winter R_{eco} and its spatial and temporal controls across North Hemisphere ecosystems. Given four different winter definitions, based on temperature below the freezing point, we found an increase in the ratio of winter to annual cumulative respiration towards higher latitude, due to the longer winters that occur at high latitudes. Therefore, due to the importance of winter processes in the carbon balance, it is important to better represent winter R_{eco} in current terrestrial carbon cycle models. The large number of sites now available provides an important source of information to improve winter carbon cycle. Our empirical characterization of temperature controls on winter R_{eco} implies that winter R_{eco} temperature sensitivity obtained on spatial and temporal scales should be treated differently. The winter R_{eco} sensitivity to temperature variation across space (Q_S) was always found to be higher than the one over time (Q_T) among different winter definitions and among different vegetation types except for the wetlands which had a limited sample size. Our result also imply that Q_S can become closer to its Q_T if spatial gradients in inter-site substrates can be more and more taken into account. Thus, if extrapolated to future warming, the winter R_{eco} temperature sensitivity to warming obtained from spatial gradients will be exaggerated without fully considering the spatial difference in substrate availability.

Temperature is an overwhelming factor in determining the spatial variation of winter R_{eco} in forests and grasslands and croplands. Although recent carbon inputs from aboveground marginally account for winter R_{eco} spatial variation, inter-site substrate availability (or biotic factors) does seem to be important since ΔLAI or GPP_gs do partly account for the difference in reference respiration across sites. Indeed, the biotic controls of winter R_{eco} were not fully explored in this study, which needs further investigation by considering belowground carbon inputs such as recently-killed rhizospheric microbial biomass and the senescence of fine roots. It should be noted that our results are mainly based on forest ecosystems and that winter carbon cycling in arctic ecosystems with limited sample size in La Thuile dataset characterized by long winters and large soil carbon pools are still not well understood. Furthermore, snow cover effects on winter R_{eco} were only explored using satellite-derived snow products, and these should be further investigated in future studies in which more in-situ snow data are available.

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Appendix A

Table A1. Winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$) comparison among different winter definitions.

Site	Type	Lat.	Lon.	D_TM	D_AT0		D_AT-2		D_AT-5		D_AT-10	
				R_{eco} (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	WLEN (SD) (d)	R_{eco} (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	WLEN (SD) (d)	R_{eco} (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	WLEN (SD) (d)	R_{eco} (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)	WLEN (SD) (d)	R_{eco} (SD) ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$)
AT-Neu	GRA	47.1	11.3	1.06(0.24)	116(16)	1.24(0.12)	92(32)	1.04(0.34)	62(22)	1.04(0.43)	–	–
BE-Vie	MF	50.3	6.0	1.10(0.16)	71(35)	1.02(0.16)	57(28)	0.89(0.15)	17	0.43	–	–
CA-Ca1	ENF	49.9	–125.3	1.48	54	1.33	–	–	–	–	–	–
CA-Ca2	ENF	49.9	–125.3	1.24(0.22)	39(31)	0.82(0.13)	–	–	–	–	–	–
CA-Let	GRA	49.7	–112.9	0.17(0.06)	138(13)	0.22(0.08)	120(21)	0.21(0.07)	100(32)	0.19(0.10)	61(37)	0.14(0.07)
CA-Mer	BWET	45.4	–75.5	0.29(0.04)	128(22)	0.32(0.03)	112(22)	0.30(0.04)	93(14)	0.28(0.04)	57(22)	0.24(0.03)
CA-Oas	DBF	53.6	–106.2	0.33(0.07)	169(17)	0.50(0.06)	157(21)	0.46(0.08)	141(13)	0.40(0.10)	101(18)	0.34(0.07)
CA-Obs	ENF	54.0	–105.1	0.27(0.04)	185(15)	0.47(0.04)	168(18)	0.42(0.04)	145(15)	0.35(0.06)	114(13)	0.30(0.03)
CA-Ojp	ENF	53.9	–104.7	0.12(0.03)	176(13)	0.24(0.02)	164(18)	0.21(0.04)	145(14)	0.17(0.05)	116(13)	0.14(0.03)
CA-Qcu	ENF	49.3	–74.0	0.13(0.01)	175(15)	0.22(0.06)	154(14)	0.19(0.04)	137(21)	0.17(0.05)	104(16)	0.12(0.01)
CA-Qfo	ENF	49.7	–74.3	0.28(0.06)	172(19)	0.44(0.07)	149(14)	0.39(0.07)	139(13)	0.37(0.05)	102(10)	0.30(0.04)
CA-SJ1	ENF	53.9	–104.7	0.08(0.04)	181(15)	0.14(0.05)	172(19)	0.13(0.04)	146(20)	0.09(0.04)	121(8)	0.08(0.04)
CA-SJ2	ENF	53.9	–104.6	0.02(0.01)	197	0.09(0.00)	167(4)	0.06(0.01)	137(17)	0.03(0.02)	123(7)	0.03(0.01)
CA-TP4	ENF	42.7	–80.4	0.67(0.02)	107(8)	0.66(0.06)	99(8)	0.65(0.04)	61(30)	0.52(0.14)	19	0.43
CA-WP1	MF	55.0	–112.5	0.12(0.00)	159(7)	0.22(0.02)	155(6)	0.21(0.02)	143(16)	0.19(0.05)	103(28)	0.14(0.02)
CH-Oe1	GRA	47.3	7.7	0.87(0.24)	85(28)	0.83(0.24)	58(13)	0.84(0.24)	43	0.73	–	–
CN-HaM	GRA	37.4	101.2	0.02	182	0.08	159	0.06	148	0.06	98(12)	0.03(0.01)
CZ-BK1	ENF	49.5	18.5	0.57(0.06)	112(19)	0.54(0.07)	105(22)	0.53(0.08)	47(1)	0.56(0.03)	–	–
DE-Bay	ENF	50.1	11.9	1.20(0.13)	127(32)	1.22(0.21)	77(30)	1.18(0.15)	91	1.11	–	–
DE-Geb	CRO	51.1	10.9	0.59(0.28)	87(7)	0.57(0.27)	34(26)	0.45(0.12)	–	–	–	–
DE-Hai	DBF	51.1	10.5	1.06(0.15)	74(22)	1.01(0.12)	68(21)	1.01(0.14)	76	0.92	–	–
DE-Meh	GRA	51.3	10.7	0.57(0.09)	96(20)	0.54(0.06)	81(4)	0.47(0.12)	–	–	–	–
DE-Tha	ENF	51.0	13.6	1.00(0.10)	85(21)	0.94(0.18)	53(29)	0.87(0.12)	48(38)	0.85(0.06)	–	–
DK-Sor	DBF	55.5	11.6	1.62(0.22)	71(35)	1.44(0.25)	63(33)	1.39(0.32)	–	–	–	–
FI-Hyy	ENF	61.8	24.3	0.47(0.14)	153(21)	0.55(0.11)	132(25)	0.50(0.13)	99(26)	0.44(0.13)	48(14)	0.42(0.13)
FI-Kaa	BWET	69.1	27.3	0.15(0.06)	191(13)	0.18(0.06)	182(9)	0.17(0.06)	147(16)	0.15(0.05)	100(19)	0.13(0.04)
FI-Sod	ENF	67.4	26.6	0.32(0.18)	183(14)	0.42(0.10)	166(9)	0.40(0.10)	146(15)	0.35(0.15)	113(11)	0.30(0.19)
FR-Hes	DBF	48.7	7.1	1.17(0.24)	57(31)	1.00(0.22)	55(28)	1.04(0.18)	–	–	–	–
HU-Bug	GRA	46.7	19.6	0.45(0.14)	92(3)	0.42(0.14)	67(25)	0.42(0.13)	33(26)	0.41(0.19)	–	–
IT-Amp	GRA	41.9	13.6	0.97(0.24)	93(23)	1.10(0.64)	43(32)	0.43(0.08)	24	0.23	–	–
IT-Col	DBF	41.8	13.6	0.75(0.15)	83(53)	0.72(0.00)	101	0.67	–	–	–	–
IT-Mbo	GRA	46.0	11.0	0.84(0.20)	141(29)	0.91(0.12)	98(19)	0.78(0.23)	68(37)	0.77(0.18)	–	–
IT-Ren	ENF	46.6	11.4	0.31(0.13)	150(19)	0.38(0.07)	118(21)	0.32(0.15)	58(35)	0.29(0.18)	–	–
JP-Tak	DBF	36.1	137.4	0.53(0.17)	123(16)	0.58(0.17)	94(11)	0.52(0.17)	77(7)	0.50(0.16)	–	–
JP-Tom	MF	42.7	141.5	0.46(0.05)	114(14)	0.51(0.02)	93(14)	0.47(0.03)	55(36)	0.46(0.06)	–	–
NL-Loo	ENF	52.2	5.7	2.06(0.43)	63(34)	1.54(0.74)	46(36)	1.41(1.02)	16	0.69	–	–
RU-Fyo	ENF	56.5	32.9	0.78(0.27)	143(19)	0.91(0.19)	130(10)	0.86(0.21)	101(29)	0.81(0.25)	62(30)	0.62(0.15)
US-Atq	AWET	70.5	–157.4	0.00(0.00)	254(14)	0.02(0.01)	231(10)	0.01(0.00)	219(3)	0.01(0.00)	185(5)	0.01(0.00)
US-Bkg	GRA	44.3	–96.8	0.13(0.10)	124(5)	0.15(0.07)	117(0)	0.14(0.08)	104(14)	0.12(0.05)	59(35)	0.11(0.05)
US-Bo1	CRO	40.0	–88.3	0.40(0.26)	96(18)	0.22(0.07)	69(28)	0.20(0.11)	31(10)	0.15(0.18)	–	–
US-Bo2	CRO	40.0	–88.3	0.53(0.49)	84(14)	0.50(0.50)	68(29)	0.53(0.47)	–	–	–	–
US-Ha1	DBF	42.5	–72.2	1.34(0.43)	110(16)	1.43(0.44)	88(3)	1.35(0.54)	59(13)	1.23(0.38)	32	1.19
US-Ho1	ENF	45.2	–68.7	0.52(0.13)	130(16)	0.62(0.13)	109(16)	0.53(0.10)	80(20)	0.46(0.11)	38(20)	0.29(0.05)
US-IB2	GRA	41.8	–88.2	0.37(0.13)	103(15)	0.38(0.04)	67(28)	0.34(0.09)	60(29)	0.34(0.07)	–	–
US-Ivo	AWET	68.5	–155.8	0.03(0.02)	239(26)	0.03(0.03)	233(25)	0.03(0.02)	223(21)	0.02(0.02)	186(7)	0.02(0.01)
US-LPH	DBF	42.5	–72.2	0.75(0.21)	119(11)	0.81(0.19)	113(15)	0.79(0.20)	87(10)	0.74(0.19)	26(6)	0.62(0.28)
US-MMS	DBF	39.3	–86.4	0.91(0.18)	77(12)	0.87(0.12)	60(21)	0.84(0.12)	25(9)	0.75(0.21)	–	–
US-Moz	DBF	38.7	–92.2	0.91(0.21)	64(26)	0.76(0.38)	37	0.50	–	–	–	–
US-NR1	ENF	40.0	–105.5	0.64(0.27)	169(41)	0.77(0.19)	150(19)	0.73(0.24)	131(38)	0.70(0.22)	72	0.44
US-Ne1	CRO	41.2	–96.5	0.62(0.03)	92(10)	0.61(0.03)	73(25)	0.58(0.05)	57(17)	0.59(0.08)	–	–
US-Ne2	CRO	41.2	–96.5	0.59(0.12)	95(9)	0.58(0.11)	79(22)	0.55(0.10)	52(17)	0.51(0.12)	–	–
US-Ne3	CRO	41.2	–96.4	0.55(0.06)	94(8)	0.59(0.10)	79(17)	0.55(0.10)	58(17)	0.54(0.14)	18	0.32
US-PFa	MF	45.9	–90.3	0.53(0.12)	141(1)	0.55(0.08)	137(1)	0.54(0.09)	112(24)	0.51(0.07)	44(17)	0.44(0.15)
US-Syv	MF	46.2	–89.3	0.42(0.36)	148(20)	0.52(0.32)	131(12)	0.43(0.36)	110(29)	0.40(0.33)	87(21)	0.32(0.44)
US-UMB	DBF	45.6	–84.7	0.77(0.05)	121(21)	0.77(0.09)	110(17)	0.76(0.09)	82(17)	0.71(0.08)	53	0.73
US-WCr	DBF	45.8	–90.1	0.45(0.17)	140(17)	0.58(0.19)	118(23)	0.50(0.17)	101(17)	0.44(0.16)	73(11)	0.40(0.17)
US-Wrc	ENF	45.8	–122.0	0.84	70	1.08	–	–	–	–	–	–

Type: DBF: deciduous broadleaf forests; ENF: evergreen needleleaf forests; GRA: grasslands; CRO: croplands; BWET and AWET are boreal and arctic wetlands respectively; MF (mixed forests).
Lat. and Lon. are latitude and longitude, respectively.
WLEN is the winter length (unit: day).
R_{eco} is mean winter R_{eco} rates ($\mathrm{g\,C\,m^{-2}\,d^{-1}}$).
D_AT0, D_AT-2, D_AT-5 and D_AT-10 are defined as the period during which the 10 day smoothed air temperature remained below 0 °C, −2 °C, −5 °C and −10 °C for at least five consecutive days; D_TM is defined as the 90-day period from 1 December to 28 February.
SD is standard deviation.

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