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esa ECOSPHERE

Soil respiration in a northeastern US temperate forest: a 22-year synthesis

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Abstract. To better understand how forest management, phenology, vegetation type, and actual and simulated climatic change affect seasonal and inter-annual variations in soil respiration (R_s), we analyzed more than 100,000 individual measurements of soil respiration from 23 studies conducted over 22 years at the Harvard Forest in Petersham, Massachusetts, USA. We also used 24 site-years of eddy-covariance measurements from two Harvard Forest sites to examine the relationship between soil and ecosystem respiration (R_e).

R_s was highly variable at all spatial (respiration collar to forest stand) and temporal (minutes to years) scales of measurement. The response of R_s to experimental manipulations mimicking aspects of global change or aimed at partitioning R_s into component fluxes ranged from −70% to +52%. The response appears to arise from variations in substrate availability induced by changes in the size of soil C pools and of belowground C fluxes or in environmental conditions. In some cases (e.g., logging, warming), the effect of experimental manipulations on R_s was transient, but in other cases the time series were not long enough to rule out long-term changes in respiration rates. Inter-annual variations in weather and phenology induced variation among annual R_s estimates of a magnitude similar to that of other drivers of global change (i.e., invasive insects, forest management practices, N deposition). At both eddy-covariance sites, aboveground respiration dominated R_e early in the growing season, whereas belowground respiration dominated later. Unusual aboveground respiration patterns—high apparent rates of respiration during winter and very low rates in mid-to-late summer—at the Environmental Measurement Site suggest either bias in R_s and R_e estimates caused by differences in the spatial scale of processes influencing fluxes, or that additional research on the hard-to-measure fluxes (e.g., wintertime R_s, unaccounted losses of CO_2 from eddy covariance sites), daytime and nighttime canopy respiration and its impacts on estimates of R_e, and independent measurements of flux partitioning (e.g., aboveground plant respiration, isotopic partitioning) may yield insight into the unusually high and low fluxes. Overall, however, this data-rich analysis identifies important seasonal and experimental variations in R_s and R_e and in the partitioning of R_e above- vs. belowground.

Key words: ecosystem respiration; eddy covariance; flux partitioning; Harvard Forest; phenology; soil respiration.

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Introduction

Terrestrial ecosystems exchange ~120 gigatons of carbon (Gt C) with the atmosphere annually through photosynthesis and respiration (R_e), equivalent to one-sixth of all C present in the atmosphere, making R_e one of the largest fluxes in the global C cycle (Prentice et al. 2001). R_e is dominated by soil respiration (R_s), the sum of belowground autotrophic (roots and associated mycorrhizae) and heterotrophic (mainly microbes, microfauna, and mesofauna) respiration. Estimates of global R_s range from 68 to 98 Gt C yr^{-1} (Raich and Schlesinger 1992, Schlesinger and Andrews 2000, Bond-Lamberty and Thomson 2010*a*), or about two-thirds of all of the C emitted to the atmosphere by terrestrial ecosystems. The amount of C emitted through R_s is ~10 times more than that released through fossil fuel combustion and cement manufacturing (IPCC 2007, Peters et al. 2012), although, for the most part, R_s is closely coupled to a large photosynthetic uptake, leading to a much smaller net C exchange with the atmosphere (Schlesinger and Andrews 2000).

R_s varies substantially across space and time (Norman et al. 1997, Rayment and Jarvis 2000, Drewitt et al. 2002), implying that long-term measurements over a large area are required to constrain flux estimates. Multiple environmental factors affect R_s. For example, R_s exhibits a seasonal pattern that is generally positively correlated with temperature (Davidson and Janssens 2006). R_s peaks under optimal soil moisture conditions and becomes depressed in soils that are too wet or too dry (Davidson et al. 1998). Nitrogen additions can reduce R_s, in part because they cause declines in plant belowground C allocation (Janssens et al. 2010). Also, N additions can decrease microbial respiration by inhibiting lignolytic enzyme activity (Berg and Matzner 1997). Alternatively, where plant photosynthesis is strongly limited by low N availability, N additions can lead indirectly to increased R_s (Janssens et al. 2010) by increasing root respiration and organic matter production that fuels litter (leaves and roots) decomposition. The availability and chemistry of carbon substrates also influence the apparent temperature sensitivity of R_s (Davidson and Janssens 2006, Gershenson et al. 2009). Furthermore, environmental drivers influence the residence time of C, and a change in the drivers can induce a transient change in R_s as the carbon pool adjusts to a new steady state (e.g., Bradford et al. 2008).

R_s also varies as a function of biotic drivers, including vegetation type (Raich and Tufekcioglu 2000, Hibbard et al. 2005, Roehm 2005) and phenology (Curiel Yuste et al. 2004). Both of these are related to photosynthesis, which has an important effect on R_s because large amounts of photosynthates (C compounds) are allocated to roots and associated mycorrhizal fungi (Högberg et al. 2001, Janssens et al. 2001, Tang et al. 2005*a*, Drake et al. 2012, Hopkins et al. 2013, Savage et al. 2013). The efflux of low-molecular-weight organic compounds from roots (via rhizodeposition and root exudation) also impacts R_s by enhancing microbial activity and soil organic matter decomposition (Dijkstra and Cheng 2007, Kuzyakov 2010).

The Harvard Forest, located in north-central Massachusetts, USA, is one of the most intensively studied forests in the world (Foster and Aber 2004). In particular, carbon cycling has been extensively studied: more than 100,000 measurements of R_s have been made during the 25 years of Harvard Forest's involvement in the Long Term Ecological Research (LTER) program. R_s has been measured in several different forest

types and in response to 15 experimental manipulations simulating various aspects of global change. The Harvard Forest is also home to the world's longest-running eddy covariance (EC) system, measuring whole-ecosystem CO_2 exchange in a deciduous forest—the Environmental Measurement Site (EMS)—and a second EC site located in a mature hemlock stand. The rich datasets provide a unique opportunity to synthesize diverse data sources into a better understanding of how actual climatic change, forest management, phenology, vegetation type, and simulated global change together affect seasonal and inter-annual variations in R_s. We also compared the data on R_s to tower-based estimates of R_e to examine seasonal variations in the partitioning of above- vs. belowground respiration in mature hardwood and hemlock forests.

Methods

Site description

The Harvard Forest is a 1200-hectare LTER site located in Petersham, Massachusetts, USA (Fig. 1). Elevation ranges from 220 m to 410 m above sea level. Mean annual air temperature (1964–2010) is 7.5°C; January is the coldest month (–6.1°C) and July and August, the warmest (20.1°C and 19.3°C, respectively). Precipitation (rain and snow water equivalent) averages 1119 mm yr^{-1} and is well distributed throughout the year. Background nitrogen deposition is 0.66 g m^{-2} yr^{-1} (Munger et al. 1998). Throughout Harvard Forest, soils are predominantly Typic Dystrochrepts—sandy loams overlying a glacial till. Poorly drained forested swamps are also found in some areas; in the well-surveyed Prospect Hill Tract, about 3% of the surface area is covered by peat deposits and 22% is poorly or very poorly drained (Foster and Motzkin 2003). Because of the presence of glacial till, rocks are ubiquitous, covering 7.2% of the surface area (Foster and Motzkin 2003). Rocks also represent up to 25.8% of the soil volume from 0- to 50-cm depth in the Prospect Hill Tract (Raymer et al. 2013). The most common dominant tree species are red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.).

The Harvard Forest has a history of agricultural use, mainly as pastures and woodlots, dating back to the mid-18th century; current land cover is heavily influenced by prior land use as well as natural disturbances (Foster 1992). Slightly more than half of the originally forested areas were cleared, but remote areas and locations where swamps or steep rocky sites predominate were cut only selectively for a variety of wood products. Beginning in the mid-19th century, large areas of farmland were abandoned and forests regrew. Logging, mainly of white pine (*Pinus strobus* L.), increased in the late 19th and early 20th century. Large swaths of the forest experienced extensive hurricane damage in 1938 when as much as 75% of the timber—mostly white pine stands, older hardwood forests, and conifer plantations—was blown down (Foster and Boose 1992). Hardwood forests of oaks, maples and birches (*Betula* spp.) often replaced the pine stands. More than 10% of the trees were damaged, but not killed, in a 2008 ice storm (Yao 2011).

Soil respiration measurements

In this paper "soil respiration" (R_s) refers to total soil CO_2 efflux, the respiration of soil fauna, roots, and mycorrhizae and other microbes. We compiled data from 23 studies of R_s, identified herein as S1 to S23 (Tables 1–2). In all cases, R_s was measured in fixed locations on a given sampling day, generally where PVC or aluminum collars had been inserted and left in the soil, usually for the duration of the study. Because comprehensive descriptions of the methods of measurement have already been published, we summarize them only briefly here.

Four methods were used to measure R_s, in order of increasing measurement frequency: (1) soda-lime systems where pellets were left beneath a closed chamber for 24 hours to absorb CO_2 emitted from the soil, (2) static chamber systems where a chamber was placed on each collar and headspace air samples were taken at fixed intervals over 15 to 30 minutes and subsequently analyzed with an infrared gas analyzer (IRGA) or a gas chromatograph, (3) dynamic chamber systems in which a chamber was placed on each collar, chamber air was circulated to and from a portable IRGA system, and the rate of increase in CO_2 concentration was measured in situ for a period of five minutes, and

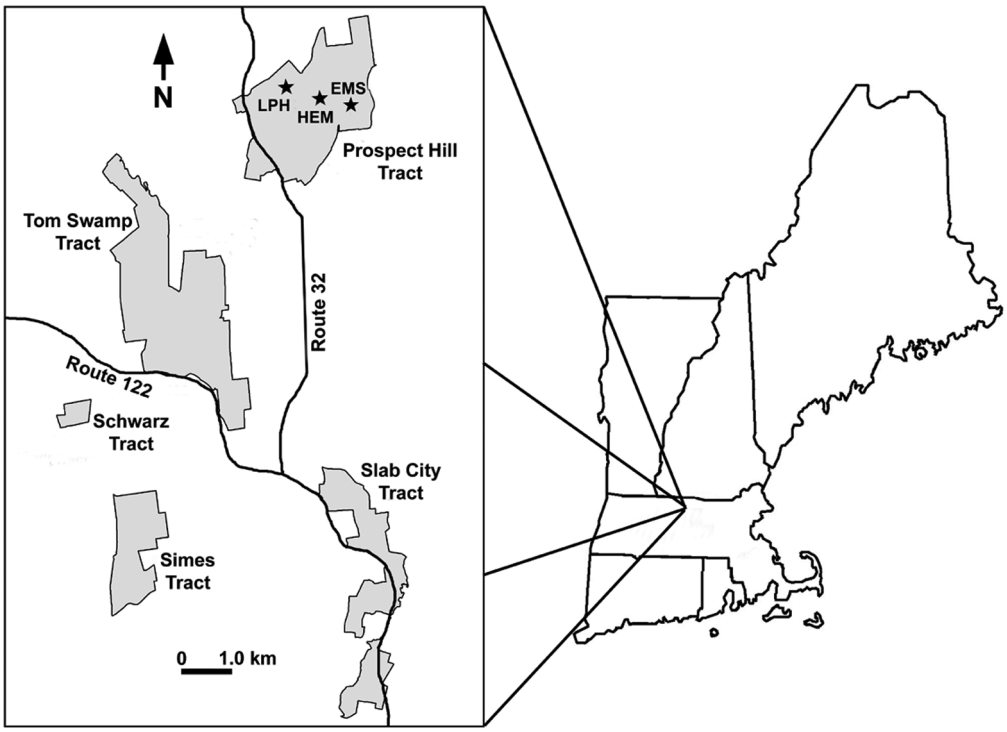

Fig. 1. Map of Harvard Forest and New England. The location of the different tracts and of the Environmental Measurement Site (EMS), Hemlock (HEM) and Little Prospect Hill (LPH) flux towers is indicated. The coordinates of the center of the Harvard Forest map are 42°29′58″ N, 72°11′37″ W.

(4) automated chamber systems (herein autochambers), in which a datalogger-controlled system closed one chamber at a time and circulated the headspace air through an IRGA. Although criticized early on, the soda-lime technique, used in one of the oldest studies, has shown good correspondence with other methods (e.g., Raich et al. 1990, Keith and Wong 2006). Importantly, the use of soda-lime data was restricted to the analysis of experimental treatments on R_s; they were not used in comparisons with R_e. The four methods were never used side-by-side, so we cannot formally analyze whether there were systematic, method-based biases, although Savage and Davidson (2003) found no significant differences in seasonal flux estimates and in fluxes measured within one hour using the autochamber and dynamic chamber methods at Harvard Forest. For >70% of collars, soil temperature was measured at 10-cm depth. In all other instances, soil temperature was measured between 2- and 8.5-cm depth.

Fourteen of the 23 studies were observational in nature and hence measured R_s in untreated or "control" plots only (Table 1). These studies covered a broad range of ecosystem types—natural and planted forests, wetlands—and times since most recent disturbances. The remaining data were collected from field experiments. In these studies, R_s was measured in control plots as well as in treated plots. Wetlands data were from accessible wetlands only; no measurements were made in flooded areas.

The experimental treatments (Table 1) were as follows: in S2, half of the plots were subjected to a simulated drought. Translucent roofs and rain gutters were used to prevent rainfall from reaching the ground. In the experimental warming studies S15, S19, and S20, soil was heated to 5°C above ambient temperature using underground heating cables. S20 also included a soil disturbance control in which heating cables were inserted in the ground but not activated. S15 is a soil warming × N fertilization (5 g N m^{-2} yr^{-1}) factorial. In S16, nitrogen fertilizer was applied at two levels (5 g N m^{-2} yr^{-1} and 15 g N m^{-2} yr^{-1})

Table 1. Location of the studies used in the synthesis, vegetation types present and experimental manipulations applied.

Principal investigator	Study	Harvard Forest tract	Vegetation types†	Treatments‡
Davidson	S1	Prospect Hill/EMS	D	C
	S2	Prospect Hill	D	C, D
	S3	Simes	C	C, G, L
	S4	Prospect Hill/EMS	D	C
	S5	Prospect Hill/EMS	D	C
	S6	Prospect Hill/EMS	D	C
	S7	Prospect Hill/EMS	D	C
	S8	Prospect Hill/EMS	W	C
	S9	Prospect Hill/EMS	C	C
	S10	Prospect Hill/EMS	D	C
	S11	Prospect Hill/EMS	D	C
	S12	Prospect Hill/EMS	D	C
	S13	Prospect Hill/EMS	D	C
Ellison	S14	Simes	D, C	C, G, L
Frey	S15	Prospect Hill	D	C, Fl, H, HFl
Frey and Ollinger	S16	Prospect Hill	D, P	C, Fh, Fl
Hadley	S17	Prospect Hill	C	C
	S18	Prospect Hill/LPH	D, C, M, P, W	C
Melillo	S19	Slab City/Barre Woods	D	C, H
	S20	Prospect Hill	D	C, DC, H
Munger	S21	Prospect Hill	D, M, W	C, PL
Nadelhoffer	S22	Tom Swamp	D	C, DL, NA, NI, NL, NR
Varner and Crill	S23	Prospect Hill/EMS	D, W	C

† Vegetation types are: conifers (C), deciduous (D), mixed conifers-deciduous (M), red pine plantation (P) and wetlands (W, including swamps, bogs, and wetland margins).

‡ Treatments are: control (C), drydown (D), disturbance control (DC), doubling of annual aboveground litter (DL), high nitrogen fertilization (Fh, 15 g N m^{-2} yr^{-1}), low nitrogen fertilization (Fl, 5 g N m^{-2} yr^{-1}), girdling (G), heating (H), heating + nitrogen fertilization (HFl, 5 g N m^{-2} yr^{-1}), logging (L), organic and A horizons replaced with B-horizon soil (NA), exclusion of aboveground litter (NL), exclusion of root inputs by trenching (NR), exclusion of aboveground litter and root inputs (NI), and partial logging (PL).

for 20 years to assess the impact of long-term N amendment on adjacent hardwood and red pine stands.

S22 assessed the impact of plant inputs on R_s. Treatments included the doubling of annual aboveground litterfall, excluding aboveground litter, excluding root inputs by trenching, excluding aboveground litter and root inputs, and replacing the organic and A horizons with B-horizon soil.

Located in hemlock-dominated areas, studies S3 and S14 examined the impacts of harvesting or of an invasive insect, the hemlock woolly adelgid (*Adelges tsugae* Annand), on R_s. The treatment plots consisted of girdled hemlock trees (i.e., the removal by chainsaw or knife of a strip of bark and cambium that kills the tree without cutting it down) or hemlock logging simulating a management decision to harvest trees before adelgid infestation. Finally, S21 was located in a selectively harvested deciduous stand in which 27% of the tree stems and basal area was removed for the production of saw timber and firewood.

Ecosystem-scale CO_2 measurements

The EMS tower (Fig. 1) has been in operation since 1990. It uses EC to make nearly continuous measurements of CO_2, H_2O, and energy fluxes between the surrounding forest and the atmosphere (Wofsy et al. 1993, Goulden et al. 1996, Urbanski et al. 2007). Air and soil temperature, photosynthetic photon flux density (PPFD), net solar radiation, and other environmental measurements are taken concurrently.

Red oak and red maple trees dominate the 75- to 110-year-old forest surrounding the tower (Urbanski et al. 2007). Small stands of eastern hemlock, white pine and red pine (*Pinus resinosa* Aiton) are also present. In 2006, an extensive survey found that the basal area of trees and shrubs (>1 cm DBH) was 38.7 m^2 ha^{-1} around the EMS tower (Goldman et al. 2006).

The Hemlock (HEM) eddy covariance tower is located ~500 m west of EMS in an eastern hemlock-dominated forest surrounded by stands of red oak and red maple, a red pine plantation, and a swamp forest overlying 1–5 m of peat sediments. The hemlock trees are 100 to 230 years

Table 2. Soil respiration measurement methods used in each study, measurement years and number of valid measurements used in the analysis, and main references.

Study	Method used	Measurement years	No. measurements used in analysis	References
S1	Autochamber	2003	43656	Savage et al. (2008)
S2	Manual, portable IRGA	2001–2004	2202	Borken et al. (2006)
S3	Manual, portable IRGA	2003–2009	2283	Ellison et al. (2010)
S4	Manual, portable IRGA	2004–2008	335	Davidson and Savage (2010)
S5	Manual, portable IRGA	1996–1998	275	Davidson and Savage (2010)
S6	Manual, portable IRGA	1996–1998	283	Davidson and Savage (2010)
S7	Manual, portable IRGA	2005–2008	258	Davidson and Savage (2010)
S8	Manual, portable IRGA	1995–1999/ 2003–2006	757	Davidson et al. (1998) Savage and Davidson (2001)
S9	Manual, portable IRGA	1995–2001/ 2003–2008	1175	Davidson et al. (1998) Savage and Davidson (2001)
S10	Manual, portable IRGA	1995–2008	1474	Davidson et al. (1998) Savage and Davidson (2001)
S11	Manual, portable IRGA	1995–2004	1094	Davidson et al. (1998) Savage and Davidson (2001)
S12	Manual, portable IRGA	1995–2004	1121	Davidson et al. (1998) Savage and Davidson (2001)
S13	Manual, portable IRGA	1995–2001	818	Davidson et al. (1998) Savage and Davidson (2001)
S14	Manual, portable IRGA	2006–2008	445	Ellison et al. (2010) Orwig et al. (2013)
S15	Manual, static chamber	2006–2009	1204	Contosta et al. (2011)
S16	Manual, static chamber and portable IRGA	1988–1989/ 2009	764	Aber and Magill (2004) Bowden et al. (2004)
S17	Manual, portable IRGA	1997–2001 / 2004–2007	1746	Hadley and Schedlbauer (2002)
S18	Manual, portable IRGA	2003–2007	2164	Hadley et al. (2008)
S19	Manual, static chamber	2002–2009	2286	Melillo et al. (2011)
S20	Manual, static chamber	1991–2009	4172	Peterjohn et al. (1994) Melillo et al. (2002)
S21	Manual, portable IRGA	1998–2000/ 2002–2003	4630	Munger and Wofsy (2006)
S22	Manual, soda lime and portable IRGA	1992–1995/ 2000–2001	2008	Bowden et al. (1993) Boone et al. (1998) Nadelhoffer et al. (2004)
S23	Autochamber	2003–2006	34640	Phillips et al. (2010)

old and the stand has been selectively logged but never completely cleared. EC measurements at HEM were made in 2000–2001 and from 2004 to present (Hadley and Schedlbauer 2002, Hadley et al. 2008). In this synthesis, we used 18 consecutive years of measurements from the EMS tower (1992–2009) and 6 consecutive years from the HEM tower (2004–2009).

Eddy covariance measurements were used to calculate net ecosystem exchange (NEE), the difference between the amount of CO_2 fixed by the ecosystem and the amount released to the atmosphere. Power outages, equipment failures, and invalid or out-of-range data caused gaps in the two series of half-hourly or hourly NEE used in this study (Appendix: Fig. A1). These factors caused the loss of 60% of the NEE data at the EMS tower, and 81% at the HEM tower. At EMS, 31% of the lost data was caused by gaps less than 24 hours long, 34% by 1 to 7-day long gaps and 35% by gaps longer than 7 days. At HEM, 25% of the lost data was caused by gaps less than 24 hours long, 50% by 1 to 7-day long gaps and 25% by gaps longer than 7 days. A larger proportion of the dataset had to be discarded at the HEM site because only EC measurements for winds from the southwest are representative of the hemlock stand; observations for other wind directions were not used. Generally, gaps were evenly distributed throughout the year at both sites.

We used the method and algorithm of Urbanski et al. (2007) to partition NEE into gross ecosystem exchange (GEE) and ecosystem respiration (R_e) and to gap-fill the EMS-tower dataset. Gaps in HEM data were filled using non-linear regression (Hadley et al. 2008). For those times when neither partitioned nor gap-filled NEE data

were available for the HEM tower, we used the Fluxnet-Canada Research Network (FCRN) gap-filling procedure (Barr et al. 2004, Amiro et al. 2006) to estimate R_e because it gave good agreement with available gap-filled values from HEM (Appendix: Fig. A2). For both EMS and HEM data, we summed the gap-filled half-hourly or hourly averages of R_e to obtain daily and monthly fluxes.

It is important to keep in mind that R_e values determined from eddy covariance are a model-based estimate of ecosystem respiration assuming that observed NEE at night can be scaled to the daytime using its relationship to temperature. Calm periods are excluded to avoid a low bias in the fluxes due to advective losses and transport not associated with turbulent eddies. For EMS tower data, we fit a linear dependence of nighttime NEE against the difference in temperature from the mean over short (10–20 day) intervals. Ecosystem respiration during daylight was predicted by assuming that the nighttime dependence of R_e on temperature applied equally to daytime R_e.

We estimated the spatial extent of the flux-tower footprints using inverse Lagrangian modeling (Kljun et al. 2004) to estimate the proportion of the footprint area represented by the different vegetation cover types. Because the footprint varies with season, we computed it separately for the snow-free, intermittent, and permanent snow cover seasons. For each flux tower in each season, we computed the average footprint contributing 90% of the measured fluxes.

Tree phenology

To link soil and ecosystem respiration to annual aboveground phenology, we used phenological data collected at Prospect Hill from 1992–2010 (O'Keefe 2011). The date of bud break was defined as the first day when at least 50% of the buds on a tree had recognizable leaves. Full leaf out was estimated as the day when >90% of the leaves on a given tree reached at least 95% of their final size. In autumn, the process of leaf abscission was noted as "leaf coloration" and was estimated as the day when at least 20% of the leaves on a given tree had changed color. We computed the average date of occurrence of bud break, leaf out, and leaf coloration for four red oak trees and five red maples, the two dominant tree species present in the EMS-tower footprint, or for five hemlock trees, the dominant species in the HEM-tower footprint, and averaged the results across years.

Snow cover

The presence or absence of a snow cover was used in our analyses as a potential driver of seasonal R_s patterns and to adjust the extent of the flux-tower footprint. Since snow depth or cover was not routinely measured before 2010, we identified days with snow cover by calculating the daily ratio of daytime upward to downward PPFD measured at the top of the EMS tower (Coursolle et al. 2012). This method is based on the principle that snow has a higher albedo than the soil surface, so snow cover increases the ratio of upward-to-downward PPFD. Data were available for 1992–2007. Because PPFD data are noisy, we combined data across years and identified a day of year (DOY) as having "persistent snow cover" when the daily ratio of upward to downward PPFD was at least 0.06 in at least 8 out of the 16 years. We identified the DOY as having "intermittent snow cover" when 4–7 years were above the threshold, and as "snow-free" when 3 years or less were above the threshold.

Calculation of the response of R_s to T_s

All data are publicly and freely available via the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-archive; key datasets are HF000, HF001 [Harvard Forest meterological data], HF003 [phenology], HF004 [EMS EC tower], HF072 [Little Prospect Hill EC tower], HF103 [Hemlock EC tower], HF194 [main R_s dataset]). We used all data from the period 1988–2009 when both R_s and related soil temperature (T_s) were available. A total of 31,148 usable R_s measurements were made manually and 78,296 were made using autochambers.

The number of R_s studies synthesized here, and hence data coverage, varied greatly during the 22 years (from 1 to 12 different study locations per year; Table 2, Fig. 2A). Temporal resolution was also widely variable; the studies using autochambers produced R_s measurements every 30 minutes (S1) or 4 hours (S23) but R_s measured manually was usually available only

once every few days/weeks for any given study. Similarly, very few measurements were made during winter because of the difficulty of measuring R_s through a snowpack. Wintertime estimates of R_s were based on the apparent temperature sensitivity of R_s derived from snow-free periods. Besides temperature, we did not include other drivers, such as soil moisture content, in the extrapolation because these data were not available for all studies.

We assessed the response of R_s to T_s using the linearized Q_{10} function in Humphreys et al. (2005):

$$\ln(R_s) = A + BT_s. \quad (1)$$

The logarithmic transformation yielded a linear function with homoscedastic errors. The parameters of this equation were then used to estimate the apparent Q_{10} of soil respiration, which measures the factor of increase in soil respiration associated with an increase of 10°C in soil temperature:

$$Q_{10} = \exp(10B). \quad (2)$$

We then calculated R_{10}, the rate of soil respiration at 10°C:

$$R_{10} = Q_{10} \times \exp(A). \quad (3)$$

Because Eq. 1 represents the *apparent*, and not actual, temperature response when used on data at the seasonal to annual time scale (Davidson et al. 2006*b*, Subke and Bahn 2010), we used the temperature model to capture seasonal trends in R_s. In this case, T_s is effectively used as a driver of R_s but also as a proxy for other drivers that correlate with temperature, such as plant phenology, soil water content and substrate supply, among others.

Estimation of R_s at eddy-covariance sites

The exceptionally large number of observations in the R_s dataset created the opportunity to compare seasonal variations in the magnitude and timing of R_s to that of R_e. We created an 18-year time series of R_s for the EMS and HEM tower sites ($R_{s\mathrm{EMS}}$ and $R_{s\mathrm{HEM}}$, respectively) using a "reference" soil temperature at 10-cm depth (herein $T_{s\mathrm{ref}}$), the depth of most T_s measurements. Because no single site has 18 years of continuous measurements of soil temperature at 10-cm depth, we combined T_s data from all available sources. We first computed $T_{s\mathrm{ref}}$ and then calculated site-specific temperature records for each vegetation type of each study listed in Table 1 based on measured relationships between $T_{s\mathrm{ref}}$ and site-specific T_s.

The longest time series of soil temperature at 10-cm depth in a forested area was collected at the Little Prospect Hill (LPH) eddy-covariance site, with half-hourly data available from 2002 to 2009 (herein $T_{s10,\mathrm{LPH}}$; Hadley et al. 2008). Red oak is the dominant tree species at the LPH site; this is the same species that dominates the EMS tower footprint, although the LPH stand is younger.

Using T_s from LPH, we generated the 18-year time series of $T_{s\mathrm{ref}}$ by regressing $T_{s10,\mathrm{LPH}}$ against soil-temperature data measured at the other tower sites for periods of time when the data series overlapped (Appendix: Fig. A3). The parameters of these quadratic regressions were then used to estimate T_s at 10-cm depth and to extend the LPH data series across 18 years. This approach assumes the scaling relationships are the same over the 18-year time interval. Because the EMS 20-cm depth T_s data series had gaps, we also used soil-surface data from the same site to estimate the missing values in 1991–2000 (Appendix: Fig. A3D, E).

We used the $T_{s\mathrm{ref}}$ time series to estimate study-specific T_s values that were consistent in nature (e.g., depth of measurement) across all studies. Predicted T_s for a given study site was increased or decreased based on the parameters relating $T_{s\mathrm{ref}}$ to the observed T_s for each soil collar from control plots in a study.

Using the study-specific T_s datasets, we computed Q_{10} (Eq. 2) and R_{10} (Eq. 3) coefficients employing parameters from Eq. 1 with the R_s measurements and used these coefficients to create an 18-year series of estimated half-hourly R_s for each vegetation cover type in control plots of each study. The back-transformation of the linear Q_{10} model produced a model of the median response. Because we were interested in a model of the mean response and the R_s data were not normally distributed, we corrected the bias between median and mean following Miller (1984; Appendix: Fig. A4). To scale R_s estimates to the same spatial scale as the tower measurements, we adjusted half-hourly $R_{s\mathrm{EMS}}$ and $R_{s\mathrm{HEM}}$ according to the proportion of the tower footprint area represented by the different vegetation

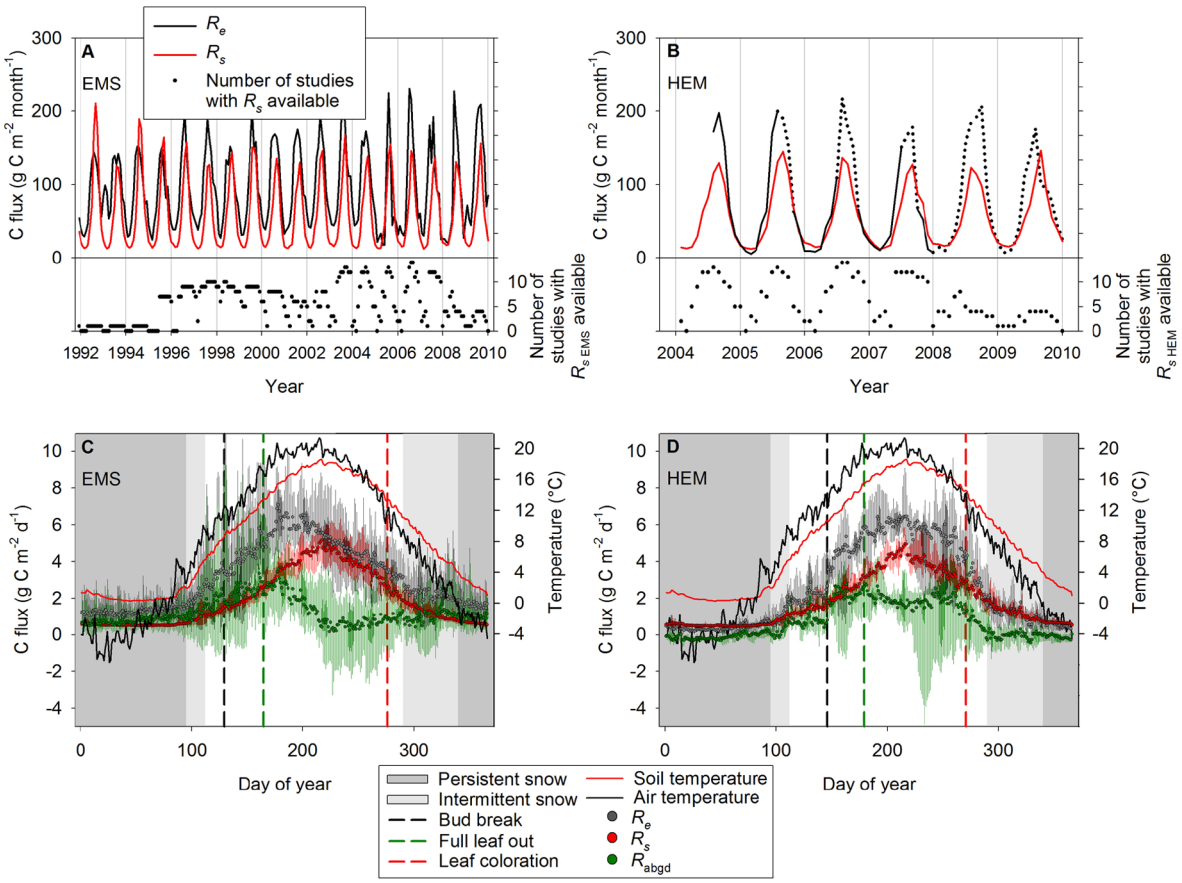

Fig. 2. Monthly ecosystem respiration (R_e) and soil respiration (R_s) for (A) 18 years of measurements at the EMS tower and (B) for 6 years at the HEM tower (left axis). In (A) and (B), the number of studies where R_s measurements were available for a given month (lower plots, right axis). On (B), the black solid line represents periods when the principal investigator's gap-filled R_e was available while the dotted line shows periods when we used the Fluxnet-Canada gap-filling algorithm to estimate R_e. Daily R_e (dark gray), R_s (red) and aboveground respiration (R_{abgd}; green) for (C) 1996–2009 at the EMS tower and (D) 2004–2009 at the HEM tower. Dots represent the median flux and vertical lines the 5th and 95th percentile. Shaded areas represent the periods when the ground was generally (medium gray) or intermittently (light gray) covered with snow. Daily mean air and soil temperature are shown as solid black and red lines, respectively. Also presented are the mean date of occurrence of bud break, full leaf out, and appearance of autumn leaf coloration (bold vertical dashed lines) for (C) red oak and red maple and (D) hemlock.

types and the fraction of the soil surface covered by rocks and tree basal area, which we assumed had a flux of zero. Seasonally adjusted (i.e., snow free, intermittent, and permanent snow cover) estimates of the mean flux footprint were used to adjust the proportion of the different vegetation types. We aggregated the results to daily and monthly sums for further analysis. A total of 27 R_s series were used to estimate R_{sEMS} and R_{sHEM}.

Annual R_s estimation

Bahn et al. (2010) used a compilation of soil respiration measurements (57 sites, 80 site-years) and modeling to suggest that annual soil respiration ($R_{sannual}$) could be estimated from measurements of soil respiration at mean annual temperature (R_{sMAT}). In their analysis, however, they used the predicted value of R_{sMAT} rather than observations of R_{sMAT}, raising the possibility that autocorrelation between the modeled values

of $R_{sannual}$ and R_{sMAT} accounted for this relationship. The data for the relationship depended on site-specific, exponential equations relating R_s measurements to soil temperature, which were used to estimate $R_{sannual}$ and R_{sMAT}. We recreated Bahn et al.'s (2010) approach by producing a relationship between $R_{sannual}$ and modeled R_{sMAT} at the Harvard Forest and tested its validity using observed R_s data.

Calculation of treatment effects

To compare the effects of experimental treatments on R_s within and among studies through time, we computed a "response ratio", or effect size, of R_s in the treatment plots (R_{strt}) and the corresponding control plots (R_{sctl}) of each study. We used an approach similar to the one described in the section *Estimation of R_s at eddy-covariance sites* to obtain series of estimated R_s, but the temperature response of R_s was calculated for each measurement year (instead of all years together) to avoid masking variability that might have been caused by inter-annual variations in environmental conditions. Since very few R_s measurements were made during winter in any study, we used data from April to October only, the period with the best data coverage. To estimate the uncertainty in the response ratio, we randomly removed 20% of the collars from each experiment and treatment. Using the new dataset, we rescaled the T_{sref} series to T_s of the study, recomputed the relationship between R_s and T_s using Eq. 1 and used the resulting Q_{10} and R_{10} coefficients to produce series of estimated R_{sctl} and R_{strt} for each measurement year. We then computed the new response ratio. This process was repeated 200 times and we used the results to calculate non-parametric confidence intervals.

Spatial variability of R_s

To study the spatial variability of soil respiration at Harvard Forest, we examined the correlation of small-scale fluctuations at neighboring collars. For example, we analyzed R_s data from a transect of nine collars that were measured on multiple days. On each measurement day, every collar was measured. A linear model of $\log(R_s)$ on $\log(T_s)$ was fit separately at each collar, and correlation among collars was examined with a scatterplot matrix of residuals (Appendix: Fig. A5). We observed no more correlation among neighboring collars than among distant collars, suggesting that non-modeled effects are not spatially correlated at this fine scale.

Statistics

We analyzed variations in R_{10} and Q_{10} among vegetation types using one-way ANOVA with post-hoc comparisons using Tukey's Honestly Significant Difference test in R (R Development Core Team, version 0.96.230). In this analysis, the unit of replication was the soil-respiration collar (Fig. 3). Data from all years collected at a collar were used to fit the linearized Q_{10} function, Eq. 1. Gap-filling and regression analyses were conducted in Matlab version 7.11.0 (MathWorks, Natick, Massachusetts, USA).

Results

Soil respiration across measurement locations

Among the studies included in this synthesis, basal respiration at 10°C (R_{10}) varied from 0.5 to 4 μmol C m^{-2} s^{-1}, and was normally distributed with a mean and standard error of 1.70 ± 0.02 μmol C m^{-2} s^{-1} (Fig. 3A, B). Mixed deciduous-coniferous stands had the highest R_{10} (2.01 ± 0.06), whereas wetland locations and red pine plantations had the lowest R_{10} of all vegetation types (0.90 ± 0.07 μmol C m^{-2} s^{-1} and 1.42 ± 0.10 μmol C m^{-2} s^{-1}, respectively; Fig. 3A). Mean R_{10} for deciduous and hemlock stands were 1.74 ± 0.03 and 1.73 ± 0.05 μmol C m^{-2} s^{-1}, respectively.

The apparent temperature sensitivity of soil respiration (Q_{10}) estimated for each collar varied from about 1 to 9, with most values between 2 and 5 (Fig. 3C, D). In general, the Q_{10} estimates were more broadly distributed than the R_{10} estimates (Fig. 3B, D). Mean Q_{10} was lowest at 2.53 ± 0.11 for red pine, intermediate at 2.93 ± 0.11 and 3.04 ± 0.12 for mixed and hemlock stands, respectively, and was highest at 3.83 ± 0.09 in deciduous and 3.97 ± 0.15 in wetland sites (Fig. 3C). The mean Q_{10} of deciduous stands was slightly higher and that of hemlock stands slightly lower than the average calculated from Bond-Lamberty and Thomson (2010*b*; global means = 3.46 ± 0.10 and 3.44 ± 0.16).

Among the five different vegetation types, annual soil respiration ($R_{sannual}$) varied from 469 to 951 g C m^{-2} yr^{-1} (Table 3). On average, $R_{sannual}$

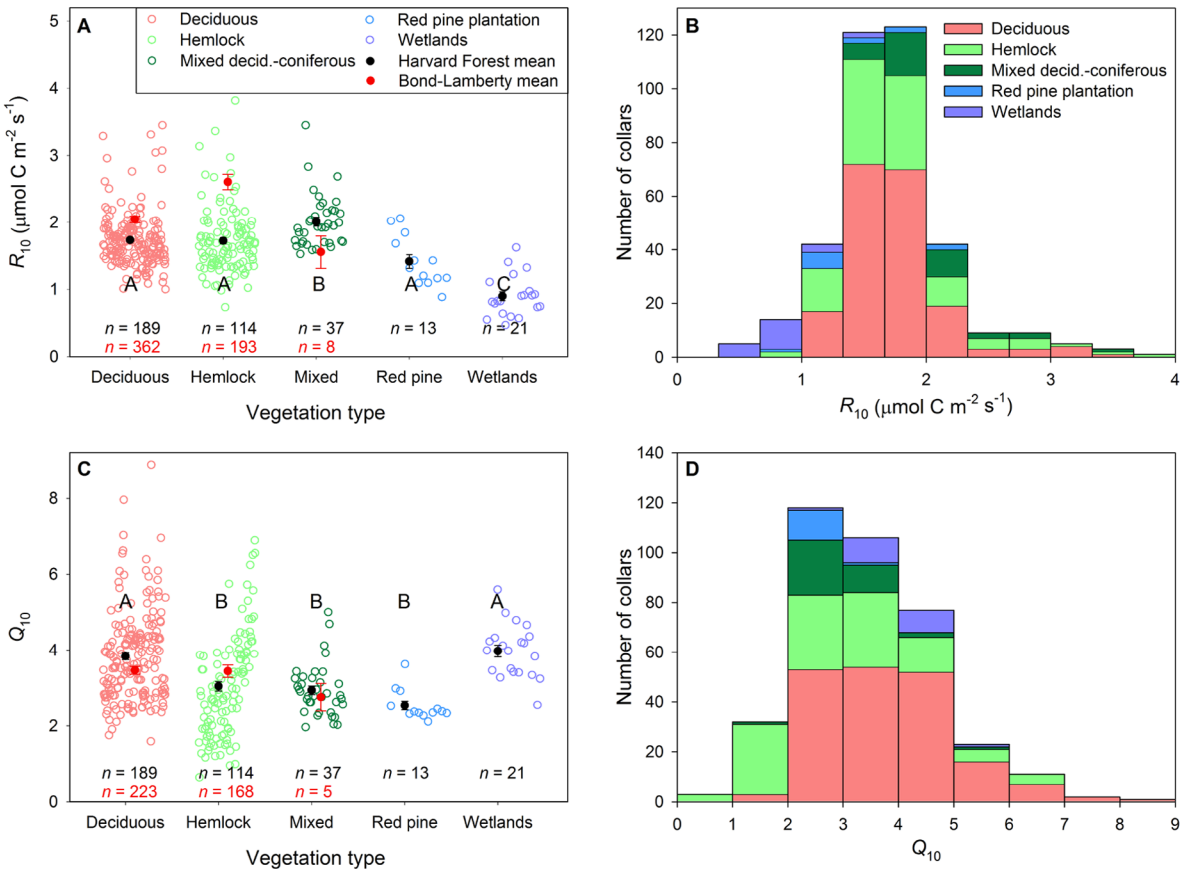

Fig. 3. (A) Soil respiration at 10°C (R_{10}) and (C) the ratio of increase in soil respiration associated with an increase of 10°C in soil temperature (Q_{10}) with respect to the vegetation type present at each measurement location. R_{10} and Q_{10} were calculated for each collar of the studies included in this synthesis using Eqs. 1, 2 and 3. The mean and standard error (SE) are presented with black circles and error bars for each vegetation type. Different letters indicate significant differences between the Harvard Forest means ($p < 0.05$). The average R_{10} and Q_{10} (± SE) computed from Bond-Lamberty and Thomson's global soil respiration database (version 20120510a) for mature deciduous, coniferous, and mixed temperate forests where no experimental treatment was applied is shown in red. The number (n) of data used to compute the means is shown in black (Harvard Forest) and red (Bond-Lamberty). Also presented are the frequency distributions of (B) R_{10} and (D) Q_{10} of Harvard Forest measurements.

of wetlands was almost 200 g C m^{-2} yr^{-1} lower than for other forest types.

Annual soil respiration estimation

We found a robust relationship between $R_{sannual}$ and modeled R_{sMAT} when data from all studies and vegetation types were used (Fig. 4A). However, in contrast to the predictions of Bahn et al. (2010), we found no significant relationship between $R_{sannual}$ and values of R_s measured manually in the field within 0.5°C of soil MAT under varying environmental conditions ($R_{s0.5°C\text{-}MAT}$; Fig. 4B).

Respiration and phenology

There was large inter-annual variability in soil and ecosystem respiration (Table 4; Fig. 2A, B). At the EMS site, R_{eEMS} ranged from 826 to 1456 g C m^{-2} yr^{-1} and R_{sEMS} varied between 621 and 882 g C m^{-2} yr^{-1}. The annual R_{sEMS}/R_{eEMS} ratio varied from 0.49 to 0.92. Annual ecosystem respiration at the HEM site (R_{eHEM}) varied

Table 3. Annual soil respiration ($R_{sannual}$) for the five main vegetation types present at Harvard Forest.

Year	$R_{sannual}$ (g C m^{-2} yr^{-1})				
	Deciduous	Hemlock	Mixed	Red pine	Wetlands
1992	913	853	842	951	647
1993	663	616	618	676	483
1994	839	783	777	869	600
1995	781	728	725	804	562
1996	750	698	696	770	541
1997	644	598	601	656	469
1998	752	700	699	772	544
1999	818	762	758	844	587
2000	696	646	648	710	506
2001	663	616	618	676	483
2002	748	696	695	767	541
2003	768	715	713	789	554
2004	734	682	682	752	531
2005	783	729	726	806	563
2006	751	699	698	770	544
2007	704	655	655	720	511
2008	721	670	671	736	524
2009	740	688	688	757	536
Mean ± SD	748 ± 64	696 ± 61	695 ± 58	768 ± 70	540 ± 42

between 803 and 1049 g C m^{-2} yr^{-1}, whereas soil respiration ($R_{s\mathrm{HEM}}$) ranged from 640 to 711 g C m^{-2} yr^{-1}, resulting in $R_{s\mathrm{HEM}}/R_{e\mathrm{HEM}}$ ratios of 0.62 to 0.80. We found no significant correlations between annual R_e, R_s, and the R_s/R_e ratio and meteorological variables such as precipitation, temperature, and PPFD at either site. The rank orders of the R_s/R_e ratios from 2005 to 2009 at the EMS and HEM sites differed, with 2005 > 2008 > 2007 ≈ 2006 > 2009 at the EMS site and 2009 = 2007 > 2006 ≈ 2005 > 2008 at the HEM site (Table 4).

To compare the annual cycle of R_e and R_s, we computed the median daily fluxes using our 6-year HEM dataset and the last 14 years of our EMS dataset (Fig. 2C, D). We did not use the first 4 years of the EMS dataset because only one study took place during these years and using data from later years to estimate R_s in the first four years resulted in unrealistic fluxes such as higher monthly R_s than R_e (Fig. 2A).

Although both R_s and R_e followed annual

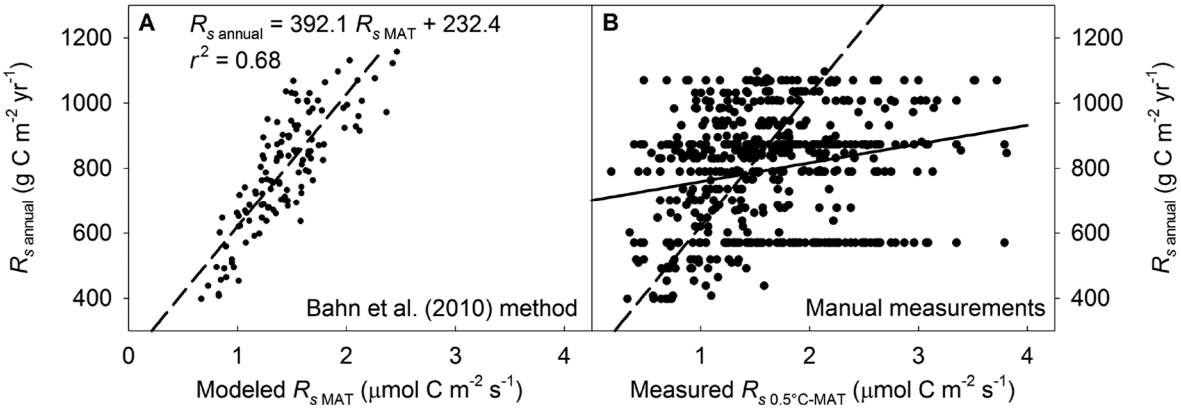

Fig. 4. (A) Relationship between annual soil respiration ($R_{sannual}$) and modeled soil respiration at mean annual soil temperature ($R_{s\mathrm{MAT}}$) as suggested by Bahn et al. (2010). The linear relationship is shown as a dashed line. (B) Relationship between $R_{sannual}$ and all unique manual measurements of R_s collected within 0.5°C of MAT ($R_{s\ 0.5°\mathrm{C–MAT}}$). The best linear relationship is shown (solid line). For reference, the relationship in (A) is reproduced as a dashed line in (B).

Table 4. Annual total ecosystem respiration (R_e), soil respiration (R_s) and R_s/R_e ratio for the EMS and HEM sites.

Year	$R_{e\mathrm{EMS}}$ (g C m^{-2} yr^{-1})	$R_{s\mathrm{EMS}}$ (g C m^{-2} yr^{-1})	$R_{s\mathrm{EMS}}/R_{e\mathrm{EMS}}$	$R_{e\mathrm{HEM}}$ (g C m^{-2} yr^{-1})	$R_{s\mathrm{HEM}}$ (g C m^{-2} yr^{-1})	$R_{s\mathrm{HEM}}/R_{e\mathrm{HEM}}$
1992	1007	882	0.88	...	...	...
1993	1181	640	0.54	...	...	...
1994	1064	811	0.76	...	...	...
1995	973	754	0.78	...	...	...
1996	1133	724	0.64	...	...	...
1997	1240	621	0.50	...	...	...
1998	1056	726	0.69	...	...	...
1999	1188	790	0.66	...	...	...
2000	1185	671	0.57	...	...	...
2001	1212	640	0.53	...	...	...
2002	1244	722	0.58	...	...	...
2003	1324	741	0.56	...	...	...
2004	1248	708	0.57	...	667	...
2005	826	756	0.92	963	711	0.74
2006	1197	725	0.61	912	682	0.75
2007	1085	680	0.63	803	640	0.80
2008	988	695	0.70	1049	655	0.62
2009	1456	714	0.49	848	672	0.79
Mean ± SD	1145 ± 142	722 ± 62	0.64 ± 0.12	915 ± 86	671 ± 22	0.74 ± 0.06

cycles, in which respiration was lowest during winter and highest during the warmest months of the year, there were marked differences in fluxes within and between tower sites. The largest relative differences between daily $R_{e\mathrm{EMS}}$ and $R_{s\mathrm{EMS}}$ occurred during winter, the first half of the growing season, and late in the fall (Fig. 2C). Mean winter (December–March) $R_{s\mathrm{EMS}}$ represented only 40% of $R_{e\mathrm{EMS}}$, whereas it was 65% of $R_{e\mathrm{EMS}}$ on average during the 8 other months of the year. During August and September, mean daily $R_{s\mathrm{EMS}}$ increased to 87% of $R_{e\mathrm{EMS}}$. Respiration at the HEM site differed from that of the EMS site: $R_{e\mathrm{HEM}}$ and $R_{s\mathrm{HEM}}$ were almost equal during winter, and $R_{s\mathrm{HEM}}$ represented 68% of $R_{e\mathrm{HEM}}$ during the rest of the year (Fig. 2D). $R_{e\mathrm{HEM}}$ and $R_{s\mathrm{HEM}}$ both peaked in early August, whereas $R_{e\mathrm{EMS}}$ attained its maximum approximately four weeks earlier than $R_{s\mathrm{EMS}}$ (Fig. 2C, D).

At the EMS site, aboveground plant respiration (R_{abgdEMS})—the difference between $R_{e\mathrm{EMS}}$ and $R_{s\mathrm{EMS}}$—was ~0.8 g C m^{-2} d^{-1} during winter and started increasing immediately before snowmelt (Fig. 2C). R_{abgdEMS} reached its highest value between late May and early July, when leaf development reached completion, and decreased thereafter, attaining its minimum in August. R_{abgdEMS} later slowly increased, reaching its winter average rate of ~0.8 g C m^{-2} d^{-1} at the beginning of October, coincident with the emergence of leaf coloration in the autumn. At the HEM site, R_{abgdHEM} was near zero during winter, increased rapidly during snowmelt, and reached its peak in June, at the time of full leaf out (Fig. 2D). R_{abgdHEM} declined slightly during midsummer, increased again until it reached almost as high as the annual maximum in early September, and decreased sharply thereafter until it reached zero at the onset of the winter snowpack. The annual cycle of R_{abgd} presented some oddities that will be discussed in detail in sections *Seasonal variation in R_s is linked to temperature and phenology* and *Methodological advances are needed to reduce uncertainty in R_s, R_e and NEE*.

Effect of experimental treatments on soil respiration

Two main categories of experimental treatments have been used: treatments mimicking different aspects of global change and experiments aimed at partitioning R_s into component fluxes. Some of these manipulations had large effects on annual R_s ranging from −70% to +52% of that in control plots (Fig. 5). Not surprisingly, the direction of the effect was generally related to the change in C inputs, with girdling, logging, trenching, diminution of litter inputs, and removal of O and A horizons resulting in lower CO_2 emissions, while increasing litter inputs caused an increase in emissions. N additions and soil warming also increased CO_2 efflux, with the largest effects of these manipulations in the first few years of the treatment.

Variability of soil respiration

To assess variation in R_s due to spatial variability, interannual variations, and experimental treatments, we calculated the coefficient of variation (CV) of soil respiration totals from April to October ($R_{sAp–Oc}$) in all studies (Table 5). To remove the effect of varying climate conditions between years and isolate the effect of experimental treatments, we calculated the CV of the average R_{strt}/R_{sctl} ratio of all studies. Removing the three least realistic treatments from study S22 (no roots, no roots nor litter, no O and A horizons) strongly decreased the CV. The impact of spatial variability on R_s was represented by the CV of the average $R_{sAp–Oc}$ in control plots for each vegetation type in each study. The effect of spatial variability was similar to the variability introduced by interannual variations in climate and biological processes in control plots for the three studies with at least 11 years of measurements (Table 5).

Discussion

We analyzed more than 100,000 individual measurements of soil respiration (R_s) from 23 observational or experimental studies executed over nearly a quarter century in five different forest types at the Harvard Forest. These data were coupled with 24 site-years of net ecosystem exchange (NEE) data collected using eddy covariance (EC) measurements—including the longest time-series of EC data in the world—that allowed us to examine in detail the relationship between R_s and ecosystem respiration (R_e). These data and the relationships they reveal are especially valuable in light of a recent analysis suggesting that measurements of R_s are among the most important data for reducing the uncertainty of process-based models of forest carbon dynamics (Keenan et al. 2013).

We draw five main observations from our analyses and synthesis:

1. Responses in R_s caused by experimental manipulations appear to follow changes in substrate availability with treatments increasing C supply stimulating R_s and those decreasing C supply reducing the rate of R_s. The magnitudes of the effects reported here are similar in size to those reported in the literature from global change manipulations in other vegetation types.
2. Variations in measurements of R_s at unique sample points can be as large as or larger than variations in annual R_s within studies and forest types or in responses to experimental manipulations.
3. Seasonal variations in R_s and R_e are linked to variations in temperature and vegetation phenology, with the majority of R_e driven by aboveground respiration from bud break through leaf out followed by the continued increase in soil respiration and its dominance of R_e throughout the remainder of the growing season. On average, the peak in aboveground respiration occurs 38 days earlier than the peak in belowground respiration.
4. Variations in R_s caused by inter-annual variations in weather and phenological events are of the same order of magnitude as responses caused by experimental manipulations. Thus it appears that climatic controls over R_s are of similar importance as other drivers of global change (i.e., invasive insects, forest management practices, N deposition).
5. It remains difficult to partition R_e into above- and belowground components, in part because of the different spatial scales of R_s and R_e measurements and possible errors associated with the two techniques. Progress in making the "hard" measurements, such as R_s during winter, properly dealing with stable conditions in eddy covariance measurements, daytime vs. nighttime canopy respiration and its impacts on estimates of R_e, and independently verifying the partitioning of NEE into R_e is likely to lead to increases in the confidence of estimates of R_s, R_e, and NEE.

Experimental manipulations appear to influence R_s through substrate availability

Overall, R_s increased in response to soil warming, nitrogen fertilization and doubling of litter inputs, and declined because of simulated drought, logging, girdling, trenching, diminution of litter inputs, and removal of O and A horizons (Fig. 5). Both responses appear to arise from experimentally induced changes in substrate

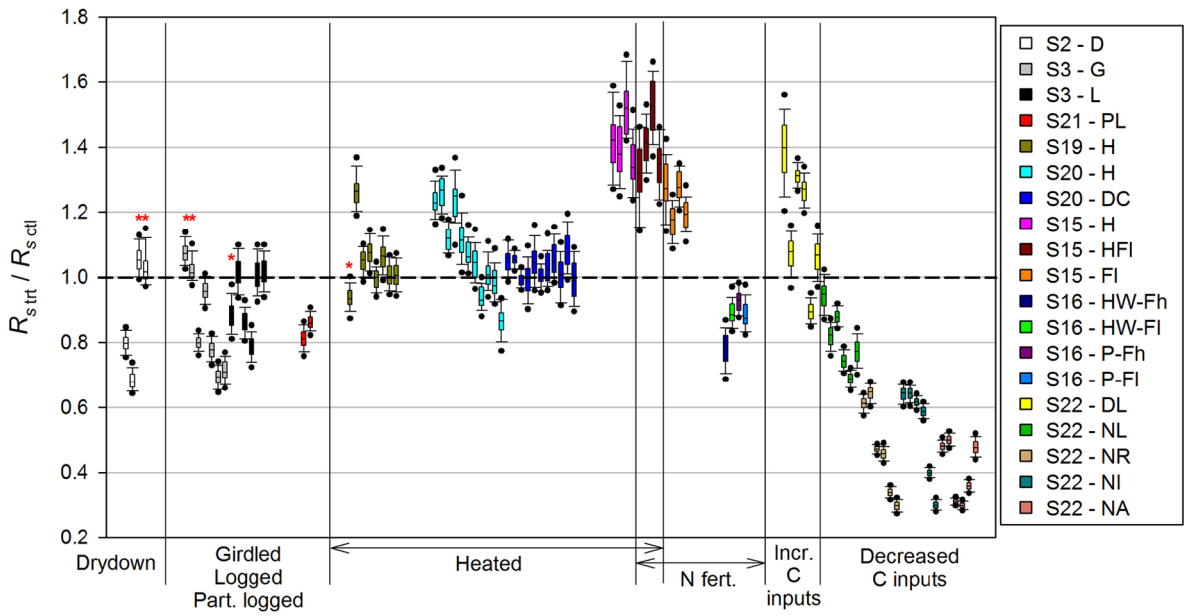

Fig. 5. Box plots of ratios of total soil respiration for the April-to-October period for treatments relative to their respective control soil respiration total for each measurement year, shown in chronological order. The boundary of the box closest to zero indicates the 25th percentile and the boundary farthest from zero, the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles while the black points above and below the whiskers indicate the 5th and 95th percentiles. The horizontal dashed line represents a ratio of 1. A ratio above 1 indicates an increase in R_s caused by the treatment, while a ratio lower than 1 indicates a decrease. Red asterisks denote years when data were available for the treated plots before/after the treatments were applied. Boxes without asterisks represent years during which the plots were treated. The categories of treatments are indicated on the *x*-axis. Treatments codes are as in Table 1. In study S16, treatments were applied to hardwood (HW) and red pine (P) plots.

availability that are caused by changes in the size of soil C pools (e.g., addition of labile litter, removal of soil horizons), belowground C fluxes (e.g., N fertilization, trenching, girdling or logging), or environmental conditions (e.g., drydown, warming). The magnitude (range: −70% to +52%) of the observed changes in R_s following manipulations was similar to those reported in the literature (drought: Wu et al. 2011; logging: Luo and Zhou 2006; N addition: Janssens et al. 2010; selective harvest: Tang et al. 2005*b*, Nave et al. 2011; warming: Rustad et al. 2001). In some cases (e.g., logging, warming studies S19 and S20), experimental effects on R_s were clearly

Table 5. Coefficient of variation (CV) of the average soil respiration totals from April to October for spatial and interannual variability and CV of the annual R_{strt}/R_{sctl} ratio for experimental manipulations variability.

Source of variability		CV	*n*
Spatial		0.18	29
Interannual variations in climate and phenology†	S9	0.15	11
	S10	0.20	12
	S20	0.17	11
Experimental manipulations	All treatments	0.31	19
	Without NA, NR, and NI treatments‡	0.22	16

† Only studies with at least 11 years of R_s measurements available are presented.
‡ NA: organic and A horizons replaced with B-horizon soil; NR: exclusion of root inputs by trenching; NI: exclusion of aboveground litter and root inputs.

transient, but in other cases the duration of observations following single or repeated manipulations ("pulse" and "press" experiments, respectively, sensu Bender et al. 1984) were too short to distinguish between transient dynamics and permanent change in R_s. It remains difficult to pinpoint the cause of differences in the effects of similar manipulations in different studies (e.g., the greater impact of warming in study S15 than in S19 and S20; Fig. 5) since the experiments were not all designed to be compared to each other and not all environmental parameters and carbon pools were measured.

Small-scale spatial variation in R_s can exceed variation among forest types

Our data clearly illustrate that R_s is highly variable at all spatial and temporal scales of measurement (Figs. 2, 3; see also Norman et al. 1997, Rayment and Jarvis 2000, Drewitt et al. 2002). Variability among R_s measurements made at collars within a single observational or experimental study was as large as or larger than inter-annual variability in estimated $R_{sannual}$ (cf. Raich et al. 1990). For example, R_s measured between July 1–10 during a single year on unique collars in undisturbed plots varied by up to 1426% (median: 31%, mean: 99%) over those 10 days, whereas $R_{sannual}$ varied by a maximum of 127% within studies (median: 39%, mean: 47%) and 197% among all studies and vegetation types. This suggests that unquantified heterogeneity in substrate or activity by roots or microbes is a critical factor that needs to be explored in more detail. Deciduous and hemlock forests, the main types of vegetation studied, had similar R_{10} rates (Fig. 3A) that were lower than predicted from Bond-Lamberty and Thomson's global soil respiration database (version 20120510a) for mature deciduous and coniferous temperate forests (2.04 ± 0.05 and 2.61 ± 0.11 μmol C m^{-2} s^{-1}, respectively; data available at http://code.google.com/p/srdb; Bond-Lamberty and Thomson 2010*b*). R_{10} and $R_{sannual}$ were lowest in wetlands, likely because of lower plant productivity and reduced C inputs to the soil (Davidson et al. 1998) and lower decomposition under anoxic conditions (Skopp et al. 1990). Although spatial variation in fluxes is large, it does not preclude understanding and statistically resolving important temporal variations in R_s at sub-seasonal to inter-annual time scales or variations in response to properly designed experimental treatments.

Predicting annual rates of soil respiration

Similar to Bahn et al. (2010), we were able to predict annual soil respiration ($R_{sannual}$) from soil respiration at mean annual temperature (R_{sMAT}), but only when we used a large number of R_s measurements taken over a wide range of temperatures to estimate R_{sMAT} (Fig. 4A), not when using only actual R_s measurements made at MAT (Fig. 4B). Our analysis suggests that estimates of $R_{sannual}$ based on only a small number of measurements of R_s at MAT will have high uncertainty, probably driven by spatial and temporal variations in R_s.

Seasonal variation in R_s is linked to temperature and phenology

At both the deciduous EMS and hemlock-dominated HEM sites, R_s was correlated with phenological events driven by abiotic factors such as soil and air temperature (Fig. 2C, D). When estimated at the seasonal or annual time scale, the response of R_s to temperature using Eq. 1 represents the *apparent* rather than *intrinsic* temperature sensitivity (Davidson and Janssens 2006). This occurs because field-based measurements of R_s provide an integrated measure of various factors including the intrinsic temperature sensitivity of the various C pools metabolized by microbes and plant roots in addition to the effects of substrate supply and diffusion, plant phenology and C allocated belowground (e.g., Davidson et al. 2006*a*, *b*, Subke and Bahn 2010).

Plant phenology drives seasonal R_s rates through above- and belowground litter inputs, root respiration, and root exudates. Hence, seasonal variations in R_s are correlated with both aboveground plant phenology and seasonal temperature changes (Curiel Yuste et al. 2004, Savage et al. 2013), as our analysis reiterates (Fig. 2C, D). R_e and R_s were at their lowest in winter, when deciduous trees are leafless and soil temperature (T_s) is lowest. As soon as snow started melting, T_s increased rapidly, leading to a sharp increase in respiration (Fig. 2C, D). Furthermore, the rapid fine-root growth, which occurs mainly in April and May in Harvard

Forest's hardwoods and red pine stands (McClaugherty et al. 1982), also contributed to the increase in R_s at that time of the year.

Not surprisingly, R_s and R_e in conifer- and hardwood-dominated stands responded differently to climatic drivers as suggested by the varying rank order of the R_s/R_e ratios at the two sites (Table 4). At both sites, R_s followed changes in soil temperature (see also Davidson et al. 1998, Bahn et al. 2010, Subke and Bahn 2010). The peak of R_e, however, seemed to better correspond with the timing of maximum air temperature than that of soil temperature (Fig. 2C, D). The earlier peak in $R_{e\mathrm{EMS}}$ was apparently the result of earlier and greater quantity of leaf and shoot development compared to the growth of new shoots and leaf biomass in the conifer site (cf. Phillips et al. 2010). Indeed, bud break and complete leaf expansion occurred two weeks earlier in the deciduous stand compared to the hemlock forest (Fig. 2C, D). The timing of maximum ecosystem and soil respiration at the HEM site is comparable to C-flux measurements from a spruce-hemlock forest in Maine (Davidson et al. 2006*b*).

At both sites, R_{abgd} started increasing just before snowmelt (Fig. 2C, D). At the HEM site, it reflected increasing metabolic activity in conifers, as has been reported elsewhere (Davidson et al. 2006*b*). At the hardwood-dominated EMS site, R_{abgd} was more likely initially driven by pre-leaf out metabolic activity associated with bud break, branch elongation, and wood production in ring-porous species such as oak that dominate this site (Hadley et al. 2009). We estimated aboveground metabolic activity and growth during the early growing season represents ~60% of $R_{e\mathrm{EMS}}$ but only ~33% of $R_{e\mathrm{HEM}}$ from snowmelt until the end of May.

At EMS, after full leaf expansion, the relative contribution of R_{abgd} to R_e decreased rapidly and substantially until it was ~10% in August. Thereafter, R_{abgd} slowly increased until leaf-fall in late September and October (Fig. 2C), possibly reflecting increasing metabolic activity associated with the breakdown and translocation of carbohydrates, nucleic acids, and nutrients during the senescence process (Chapin and Kedrowski 1983). In addition to the surprisingly low mid- to late-summer values of R_{abgd} at EMS noted above, we also observed surprisingly high R_{abgd} in winter at EMS, a time when most respiration is expected to occur in the soil with little coming from aboveground vegetation (Davidson et al. 2006*b*).

Despite the large volume of data brought to bear in this analysis, we cannot clearly attribute the unusual patterns in respiration to uncertainty in R_e or spatial and temporal extrapolations associated with the measurements of R_s. The inability to attribute uncertainty may result from "irreconcilable differences" in methodology (sensu Strand et al. 2008); the spatial and temporal scales of measurements may simply not allow for robust cross comparisons. The substantial differences between R_{abgd} at HEM and EMS may also reflect methodological challenges and uncertainties in the dataset and estimates (see *Methodological advances are needed to reduce uncertainty in R_s, R_e and NEE*).

Finally, it appears that spatial variability and temporal variations in weather and phenology induced variation among annual R_s estimates that was similar to differences in R_s among the experimental treatments, with the exception of some of the R_s partitioning manipulations (Table 5). Our results imply that R_s is regulated simultaneously by several biotic and abiotic factors, and that any factor can have a large impact on R_s at a given time through its direct or indirect effect on substrate availability.

Methodological advances are needed to reduce uncertainty in R_s, R_e and NEE

The dataset analyzed here includes 109,444 measurements of R_s taken over two decades in different vegetation types found within two EC tower sites, and 24 site-years of EC data. Before computing seasonal or annual estimates of R_s, data were adjusted to account for soil surface area covered by trees or rocks and seasonal variation of tower footprint size. Despite these adjustments, we observed unusual patterns in R_{abgd} at the EMS site that cannot be explained by ecosystem processes and physiology alone, and differences between our observations and estimates of R_s and R_e at other temperate sites.

For example, from December through March, a time of year when the ground is generally covered by snow, mean daily $R_{e\mathrm{EMS}}$ ranged from 0.79 to 2.70 g C m^{-2} d^{-1} depending on the year (median: 1.47; mean: 1.48; SD: 0.40 g C m^{-2} d^{-1}) and was on average more than twice as high as

R_{sEMS} (median: 0.59; mean: 0.58; SD: 0.05 g C m^{-2} d^{-1}). Furthermore, wintertime R_{eEMS} was considerably higher than what has been measured in four other North American temperate deciduous forests (AmeriFlux online database, http://public.ornl.gov/ameriflux), where mean daily R_e varied between 0.22 and 0.60 g C m^{-2} d^{-1} for the December to March period during 17 site-years at the Morgan Monroe State Forest (Indiana), UMBS (Michigan), Park Falls (Wisconsin), and Willow Creek (Wisconsin).

Some of the higher wintertime R_e at the EMS site compared to other temperate U.S. forests may be caused by differences in aboveground biomass and temperature, but these factors are likely not sufficient to explain the large difference in R_e. Morgan Monroe State Forest's aboveground biomass is 19.52 kg m^{-2} (~9.37 kg C m^{-2}; Schmid et al. 2000), which is similar to the aboveground biomass at the EMS site (~10 kg C m^{-2}; Urbanski et al. 2007). Aboveground biomass at UMBS is 7.23 kg C m^{-2} (AmeriFlux online database, http://public.ornl.gov/ameriflux), approximately 25% lower than EMS, but the difference in wintertime R_e was much larger than that. We did not find biomass data for the Park Falls and Willow Creek sites.

Average December-to-March air temperature is −2.4°C at Harvard Forest (Harvard Forest Data Archive, http://harvardforest.fas.harvard.edu/data-archive) while it is 1.49°C at Morgan Monroe State Forest, −3.81°C at UMBS, −6.26°C at Park Falls and −6.32°C at Willow Creek (AmeriFlux online database, http://public.ornl.gov/ameriflux). Given that aboveground biomass is essentially the same at the EMS and Morgan Monroe sites and that temperature is higher at the latter, EMS should not show much higher wintertime R_e. Park Falls, Willow Creek, and UMBS are all colder than EMS during the winter, but at these low temperatures the exponential relationship between temperature and respiration is almost flat—an increase of 2–4°C in low temperatures does not induce a large absolute change in respiration. In conclusion, we did not find a satisfying explanation of why wintertime R_e is higher at the EMS site than elsewhere.

Underestimation of R_{sEMS} or overestimation of R_{eEMS} could explain the high apparent rate of $R_{abgdEMS}$ during the winter period. Uncertainties in the estimates of both fluxes make it difficult to determine which process is contributing more to the high estimate of wintertime $R_{abgdEMS}$. To examine whether the temperature-dependent model used to estimate R_e from net ecosystem exchange (NEE) is biasing the result, we examined the nighttime NEE data; median R_e values were ~1 g C m^{-2} d^{-1}, which still greatly exceeds the soil respiration. Emissions from soils and open water in the wetlands in the northwest sector cannot account for high R_e; ecosystem respiration values for the southwest sector, which is entirely uplands, were at most 10% lower than R_e estimated for the entire dataset that includes wetlands in the northwest sector. Goulden et al. (1996) previously noted enhanced R_e during periods of high wind in winter at Harvard Forest, and this accounts for some of the extremely large values of R_e, but excluding them does not bring R_e estimates down to the range of R_s.

Our estimates of R_e are based on excluding periods of low turbulence ($u^* < 0.2$ m s^{-1}) based on the premise developed for summer that CO_2 fluxes are biased low during stable atmospheric conditions due to advective losses (Staebler and Fitzjarrald 2004, Barr et al. 2013). Whether or not a friction velocity (u^*) filter is appropriate during wintertime may need to be re-examined. Deep snowpacks are a diffusion barrier allowing CO_2 from soil respiration to accumulate. If high winds are ventilating the snowpack where CO_2 has been accumulating, then averaging the high and low u^* data together, which would bring down the estimate of R_e, may be necessary to get an unbiased estimate of R_e.

On the other hand, R_{sEMS} could be systematically underestimated because there are very few wintertime R_s measurements through a snowpack. As such, the wintertime R_s estimate is based on an extrapolation of data beyond the range of values measured: the temperature-response relationship used to estimate R_s for cold soil during winter was established using data collected mainly when the soil was warm, and the influence of snow cover is not accounted for. The response of R_{sEMS} to temperature during winter might differ from that during the warmer months of the year due to shifts in soil microbial assemblages that have higher temperature sensitivity at cold temperatures than growing-season-adapted microbial communities (Monson et al.

2006, Bradford et al. 2008). Importantly, however, modeled R_s generally *overestimated* the available wintertime measurements (Fig. 6). Another possibility is that scaling R_s to the landscape level introduced a bias. Since there is large variation in R_s within each vegetation type (Fig. 3), predominance of a given vegetation type within an EC footprint does not mean that R_s is uniform within the footprint. The deciduous stands located to the south and west of the EMS tower are on a soil series different from (deeper and less rocky, with higher R_s) that beneath the deciduous stands to the north and east. When the footprint includes stands south and west of the tower, actual R_s within the footprint may be higher than our weighted R_s. As fine-tuned as our scaling of R_s to the EC tower footprint is, it remains difficult, if not impossible, to scale it perfectly. Hence, a mismatch between the footprints of R_e and R_s cannot be ruled out.

R_s accounts for the majority of R_e late in the growing season when soils reach their maximum temperature (Fig. 2; see also Curiel Yuste et al. 2005, Davidson et al. 2006*b*, Bergeron et al. 2009). The majority of the soil respiration measurements at Harvard Forest were made during the growing season when soil temperature was between 5–20°C, suggesting that the estimate of $R_{s\mathrm{EMS}}$ during summer is robust (Fig. 7). In contrast, during summer, mean wind speed and friction velocity decline substantially from that observed in the other seasons (Fig. 8). Although our EC estimates were based on fluxes when u^* was >0.2 m s^{-1}, the minimum value when EC fluxes are considered valid at the EMS site (Urbanski et al. 2007), low wind speeds during the summer are likely to exacerbate advective losses of CO_2 at this site even when friction velocity is above the minimum threshold (Staebler and Fitzjarrald 2004). Furthermore, NEE values are dependent on the u^* threshold selected (Barford et al. 2001, Barr et al. 2013). A bias in NEE would bias the estimate of R_e. The net effect may be low estimates of R_e and seemingly very low R_{abgdEMS} during the late summer months. Intermittent transport of CO_2 or its transport too fast or too slow to be captured by the EC system may also result in the underestimation of R_e (Staebler and Fitzjarrald 2004). It has been suggested that the HEM site may be less subject to advection than the EMS site because of the site topography (Hadley and Schedlbauer 2002).

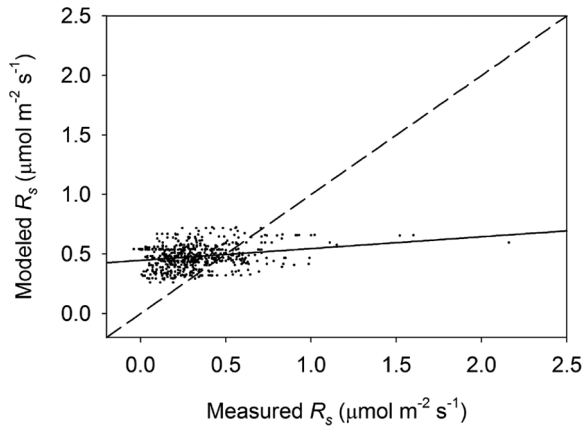

Fig. 6. Relationship between all R_s measurements made from January to March and corresponding modeled R_s. The linear relationship is represented by the solid line while the dashed line has a 1:1 slope.

Another important issue is that the NEE partitioning method assumes that nighttime NEE when u^* is high can be used to define the dependence of R_e on temperature and predict daytime R_e. However, if ecosystem or soil respiration is not adequately predicted by temperature alone, the daily sums may be incorrect. It might be the case, for example, if canopy dark respiration is inhibited during the day as recent studies suggest (e.g., Heskel et al. 2013), implying that daytime R_e is overestimated when the nighttime relationship between NEE and temperature is used to do the partitioning. Although the observation scales may not always be well matched, comparisons between R_s and estimated R_e provide a useful constraint for evaluating the validity of NEE partitioning models.

Additional research on the hard-to-measure fluxes (e.g., wintertime R_s, non-turbulent transport of CO_2) and independent measurements confirming flux partitioning (e.g., aboveground plant respiration, isotopic partitioning of NEE) might yield the greatest insights into partitioning R_e between above- and belowground components. Such an approach may be necessary to both resolve current uncertainties as well as to link remotely sensed products of vegetation phenology (e.g., satellite- and tower-based camera observations) with fluxes of C on the ground (see also Keenan et al. 2013).

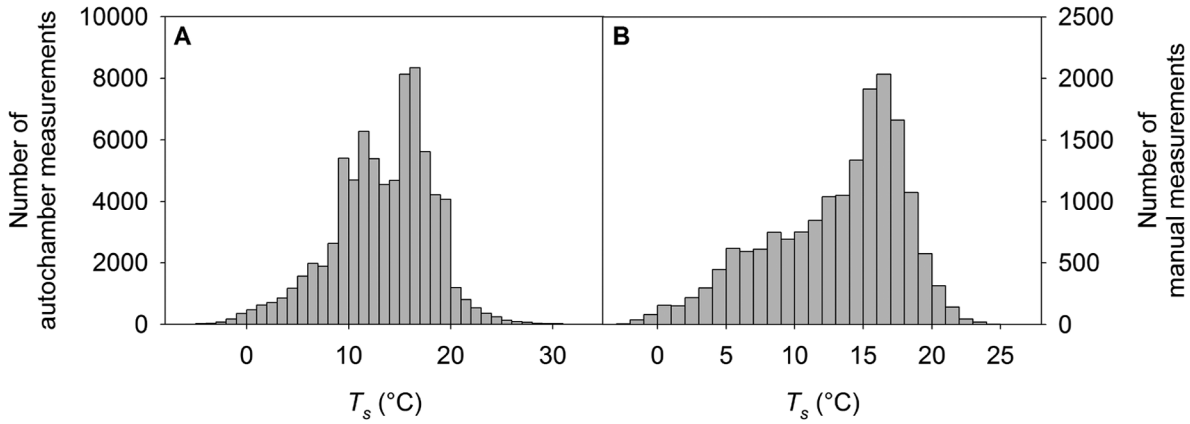

Fig. 7. Distribution of (A) autochamber and (B) manual soil respiration measurements as a function of soil temperature.

Conclusions

Using one of the largest site-specific collections of R_s measurements in the world, we found strong seasonal and inter-annual variations in R_s that were linked both to temperature and vegetation phenology and that experiments intended to simulate aspects of global and environmental change influenced R_s to the same extent as that found at seasonal to annual time scales. We then used this robust dataset to partition R_e into above- and belowground fluxes. Given the number of R_s and R_e observations brought to bear, our partitioning estimates of above- vs. belowground respiration are as robust as currently possible. We found a distinct pattern of ecosystem respiration dominated by above-ground processes early in the growing season and belowground processes after the time of full canopy development in deciduous and conifer forests. While the absolute magnitude of the partitioning above- vs. belowground remains in

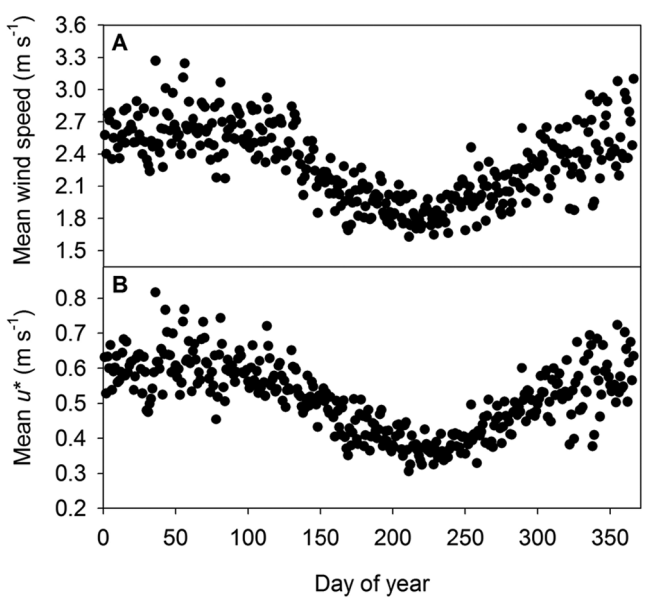

Fig. 8. Annual cycle of (A) daily mean wind speed and (B) daily mean friction velocity (u^*) at the EMS site.

question, the temporal variation is clear. This analysis suggests a greater emphasis be placed on accurately characterizing wintertime R_s fluxes, the size of eddy-covariance tower footprints, the scaling up of the soil respiration chambers measurements, and accounting for C flux bias during stable periods throughout the year and particularly in the late summer. An in-depth evaluation of C flux partitioning is also needed, possibly based on a comparison with reliable and representative soil and aboveground plant respiration measurements.

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Supplemental Material

Appendix

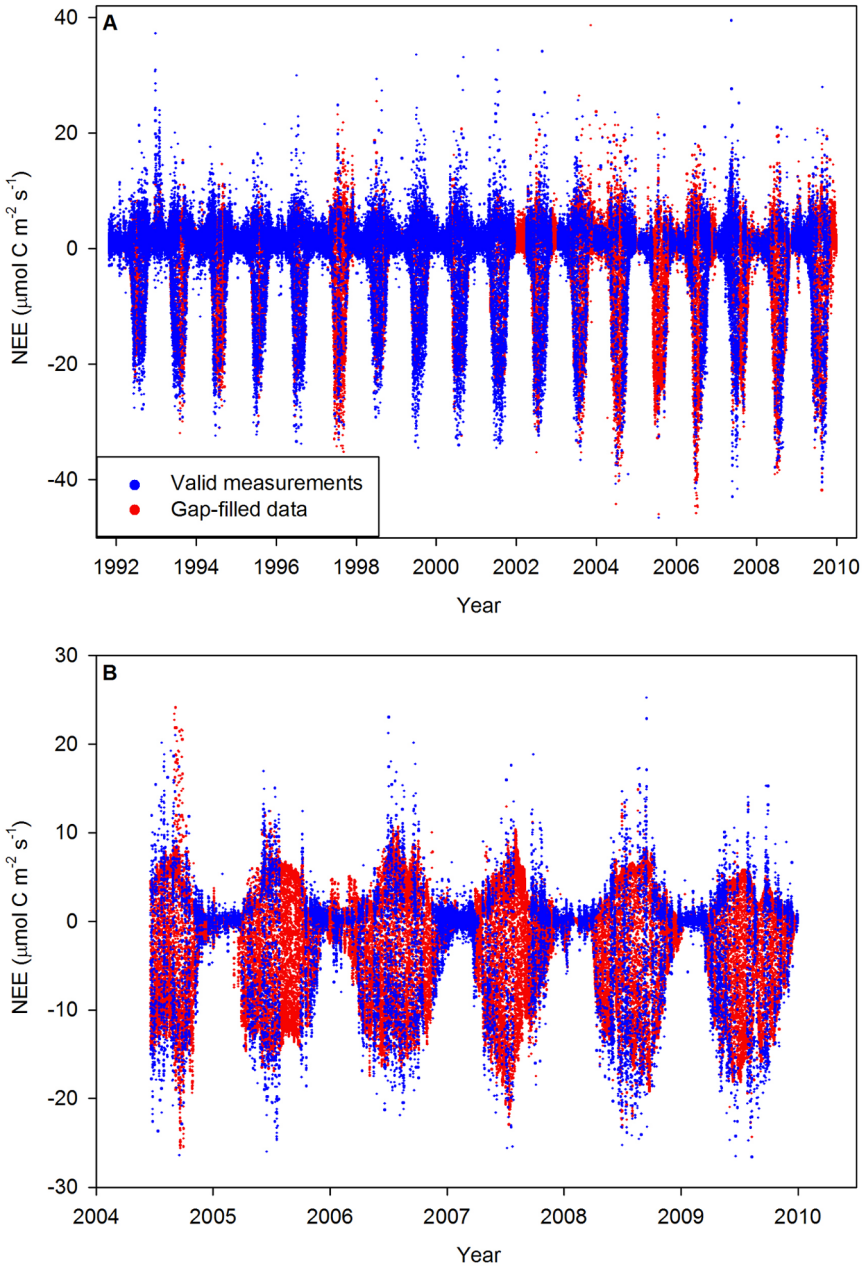

Fig. A1. Valid net ecosystem exchange measurements (NEE; blue) and gap-filled data (red) at (A) the EMS and (B) HEM eddy covariance tower sites. Missing or invalid measurements were caused by power outages, equipment failures, out-of-range values, friction velocity below the site-specific threshold or, at the HEM tower only, when winds were not from the southwest.

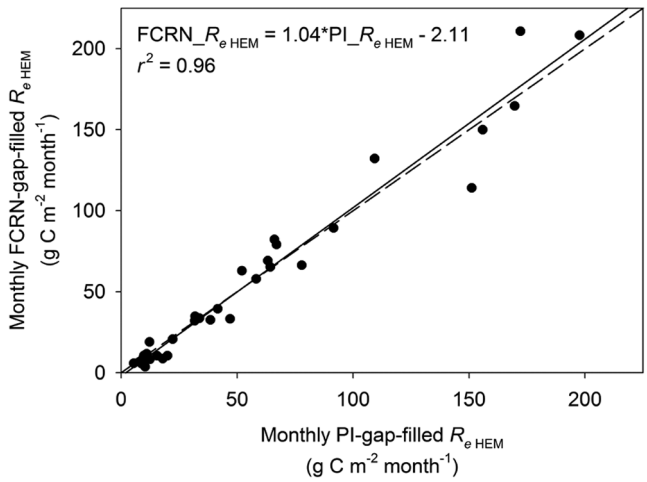

Fig. A2. Relationship between monthly totals of ecosystem respiration gap-filled and partitioned using the Fluxnet-Canada Research Network procedure (FCRN; *y*-axis) and by the HEM site principal investigator (PI; *x*-axis). The linear relationship is represented by the solid line while the dashed line has a 1:1 slope.

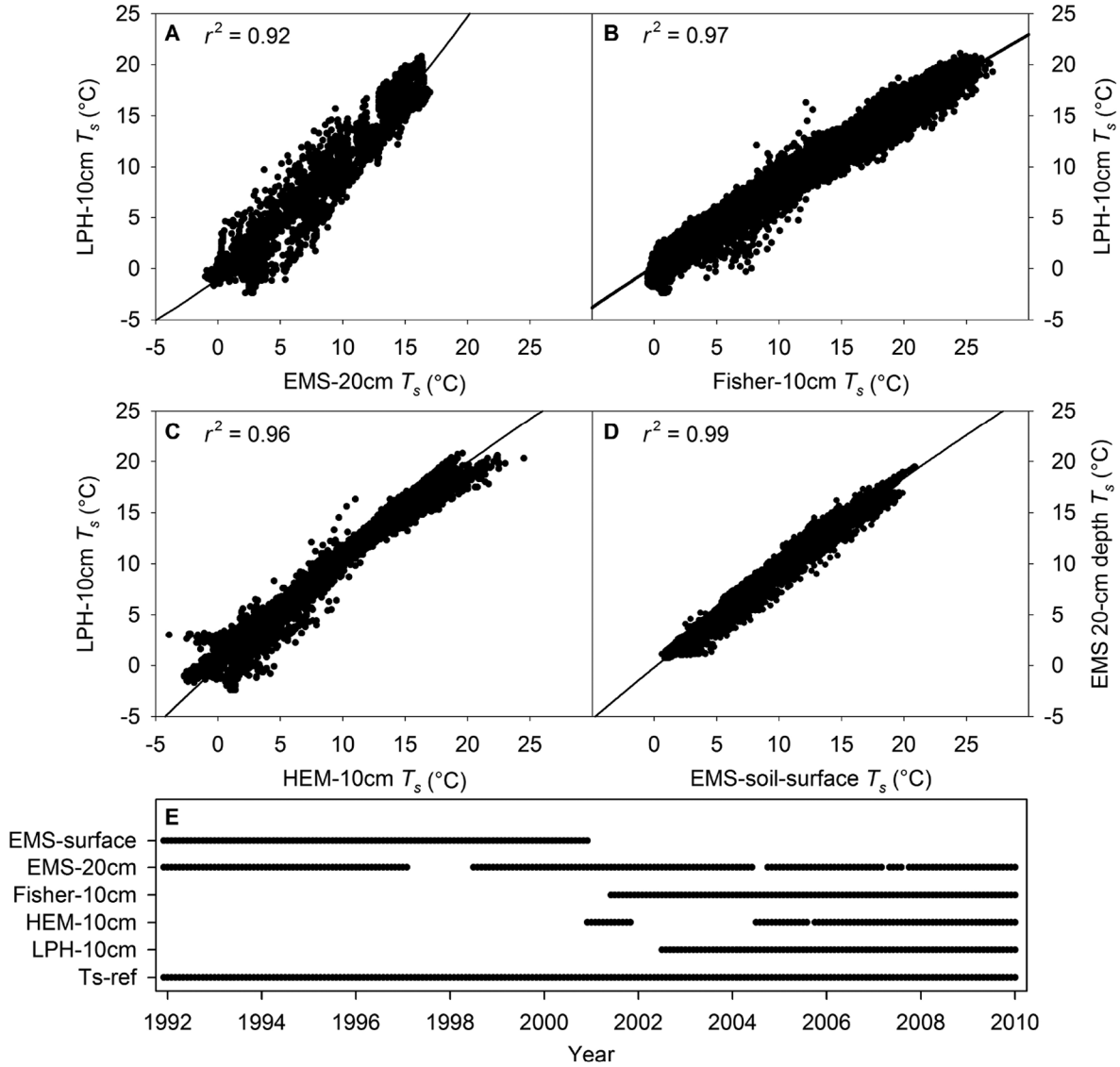

Fig. A3. Relationship between LPH soil temperature at 10-cm depth, the series used as a base for T_{sref}, and the soil temperatures used to fill gaps in that series: (A) EMS-20cm, (B) Fisher meteorological station 10cm, and (C) HEM-10cm. (D) Relationship between EMS 20-cm depth and soil-surface temperature. Soil-surface temperature was used to gap-fill EMS-20cm T_s during the period when they were the only T_s data series available. (E) Temporal availability of T_s measurements. A black dot indicates measurements were available during a given month at a given site.

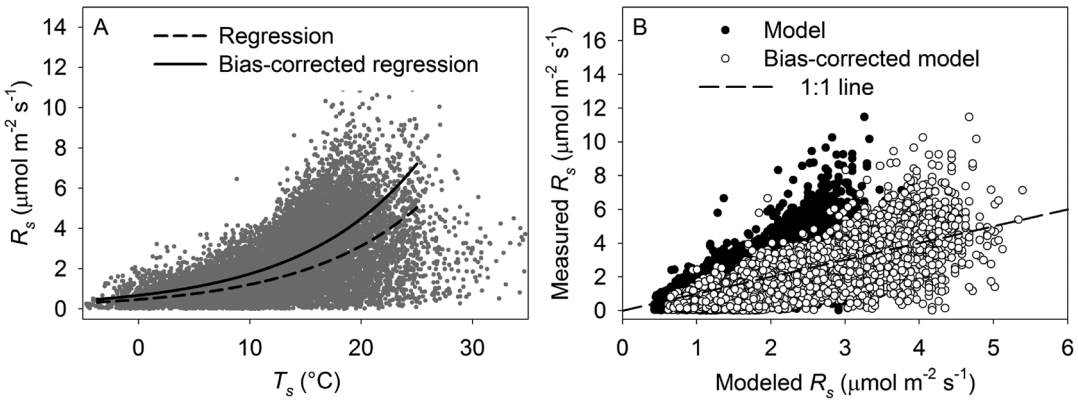

Fig. A4. (A) Example relationship between soil respiration and soil temperature. The back-transformed linear Q_{10} model (Eq. 1) is shown by the dashed line while the solid line represents the bias-corrected model. (B) Relationship between modeled and measured R_s for the uncorrected and bias-corrected models shown in (A). Only data from the wet microsites of study S23 were used in these plots.

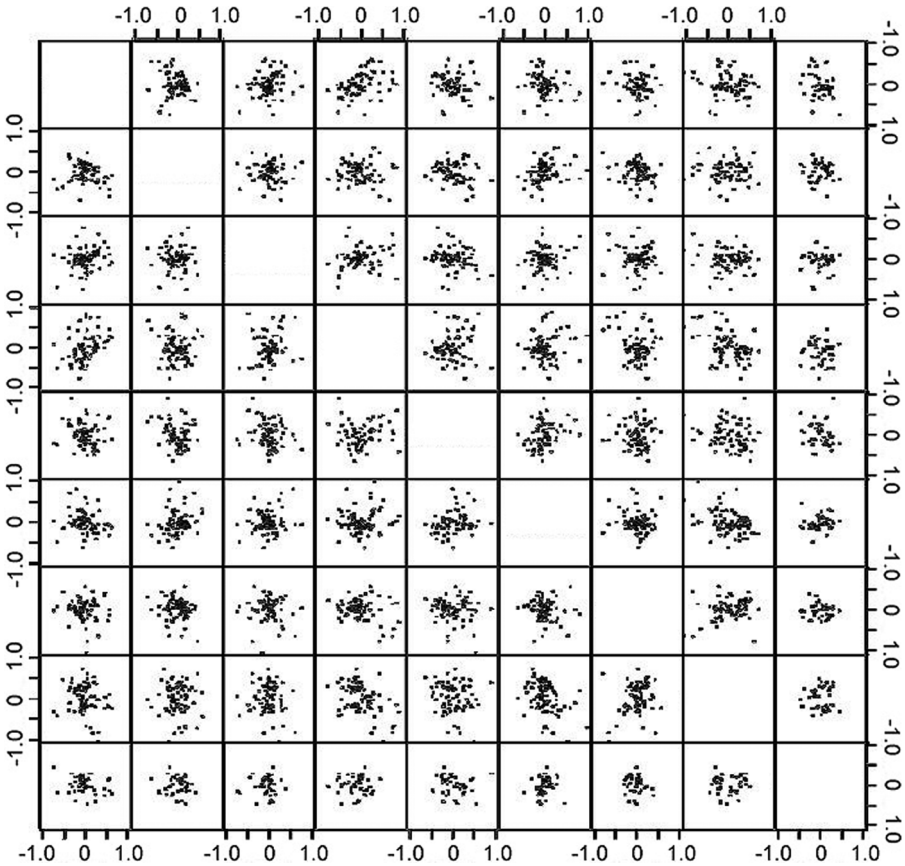

Fig. A5. Scatterplot matrix of residuals from the linear model of log(R_s) on log(T_s) for 9 soil respiration collars located along a transect. No correlation was observed among residuals of soil respiration measured on different collars.