

Comparing ecosystem and soil respiration: Review and key challenges of tower-based and soil measurements



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ABSTRACT

The net ecosystem exchange (NEE) is the difference between ecosystem CO₂ assimilation and CO₂ losses to the atmosphere. Ecosystem respiration (R_{eco}), the efflux of CO₂ from the ecosystem to the atmosphere, includes the soil-to-atmosphere carbon flux (i.e., soil respiration; R_{soil}) and aboveground plant respiration. Therefore, R_{soil} is a fraction of R_{eco} and theoretically has to be smaller than R_{eco} at daily, seasonal, and annual scales. However, several studies estimating R_{eco} with the eddy covariance technique and measuring R_{soil} within the footprint of the tower have reported higher R_{soil} than R_{eco} at different time scales. Here, we compare four different and contrasting ecosystems (from forest to grasslands, and from boreal to semiarid) to test if measurements of R_{eco} are consistently higher than R_{soil}. In general, both fluxes showed similar temporal patterns, but R_{eco} was not consistently higher than R_{soil} from daily to annual scales across sites. We identified several issues that apply for measuring NEE and measuring/upscaling R_{soil} that could result in an underestimation of R_{eco} and/or an overestimation of R_{soil}. These issues are discussed based on (a) nighttime measurements of NEE, (b) R_{soil} measurements, and (c) the interpretation of the functional relationships of these fluxes with temperature (i.e., Q₁₀). We highlight that there is still a need for better integration of R_{soil} with eddy covariance measurements to address challenges related to the spatial and temporal variability of R_{eco} and R_{soil}.

1. Introduction

The net ecosystem exchange (NEE) is the difference between atmospheric carbon dioxide (CO₂) assimilation through photosynthesis (gross primary production; GPP) and the efflux of CO₂ released back to the atmosphere through respiration processes (ecosystem respiration; R_{eco}) (Baldocchi, 2003). R_{eco} is a composite of different complex biological and non-biological sources. These include aboveground respiration, mainly from leaves (R_L) and woody tissues (R_w) (Brüggemann et al., 2011), and belowground respiration, derived from soil

respiration (R_{soil}, the sum of both autotrophic and heterotrophic processes) (Ryan and Law, 2005), carbonate weathering (CW) (Mörner and Etiope, 2002; Rey, 2014), subterranean ventilation (SV) (Sanchez-Cañete et al., 2011), or photo-degradation (PD) (Austin and Vivanco, 2006). Therefore, R_{eco} can be defined as:

$$R_{eco} = R_{soil} + R_L + R_w + CW + SV + PD \quad (1)$$

R_{soil} is expected to be the largest component of R_{eco} (Davidson et al., 2006), but it is still a fraction and theoretically has to be smaller than R_{eco} (i.e., R_{eco} > R_{soil}) at annual, seasonal, daily, or sub-daily scales.

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Nonetheless, several studies have found discrepancies between measurements of R_{eco} and R_{soil} , with R_{soil} being higher than R_{eco} (Barron-Gafford et al., 2011; Phillips et al., 2016; Speckman et al., 2015; Van Gorsel et al., 2007; Wang et al., 2010). These studies have combined ecosystem-scale measurements of CO_2 fluxes, using the eddy covariance (EC) technique, with independent site-specific automated R_{soil} measurements within the footprint of an EC tower. Studies performed across deciduous and temperate forests, managed meadows, semiarid grasslands, and rainforests have shown that R_{eco} could be between 27% and 50% lower than R_{soil} (Van Gorsel et al., 2007; Wang et al., 2010). Thus, it is critical to identify discrepancies between these two fluxes, and examine measurements of R_{soil} and estimates of R_{eco} as inconsistencies could lead to biased local to global carbon budgets and partitioning of ecosystem fluxes. A recent review has identified this topic as one of the three major challenges for interpreting respiration processes in ecosystems (Phillips et al., 2016).

The EC technique allows a direct estimate of NEE, using micrometeorological theory to quantify the covariance between turbulent fluctuations of the vertical wind speed and CO_2 (Aubinet et al., 1999; Baldocchi, 2003). The EC technique has been used to measure NEE at the ecosystem scale with more than 650 EC towers distributed in a wide variety of ecosystems (Baldocchi, 2014), improving our knowledge of the exchange of energy and matter between ecosystems and the atmosphere around the world (Beer et al., 2010; Jung et al., 2010; Mahecha et al., 2010).

As with any technique, the EC approach comes with some limitations. Several studies have discussed these challenges (Finnigan, 2008; Massman and Lee, 2002; Schimel et al., 2008) or how to quantify errors in measurements (Goulden et al., 1996; Hollinger and Richardson, 2005; Loeschner et al., 2006; Moncrieff et al., 1996). Arguably, the largest limitation of EC CO_2 flux measurements comes from low atmospheric mixing at night (Aubinet, 2008; Barba and Anderson, 2010; Gu et al., 2005). During calm and stable night conditions, advection may be predominant (Cooper et al., 2006; Gu et al., 2005; Horst and Doran, 1986; Massman and Lee, 2002; Van Gorsel et al., 2007); thus, CO_2 produced near the ground can be transported laterally, and not measured by the EC tower (Aubinet et al., 2003; Baldocchi et al., 2000; Feigenwinter et al., 2008; Finnigan, 1999; Lee, 1998; Roland et al., 2015; Speckman et al., 2015). In contrast, during daytime, convective mixing often minimizes advection (Galvagno et al., 2017), creating appropriate micrometeorological conditions to apply the EC technique. Finally, since NEE is the difference between GPP and R_{eco} there are two general ways to estimate R_{eco} from EC (Desai et al., 2008): 1) estimating GPP using light-response curves fitted to daytime NEE (NEE_{Day}) to estimate daytime R_{eco} as the difference of GPP and NEE (Lasslop et al., 2010); and 2) estimating R_{eco} using nighttime NEE ($\text{NEE}_{\text{Night}}$) to fit an exponential relationship with air or soil temperature (Arrhenius, 1889) and extrapolating to daytime (thus, assuming that temperature functional relationship is the same for night and daytime); consequently, GPP is derived by adding NEE and R_{eco} (Reichstein et al., 2005). For both approaches, a bias in the estimation of one component may result in an over- or under-estimation of the other component. Previous studies have argued that both partitioning approaches result in similar cross-site results and are widely used across studies (Desai et al., 2008; Falge et al., 2001; Lasslop et al., 2010; Moffat et al., 2007).

R_{soil} has been commonly measured using static (non-) steady-state, (non-) through-flow chambers (Livingston and Hutchinson, 1995; Pumpanen et al., 2004), and most recently with the soil gradient method (Hirano et al., 2003; Tang et al., 2003), making continuous automated measurements of R_{soil} possible (Vargas et al., 2011). Previous studies have provided intercomparisons among different instruments designs and techniques to measure R_{soil} suggesting comparable results (Görres et al., 2016; Pumpanen et al., 2004; Pumpanen et al., 2003; Riveros-Iregui et al., 2008). However, high-temporal frequency measurements of R_{soil} have pitfalls due to the lack of spatial representation and the small area of the measurements (i.e., single point-

measurements (Savage and Davidson, 2003)). Such measurements are usually performed at a few locations assumed to be representative of the whole ecosystem (in both patterns and magnitudes), but may underrepresent the spatial variability of R_{soil} (Barba et al., 2013), especially in those ecosystems where hotspots and high flux events are present (Jenerette et al., 2008; Leon et al., 2014). Thus, a scientific challenge is to properly represent R_{soil} spatial heterogeneity to capture spatial and temporal trends that are representative at the ecosystem scale.

The main goal of this study is to bring attention to issues and challenges related to discrepancies between R_{eco} and R_{soil} and, in light of the 20th anniversary of the AmeriFlux network, encourage new research to improve our understanding of respiration processes at the ecosystem scale. To this end we take advantage of four contrasting ecosystems (from forests to grasslands, and from boreal to semiarid ecosystems) to analyze how R_{eco} , estimated using the EC technique, compares with site-specific continuous measurements of R_{soil} . We hypothesize that 1) nighttime NEE ($\text{NEE}_{\text{Night}}$) should be similar to nighttime estimates of R_{eco} (R_{ecoNight}); 2) the temperature sensitivity (i.e., Q_{10}) of $R_{\text{soilNight}}$ and R_{soilDay} should be similar, thus justifying the use of nighttime functional relations to estimate daytime fluxes; 3) the temperature sensitivity and temporal patterns of R_{eco} and R_{soil} should be similar within each study site, since R_{soil} is the main component of R_{eco} ; but 4) R_{eco} should be higher than R_{soil} at annual, seasonal and daily scales at each site. We conclude with a review about issues influencing nighttime measurements of NEE, R_{soil} measurements, and the interpretation of the functional relationships between R_{soil} and R_{eco} with temperature.

2. Material and methods

2.1. Study sites

We consider four contrasting experimental sites with NEE measurements using the EC technique, and R_{soil} measurements collected within the footprint of the EC tower. The study sites include: a boreal evergreen forest, a temperate broadleaf forest, a temperate grassland, and a semiarid savanna.

The first site is a boreal evergreen forest (FI-Hyy, also known as SMEARII), located nearby the Hyttälä Forestry Field Station, Finland. The vegetation is characterized by ~52 yr old boreal coniferous forest dominated by Scots pine (*Pinus sylvestris* L.). The soil type is a Haplic podzol. The EC system is composed by a three-dimensional sonic anemometer (R3IA; Gill Instruments Ltd) and a closed-path $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (LI6262; Li-Cor Inc.) installed above the forest canopy at a height of 23 m. R_{soil} was measured using automatic chambers based on the closed dynamic chamber technique (Pumpanen et al., 2015). R_{soil} could not be measured when soils were covered by snow (135 days of the year). FI-Hyy data used in this study were measured during 2008. Environmental conditions during the study period are shown in Sup. Fig. 1. We refer to specific bibliography for further information on instrumentation and characteristics of this study site (Bäck et al., 2012; Hari and Kulmala, 2005; Vesala et al., 2005).

The second site is a temperate grassland (AT-Neu), located in a meadow in the vicinity of the village Neustift in the Stubai Valley, Austria. The vegetation consists mainly of a few dominant graminoids (*Dactylis glomerata* L., *Festuca pratensis* Huds., *Phleum pratensis* L., *Trisetum flavescens* (L.) Beauv.), and forbs (*Ranunculus acris* L., *Taraxacum officinale* G.H. Weber ex Wiggers, *Trifolium pratense* L., *Trifolium repens* L., *Carum carvi* L.). The soil type is a Gleyic fluvisol. The EC system included a three-dimensional sonic anemometer (R3IA; Gill Instruments) and a closed-path $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (LI6262; Li-Cor Inc.) installed above the grassland at a height of 3 m (Wohlfahrt et al., 2008). R_{soil} was measured using solid-state CO_2 sensors installed at 5 and 10 cm depth, employing the gradient flux method and located within the footprint of the flux tower (Vargas et al., 2011). AT-Neu data

Table 1

General information of study sites. Annual R_{eco} and R_{soil} represent the cumulative sum for all days of the year. Uncertainty in the cumulative flux is calculated by the sum of daily standard deviations and random errors (see Sup. Table 1). Growing season length represents the days of the year (DOY) where there is a net ecosystem carbon uptake.

Fluxnet ID	Site name	Land Cover Type	Latitude (N)	Longitude (W)	Elevation (m)	Cumulative R_{eco} (g C m^{-2} period ⁻¹) ^a	Cumulative R_{soil} (g C m^{-2} period ⁻¹) ^a	Growing Season (DOY)
FI-Hyy	Hyytiälä	Evergreen coniferous forest	61.8474	24.2948	181	662.3 ± 50.2	794.6 ± 86.4	101–282
AT-Neu	Stubai Valley	Temperate grassland	47.1167	11.3175	970	2107.6 ± 344.4	1821.4 ± 164.7	104–290
US-MOz	Missouri Ozark	Deciduous broadleaf forest	38.7441	–92.2	210	1031.0 ± 101.6	959.4 ± 124.4	116–287
US-SRM	Santa Rita Mesquite	Semiarid savanna	31.8214	–110.8661	1116	287.3 ± 44.4	385.6 ± 81.6	210–292

^a We calculated the cumulative sum of R_{eco} and R_{soil} for the available data. Therefore, period⁻¹ represents the number of days with available measurements at each study site: FI-Hyy 229 available days, AT-Neu 360 available days, US-MOz 365 available days, and US-SRM 342 available days.

used in this study were measured during 2006. Environmental conditions during the study period are shown in Sup. Fig. 1. We refer to specific bibliography for further information on instrumentation and characteristics of this study site (Schmitt et al., 2010; Wohlfahrt et al., 2008; Table 1).

The third site is a temperate broadleaf forest (US-MOz), located 30 km southeast of Columbia, in central Missouri, USA. The vegetation is dominated by *Quercus alba* L. with Hapludal & Argiudoll soils. The EC system included a three-dimensional sonic anemometer (81000; RM Young, Traverse City, MI, USA) and an open-path $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (LI7500, Li-Cor Inc.) installed at a height of 32 m above the ground (Cescatti et al., 2012; Gu et al., 2007). R_{soil} was measured using automated self-constructed open-path chambers (Edwards and Riggs, 2003) coupled with an IRGA (LI7000, Li-Cor Inc). Chambers were located within the footprint of the flux tower. US-MOz data used in this study were measured during 2006. Environmental conditions during the study period are shown in Sup. Fig. 1. We refer to specific bibliography for further information on instrumentation and characteristics of this study (Gu et al., 2007, Table 1).

The fourth site is a semiarid savanna (US-SRM), located in the Santa Rita Experimental Range, outside of Tucson, Arizona, USA. The site is dominated by velvet mesquite (*Prosopis velutina* Woot.) and bunchgrasses (*Eragrostis lehmanniana* Nees, *Digitaria californica* Beth, *Muhlenbergia porter*, and *Bouteloua eripoda*), with thermic Ustic Torrifluvents soils. The EC system included a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Inc., Logan UT) and an open path $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (LI7500, Li-Cor Inc.) installed at a height of 7 m (Scott et al., 2009). R_{soil} was measured using solid-state CO_2 sensors installed at 2 and 10 cm depth, employing the gradient flux method. US-SRM data used in this study was measured during 2007. Environmental conditions during the study period are shown in Sup. Fig. 1. We refer to specific bibliography for further information on instrumentation and characteristics of this study site (Barron-Gafford et al., 2011; Scott et al., 2009; Table 1).

2.2. Measurements

NEE and R_{eco} data measured with EC technique were collected from the La Thuile 2007 FLUXNET 2.0 v dataset (<http://www.fluxdata.org>) where data has been harmonized for quality control of NEE and calculation of R_{eco} using standardized protocols (Papale et al., 2006; Reichstein et al., 2005). NEE and R_{eco} data from US-SRM was directly provided by the site principal investigator (R. Scott). R_{eco} was estimated at all sites from EC, fitting an exponential relationship between $\text{NEE}_{\text{Night}}$ and temperature and extrapolating to daytime (Reichstein et al., 2005). Information on R_{soil} measurements for FI-Hyy, US-MOz, and AT-Neu were discussed in Vargas et al. (2010), where little differences between chamber and gradient method measurements were found across study sites. The same applies to R_{soil} at US-SRM (Barron-Gafford et al., 2011).

This study includes analyses of (sub-) hourly measurements of R_{soil}

and ancillary measurements of soil moisture, photosynthetic active radiation (PAR), air temperature, and volumetric water content for one year at each study site. All subsequent analyses were performed with original time series (i.e., without gap-filling).

2.3. Data and analysis

To evaluate our hypotheses, we organized the data in different categories based on: 1) *Season* (growing season [GS] or non-growing season [NGS]); and 2) *Time of the day* (daytime or nighttime). The GS was defined as the period of the year when mean daily NEE was continuously a net carbon sink, and conversely, NGS was the part of the year when ecosystem was a net carbon source (Churkina et al., 2005). Daytime and nighttime thresholds were established for each site using estimates of global radiation from photosynthetic active radiation measurements according to Al-Shooshan (1997). Thus, daytime is considered when global radiation $\geq 20 \text{ W m}^{-2}$ and nighttime when global radiation $< 20 \text{ W m}^{-2}$.

Annual R_{eco} and R_{soil} were estimated as the sum of their respective daily values, and standard deviation and random errors were calculated to test for differences between these effluxes according to Wohlfahrt et al. (2005) and Moncrieff et al. (1996). The number of days in which daily R_{soil} was larger than R_{eco} (i.e., $R_{\text{soil}(i)} > R_{\text{eco}(i)}$) was calculated for GS and NGS at each study site. We also considered the cumulative fluxes for days when R_{soil} was larger than R_{eco} , and their contribution (%) to the respective seasonal (i.e., GS or NG) sum of CO_2 emissions.

The relationships between nighttime NEE and R_{eco} , R_{eco} and R_{soil} , or R_{soilDay} and $R_{\text{soilNight}}$ were evaluated, for all available data (i.e., one year) or split by seasons, for each study site using linear regression models, reporting the slope and associated 95% confidence intervals (CI).

The temperature sensitivity of R_{ecoNight} , $R_{\text{soilNight}}$ and R_{soilDay} was estimated using daily means of each flux and air temperature by means of a Q_{10} function (Van 't Hoff, 1898):

$$F = F_{10} Q_{10}^{((T-10)/10)} \quad (2)$$

where F represents the different fluxes (i.e., R_{ecoNight} , $R_{\text{soilNight}}$, or R_{soilDay}), F_{10} is the simulated flux at 10 °C, Q_{10} is the so-called temperature sensitivity of the flux, and T is the air temperature. Differences between Q_{10} values were evaluated using 95% CI as recommended previously (Vargas et al., 2012). Thus, if the 95% CIs of Q_{10} do not overlap, then differences were considered to be significant. All the analyses were performed using MATLAB (R2014a, Mathworks Inc).

3. Results

R_{eco} and R_{soil} had similar temporal trends following similar seasonal patterns with high fluxes during the GS and lower fluxes during NGS across each study site (Fig. 1A–D). No differences in annual cumulative sums were found between R_{eco} and R_{soil} within sites (Table 1).

Table 2

Summary table to denote when $R_{soil} > R_{eco}$ and vice versa and which is the relative contribution of these seasonal cumulative fluxes. The Days column shows the number of days for each season and study site. NGS Days for FI-Hyy for FI-Hyy does not show the number of all days but only the number where both R_{eco} and R_{soil} were measured.

Sites	Season	Days	% Days		Flux (%)	
			$R_{eco} < R_{soil}$	$R_{eco} > R_{soil}$	$R_{eco} < R_{soil}$	$R_{eco} > R_{soil}$
FI-Hyy	NGS	49	28.6	71.4	8.0	26.5
	GS	181	58.6	41.4	29.5	18.4
AT-Neu	NGS	179	30.7	69.3	73.3	39.0
	GS	186	24.7	75.3	13.5	34.7
US-MOz	NGS	194	12.4	87.6	14.1	35.1
	GS	171	49.1	50.9	18.5	15.7
US-SRM	NGS	283	70.7	29.3	41.6	25.3
	GS	82	92.7	7.3	25.8	13.3

However, the uncertainties of these annual cumulative sums were very large (deviation of annual cumulative fluxes included both daily standard deviation and random error). Random errors of measurements were similar between R_{eco} and R_{soil} , ranging from 1.81% to 4.50% (Sup. Table 1).

However, R_{eco} was not consistently higher than R_{soil} at daily scale at any of the study sites. Days where R_{soil} was larger than R_{eco} showed a strong seasonal dependency (Figs. 1E–H) and its proportion ranged from 12 to 71% of the total number of days during NGS (US-MOz and US-SRM, respectively; Table 2) and 25–93% of days during GS (AT-Neu and US-SRM, respectively; Table 2). For those days when R_{soil} was larger than R_{eco} , the cumulative sum of R_{soil} was between 8 and 73% higher than the cumulative sum of R_{eco} during NGS (i.e., FI-Hyy and AT-Neu; Table 2), or 14 and 30% higher than the cumulative sum of R_{eco} during GS (i.e., AT-Neu and FI-Hyy; Table 2).

The annual cumulative sum of NEE_{Night} was not statistically different from the annual cumulative sum of $R_{ecoNight}$, including both random errors and cumulative standard deviations (Sup. Table 2).

However, the 1:1 comparison revealed that daily $R_{ecoNight}$ was systematically higher than daily NEE_{Night} at three sites (Fig. 2A–D; regression slopes for FI-Hyy, AT-Neu and US-MOz were significantly lower than 1). Notably, the overall magnitude of the respective daily fluxes was similar, as the linear regressions between NEE_{Night} and $R_{ecoNight}$ showed slopes close to 1 and a high fraction of explained variance ($R^2 > 0.82$; Fig. 2A–D). When data was analyzed between seasons, we found similar trends at three sites between GS and NGS with slopes significantly lower than 1 (Table 3). Only FI-Hyy during NGS and US-SRM during GS showed similar NEE_{Night} and $R_{ecoNight}$ (i.e., CI of regression slopes overlapped with 1).

The annual cumulative sum of $R_{ecoNight}$ was lower than the annual cumulative sum of $R_{soilNight}$ at FI-Hyy and US-SRM, but no significant differences were found at AT-Neu or US-MOz (Sup. Table 2). The daily fluxes of $R_{ecoNight}$ were consistently lower than the daily fluxes of $R_{soilNight}$ as linear regressions showed slopes ranging from 0.78 to 0.52 (AT-Neu and FI-Hyy, respectively) (Fig. 2A–D). This bias was accentuated during GS for all sites with even higher $R_{soilNight}$ fluxes compared

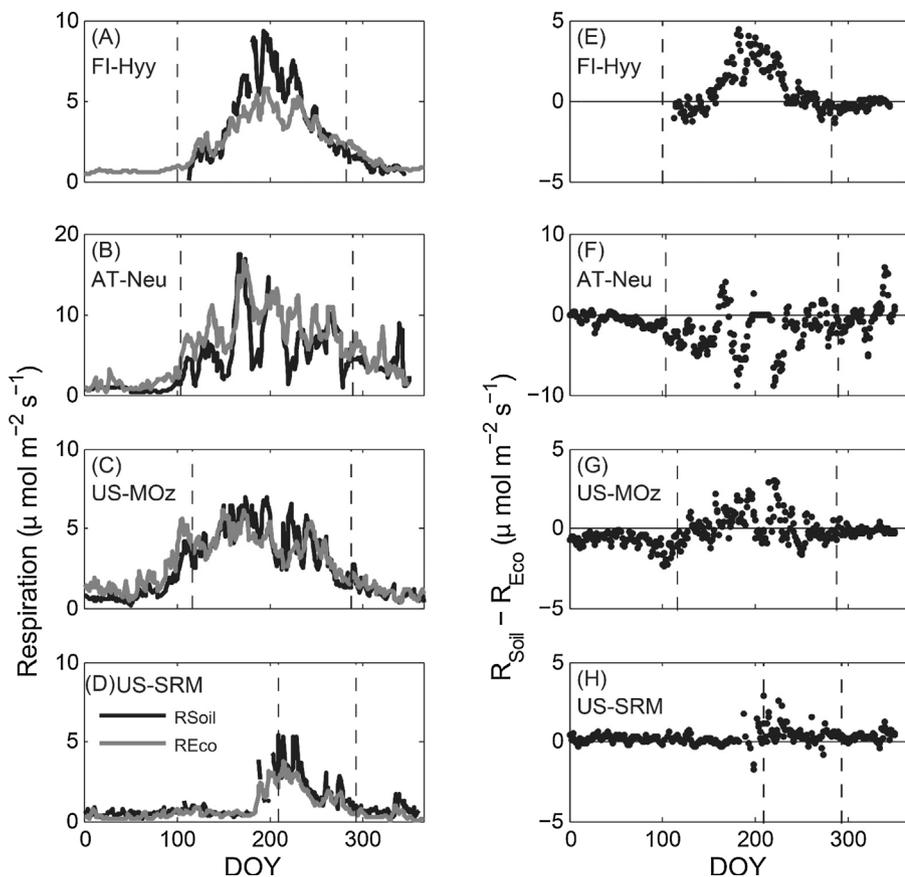


Fig. 1. Seasonal course of daily averages of R_{eco} (grey) and R_{soil} (black) across study sites (FI-Hyy, AT-Neu, US-MOz and US-SRM) (panels A–D) and the difference between R_{soil} and R_{eco} (panels E–H). Growing season is the period between the two dashed lines. Note the different y-axis scale for AT-Neu required to represent the higher fluxes at this site.

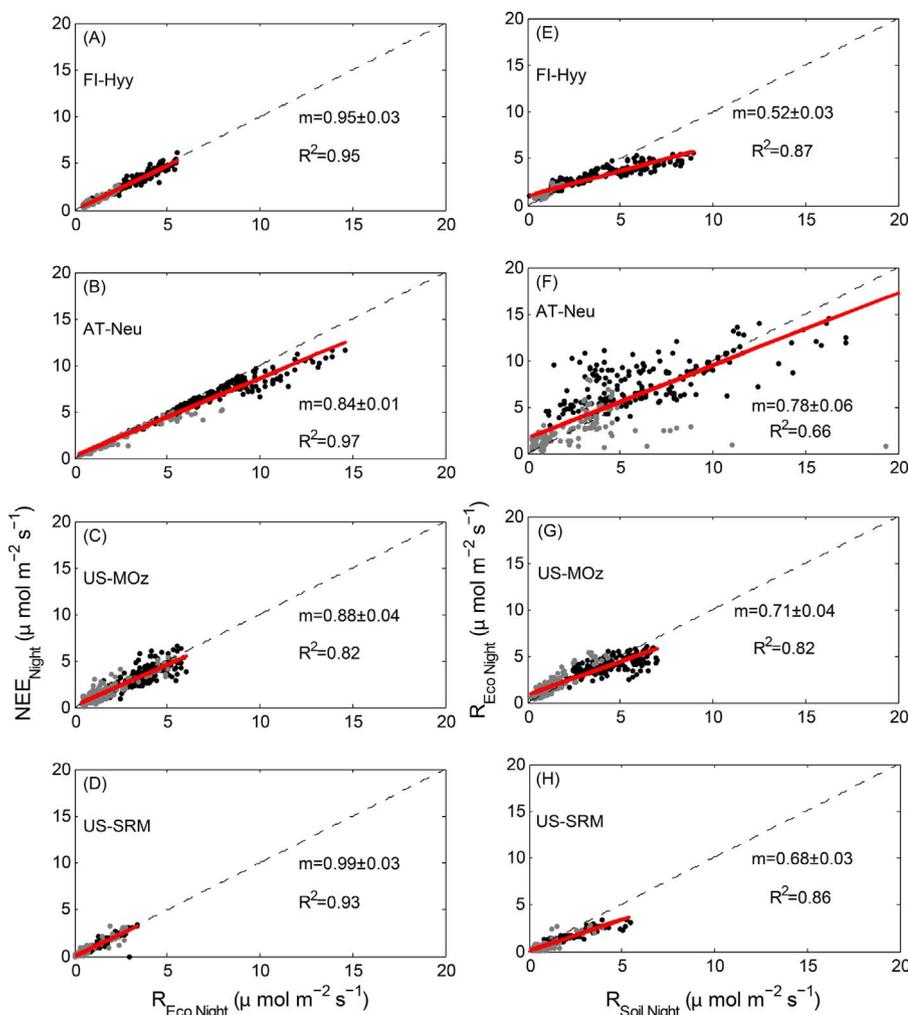


Fig. 2. Comparison of daily averages of NEE_{Night} and $R_{ecoNight}$ (A–D) and $R_{ecoNight}$ and $R_{soilNight}$ (E–H) across study sites (FI-Hyy, AT-Neu, US-MOz and US-SRM). Parameter m shows slope (mean \pm 95% of CI) of the regression with the whole annual data. Grey and black colors indicate non growing season (NGS) and growing season (GS) data, respectively.

Table 3
Regressions of daily averages of NEE_{Night} versus $R_{ecoNight}$ and $R_{ecoNight}$ versus $R_{soilNight}$ across study sites by seasons (slope \pm 95% of CI).

Site	Period	NEE_{Night} vs $R_{ecoNight}$	R^2	$R_{ecoNight}$ vs $R_{soilNight}$	R^2
FI-Hyy	GS	0.93 ± 0.04	0.92	0.45 ± 0.03	0.84
	NGS	0.99 ± 0.10	0.86	1.19 ± 0.18	0.75
AT-Neu	GS	0.75 ± 0.03	0.92	0.50 ± 0.07	0.49
	NGS	0.77 ± 0.03	0.95	0.59 ± 0.11	0.41
US-Moz	GS	0.87 ± 0.11	0.59	0.53 ± 0.07	0.60
	NGS	0.88 ± 0.06	0.80	1.19 ± 0.08	0.84
US-SRM	GS	1.02 ± 0.06	0.93	0.60 ± 0.06	0.82
	NGS	0.95 ± 0.04	0.85	0.72 ± 0.06	0.70

Table 4
Summary of Q_{10} estimates of NEE_{Night} , $R_{ecoNight}$, $R_{soilNight}$ and $R_{soilDay}$ for each site and season (mean \pm 95% CI). Different lowercase letters indicate significant differences in Q_{10} between fluxes within sites and seasons (95% CI not overlapped). Mean annual T, SWC and u^* are reported with their standard deviation.

Site	Season	$Q_{10} NEE_{Night}$	$Q_{10} R_{ecoNight}$	$Q_{10} R_{soilNight}$	$Q_{10} R_{soilDay}$	T (°C)	SWC ($m^3 m^{-3}$)	u^* ($m s^{-1}$)
FI-Hyy	GS	1.97 ± 0.2^a	2.03 ± 0.2^b	3.3 ± 0.6^c	2.3 ± 0.3^b	10.4 ± 4.9	0.34 ± 0.07	0.45 ± 0.25
	NGS	2.6 ± 0.5^a	2.6 ± 0.4^a	2.3 ± 0.4^a	2.3 ± 0.6^a	2.4 ± 5.8	0.46 ± 0.02	0.45 ± 0.25
AT-Neu	GS	1.8 ± 0.1^a	1.9 ± 0.1^a	2.4 ± 0.3^b	2.4 ± 0.3^b	14.0 ± 6.6	0.31 ± 0.08	0.18 ± 0.11
	NGS	2.5 ± 0.2^a	2.6 ± 0.3^a	1.8 ± 0.4^b	1.6 ± 0.4^b	-0.70 ± 7.3	0.39 ± 0.09	0.17 ± 0.13
US-MOz	GS	1.4 ± 0.1^a	1.3 ± 0.1^a	1.5 ± 0.2^a	1.4 ± 0.1^a	21.2 ± 6.6	0.24 ± 0.06	0.34 ± 0.24
	NGS	1.8 ± 0.2^a	1.9 ± 0.1^a	2.0 ± 0.1^a	1.8 ± 0.1^a	7.1 ± 7.9	0.32 ± 0.05	0.47 ± 0.30
US-SRM	GS	2.7 ± 1.0^a	2.7 ± 0.9^a	2.0 ± 0.7^a	0.9 ± 0.3^b	27.4 ± 5.2	0.05 ± 0.02	0.32 ± 0.18
	NGS	1.7 ± 0.2^{ab}	1.8 ± 0.2^a	1.2 ± 0.1^b	1.1 ± 0.1^b	19.9 ± 9.2	0.04 ± 0.02	0.37 ± 0.28

to $R_{ecoNight}$, and regression slopes between 0.60 and 0.45 (US-SRM and FI-Hyy, respectively) (Table 3). During NGS two sites (FI-Hyy, US-MOz) showed that $R_{ecoNight}$ fluxes were higher than $R_{soilNight}$ (slopes were 1.19 for both sites) and two other sites (AT-Neu, US-SRM) showed the opposite pattern (slopes were 0.59 and 0.72, respectively) (Table 3). Despite these systematic differences in fluxes, we did not find a clear pattern in temperature sensitivity between $R_{ecoNight}$ and $R_{soilNight}$. Similar Q_{10} between $R_{ecoNight}$ and $R_{soilNight}$ were found for US-MOz and US-SRM during GS and for FI-Hyy and US-MOz during NGS, but different for FI-Hyy GS, AT-Neu GS and NGS, and US-SRM NGS ($R_{ecoNight}$ Q_{10} was higher than $R_{soilNight}$ in two cases but lower in other two) (Table 4). Finally, similar temperature sensitivity was found in R_{soil} between nighttime and daytime divided by seasons across sites (Table 4).

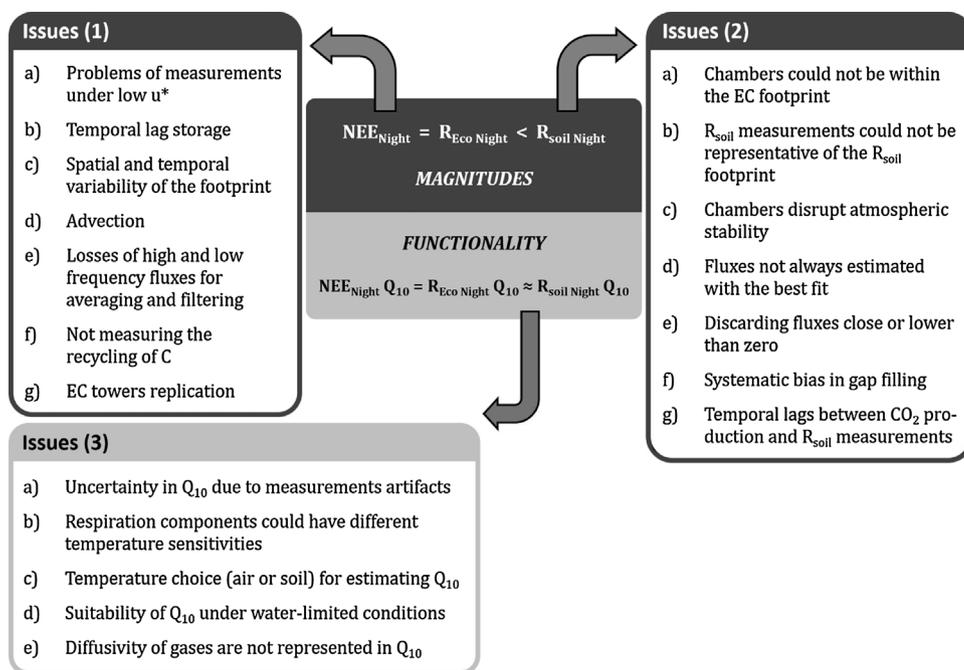


Fig. 3. Review diagram of key issues identified in this study. Issues (1) are related to nighttime measurements of NEE. Issues (2) are related to R_{soil} measurements. Issues (3) represent challenges related to the interpretation of the functional relationships of these fluxes with temperature (i.e., Q_{10}).

4. Discussion

Annual cumulative sums of R_{eco} were similar to annual cumulative sums of R_{soil} for all studied ecosystems, but a large proportion of days from all study sites showed higher R_{soil} fluxes than R_{eco} , with a clear seasonal pattern (Fig. 1E–H, Table 2). Despite the fact that R_{eco} should be higher than R_{soil} , other studies in a variety of ecosystems, from boreal forests (Lavigne et al., 1997) to temperate ecosystems (Speckman et al., 2015), have observed similar discrepancies. Here, we identify and discuss different challenges and opportunities (Fig. 3) that should be addressed in order to improve the estimation of R_{eco} and R_{soil} : extrapolation of day-to-night functionality (Section 4.1); comparison between NEE_{Night} and $R_{ecoNight}$ (Section 4.2); comparison between $R_{ecoNight}$ and $R_{soilNight}$ (Section 4.3); and their temperature sensitivity (Section 4.4).

4.1. Extrapolation of nighttime to daytime functionality

One of the main assumptions for estimating daily values of R_{eco} with the nighttime flux partitioning approach is that R_{eco} nighttime functional relations can be extrapolated to daytime R_{eco} (Reichstein et al., 2005). In general, our simple approach showed that the temperature sensitivity of R_{soil} was similar between nighttime and daytime across seasons and sites (confirming H2). Provided that R_{soil} represents the largest component of R_{eco} (Davidson et al., 2006), as is usually the case, it seems reasonable to assume that the Q_{10} of R_{eco} and R_{soil} may be similar, thus justifying the use of functional relations based on $R_{ecoNight}$ to estimate R_{ecoDay} . That said, previous studies have described processes with different functioning between daytime and nighttime, such as leaf mitochondrial respiration (Wehr et al., 2016; Wohlfahrt and Gu, 2015), fine roots respiration or exudates supply (Kodama et al., 2008; Savage et al., 2013), and problems related to phase shifts between driving temperatures of various respiration processes (Lasslop et al., 2012; Wohlfahrt and Galvagno, 2017). This may be the case for site-specific conditions during the growing season, for example in water-limited or boreal ecosystems where Q_{10} may be confounded by other factors (e.g., soil moisture, plant phenology or ecosystem productivity). Thus, suggesting that the universal applicability of nighttime functional relations to daytime R_{eco} is still an open scientific debate and deserves more comprehensive studies.

4.2. Comparison of NEE_{Night} and $R_{ecoNight}$

The main assumption to estimate R_{eco} from nighttime NEE is that only respiration processes occur during nighttime, and that these can be described by an Arrhenius type relationship with temperature (Reichstein et al., 2005). Thus, it has been widely interpreted that NEE_{Night} (direct measurements) is the same as $R_{ecoNight}$ (model result). Although we found similar NEE and R_{eco} during nighttime at the annual scale (supporting this expectation), we found systematic higher R_{eco} than NEE during nighttime at three different sites at daily scale. These small differences in magnitudes could be explained because $R_{ecoNight}$ is not exactly NEE_{Night} ; as $R_{ecoNight}$ is a semi-empirical prediction of NEE_{Night} based on a temperature relationship (Reichstein et al., 2005). Despite statistically significant daily differences between NEE_{Night} and $R_{ecoNight}$, the slopes were close to 1 and therefore we interpret that both fluxes are overall similar; supporting H1 (Fig. 2A–D). Consequently, we propose that observed differences between R_{eco} and R_{soil} are likely not due to a wrong estimation of $R_{ecoNight}$ from NEE_{Night} . Thus, these results support the theoretical partitioning of R_{eco} from temperature relationships of NEE_{Night} (Reichstein et al., 2005).

4.3. $R_{ecoNight}$ and $R_{soilNight}$ comparison

Annual $R_{ecoNight}$ was not consistently higher than annual $R_{soilNight}$ (nighttime R_{soil} was not different from R_{eco} at AT-Neu and US-MOz, but higher at FI-Hyy and US-SRM). Additionally, regression slopes of daily $R_{ecoNight}$ and $R_{soilNight}$ were lower than 1 (ranging from 0.78 to 0.52; Fig. 2E–H), suggesting that differences were not only statistically significant but also ecologically relevant. Systematic differences were even more important during GS (slopes ranged from 0.6 to 0.45), when fluxes were higher (Fig. 1A–D). Given that $R_{soilNight}$ has to be smaller than $R_{ecoNight}$, there could be an underestimation of $R_{ecoNight}$, overestimation of $R_{soilNight}$, or a combination of both. Since we assume that $R_{ecoNight}$ was correctly estimated from NEE_{Night} (see previous Section 4.2), we postulate that an eventual underestimation of $R_{ecoNight}$ could result from an underestimation of measured NEE_{Night} . Currently, we do not have another independent way to estimate NEE_{Night} or R_{soil} to accurately determine the sources of errors, but different potential sources and possible improvements have been identified in Fig. 3.

4.3.1. Measurements of R_{soil}

Automatic soil respiration chambers are usually placed around an EC tower due to limitations in tubing length or electrical power, but are not necessarily consistently installed within the EC tower footprint (Fig. 3, Issue 2.a). An accurate estimate of the EC footprint before chamber deployment could contribute to better comparisons (Phillips et al., 2016). Additionally, R_{soil} measurements are usually poorly spatially replicated across EC study sites (Fig. 3, Issue 2.b), and possibly do not integrate the spatial variability of R_{soil} within the EC footprint (Leon et al., 2014). Preliminary studies with manual measurements in the EC footprint for detecting areas that are representative of the mean of R_{soil} across the space, and an effort to increase spatial replication of automatic measurements, could reduce uncertainties associated with R_{soil} measurements. Irrespective of spatial replication, soil chambers could themselves introduce an artifact during R_{soil} measurement, especially during low u^* conditions (Fig. 3, Issue 2.c). Automatic opening and closing of chambers has been demonstrated to disrupt atmospheric stability during low turbulence conditions when the air on the surface of soil could be CO_2 enriched, enhancing higher soil CO_2 emissions and resulting in a systematic R_{soil} overestimation (Brændholt et al., 2016; Conen and Smith, 1998; Riederer et al., 2014). Chambers with less movement could minimize this effect. The soil gradient method for measuring soil respiration does not produce this atmospheric disruption, but has other limitations such as the sensitivity of the calculation to soil CO_2 diffusion rates (Sánchez-Cañete et al., 2017; Vargas et al., 2010) and neglects non-diffusive transport of CO_2 (Roland et al., 2015).

Furthermore, similar to NEE measurements, R_{soil} uncertainties could be associated with errors in flux calculation and data processing. Efforts have been made to develop diffusivity models for estimating R_{soil} with the soil gradient method (Maier and Schack-Kirchner, 2014; Moldrup et al., 2001), but an empirical calibration with chamber measurements is still necessary (Fig. 3, Issue 2.d) for reliable long-term R_{soil} measurements (Roland et al., 2015; Sánchez-Cañete et al., 2017). In studies where non-steady state chambers are used, R_{soil} is usually estimated from the rate of change of CO_2 concentrations in relation to time using linear or exponential models (Kopittke et al., 2013; Pihlatie et al., 2013). However, recent studies have shown the usefulness of hierarchical Bayesian models in order to improve R_{soil} estimates (Ogle et al., 2017). When classical non-hierarchical models are used (i.e., ordinary least squares), a criterion based on minimum R^2 threshold is commonly used for discarding R_{soil} (Fig. 3, Issue 2.d). However, this criterion could systematically discard low R_{soil} since, for a given variability of a data set, R^2 parameter tends to decrease as the slope of the regression tends to be closer to 0 (i.e., R_{soil} tends towards 0). Gap filling techniques are usually applied in many studies (Gomez-Casanovas et al., 2013) (but not in the present manuscript) to estimate R_{soil} when data is missing. However, this gap filling could be skewed, since it may likely be parameterized with other R_{soil} data measured under similar environmental conditions, but with fluxes greater than 0 (the used data should have passed the R^2 threshold) (Fig. 3, Issue 2.e). Applying a lower R^2 threshold criterion at low fluxes during data quality check could reduce this bias.

The last source of R_{soil} uncertainty is related to the difference between soil CO_2 production and R_{soil} measured at the surface and their temporal lags (Fig. 3, Issue 2.g). Both concepts are usually assumed to be the same, but they could differ substantially depending on environmental conditions. Soil CO_2 production is a catabolic process of organic matter oxidation driven by fine root respiration, rhizomicrobial respiration, microbial respiration of dead plant tissues, priming effects, soil organic matter derived CO_2 , and basal respiration (Kuzakov, 2006). Each one of these components is regulated in a different way by soil temperature, moisture, symbiotic interactions, plant C supply, and quality of organic matter (Högberg et al., 2001; Jenkinson et al., 1991; Raich and Schlesinger, 1992). However, the recorded R_{soil} measurement on the soil surface also depends on factors determining gas diffusivity (i.e., soil texture, pore structure, atmospheric pressure, wind

speed, temperature or moisture). Variations in these factors may produce a temporal lag between CO_2 production in depth and measurement at the surface leading to biophysical confounding factors, since R_{soil} recorded at the surface, at a certain moment, should be a result of prior environmental conditions. Additionally, non-biological soil CO_2 sources could hinder the correct interpretation of R_{soil} and its relationship with the drivers (Rey, 2014; Sánchez-Cañete et al., 2016). The soil diffusion method could be more suitable for establishing functional relations between R_{soil} and its drivers, since it is calculated directly from soil CO_2 concentrations within the soil profile instead of soil surface emissions. However, this method shows some limitations, as it is difficult to accurately determine the diffusivity of the soil and the effect of air turbulence; both parameters influencing R_{soil} measurements. On the other hand, chamber techniques could arguably be more comparable with R_{eco} estimated from an EC system, since both techniques measure gas emissions and not production.

Most of these issues related to R_{soil} measurements and calculation produce random errors, which in turn could produce over- or underestimations of R_{soil} depending on stochasticity (Cueva et al., 2015). Furthermore, we found systematically higher $R_{soilNight}$ than $R_{ecoNight}$ across study sites and seasons, suggesting that measurements of NEE_{Night} should also be improved.

4.3.2. Estimating NEE

One of the main limitations of the EC technique to estimate NEE is its suitability under stable boundary layers (Fig. 3, Issue 1.a) producing low atmospheric turbulence (low u^*), commonly during nighttime (Aubinet, 2008; Gu et al., 2005). This could produce a temporal lag storage (Fig. 3, Issue 1.b) when CO_2 emitted under low u^* is not detected by the EC system until u^* increases and therefore is sufficient turbulent. Additionally, this CO_2 stored within the canopy during nighttime promotes a flux of CO_2 during the early morning, when the footprint is smaller, increasing the uncertainty of NEE measurements mainly in tall dense canopies (Fig. 3, Issue 1.c). Kutsch et al. (2008) suggested that discrepancies between R_{soil} and R_{eco} could also be a result of increased abundance of advection (Fig. 3, Issue 1.d) that could consequently bias NEE measurements. This interpretation is supported by the recommendation that advection needs to be taken into consideration to better derive R_{eco} measurements across the day (Van Gorsel et al., 2007). Any improvement on estimating NEE under these conditions could have an impact when calculating annual sums. Previous studies which have examined the influence of different u^* thresholds in NEE fluxes (Gu et al., 2005; Aubinet 2008; Speckman et al., 2015; Wohlfahrt et al., 2005), identified losses of high and low-frequency fluxes during the averaging and filtering process as a source of error in NEE estimations (Fig. 3, Issue 1.e).

The next issue related to NEE measurements is that the EC footprint is constantly changing depending on atmospheric stability, wind speed and direction, in comparison with the constant area measured by the soil respiration chambers. Thus, EC estimates of NEE integrate fluxes from different areas, not always including the surface area that respiration chambers measure, and possibly mismatching the spatial relation between R_{soil} and NEE (Fig. 3, Issue 1.c).

Another issue could be that an EC system may not be accounting for C recycling within the canopy (Fig. 3, Issue 1.f). CO_2 produced in soil during nighttime could reside in the canopy space and partially be fixed by photosynthesis in the morning. The interpretation of these measurements would result in an underestimation of both nighttime R_{eco} and early morning fluxes of GPP.

The last issue that we discuss for measuring NEE is the lack of formal replication of EC systems (Fig. 3, Issue 1.g). Logistical limitations and the high equipment costs hinder the explicit spatial replication of EC systems within study sites. Recently, Hill et al. (2017) have demonstrated that around four EC towers are required to properly estimate annual flux within a 95% statistical confidence interval. This number could increase further when ecosystem fluxes are small or there

is high spatial soil and canopy heterogeneity. In contrast, other studies have shown that in homogeneous landscapes there is a large similarity (within 6%) between adjacent EC measurements (Hollinger et al., 2004). Thus, this is an open challenge for individual sites and flux networks to design experiments, and evaluate network performance and data interpretation.

4.4. R_{ecoNight} and $R_{\text{soilNight}}$ temperature sensitivity

R_{ecoNight} temperature sensitivity (i.e., Q_{10}) was expected to be similar to $R_{\text{soilNight}}$ Q_{10} within sites (H3), but we found significant differences for about 50% of the cases (i.e., seasons and sites). These discrepancies could be explained either by errors in measurements or by real differences in temperature sensitivity. First, if fluxes are not well measured, then differences in the magnitudes of R_{soil} and R_{eco} could result in different Q_{10} estimates (Fig. 3, Issue 3.a). Second, R_{plant} (the other component of R_{eco}) could have different physiological responses to changes in environmental conditions (e.g., temperature, soil moisture), resulting in different Q_{10} than R_{soil} ; consequently, modifying R_{eco} Q_{10} (Fig. 3, Issue 3.b). We found systematic differences between $R_{\text{soilNight}}$ and R_{ecoNight} (i.e., R_{soil} higher than R_{eco}), but these discrepancies were not systematic for $R_{\text{soilNight}}$ and R_{ecoNight} Q_{10} among sites. Thus, more research is needed to understand Q_{10} among different components of R_{eco} , identify systematic differences in measurements, and physiological responses to changing weather conditions across ecosystems.

Another factor that could influence R_{eco} Q_{10} is related to which temperature measurement should be used (Fig. 3, Issue 3.c), since soil temperature could be more suitable for estimating soil respiration responses (one of the R_{eco} components), but other components, e.g. R_{plant} , may be more tightly coupled to air or leaf temperature (Lasslop et al., 2012; Wohlfahrt and Galvagno, 2017). Additionally, soil temperature should be measured at the depth of CO_2 production in soils, which changes with space and time (Vargas et al., 2010). Measuring soil temperature at unrepresentative depths could result in a wrong interpretation of temperature sensitivity (Phillips et al., 2011; Reichstein and Beer, 2008; Subke and Bahn, 2010; Tang et al., 2003).

Another issue that could strongly affect the estimated temperature sensitivity of NEE (and therefore R_{eco}) is that NEE_{Night} is expected to have a significant relationship with temperature in order to estimate R_{eco} (Fig. 3, Issue 3.d). However, this relationship may not exist when soil moisture is a limiting factor (Almagro et al., 2009; Leon et al., 2014). In this study, for instance, US-SRM was water-limited during the length of the NGS (three quarters of the year), but R_{ecoNight} was estimated using a temperature-dependent relationship from NEE_{Night} (using the 5-days windows (Reichstein et al., 2005)) throughout the year of measurements. We propose that interpretation of R_{eco} in water-limited ecosystems should be formally revisited as partitioning algorithms may have larger errors when soil moisture is a limiting factor.

The last issue is that changes in physical parameters could influence the diffusivity of gases, hindering the proper interpretation of temperature sensitivity (Fig. 3, Issue 3.e). The temporal lag between CO_2 production in depth and R_{soil} measured in surface or between R_{soil} and EC measurements depends on these physical parameters and shift depending on time (Maier et al., 2011).

We advocate the use of mechanistic and standardized approaches for partitioning of NEE (Lasslop et al., 2010; Reichstein et al., 2005), but we also invite the community to conduct an open discussion on the calculation and interpretation of R_{soil} and R_{eco} to identify key challenges and potential improvements upon the current approaches to measure these variables. If R_{soil} is not measured accurately, we could be overestimating soil CO_2 emissions to the atmosphere and therefore soil functionality, which could strongly affect predictions of global C emissions (Phillips et al., 2016). If R_{eco} is underestimated, then NEE partitioning will underestimate GPP and could influence the magnitude of carbon sequestration by terrestrial ecosystems. These challenges can be addressed as AmeriFlux, and other networks within FLUXNET, grow,

refine flux measurements, increase ancillary information, and test new approaches to measure ecosystem respiration.

5. Conclusions

R_{eco} and R_{soil} showed similar temporal patterns across study sites, with higher fluxes during growing season (GS) than during non-growing season (NGS). However, despite R_{soil} being a component of R_{eco} , annual, seasonal and daily values of R_{eco} were not consistently higher than R_{soil} , and exhibited strong differences between the studied ecosystems. These results suggest that there are evident underlying errors when R_{soil} is higher than R_{eco} , but we cannot discard (or identify) potential errors when R_{eco} is higher than R_{soil} .

Our results support the assumption that R_{ecoNight} information could be used for estimating daytime R_{eco} , and that NEE_{Night} is similar to R_{ecoNight} across study sites. We discussed several limitations for estimating NEE and measuring and upscaling R_{soil} , which could influence the miscalculation of these fluxes. The ultimate aim of this study is to ignite the discussion of the interpretation and calculation of R_{eco} and R_{soil} to improve measurements and modeling of respiration processes across ecosystems. Future studies should test the generalities of our findings across multiple sites with longer time series and across different climatic conditions. Discrepancies between R_{eco} and R_{soil} could be site-specific or biome-specific (e.g., arid ecosystems, boreal forests), but if discrepancies are consistent across AmeriFlux, and other flux networks, then it will represent a challenge for modeling and upscaling of R_{eco} , R_{soil} , gross primary productivity, and ultimately the regional-to-global carbon budget.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.10.028>.

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