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

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36   **Highlights**

37   - R_{soil} is a fraction of R_{eco} and theoretically must be lower than R_{eco}

38   - R_{eco} was not consistently higher than R_{soil} from daily to annual scales

39   - We discuss issues with current practices influencing under or overestimation of R_{eco} and

40   R_{soil}

41   - Flux networks need a better integration of spatial and temporal variability of R_{eco} and R_{soil}

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Abstract

The net ecosystem exchange (NEE) is the difference between ecosystem CO_2 assimilation and CO_2 losses to the atmosphere. Ecosystem respiration (R_{eco}), the efflux of CO_2 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., Q_{10}). 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 (CO_2) assimilation through photosynthesis (gross primary production; GPP) and the efflux of CO_2 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:

$$R_{eco}=R_{soil}+R_L+R_w+CW+SV+PD \qquad \textit{(eq. 1)}$$

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. 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

87 inconsistencies could lead to biased local to global carbon budgets and partitioning of ecosystem

88 fluxes. A recent review has identified this topic as one of the three major challenges for

89 interpreting respiration processes in ecosystems (Phillips et al., 2016).

90   The EC technique allows a direct estimate of NEE, using micrometeorological theory to

91 quantify the covariance between turbulent fluctuations of the vertical wind speed and CO_2

92 (Aubinet et al., 2000; Baldocchi, 2003). The EC technique has been used to measure NEE at the

93 ecosystem scale with more than 650 EC towers distributed in a wide variety of ecosystems

94 (Baldocchi, 2014), improving our knowledge of the exchange of energy and matter between

95 ecosystems and the atmosphere around the world (Beer et al., 2010; Jung et al., 2010; Mahecha

96 et al., 2010).

97   As with any technique, the EC approach comes with some limitations. Several studies

98 have discussed these challenges (Finnigan, 2008; Massman and Lee, 2002; Schimel et al., 2008)

99 or how to quantify errors in measurements (Goulden et al., 1996; Hollinger and Richardson,

100 2005; Loescher et al., 2006; Moncrieff et al., 1996). Arguably, the largest limitation of EC CO_2

101 flux measurements comes from low atmospheric mixing at night (Aubinet, 2008; Burba and

102 Anderson, 2010; Gu et al., 2005). During calm and stable night conditions, advection may be

103 predominant (Cooper et al., 2006; Gu et al., 2005; Horst and Doran, 1986; Massman and Lee,

104 2002; Van Gorsel et al., 2007); thus, CO_2 produced near the ground can be transported laterally,

105 and not measured by the EC tower (Aubinet et al., 2003; Baldocchi et al., 2000; Feigenwinter et

106 al., 2008; Finnigan, 1999; Lee, 1998; Roland et al., 2015; Speckman et al., 2015). In contrast,

107 during daytime, convective mixing often minimizes advection (Galvagno et al., 2017), creating

108 appropriate micrometeorological conditions to apply the EC technique. Finally, since NEE is the

109 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 (NEE_{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, 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

132 scientific challenge is to properly represent R_{soil} spatial heterogeneity to capture spatial and

133 temporal trends that are representative at the ecosystem scale.

134   The main goal of this study is to bring attention to issues and challenges related to

135 discrepancies between R_{eco} and R_{soil} and, in light of the 20th anniversary of the AmeriFlux

136 network, encourage new research to improve our understanding of respiration processes at the

137 ecosystem scale. To this end we take advantage of four contrasting ecosystems (from forests to

138 grasslands, and from boreal to semiarid ecosystems) to analyze how R_{eco}, estimated using the EC

139 technique, compares with site-specific continuous measurements of R_{soil}. We hypothesize that 1)

140 nighttime NEE (NEE_{Night}) should be similar to nighttime estimates of R_{eco} ($R_{eco\ Night}$); 2) the

141 temperature sensitivity (i.e., Q_{10}) of $R_{soil\ Night}$ and $R_{soil\ Day}$ should be similar, thus justifying the

142 use of nighttime functional relations to estimate daytime fluxes; 3) the temperature sensitivity

143 and temporal patterns of R_{eco} and R_{soil} should be similar within each study site, since R_{soil} is the

144 main component of R_{eco}; but 4) R_{eco} should be higher than R_{soil} at annual, seasonal and daily

145 scales at each site. We conclude with a review about issues influencing nighttime measurements

146 of NEE, R_{soil} measurements, and the interpretation of the functional relationships between R_{soil}

147 and R_{eco} with temperature.

148

2. Material and Methods

150 2.1. Study sites

151 We consider four contrasting experimental sites with NEE measurements using the EC

152 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 Hyytiälä Forestry Field Station, Finland. The vegetation is characterized by ~45 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 CO_2/H_2O 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. Figure 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 pretense 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 CO_2/H_2O 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

176 within the footprint of the flux tower (Roland et al., 2015). AT-Neu data used in this study were

177 measured during 2006. Environmental conditions during the study period are shown in Sup.

178 Figure 1. We refer to specific bibliography for further information on instrumentation and

179 characteristics of this study site (Schmitt et al., 2010; Wohlfahrt et al., 2008; Table 1).

180   The third site is a temperate broadleaf forest (US-MOz), located 30 km southeast of

181 Columbia, in central Missouri, USA. The vegetation is dominated by *Quercus alba* L. with

182 Hapludalt & Argiudoll soils. The EC system included a three-dimensional sonic anemometer

183 (81000; RM Young, Traverse City, MI, USA) and an open-path CO_2/H_2O infrared gas analyzer

184 (LI7500, Li-Cor Inc.) installed at a height of 32 m above the ground (Cescatti et al., 2012; Gu et

185 al., 2007). R_{soil} was measured using automated self-constructed open-path chambers (Edwards

186 and Riggs, 2003) coupled with an IRGA (LI7000, Li-Cor Inc). Chambers were located within the

187 footprint of the flux tower. US-MOz data used in this study were measured during 2006.

188 Environmental conditions during the study period are shown in Sup. Figure 1. We refer to

189 specific bibliography for further information on instrumentation and characteristics of this study

190 (Gu et al., 2007, Table 1).

191   The fourth site is a semiarid savanna (US-SRM), located in the Santa Rita Experimental

192 Range, outside of Tucson, Arizona, USA. The site is dominated by velvet mesquite (*Prosopis*

193 *velutina Woot.*) and bunchgrasses (*Eragrostis lehmanniana Nees, Digitaria californica Beth,*

194 *Muhlenbergia porter,* and *Bouteloua eripoda*), with thermic Ustic Torrifluvents soils. The EC

195 system included a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Inc.,

196 Logan UT) and an open path CO_2/H_2O infrared gas analyzer (LI7500, Li-Cor Inc.) installed at a

197 height of 7 m (Scott et al., 2009). R_{soil} was measured using solid-state CO_2 sensors installed at 2

198 and 10 cm depth, employing the gradient flux method. US-SRM data used in this study was

199 measured during 2007. Environmental conditions during the study period are shown in Sup.

200 Figure 1. We refer to specific bibliography for further information on instrumentation and

201 characteristics of this study site (Barron-Gafford et al., 2011; Scott et al., 2009; Table 1).

202

203 2.2. Measurements

204 NEE and R_{eco} data measured with EC technique were collected from the La Thuile 2007

205 FLUXNET 2.0v dataset (http://www.fluxdata.org) where data has been harmonized for quality

206 control of NEE and calculation of R_{eco} using standardized protocols (Papale et al., 2006;

207 Reichstein et al., 2005). NEE and R_{eco} data from US-SRM was directly provided by the site

208 principal investigator (R. Scott). R_{eco} was estimated at all sites from EC, fitting an exponential

209 relationship between NEE_{Night} and temperature and extrapolating to daytime (Reichstein et al.,

210 2005). Information on R_{soil} measurements for FI-Hyy, US-MOz, and AT-Neu were discussed in

211 Vargas et al. (2010), where little differences between chamber and gradient method

212 measurements were found across study sites. The same applies to R_{soil} at US-SRM (Barron-

213 Gafford et al., 2011).

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

215 measurements of soil moisture, photosynthetic active radiation (PAR), air temperature, and

216 volumetric water content for one year at each study site. All subsequent analyses were performed

217 with original time series (i.e., without gap-filling).

218

219 2.3. Data and analysis

220   To evaluate our hypotheses, we organized the data in different categories based on: 1)

221   *Season* (growing season [GS] or non-growing season [NGS]); and 2) *Time of the day* (daytime or

222   nighttime). The GS was defined as the period of the year when mean daily NEE was

223   continuously a net carbon sink, and conversely, NGS was the part of the year when ecosystem

224   was a net carbon source (Churkina et al., 2005). Daytime and nighttime thresholds were

225   established for each site using estimates of global radiation from photosynthetic active radiation

226   measurements according to Al-Shooshan (1997). Thus, daytime is considered when global

227   radiation $\geq$20 W m^{-2} and nighttime when global radiation <20 W m^{-2}.

228   Annual R_{eco} and R_{soil} were estimated as the sum of their respective daily values, and

229   standard deviation and random errors were calculated to test for differences between these

230   effluxes according to Wohlfahrt et al. (2005) and Moncrieff et al. (1996). The number of days in

231   which daily R_{soil} was larger than R_{eco} (i.e., $R_{soil(i)} > R_{eco(i)}$) was calculated for GS and NGS at

232   each study site. We also considered the cumulative fluxes for days when R_{soil} was larger than

233   R_{eco}, and their contribution (%) to the respective seasonal (i.e., GS or NG) sum of CO_2

234   emissions.

235   The relationships between nighttime NEE and R_{eco}, R_{eco} and R_{soil}, or $R_{soil\ Day}$ and $R_{soil\ Night}$

236   were evaluated, for all available data (i.e., one year) or split by seasons, for each study site using

237   linear regression models, reporting the slope and associated 95 % confidence intervals (CI).

238   The temperature sensitivity of $R_{eco\ Night}$, $R_{soil\ Night}$ and $R_{soil\ Day}$ was estimated using daily

239   means of each flux and air temperature by means of a Q_{10} function (Van 't Hoff, 1898):

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

241   where F represents the different fluxes (i.e., $R_{eco\ Night}$, $R_{soil\ Night}$, or $R_{soil\ Day}$), F_{10} is the simulated

242   flux at 10°C, Q_{10} is the so-called temperature sensitivity of the flux, and T is the air temperature.

243   Differences between Q_{10} values were evaluated using 95 % CI as recommended previously

244   (Vargas et al. 2012). Thus, if the 95 % CIs of Q_{10} do not overlap, then differences were

245   considered to be significant. All the analyses were performed using MATLAB (R2014a,

246   Mathworks Inc).

247

3. Results

249   R_{eco} and R_{soil} had similar temporal trends following similar seasonal patterns with high

250   fluxes during the GS and lower fluxes during NGS across each study site (Figs. 1A-D). No

251   differences in annual cumulative sums were found between R_{eco} and R_{soil} within sites (Table 1).

252   However, the uncertainties of these annual cumulative sums were very large (deviation of annual

253   cumulative fluxes included both daily standard deviation and random error). Random errors of

254   measurements were similar between R_{eco} and R_{soil}, ranging from 1.81 % to 4.50 % (Sup. Table
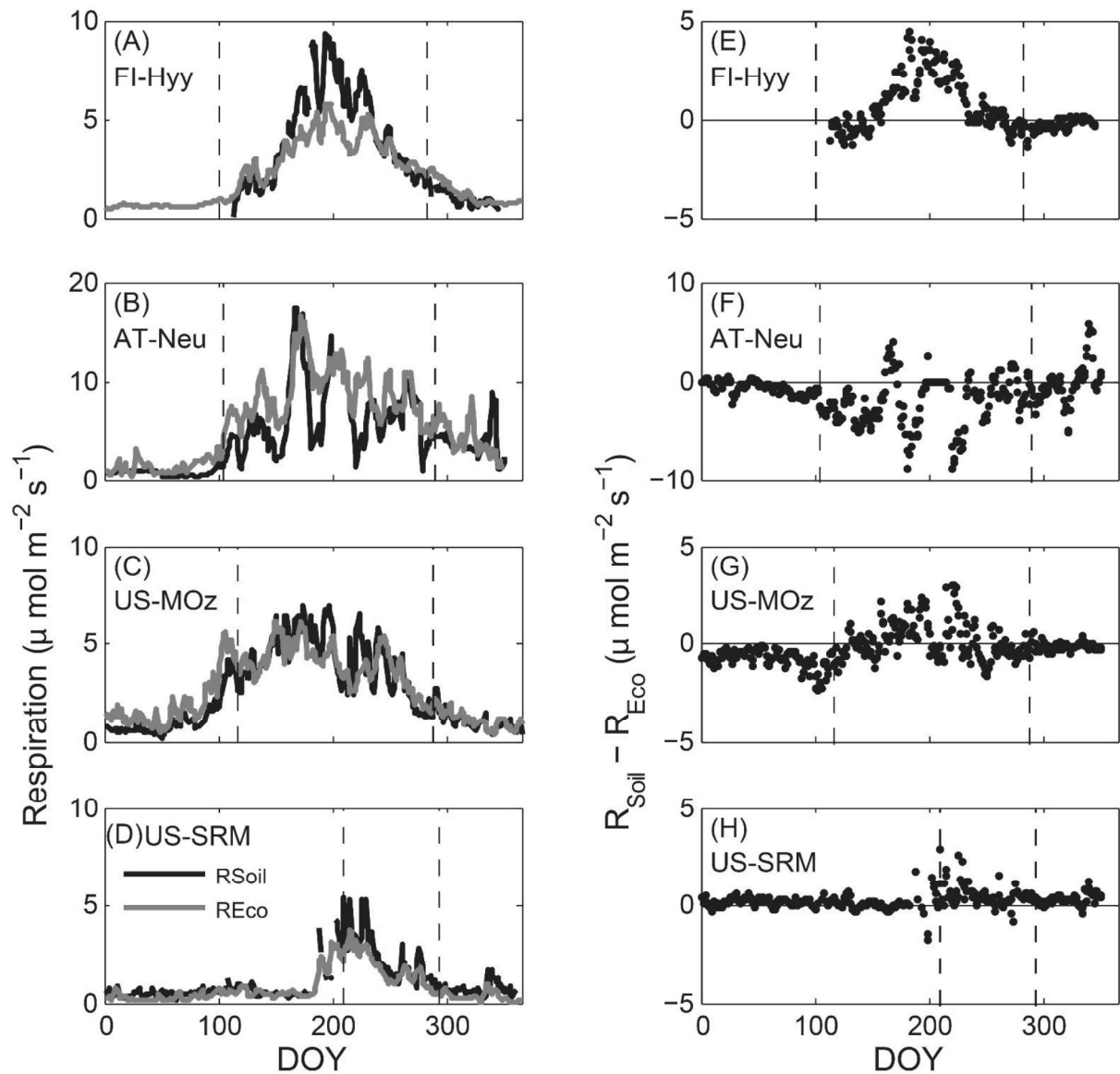
255   1).

Figure 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.

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

265 US-SRM, respectively; Table 2) and 25 to 93 % of days during GS (AT-Neu and US-SRM,

266 respectively; Table 2). For those days when R_{soil} was larger than R_{eco}, the cumulative sum of R_{soil}

267 was between 8 and 73 % higher than the cumulative sum of R_{eco} during NGS (i.e., FI-Hyy and

268 AT-Neu; Table 2), or 14 and 30 % higher than the cumulative sum of R_{eco} during GS (i.e., AT-

269 Neu and FI-Hyy; Table 2).

270 The annual cumulative sum of NEE_{Night} was not statistically different from the annual

271 cumulative sum of $R_{eco\ Night}$, including both random errors and cumulative standard deviations

272 (Sup. Table 2). However, the 1:1 comparison revealed that daily $R_{eco\ Night}$ was systematically

273 higher than daily NEE_{Night} at three sites (Figs. 2A-D; regression slopes for FI-Hyy, AT-Neu and

274 US-MOz were significantly lower than 1). Notably, the overall magnitude of the respective daily

275 fluxes was similar, as the linear regressions between NEE_{Night} and $R_{eco\ Night}$ showed slopes close

276 to 1 and a high fraction of explained variance ($R^2>0.82$; Figs. 2A-D). When data was analyzed

277 between seasons, we found similar trends at three sites between GS and NGS with slopes

278 significantly lower than 1 (Table 3). Only FI-Hyy during NGS and US-SRM during GS showed

279 similar NEE_{Night} and $R_{eco\ Night}$ (i.e., CI of regression slopes overlapped with 1).
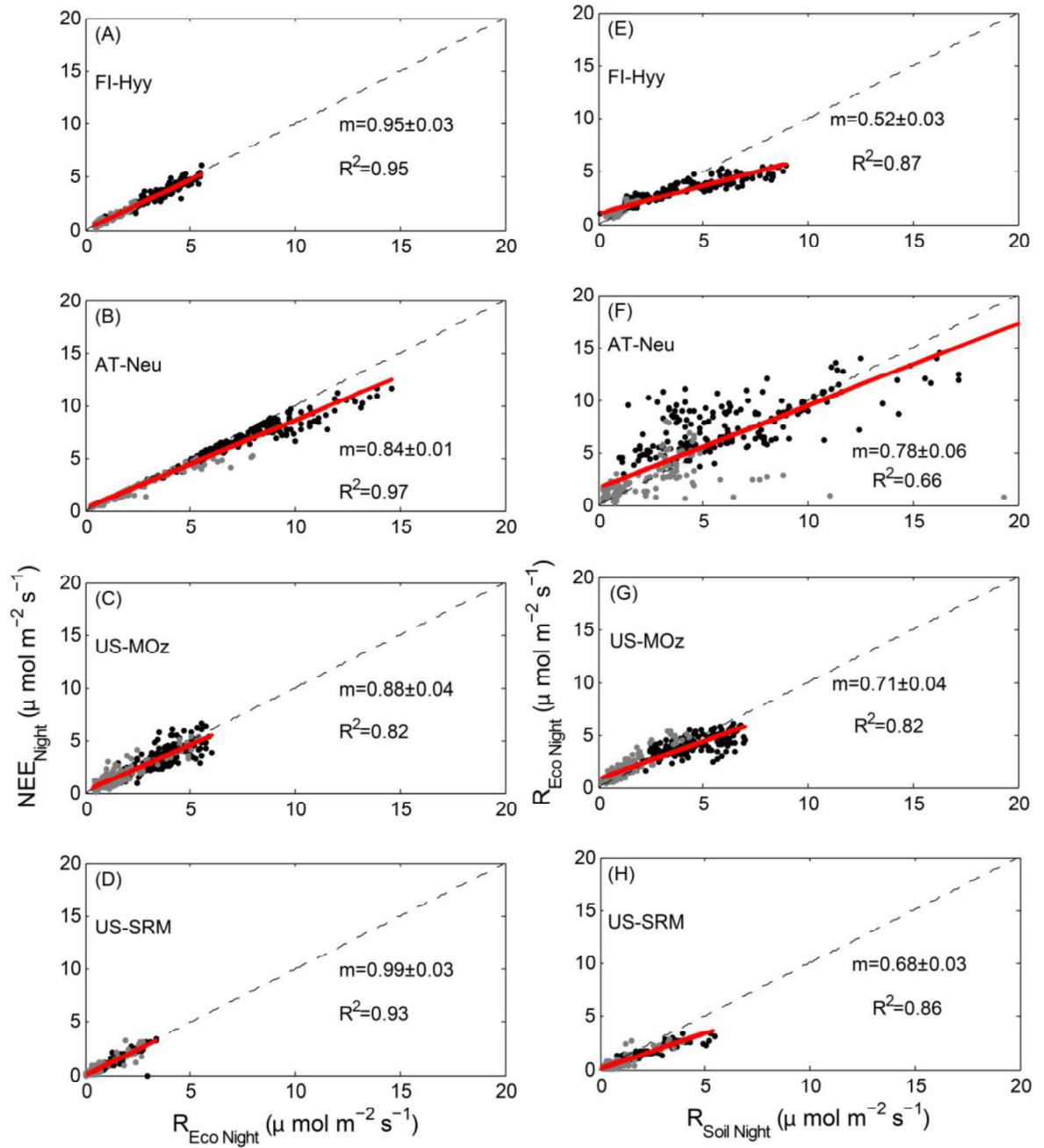
Figure 2. Comparison of daily averages of NEE_{Night} and $R_{eco\ Night}$ (A-D) and $R_{eco\ Night}$ and $R_{soil\ Night}$ (E-H) across study sites (FI-Hyy, AT-Neu, US-MOz and US-SRM). Parameter m shows slope (mean ± 95 % of CI) of the regression with the whole annual data. Grey and black colors indicate non growing season (NGS) and growing season (GS) data, respectively.

286   The annual cumulative sum of $R_{eco\,Night}$ was lower than the annual cumulative sum of R_{soil}

287    $_{Night}$ at FI-Hyy and US-SRM, but no significant differences were found at AT-Neu or US-MOz

288   (Sup. Table 2). The daily fluxes of $R_{eco\,Night}$ were consistently lower than the daily fluxes of R_{soil}

289    $_{Night}$ as linear regressions showed slopes ranging from 0.78 to 0.52 (AT-Neu and FI-Hyy,

290   respectively) (Fig. 2A-D). This bias was accentuated during GS for all sites with even higher

291    $R_{soil\,Night}$ fluxes compared to $R_{eco\,Night}$, and regression slopes between 0.60 and 0.45 (US-SRM

292   and FI-Hyy, respectively) (Table 3). During NGS two sites (FI-Hyy, US-MOz) showed that R_{eco}

293    $_{Night}$ fluxes were higher than $R_{soil\,Night}$ (slopes were 1.19 for both sites) and two other sites (AT-

294   Neu, US-SRM) showed the opposite pattern (slopes were 0.59 and 0.72, respectively) (Table 3).

295   Despite these systematic differences in fluxes, we did not find a clear pattern in temperature

296   sensitivity between $R_{eco\,Night}$ and $R_{soil\,Night}$. Similar Q_{10} between $R_{eco\,Night}$ and $R_{soil\,Night}$ were found

297   for US-MOz and US-SRM during GS and for FI-Hyy and US-MOz during NGS, but different

298   for FI-Hyy GS, AT-Neu GS and NGS, and US-SRM NGS ($R_{eco\,Night}$ Q_{10} was higher than R_{soil}

299    $_{Night}$ in two cases but lower in other two) (Table 4). Finally, similar temperature sensitivity was

300   found in R_{soil} between nighttime and daytime divided by seasons across sites (Table 4).

301

4. Discussion

303   Annual cumulative sums of R_{eco} were similar to annual cumulative sums of R_{soil} for all

304   studied ecosystems, but a large proportion of days from all study sites showed higher R_{soil} fluxes

305   than R_{eco}, with a clear seasonal pattern (Figs. 1E-H, Table 2). Despite the fact that R_{eco} should be

306   higher than R_{soil}, other studies in a variety of ecosystems, from boreal forests (Lavigne et al.,

307   1997) to temperate ecosystems (Speckman et al., 2015), have observed similar discrepancies.

308   Here, we identify and discuss different challenges and opportunities (Figure 3) that should be

309 addressed in order to improve the estimation of R_{eco} and R_{soil}: extrapolation of day-to-night

310 functionality (section 4.1); comparison between NEE_{Night} and $R_{eco\ Night}$ (section 4.2); comparison

311 between $R_{eco\ Night}$ and $R_{soil\ Night}$ (section 4.3); and their temperature sensitivity (section 4.4).

312

Issues (1)

a) Problems of measurements under low u*

b) Temporal lag storage

c) Spatial and temporal variability of the footprint

d) Advection

e) Losses of high and low frequency fluxes for averaging and filtering

f) Not measuring the recycling of C

g) EC towers replication

$$NEE_{Night} = R_{Eco\ Night} < R_{soil\ Night}$$

MAGNITUDES

FUNCTIONALITY

$$NEE_{Night}\ Q_{10} = R_{Eco\ Night}\ Q_{10} \approx R_{soil\ Night}\ Q_{10}$$

Issues (2)

a) Chambers could not be within the EC footprint

b) R_{soil} measurements could not be representative of the R_{soil} footprint

c) Chambers disrupt atmospheric stability

d) Fluxes not always estimated with the best fit

e) Discarding fluxes close or lower than zero

f) Systematic bias in gap filling

g) Temporal lags between CO_2 production and R_{soil} measurements

Issues (3)

a) Uncertainty in Q_{10} due to measurements artifacts

b) Respiration components could have different temperature sensitivities

c) Temperature choice (air or soil) for estimating Q_{10}

d) Suitability of Q_{10} under water-limited conditions

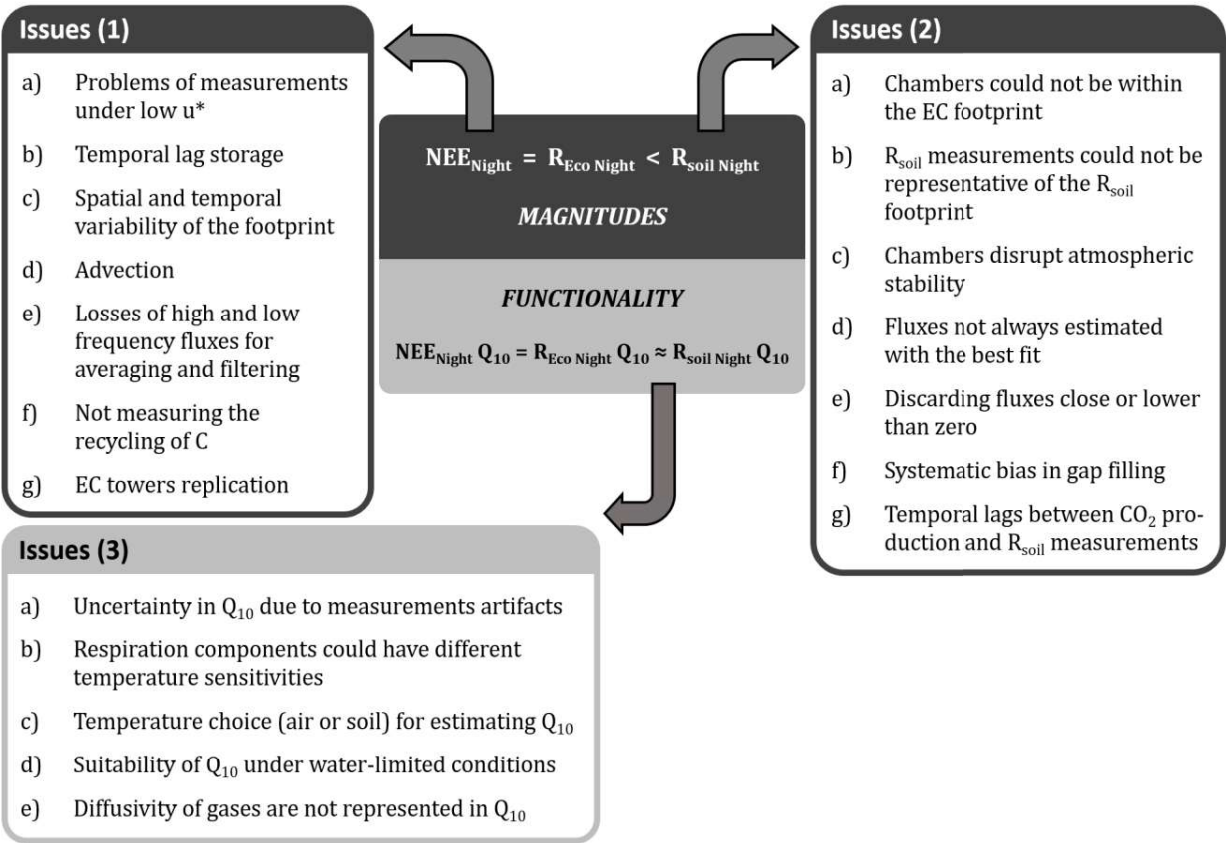e) Diffusivity of gases are not represented in Q_{10}

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

317

318 4.1 *Extrapolation of nighttime to daytime functionality*.

319   One of the main assumptions for estimating daily values of R_{eco} with the nighttime flux

320 partitioning approach is that R_{eco} nighttime functional relations can be extrapolated to daytime

321 R_{eco} (Reichstein et al., 2005). In general, our simple approach showed that the temperature

322 sensitivity of R_{soil} was similar between nighttime and daytime across seasons and sites

323 (confirming H2). Provided that R_{soil} represents the largest component of R_{eco} (Davidson et al.,

324 2006), as is usually the case, it seems reasonable to assume that the Q_{10} of R_{eco} and R_{soil} may be

325 similar, thus justifying the use of functional relations based on $R_{eco\ Night}$ to estimate $R_{eco\ Day}$. That

326 said, previous studies have described processes with different functioning between daytime and

327 nighttime, such as leaf mitochondrial respiration (Wehr et al., 2016; Wohlfahrt and Gu, 2015),

328 fine roots respiration or exudates supply (Kodama et al., 2008; Savage et al., 2013), and

329 problems related to phase shifts between driving temperatures of various respiration processes

330 (Lasslop et al., 2012; Wohlfahrt and Galvagno, 2017). This may be the case for site-specific

331 conditions during the growing season, for example in water-limited or boreal ecosystems where

332 Q_{10} may be confounded by other factors (e.g., soil moisture, plant phenology or ecosystem

333 productivity). Thus, suggesting that the universal applicability of nighttime functional relations

334 to daytime R_{eco} is still an open scientific debate and deserves more comprehensive studies.

335

336 *4.2 Comparison of NEE_{Night} and $R_{eco\ Night}$.*

337 The main assumption to estimate R_{eco} from nighttime NEE is that only respiration

338 processes occur during nighttime, and that these can be described by an Arrhenius type

339 relationship with temperature (Reichstein et al., 2005). Thus, it has been widely interpreted that

340 NEE_{Night} (direct measurements) is the same as $R_{eco\ Night}$ (model result). Although we found

341 similar NEE and R_{eco} during nighttime at the annual scale (supporting this expectation), we

342 found systematic higher R_{eco} than NEE during nighttime at three different sites at daily scale.

343 These small differences in magnitudes could be explained because $R_{eco\ Night}$ is not exactly

344 NEE_{Night}; as $R_{eco\ Night}$ is a semi-empirical prediction of NEE_{Night} based on a temperature

345 relationship (Reichstein et al., 2005). Despite statistically significant daily differences between

346 NEE_{Night} and $R_{eco\ Night}$, the slopes were close to 1 and therefore we interpret that both fluxes are

347 overall similar; supporting H1 (Fig. 2A-D). Consequently, we propose that observed differences

348 between R_{eco} and R_{soil} are likely not due to a wrong estimation of $R_{eco\ Night}$ from NEE_{Night}. Thus,

349 these results support the theoretical partitioning of Reco from temperature relationships of

350 NEE_{Night} (Reichstein et al., 2005).

351

352 4.3 $R_{eco\ Night}$ and $R_{soil\ Night}$ comparison.

353 Annual $R_{eco\ Night}$ was not consistently higher than annual $R_{soil\ Night}$ (nighttime R_{soil} was not

354 different from R_{eco} at AT-Neu and US-MOz, but higher at FI-Hyy and US-SRM). Additionally,

355 regression slopes of daily $R_{eco\ Night}$ and $R_{soil\ Night}$ were lower than 1 (ranging from 0.78 to 0.52;

356 Figs. 2E-H), suggesting that differences were not only statistically significant but also

357 ecologically relevant. Systematic differences were even more important during GS (slopes

358 ranged from 0.6 to 0.45), when fluxes were higher (Fig. 1A-D). Given that $R_{soil\ Night}$ has to be

359 smaller than $R_{eco\ Night}$, there could be an underestimation of $R_{eco\ Night}$, overestimation of $R_{soil\ Night}$,

360 or a combination of both. Since we assume that $R_{eco\ Night}$ was correctly estimated from NEE_{Night}

361 (see previous section 4.2), we postulate that an eventual underestimation of $R_{eco\ night}$ could result

362 from an underestimation of measured NEE_{Night}. Currently, we do not have another independent

363 way to estimate NEE_{Night} or R_{soil} to accurately determine the sources of errors, but different

364 potential sources and possible improvements have been identified in Fig. 3.

365

366 4.3.1 Measurements of R_{soil}.

367   Automatic soil respiration chambers are usually placed around an EC tower due to

368   limitations in tubing length or electrical power, but are not necessarily consistently installed

369   within the EC tower footprint (Fig. 3, Issue 2.a). An accurate estimate of the EC footprint before

370   chamber deployment could contribute to better comparisons (Phillips et al., 2016). Additionally,

371   R_{soil} measurements are usually poorly spatially replicated across EC study sites (Fig. 3, Issue

372   2.b), and possibly do not integrate the spatial variability of R_{soil} within the EC footprint (Leon et

373   al., 2014). Preliminary studies with manual measurements in the EC footprint for detecting areas

374   that are representative of the mean of R_{soil} across the space, and an effort to increase spatial

375   replication of automatic measurements, could reduce uncertainties associated with R_{soil}

376   measurements. Irrespective of spatial replication, soil chambers could themselves introduce an

377   artifact during R_{soil} measurement, especially during low u* conditions (Fig. 3, Issue 2.c).

378   Automatic opening and closing of chambers has been demonstrated to disrupt atmospheric

379   stability during low turbulence conditions when the air on the surface of soil could be CO_2

380   enriched, enhancing higher soil CO_2 emissions and resulting in a systematic R_{soil} overestimation

381   (Brændholt et al., 2016; Conen and Smith, 1998; Riederer et al., 2014). Chambers with less

382   movement could minimize this effect. The soil gradient method for measuring soil respiration

383   does not produce this atmospheric disruption, but has other limitations such as the sensitivity of

384   the calculation to soil CO_2 diffusion rates (Sánchez-Cañete et al., 2017; Vargas et al., 2010) and

385   neglects non-diffusive transport of CO_2 (Roland et al., 2015).

386   Furthermore, similar to NEE measurements, R_{soil} uncertainties could be associated with

387   errors in flux calculation and data processing. Efforts have been made to develop diffusivity

388   models for estimating R_{soil} with the soil gradient method (Maier and Schack-Kirchner, 2014;

389   Moldrup et al., 2001), but an empirical calibration with chamber measurements is still necessary

390　(Figure 3, Issue 2.d) for reliable long-term R_{soil} measurements (Roland et al., 2015; Sánchez-

391　Cañete et al., 2017). In studies where non-steady state chambers are used, R_{soil} is usually

392　estimated from the rate of change of CO_2 concentrations in relation to time using linear or

393　exponential models (Kopittke et al., 2013; Pihlatie et al., 2013). However, recent studies have

394　shown the usefulness of hierarchical Bayesian models in order to improve R_{soil} estimates (Ogle et

395　al., 2016). When classical non-hierarchical models are used (i.e., ordinary least squares), a

396　criterion based on minimum R^2 threshold is commonly used for discarding R_{soil} (Fig. 3, Issue

397　2.d). However, this criterion could systematically discard low R_{soil} since, for a given variability

398　of a data set, R^2 parameter tends to decrease as the slope of the regression trends to be closer to 0

399　(i.e., R_{soil} tends towards 0). Gap filling techniques are usually applied in many studies (Gomez-

400　Casanovas et al., 2013) (but not in the present manuscript) to estimate R_{soil} when data is missing.

401　However, this gap filling could be skewed, since it may likely be parameterized with other R_{soil}

402　data measured under similar environmental conditions, but with fluxes greater than 0 (the used

403　data should have passed the R^2 threshold) (Fig. 3, Issue 2.e). Applying a lower R^2 threshold

404　criterion at low fluxes during data quality check could reduce this bias.

405　　　　The last source of R_{soil} uncertainty is related to the difference between soil CO_2

406　production and R_{soil} measured at the surface and their temporal lags (Fig.3, Issue 2.g). Both

407　concepts are usually assumed to be the same, but they could differ substantially depending on

408　environmental conditions. Soil CO_2 production is a catabolic process of organic matter oxidation

409　driven by fine root respiration, rhizomicrobial respiration, microbial respiration of dead plant

410　tissues, priming effects, soil organic matter derived CO_2, and basal respiration (Kuzyakov,

411　2006). Each one of these components is regulated in a different way by soil temperature,

412　moisture, symbiotic interactions, plant C supply, and quality of organic matter (Högberg et al.,

413   2001; Jenkinson et al., 1991; Raich and Schlesinger, 1992). However, the recorded R_{soil}

414   measurement on the soil surface also depends on factors determining gas diffusivity (i.e., soil

415   texture, pore structure, atmospheric pressure, wind speed, temperature or moisture). Variations in

416   these factors may produce a temporal lag between CO_2 production in depth and measurement at

417   the surface leading to biophysical confounding factors, since R_{soil} recorded at the surface, at a

418   certain moment, should be a result of prior environmental conditions. Additionally, non-

419   biological soil CO_2 sources could hinder the correct interpretation of R_{soil} and its relationship

420   with the drivers (Rey, 2014; Sánchez-Cañete et al., 2016). The soil diffusion method could be

421   more suitable for establishing functional relations between R_{soil} and its drivers, since it is

422   calculated directly from soil CO_2 concentrations within the soil profile instead of soil surface

423   emissions. However, this method shows some limitations, as it is difficult to accurately

424   determine the diffusivity of the soil and the effect of air turbulence; both parameters influencing

425   R_{soil} measurements. On the other hand, chamber techniques could arguably be more comparable

426   with R_{eco} estimated from an EC system, since both techniques measure gas emissions and not

427   production.

428   Most of these issues related to R_{soil} measurements and calculation produce random errors,

429   which in turn could produce over- or under-estimations of R_{soil} depending on stochasticity

430   (Cueva et al., 2015). Furthermore, we found systematically higher $R_{soil\ Night}$ than $R_{eco\ Night}$ across

431   study sites and seasons, suggesting that measurements of NEE_{Night} should also be improved.

432

433   4.3.2 *Estimating NEE.*

434   One of the main limitations of the EC technique to estimate NEE is its suitability under

435   stable boundary layers (Fig. 3, Issue 1.a) producing low atmospheric turbulence (low u*),

436   commonly during nighttime (Aubinet, 2008; Gu et al., 2005). This could produce a temporal lag

437   storage (Fig. 3, Issue 1.b) when CO_2 emitted under low u* is not detected by the EC system until

438   u* increases and therefore is sufficient turbulent. Additionally, this CO_2 stored within the canopy

439   during nighttime promotes a flux of CO_2 during the early morning, when the footprint is smaller,

440   increasing the uncertainty of NEE measurements mainly in tall dense canopies (Fig. 3, Issue 1.c).

441   *Kutsch et al.*, [2008] suggested that discrepancies between R_{soil} and R_{eco} could also be a result of

442   increased abundance of advection (Fig. 3, Issue 1.d) that could consequently bias NEE

443   measurements. This interpretation is supported by the recommendation that advection needs to

444   be taken into consideration to better derive R_{eco} measurements across the day (Van Gorsel *et al.*

445   2007). Any improvement on estimating NEE under these conditions could have an impact when

446   calculating annual sums. Previous studies which have examined the influence of different u*

447   thresholds in NEE fluxes (Gu et al., 2005; Aubinet 2008; Speckman et al., 2015; Wohlfahrt et al.,

448   2005), identified losses of high and low-frequency fluxes during the averaging and filtering

449   process as a source of error in NEE estimations (Fig. 3, Issue 1.e).

450   The next issue related to NEE measurements is that the EC footprint is constantly

451   changing depending on atmospheric stability, wind speed and direction, in comparison with the

452   constant area measured by the soil respiration chambers. Thus, EC estimates of NEE integrate

453   fluxes from different areas, not always including the surface area that respiration chambers

454   measure, and possibly mismatching the spatial relation between R_{soil} and NEE (Fig. 3, Issue 1.c).

455   Another issue could be that an EC system may not be accounting for C recycling within

456   the canopy (Fig. 3, Issue 1.f). CO_2 produced in soil during nighttime could reside in the canopy

457   space and partially be fixed by photosynthesis in the morning. The interpretation of these

458   measurements would result in an underestimation of both nighttime R_{eco} and early morning

459   fluxes of GPP.

460   The last issue that we discuss for measuring NEE is the lack of formal replication of EC

461   systems (Fig. 3, Issue 1.g). Logistical limitations and the high equipment costs hinder the explicit

462   spatial replication of EC systems within study sites. Recently, Hill et al. (2016) have

463   demonstrated that around four EC towers are required to properly estimate annual flux within a

464   95 % statistical confidence interval. This number could increase further when ecosystem fluxes

465   are small or there is high spatial soil and canopy heterogeneity. In contrast, other studies have

466   shown that in homogeneous landscapes there is a large similarity (within 6 %) between adjacent

467   EC measurements (Hollinger et al., 2004). Thus, this is an open challenge for individual sites and

468   flux networks to design experiments, and evaluate network performance and data interpretation.

469

470   4.4 $R_{eco\ Night}$ and $R_{soil\ Night}$ temperature sensitivity.

471   $R_{eco\ Night}$ temperature sensitivity (i.e., Q_{10}) was expected to be similar to $R_{soil\ Night}$ Q_{10} within sites

472   (H3), but we found significant differences for about 50 % of the cases (i.e., seasons and sites).

473   These discrepancies could be explained either by errors in measurements or by *real* differences

474   in temperature sensitivity. First, if fluxes are not well measured, then differences in the

475   magnitudes of R_{soil} and R_{eco} could result in different Q_{10} estimates (Fig. 3, Issue 3.a). Second,

476   R_{plant} (the other component of R_{eco}) could have different physiological responses to changes in

477   environmental conditions (e.g., temperature, soil moisture), resulting in different Q_{10} than R_{soil};

478   consequently, modifying R_{eco} Q_{10} (Fig. 3, Issue 3.b). We found systematic differences between

479 $R_{soil\ Night}$ and $R_{eco\ Night}$ (i.e., R_{soil} higher than R_{eco}), but these discrepancies were not systematic for

480 $R_{soil\ Night}$ and $R_{eco\ Night}$ Q_{10} among sites. Thus, more research is needed to understand Q_{10} among

481 different components of R_{eco}, identify systematic differences in measurements, and physiological

482 responses to changing weather conditions across ecosystems.

483 Another factor that could influence R_{eco} Q_{10} is related to which temperature measurement

484 should be used (Fig. 3, Issue 3.c), since soil temperature could be more suitable for estimating

485 soil respiration responses (one of the R_{eco} components), but other components, e.g. R_{plant}, may be

486 more tightly coupled to air or leaf temperature (Lasslop et al., 2012; Wohlfahrt and Galvagno,

487 2017). Additionally, soil temperature should be measured at the depth of CO_2 production in soils,

488 which changes with space and time (Vargas et al., 2010). Measuring soil temperature at

489 unrepresentative depths could result in a wrong interpretation of temperature sensitivity (Phillips

490 et al., 2011; Reichstein and Beer, 2008; Subke and Bahn, 2010; Tang et al., 2003).

491 Another issue that could strongly affect the estimated temperature sensitivity of NEE

492 (and therefore R_{eco}) is that NEE_{Night} is expected to have a significant relationship with

493 temperature in order to estimate R_{eco} (Fig. 3, Issue 3.d). However, this relationship may not exist

494 when soil moisture is a limiting factor (Almagro et al., 2009; Leon et al., 2014). In this study, for

495 instance, US-SRM was water-limited during the length of the NGS (three quarters of the year),

496 but $R_{eco\ Night}$ was estimated using a temperature-dependent relationship from NEE_{Night} (using the

497 5-days windows (Reichstein et al., 2005)) throughout the year of measurements. We propose that

498 interpretation of R_{eco} in water-limited ecosystems should be formally revisited as partitioning

499 algorithms may have larger errors when soil moisture is a limiting factor.

500 The last issue is that changes in physical parameters could influence the diffusivity of

501 gases, hindering the proper interpretation of temperature sensitivity (Fig. 3, Issue 3.e). The

25

502   temporal lag between CO_2 production in depth and R_{soil} measured in surface or between R_{soil} and

503   EC measurements depends on these physical parameters and shift depending on time (Maier et

504   al., 2011).

505   We advocate the use of mechanistic and standardized approaches for partitioning of NEE

506   (Lasslop et al., 2010; Reichstein et al., 2005), but we also invite the community to conduct an

507   open discussion on the calculation and interpretation of R_{soil} and R_{eco} to identify key challenges

508   and potential improvements upon the current approaches to measure these variables. If R_{soil} is not

509   measured accurately, we could be overestimating soil CO_2 emissions to the atmosphere and

510   therefore soil functionality, which could strongly affect predictions of global C emissions

511   (Phillips et al., 2016). If R_{eco} is underestimated, then NEE partitioning will underestimate GPP

512   and could influence the magnitude of carbon sequestration by terrestrial ecosystems. These

513   challenges can be addressed as AmeriFlux, and other networks within FLUXNET, grow, refine

514   flux measurements, increase ancillary information, and test new approaches to measure

515   ecosystem respiration.

516

517   **5. Conclusions**

518   R_{eco} and R_{soil} showed similar temporal patterns across study sites, with higher fluxes during

519   growing season (GS) than during non-growing season (NGS). However, despite R_{soil} being a

520   component of R_{eco}, annual, seasonal and daily values of R_{eco} were not consistently higher than

521   R_{soil}, and exhibited strong differences between the studied ecosystems. These results suggest that

522   there are evident underlying errors when R_{soil} is higher than R_{eco}, but we cannot discard (or

523   identify) potential errors when R_{eco} is higher than R_{soil}.

524   Our results support the assumption that $R_{eco\ Night}$ information could be used for estimating

525   daytime R_{eco}, and that NEE_{Night} is similar to $R_{eco\ Night}$ across study sites. We discussed several

526   limitations for estimating NEE and measuring and upscaling R_{soil}, which could influence the

527   miscalculation of these fluxes. The ultimate aim of this study is to ignite the discussion of the

528   interpretation and calculation of R_{eco} and R_{soil} to improve measurements and modeling of

529   respiration processes across ecosystems. Future studies should test the generalities of our

530   findings across multiple sites with longer time series and across different climatic conditions.

531   Discrepancies between R_{eco} and R_{soil} could be site-specific or biome-specific (e.g., arid

532   ecosystems, boreal forests), but if discrepancies are consistent across AmeriFlux, and other flux

533   networks, then it will represent a challenge for modeling and upscaling of R_{eco}, R_{soil}, gross

534   primary productivity, and ultimately the regional-to-global carbon budget.

535

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TABLES

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.

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 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 $R_{eco} < R_{soil}$	% Days $R_{eco} > R_{soil}$	Flux (%) $R_{eco} < R_{soil}$	Flux (%) $R_{eco} > R_{soil}$
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

898   Table 3. Regressions of daily averages of NEE_{Night} versus $R_{eco\ Night}$ and $R_{eco\ Night}$ versus $R_{soil\ Night}$

899   across study sites by seasons (slope ± 95 % of CI).

Site	Period	NEE_{Night} vs $R_{eco\ Night}$	R^2	$R_{eco\ Night}$ vs $R_{soil\ Night}$	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

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901   Table 4. Summary of Q_{10} estimates of NEE_{Night}, $R_{ecoNight}$, $R_{soilNight}$ and $R_{soilDay}$ for each site and

902   season (mean $\pm$ 95 % CI). Different lowercase letters indicate significant differences in Q_{10}

903   between fluxes within sites and seasons (95 % CI not overlapped). Mean annual T, SWC and u*

904   are reported with their standard deviation.

Site	Season	Q_{10} NEE_{Night}	Q_{10} $R_{eco\,Night}$	Q_{10} $R_{soil\,Night}$	Q_{10} $R_{soil\,Day}$	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

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