Forest ecosystem respiration estimated from eddy covariance and chamber measurements under high turbulence and substantial tree mortality from bark beetles

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Abstract

Eddy covariance nighttime fluxes are uncertain due to potential measurement biases. Many studies report eddy covariance nighttime flux lower than flux from extrapolated chamber measurements, despite corrections for low turbulence. We compared eddy covariance and chamber estimates of ecosystem respiration at the GLEES Ameriflux site over seven growing seasons under high turbulence [summer night mean friction velocity (u*) = 0.7 m s^{-1}], during which bark beetles killed or infested 85% of the aboveground respiring biomass. Chamber-based estimates of ecosystem respiration during the growth season, developed from foliage, wood, and soil CO_2 efflux measurements, declined 35% after 85% of the forest basal area had been killed or impaired by bark beetles (from 7.1 ± 0.22 μmol m^{-2} s^{-1} in 2005 to 4.6 ± 0.16 μmol m^{-2} s^{-1} in 2011). Soil efflux remained at ~3.3 μmol m^{-2} s^{-1} throughout the mortality, while the loss of live wood and foliage and their respiration drove the decline of the chamber estimate. Eddy covariance estimates of fluxes at night remained constant over the same period, ~3.0 μmol m^{-2} s^{-1} for both 2005 (intact forest) and 2011 (85% basal area killed or impaired). Eddy covariance fluxes were lower than chamber estimates of ecosystem respiration (60% lower in 2005, and 32% in 2011), but the mean night estimates from the two techniques were correlated within a year (r^2 from 0.18 to 0.60). The difference between the two techniques was not the result of inadequate turbulence, because the results were robust to a u* filter of >0.7 m s^{-1}. The decline in the average seasonal difference between the two techniques was strongly correlated with overstory leaf area (r^2 = 0.92). The discrepancy between methods of respiration estimation should be resolved to have confidence in ecosystem carbon flux estimates.

Keywords: bark beetles, chambers, disturbance, EC, ecosystem respiration, respiration modeling, soil efflux, turbulence, u* filtering

Introduction

Each year, terrestrial ecosystems sequester 2.3 GT of carbon, roughly 26% of annual anthropogenic global carbon emissions (Le Quere *et al.*, 2009). The balance between photosynthesis and respiration determines carbon storage, but respiration appears to vary with the environment more than photosynthesis, and to largely control ecosystem carbon loss or gain (Valentini *et al.*, 2000). Despite its importance, respiration is less studied than photosynthesis and there are numerous uncertainties in its measurements (Valentini *et al.*, 2000).

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Most ecosystem respiration (R_e) measurements are derived from eddy covariance (EC), and currently there are >500 EC towers established across the globe, providing nearly continuous fluxes from a wide variety of ecosystems (Baldocchi *et al.*, 2001, www.fluxnet.ornl. gov). EC measurements have greatly improved our understanding of the response of ecosystem carbon and water fluxes to the environment and to disturbance (Wofsy *et al.*, 1993; Goulden *et al.*, 1998; Valentini *et al.*, 2000; Law *et al.*, 2002; Baldocchi, 2003; Amiro *et al.*, 2010). However, uncertainties in EC fluxes measured at night (Goulden *et al.*, 1996; Lavigne *et al.*, 1997; Baldocchi, 2003; Thomas *et al.*, 2013) make inferences difficult for R_e, photosynthesis or gross primary productivity,

and daily, seasonal, and annual sums of net ecosystem exchange.

The largest uncertainty in EC measurements of R_e is that the atmospheric mixing required for the technique may be lower, absent, or different at night (Goulden *et al.*, 1996; Lavigne *et al.*, 1997; Baldocchi, 2003; Thomas *et al.*, 2013). During the daytime, convective heating mixes the atmosphere and flux can be recorded by the tower's EC instrumentation (Massman & Lee, 2002). At night, there is no convective heating from the surface and in the absence of mechanical mixing, which may not penetrate the canopy from above (Aubinet, 2008; Wharton *et al.*, 2009; van Gorsel *et al.*, 2011; Thomas *et al.*, 2013), CO_2 produced near the ground may be advected downhill. Advective fluxes are not recorded by the EC tower, causing a systematic underestimation of the true nighttime ecosystem carbon flux. If unaddressed this 'night problem' makes ecosystems appear to be unrealistically large sinks of carbon, when they could be a carbon source (Goulden *et al.*, 1996; Aubinet, 2008).

The traditional method for dealing with a lack of turbulence in EC is a procedure known as u* filtering, in which all measurements below a certain friction velocity (u*) threshold are removed and then replaced via gap filling (Goulden *et al.*, 1996). There are many limitations of u* filtering (Ruppert *et al.*, 2006; Van Gorsel *et al.*, 2007; Aubinet, 2008), such as the selection of the u* threshold is subjective (Gu *et al.*, 2005), and a small difference in the u* threshold can change the flux from a carbon sink to a carbon source (Miller *et al.*, 2004; Ruppert *et al.*, 2006). Through u* filtering, many sites lose ~50% of their nighttime EC values, causing further uncertainty of the true nighttime flux (Feigenwinter *et al.*, 2004; Misson *et al.*, 2007).

Another large and perhaps related uncertainty for EC estimates of R_e (R_{EC}) is the nearly universal and systematic bias between R_{EC} and R_e estimated using chamber measurements of components and extrapolation models (R_T; see Table 1). R_{EC} and R_T should generate similar numbers, but studies in a variety of ecosystems reported that u* filtered R_{EC} that were significantly

lower than R_T. For example, EC estimates of respiration were 27% lower than chamber measurements and poorly correlated ($r^2 = 0.06$–0.27) in Canadian boreal forest (Lavigne *et al.*, 1997). In a deciduous forest in northern USA, EC respiration estimates were 50% lower than chamber estimates, despite a good correlation between them ($r^2 = 0.62$, Bolstad *et al.*, 2004). Similar results were described in Chinese temperate forests (Wang *et al.*, 2010), a eucalyptus forest in the Australian highlands (Van Gorsel *et al.*, 2007), managed meadows in the European Alps (Wohlfahrt *et al.*, 2005), North American semiarid grasslands (Myklebust *et al.*, 2008), and Brazil's Amazon rainforest (Chambers *et al.*, 2004). Many other studies have shown EC estimates of R_e to be lower than chamber estimates (Table 2).

We compared EC and chamber estimates of R_e at the windiest EC site in North America, where bark beetle mortality also killed most of the aboveground biomass during the study (Fig. 1). If a lack of turbulence and advection cause the discrepancy between R_{EC} and R_T, then the two measurement types should be roughly equal in this highly turbulent environment. We set out to determine: (i) if the EC and chamber methods for estimating nightly mean R_e differed; (ii) if any difference between the methods decreased as turbulence increased; (iii) if the methods differed in estimating the impact of 85% tree mortality on R_e; and (iv) if any difference between the methods decreased as the tree canopy died and changed the coupling between the subcanopy (including the forest floor) and the atmosphere.

Materials and methods

Study area

Glacier Lake Ecosystem Experimental Site (GLEES) is a subalpine forest located in Wyoming's Snowy Range, approximately 55 km west of Laramie (41°21.992′ N, 106°14.397′ W). This high elevation site (3190 m), maintained by the US Forest Service Rocky Mountain Research Station (Musselman *et al.*, 1994), has a mean annual temperature of -2 °C and a mean annual precipitation of 1200 mm, mostly as snow. The forest is dominated by old growth Engelmann spruce (*Picea engelmannii* Parry ex Englem) and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt] with an average canopy height of 18 m. The age distribution of the forest at GLEES suggests either a stand-replacing disturbance >400 years ago with a very slow recovery, or a series of smaller disturbances over the last 400 years (Bradford *et al.*, 2008). Mean annual u* is 0.94 m s^{-1}, higher than any other tower (www.fluxnet.ornl.gov).

EC data collection and processing

The GLEES Ameriflux EC tower was established in its current location in 2004; the tower is 23 m tall, with the above-canopy

Table 1 Terms used for the paper

R_e	The true nighttime ecosystem respiration.
R_{EC}	Eddy covariance estimates of R_e using u* filtered nighttime data.
R_T	Chamber estimate of R_e. Calculated from Eqn (4).
R_W	Respiration from woody tissues as estimated by chambers.
R_F	Respiration from foliage as estimated by chambers.
R_S	Soil respiration as estimated by chambers.
R_{light}	Ecosystem respiration estimated from daytime EC light response curves.

Table 2 List of studies documenting EC estimates of R_e being lower than chamber estimates

Reference	Ecosystem type	Site location	Comparison
Barr et al., 2002	Boreal Forest, aspen	Saskatchewan, Canada	EC < chambers
Bolstad et al., 2004	Deciduous hardwoods	Wisconsin, USA	EC 50% < chambers, $r^2 = 0.66$
Chambers et al., 2004	Brazilian rainforest	Manaus, Brazil,	EC < chambers
Cook et al., 2008	Deciduous hardwoods	Wisconsin, USA	EC < chambers
Dore et al., 2003	Scrub-oak peatland	Florida, USA	EC < chambers
Flanagan & Johnson, 2005	Mixed grassland	Alberta, Canada	EC < chambers, but within uncertainty
Goulden et al., 1996	Deciduous hardwoods	Massachusetts, USA	EC < chambers
Grunwald & Bernhofer, 2007	Subalpine spruce forest	Tharandt, Germany	EC < chambers*
Hermle et al., 2010	Boreal Forest, black spruce	Quebec, Canada	EC < chambers
Kutsch et al., 2008	Deciduous hardwoods	Thuringia, Germany	EC < chambers
Lavigne et al., 1997	Boreal Forest, black spruce	Quebec, Canada	EC 27% < chambers, $r^2 < 0.27$
Myklebust et al., 2008	Semiarid grassland	Idaho, USA	EC < chambers
Nagy et al., 2011	Sandy grassland	Bugac, Hungary	EC < chambers
Ohkubo et al., 2007	Cypress evergreen forest	Shiga Prefecture, Japan	EC < chambers
Reth et al., 2005	Meadow and brownfield	Lindenberg, Germany	EC < chambers, $r^2 = 0.69$
Riveros-Iregui & McGlynn, 2009	Mountain pine forest	Montana, USA	EC < chambers*
Schrier-Uijl et al., 2010	Peatland dairy farm	Oukoop, Netherlands	EC 16% < chambers
Tang et al., 2008	Deciduous hardwoods	Michigan, USA	EC < chambers
Thomas et al., 2013	Douglas-fir forest	Oregon, USA	EC < Chambers
Van Gorsel et al., 2007	Highland eucalyptus forest	New South Wales, Australia	EC < Chambers, converge with alterative to u* filter
Wang et al., 2010	Mixed temperate forest	Changbai Mountain, China	EC < chambers during summer
Wharton et al., 2009	Douglas-fir forest	Oregon, USA	EC < chambers*
Wohlfahrt et al., 2005	Mountain meadow	Neustift, Austria	EC 26% < chambers, within uncertainty
Zha et al., 2007	Mountain pine forest	Huhus, Finland	EC 29% < chambers

*Study only measured soil respiration, which roughly equaled eddy covariance data. It is assumed that aboveground fluxes are >0, resulting in total chamber flux being greater than eddy covariance numbers.

sensors installed between 22.6 and 25.8 m in height. Air temperature (T_a) was measured by a RTD-810 resistance thermometer with an OM5-1P4-N100-C signal-conditioning module (Omega Engineering, Inc., Stamford, CT, USA) and a Met–One radiation shield (076B-4 radiation shield, Met One Instruments, Inc., Grants Pass, OR, USA). Soil temperature was measured at 0.05, 0.10, 0.20, 0.50, and 1.02 m depths using a Hydra probe (Vitel, Inc., Chantilly, VA, USA) (Frank et al., 2014).

At GLEES, net ecosystem exchange of carbon (NEE), water, and energy are calculated from the sum of vertical flux (eddy covariance) and changes in carbon canopy storage (Lee et al., 2004). CO_2 concentration for the EC was measured using a LI-Cor 7500 (Li-Cor Biosciences, Lincoln, NE, USA), collected at a frequency of 20 Hz and compiled into 30 min statistics. Canopy storage of CO_2 was estimated from a vertical profile of CO_2 concentration, measured once a minute at eight different heights (LI-Cor 6262, until August 2008, then a LI-Cor 7000). Wind speed and direction were measured using a sonic anemometer (model SATI/3Vx, Applied Technologies, Inc., Longmont, CO, USA).

Our comparison of R_{EC} and R_T estimates of R_e used nightly (PAR < 2 μmol m^{-2} s^{-1}) averages of NEE collected with EC during the snow-free summer nights (July 1st–October 1st)

from 2004 to 2011 when mean u* was >0.2 m s^{-1} (Goulden et al., 1996; Gu et al., 2005) for every half hour of the night. The nights used for the respiration comparison had a mean u* of 0.74 m s^{-1}, lower than the annual mean of 0.94 m s^{-1}.

EC footprint and forest mortality

Fluxes observed by the EC tower originate from a 'footprint' upwind of the tower (Massman & Lee, 2002). We used wind direction to determine the GLEES EC tower footprint, and used forest survey plots within the footprint for measurements of leaf area and sapwood volume needed to extrapolate foliar respiration and wood CO_2 efflux, and annual changes with tree mortality (Bradford et al., 2008; Frank et al., 2014). In 2004, 36 circular survey plots (each 201 m^2), arranged into nine clusters, were established to estimate carbon pools in live vegetation, dead wood, and soil to a depth of 30 cm, and the fluxes of annual litter fall and wood net primary production (Bradford et al., 2008). Twenty four of the 36 plots were within the footprint, and we used measurements of tree species, diameter, and height from these plots to compute tree leaf area, live and tree biomass, standing dead tree biomass, sapwood volume, and growth increment using allometric
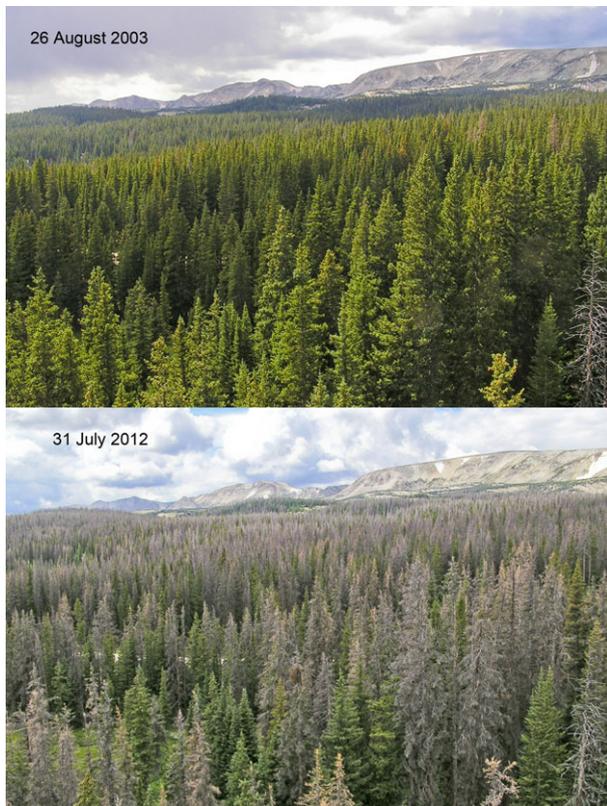
Fig. 1 Repeat photography from the GLEES EC tower contrasting the forest in 2003 with 65 m^2 ha^{-1} healthy tree basal area, and the aftermath of massive bark beetle tree mortality in 2012 with <10 m^2 ha^{-1} healthy tree basal area.

Fig. 2 From 2008 to 2011, the bark beetle epidemic greatly reduced live basal area at GLEES. In 2011, only 15% (10 of 65 m^2 ha^{-1}) of the original forest basal area remained alive and uninfected by bark beetles. Mortality survey was not conducted 2006–2008 (marked *), numbers are estimated from dendrological data (see text for details).

equations (Kaufmann & Troendle, 1981; Kaufmann *et al.*, 1982; Ryan, 1989).

Bark beetles are endemic to the study site, but starting in 2007–2008, their population rose and the rate of tree mortality dramatically increased (Figs 1 and 2). Mortality from the bark beetle epidemic was assessed by annual surveys of all plots from 2009 to 2011. Trees with a DBH >10 cm were classified as 'infested' if they displayed any evidence of bark beetles such as pitch tubes, beetle entrance holes, or boring dust. Trees were classified as 'dead' once they lacked any green needles. In 2011, it was estimated that ~85% of the forest basal area was infested or killed by bark beetles. Because the forest survey was not conducted in 2006–2008, forest mortality for these years were modeled using a logistic regression, a shape suggested by dendrochronology data and MODIS estimates of leaf area (Frank *et al.*, 2014).

Overview of chamber measurements

All chamber measurements were taken using a closed-system approach (Field *et al.*, 1991), except where noted. For each measurement, a chamber was attached to a biological substrate (such as a leaf, wood, or soil); tubing connected the chamber to a portable infrared gas analyzer (IRGA) that mea-
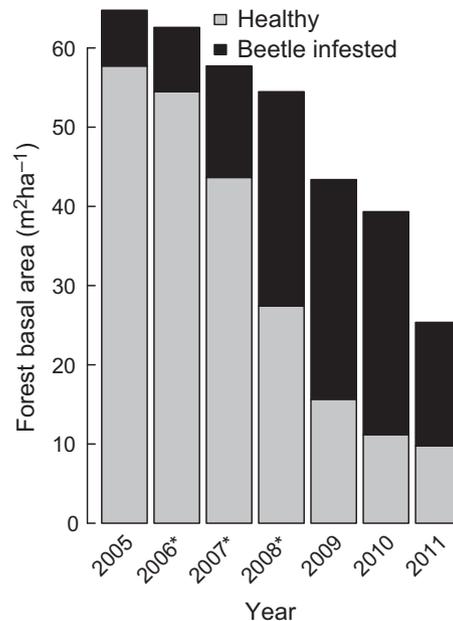
sured the increase in CO$_2$ over time. For woody and foliage measurements, airflow into and from the chamber was measured to check for leaks. For soil respiration measurements, the collar was inserted into the mineral soil. Air inside the chamber was then flushed with outside air to lower the CO$_2$ concentration to ambient prior to starting the measurements, and during flushing and measurements a fan within the chamber ensured that the air was mixed for the foliage and wood samples (the soil chamber used tubing with many small holes to mix the air within the chamber). Fluxes were calculated from the linear or exponential change in CO$_2$ concentration over time (~60 s) in a known volume of air (Field *et al.*, 1991) and fits with $r^2 < 0.98$ were excluded. The equipment used for each measurement type and period is listed in Table 3.

Chamber measurements of wood CO$_2$ efflux

CO$_2$ efflux from wood was measured on 14 Engelmann spruce and 11 subalpine fir live stems (across the range of age, diameter, and canopy position), and on four recently dead trees (two fir and two spruce). All trees were located within 100 m of the EC tower. Measurements were made three times during the summer of 2010 and five times in the summer of 2011. Measurements of CO$_2$ efflux from wood were made using a 250 ml clear polycarbonate chamber, temporarily strapped to the neoprene gasket on a 7 × 10 cm aluminum plate attached with putty to the smoothed outer bark at ~1.3 m height. These plates remained attached to the tree from summer 2010

Table 3 Summary chamber measurements

Type	Measurements taken	Time frame	IRGA used	Manufacturer
Woody Tissues	146 on 25 live boles	2010	LCA-4 (open path)	ADC, Hoddeston, England
	39 on 4 dead boles	2010	LI-820 (closed path)	Li-Cor Biosciences, Lincoln, NE, USA
		2011	Ciras-2 (closed path)	PP Systems, Amesbury, MA, USA
Foliage	85 on 26 branches	2010	LI-820 (closed path)	Li-Cor Biosciences, Lincoln, NE, USA
		2011	Ciras-2 (closed path)	PP Systems, Amesbury, MA, USA
Soil	1282 on 84 collars	2004–2006, 2009–2011	LI-820 (closed path)	Li-Cor Biosciences, Lincoln, NE, USA

through autumn 2011. System volume was calculated as the sum of volume of the chamber, tubing, IRGA, and gasket-to-tree bark space (measured for each tree). Wood CO_2 efflux measurements were expressed per unit sapwood volume (μmol m^{-3} of sapwood s^{-1}), and the sapwood volume underneath each gasket was calculated using an allometric equation and geometric formulas for a cylinder and wedge (Ryan, 1990).

Chamber measurements of foliar respiration

Foliar respiration was measured *in situ* on five spruce and five fir branches at night once during the summer of 2010 (from the EC tower and from the ground), and on eight spruce and eight fir branches three times during the summer of 2011 (at a height of 2–3 m on trees within 100 m of the EC tower). Sampled branches represented the range of tree sizes and light positions (even for trees sampled near the ground), included a range of foliage ages including new growth, were ~30 cm long, ~1 cm diameter at the proximal end, and had about ~350 cm^2 of projected leaf area. Foliage chambers were clear polycarbonate and split length-wise, with a neoprene gasket sealing the chamber around the branch. In 2010, 5 l chambers were used (each half 30 × 15 × 7.5 cm), and in 2011 these chambers were replaced by smaller 3 l chambers (each half 30 × 15 × 2 cm). Leaf temperatures were measured with an infrared thermometer. Fluxes were scaled by the effective projected of leaf area (μmol m^{-2} of effective projected LAI s^{-1}) (Kaufmann & Troendle, 1981; Scurlock et al., 2001).

At the end of each summer, branches were harvested and leaf area measured using a volume displacement method (Chen et al., 1997). After the final 2011 measurements, branches were harvested, immediately recut underwater, and their stems were kept submerged during transport to the lab. Within 18 h of cutting, foliar respiration was again measured in the laboratory at 22 °C. Temperature response curves were tested on a subset of five branches (three spruce and two fir), measuring respiration at 5, 10, 15, and 20 °C using a temperature controlled cuvette (Hubbard et al., 1995). Foliage was allowed to acclimate to the new temperature for 10 min prior to each measurement.

Chamber measurements of soil respiration

Soil respiration was measured with survey chambers throughout the EC footprint, from 2004 to 2011, before and during the extensive tree mortality. For survey measurements, 108 collars were permanently installed in the 36 plots located in a km^2 around the EC tower (described above), and 84 of these collars were within the probable EC footprint (Frank et al., 2014) and used for constructing the model for soil respiration. Collars were circular (731 cm^2 area), made of PVC pipe, and installed ~5 cm depth in the mineral soil, leaving ~5 cm of collar above the soil. A 6 l PVC chamber was placed on the collar for measurement. Soil respiration at each collar was measured ~3 times per summer in 2004–2006 and 2009–2011, but not measured from collars containing standing water (a few collars in the first measurement after snow melt). Soil temperature was measured at 10 cm depth using a Penetration Probe (Omega Engineering, Stamford, CT, USA) and soil moisture was measured at 10 cm depth in three different spots near the collar (HydroSense, Campbell Scientific, Logan, UT, USA). Fluxes were expressed as μmol m^{-2} of ground area s^{-1}.

Modeling observed chamber fluxes

To compare with nightly EC means, we developed models for continuous estimates of respiration fluxes for each ecosystem component (woody tissues, foliage, and soils). Models used substrate temperature, moisture, phenology, and tree species; model quality was evaluated using AIC and r^2.

CO_2 efflux from woody tissues displayed strong seasonal variability, and was modeled with the log-linear model:

$$R_w = S_v \exp\left(w_0 + w_1 D + w_2 D^2 + w_3 S\right) \qquad (1)$$

where R_W is observed woody respiration rates (μmol m^{-3} of sapwood volume s^{-1}), D is day of year, S is a species identifier, and w_0–w_3 are model coefficients. To convert to units of flux per ground area (R_W, μmol m^{-2} s^{-1}), respiration is multiplied by the average sapwood volume per ground area per species (S_v, cm^3 m^{-2}) from the plot sampling (Ryan, 1990; Sprugel, 1990; Lavigne et al., 1997), adjusted for mortality each year. Bark beetles infect sapwood with blue-stain fungus, and we assumed that wood CO_2 efflux from beetle-infested trees was 50% of uninfected trees (likely an overestimate; sensitivity analysis in discussion).

Foliar respiration was modeled with the log-linear equation:

$$R_F = LAI \exp\left(f_0 + f_1 T_A\right) \qquad (2)$$

where R_F is foliar respiration per unit ground area (μmol m^{-2} s^{-1}), T_A is air temperature (°C) as observed by

the EC tower, and f_0–f_1 are model coefficients. Equation (2) is a mathematically equivalent to the commonly used Q_{10} equation (Lloyd & Taylor, 1994). To model foliar respiration to units of flux per ground area, we multiplied $\exp(f_A + f_B\ T_A)$ by the average effective projected leaf area (LAI, $m^2\ m^{-2}$) of the EC footprint, estimated from the annual forest inventory survey and adjusted for mortality each year. Continuous measurements of T_A were provided by the EC tower. Bark beetle-infested trees retain needles for ~2 years after infection, but with greatly impaired physiology (Frank *et al.*, 2014). We assumed that foliar respiration for beetle-infested trees had 50% of the rate of uninfested trees.

Soil respiration was modeled using the linear model:

$$R_s = s_0 + s_1 T_s + s_2 \theta \qquad (3)$$

where R_S is soil respiration per ground area ($\mu mol\ m^{-2}\ s^{-1}$), T_S is soil temperature at 10 cm (°C) for collars, θ is percent volumetric water content for collars, and s_0–s_2 are model coefficients. Equation (3) was fit using mean values of R_S, T_S, and θ observed during each field session from the 84 soil collars in the EC footprint, and used with continuous measurements of T_S and θ from probes buried at 10 cm depth near the EC tower to generate continuous estimates.

Continuous estimates of fluxes from woody tissues, foliage, and soils from the models in Eqns (1–3) were averaged for the same time period as used for the night EC measurements to estimate total ecosystem respiration from chambers [R_T, Eqn (4)]:

$$R_T = R_W + R_F + R_S \qquad (4)$$

Values of R_T were compared to u*-filtered EC (R_{EC}), using linear regression and paired *t*-tests.

Results

Tree mortality from bark beetles

Healthy tree basal area declined from 65 $m^2\ ha^{-1}$ in 2005 to 10 $m^2\ ha^{-1}$ in 2011 (85% decrease, Figs 1 and 2). In 2011, 15 $m^2\ ha^{-1}$ of basal area still retained needles, but was infested by bark beetles. Trees attacked by bark beetles have severely impaired physiology, likely respire little, and will die completely in 1–2 years physiology (Frank *et al.*, 2014). Trees which survived the bark beetle epidemic are smaller than their predecessors (mean stand live DBH in 2005 was 24.5 cm, vs. 18.2 cm in 2011). Healthy sapwood volume decreased from 330 $m^3\ ha^{-2}$ in 2005 to 21 $m^3\ ha^{-2}$ in 2011 (6% of the original). Healthy effective projected leaf area similarly decreased from 6.1 $m^2\ m^{-2}$ (±1.7, 95% confidence interval) in 2005 to 0.9 ± 0.3 $m^2\ m^{-2}$ in 2011 (7% of the 2005 values). These allometeric estimates of LAI are slightly higher than MODIS estimates for the same site (Frank *et al.*, 2014), a trend commonly observed in conifer forests (Wang *et al.*, 2004).
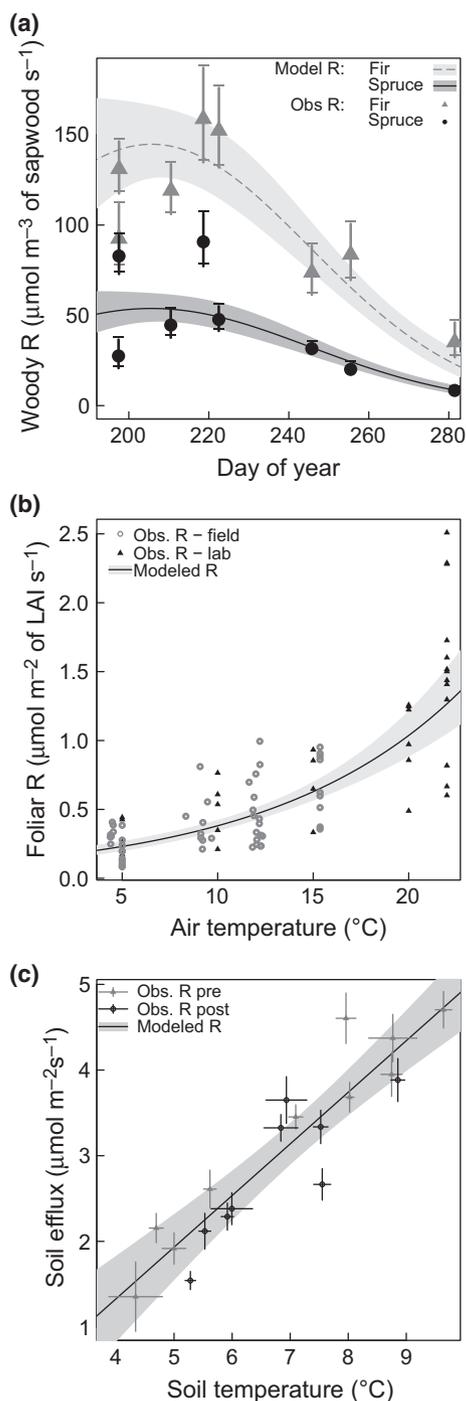
Chamber respiration measurements

CO_2 efflux from woody tissues (R_W) increased until the end of July and decreased afterward (Fig. 3a), a pattern attributed to seasonal changes in wood growth and photosynthetic activity (Ryan, 1990). This trend was similar in 2010 and 2011, and modeled using Eqn (1) ($R_W = \exp\ (-9.57 + 1.31\ D - 0.00032\ D^2 + 1.00\ S,\ r^2 = 0.67,\ n = 146$, Fig. 3a). Firs respired more per unit sapwood volume than Engelmann spruce, but had less sapwood volume per unit of tree basal area. We did not measure diurnal variation in CO_2 flux with sapwood temperatures (Ryan *et al.*, 1995), however, seasonal variation in sapwood temperature was not a significant predictor of R_W after accounting for seasonal trends. Respiration from dead tree boles was zero (39 measurements on 4 trees).

Foliar respiration (R_F) varied with temperature, but temperature corrected foliage respiration did not vary across season [$R_F = \exp\ (-1.96 + 0.10\ T_A),\ r^2 = 0.63,\ n = 85$, Fig. 3b]. For every 10 °C increase in air temperature (Q_{10}), R_F increased by a factor of 2.7 ± 0.2. Foliar respiration per leaf area did not differ between firs and spruces.

Soil respiration (R_S) was influenced both by temperature and soil moisture (soil temperature was the dominant influence, $R_S = -1.98 + 0.60\ T_S + 0.044\ \theta$, $r^2 = 0.83,\ n = 1282$, Fig. 3c). Model fit was substantially better using a linear rather than an exponential temperature response. R_S did not decline after the bark beetle epidemic, nor was there any significant relationship between observed soil respiration rates and distance to live or dead trees ($t > 0.1$ both when comparing collars near vs. far from trees, and collars before vs. after the death of nearby). Mean R_S was estimated to be 3.3 ± 0.09 $\mu mol\ m^{-2}\ s^{-1}$ in 2005, and 3.8 ± 0.13 $\mu mol\ m^{-2}\ s^{-1}$ in 2011 (2011 values slightly higher because of the heavy precipitation that year).

The total ecosystem mean summer nightly respiration estimated from chambers (R_T) was estimated to have declined 35% after 85% of the tree basal area was killed or infested with bark beetles, from 7.1 ± 0.22 $\mu mol\ m^{-2}\ s^{-1}$ in 2005 to 4.6 ± 0.16 $\mu mol\ m^{-2}\ s^{-1}$ in 2011 (Fig. 4a). This decrease was entirely from the loss of aboveground biomass: R_W declined 82% after the epidemic (1.4 ± 0.06 $\mu mol\ m^{-2}\ s^{-1}$ in 2005 to 0.26 ± 0.02 $\mu mol\ m^{-2}\ s^{-1}$ in 2011, Fig. 4b), and R_F declined 75%, from 2.4 ± 0.10 $\mu mol\ m^{-2}\ s^{-1}$ in to 2005 to 0.60 ± 0.03 $\mu mol\ m^{-2}\ s^{-1}$ in 2011, Fig. 4c). R_S did not decrease in response to bark beetle tree mortality; however, R_S in 2011 was slightly higher than other years due to high soil moisture that year (3.3 ± 0.09 $\mu mol\ m^{-2}\ s^{-1}$ in 2005 to 3.8 ± 0.1 $\mu mol\ m^{-2}\ s^{-1}$ in 2011, Fig. 4d).

In 2005, 19% ($\pm$0.5% standard error) of R_T was estimated to originate from woody tissue efflux, 34% ($\pm$0.6%) from foliage respiration, and 47% ($\pm$0.6%) from soils. These proportions are similar to those found in other studies (Lavigne *et al.*, 1997). In 2011, after 85% of the tree basal area had been killed of beetle infested, only 5% ($\pm$0.2%) of R_T came from woody tissues, 13% ($\pm$0.4) from foliage, and the remaining 82% ($\pm$0.5%) from soils.

(a)

(b)

(c)

EC and comparison to chambers

Unlike chamber estimates, nighttime EC measurements of respiration (R_{EC}) did not decline after 85% of the forest basal area had been infested or killed by bark beetles (*F*-test, $P > 0.1$), with a mean nighttime NEE of 2.9 µmol m^{-2} s^{-1} in 2005 ($\pm$0.2) and 3.1 in 2011 ($\pm$0.1; Fig. 6a).

We also used daytime EC data to estimate R_e from the intercept of light response curves (R_{light}, Hutyra *et al.*, 2008). These intercepts remained constant throughout the epidemic (R_{light} of 2.4 $\pm$ 0.3 µmol m^{-2} s^{-1} in 2005 and 2011; Fig. 6a). However, maximum CO_2 assimilation rates (A_{max}) and quantum yield of photosynthesis (Φ) both declined 50% due to the epidemic (Frank *et al.*, 2014). Using Bayesian analysis, daytime EC data were able to correctly approximate the degree of bark beetle mortality independent of actual forest inventories (Frank *et al.*, 2014). Other EC sites have shown an increase in estimates of R_e following an insect epidemic (Clark *et al.*, 2010; Mathys *et al.*, 2013).

Daytime and night EC values consistently estimated R_e values much lower than those estimated by chambers, but the difference between R_{EC} and R_T declined as tree mortality increased (Figs 4a, 5, and 6a; accessed via paired *t*-test, $t > 0.1$). In 2005, before the bark beetle tree mortality, EC estimated R_e to be on average 60% lower than chamber estimates ($\pm$0.14%). In 2011, EC estimates of R_e were only 32% lower than chambers ($\pm$0.02%). Despite the large difference in absolute values, the two estimates of R_e were correlated (yearly r^2 ranging from 0.17 to 0.60) with the slopes for each year ~0.9, which implies a ~constant slope and an intercept that decreased with tree mortality. After 85% of the aboveground biomass was killed or infected by bark beetles,

Fig. 3 The variability in chamber measurements of wood, foliage, and soil CO_2 efflux were fit to models driven by environmental variability or phenology. (a) Observed and modeled CO_2 efflux from woody tissues measured on live boles in 2010 and 2011 was highly seasonal, varied with sapwood volume, and was greater for fir. Data points are mean efflux and standard error for each species during each measurement session (*n* ~10). (b) Observed and modeled foliar respiration varied with temperature. Data points represent foliage respiration rates observed in the field (circles) and lab (triangles). (c) Observed and modeled soil efflux rates varied with soil temperature and moisture and did not differ between the mostly intact forest measurements (2004–2006) and high tree mortality years (2009–2011). Data points are mean and standard error soil CO_2 efflux for each measurement period (*n* ~84 measurements, taken over 2–3 days), standardized to 20% volumetric soil moisture.
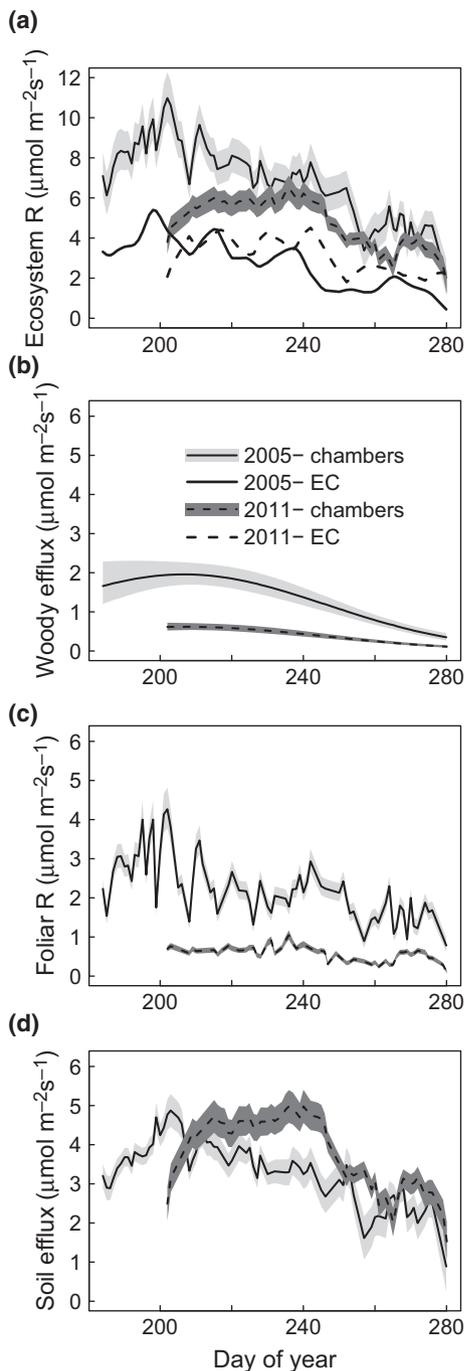
(a)

(b)

(c)

(d)

Fig. 4 R_e estimated by EC and chambers for 2005 (65 m^2 ha^{-1} healthy tree basal area), and in 2011 (10 m^2 ha^{-1} healthy tree basal area). (a) EC estimates of R_e are significantly lower than chamber estimates, and EC R_e did not decline over 2005–2011 period, while chamber estimates of R_e decreased 35%. The shaded area is 95% confidence interval (CI), and EC values are smoothed splines of nightly mean NEE measurements where u* > 0.2 m s^{-1}. Modeled respiration and 95% CI from chambers in 2005 and 2011 for woody tissues (b), foliage (c), and soils (d). Respiration declined 72% for live wood 74% for foliage, but soil respiration was greater in 2011.
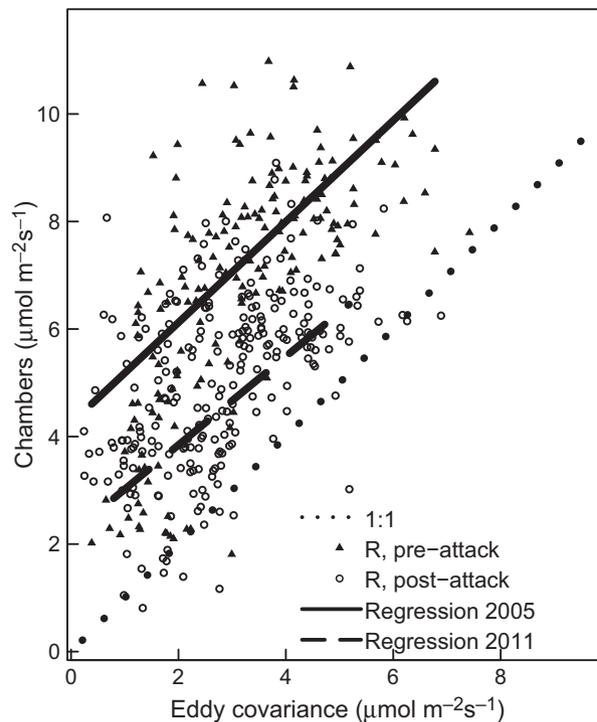

Fig. 5 Estimates of mean R_e at night estimated by EC (R_{EC}, u* > 0.2 m s^{-1}) and chambers (R_T) for qualifying nights from 2005 to 2011 were correlated within a year (r^2 0.18–0.60), but chamber estimates of R_e were greater (see Table 4 for regression fits). Years 2005–2007 (less tree mortality) are gray circles, years 2008–2011 (high tree mortality) are black triangles.

R_T estimated from chamber measurements decreased by 35%, with no change in EC estimates of R_e (Fig. 4a and 5). The difference between R_T and R_{EC} was strongly related to live leaf area, which declined with tree mortality (Fig. 6b, $r^2 = 0.92$).

Discussion

Ecological implications of chamber measurements

Chamber measurements enable discerning how individual ecosystem components react to environmental factors and disturbances. Over the bark beetle mortality period assessed, modeled mean CO_2 efflux from woody tissues declined 72% and foliage respiration declined 74% from the loss of sapwood and live foliage. Standing dead tree boles had no measurable CO_2 efflux, and decomposition of standing aboveground dead wood will likely remain negligible until the trees fall (Harmon *et al.*, 2011).

Unlike the wood and foliage, soil respiration remained constant during the large tree mortality from the bark beetles (F-test, P > 0.1). This result was consistent with another study of soil respiration after
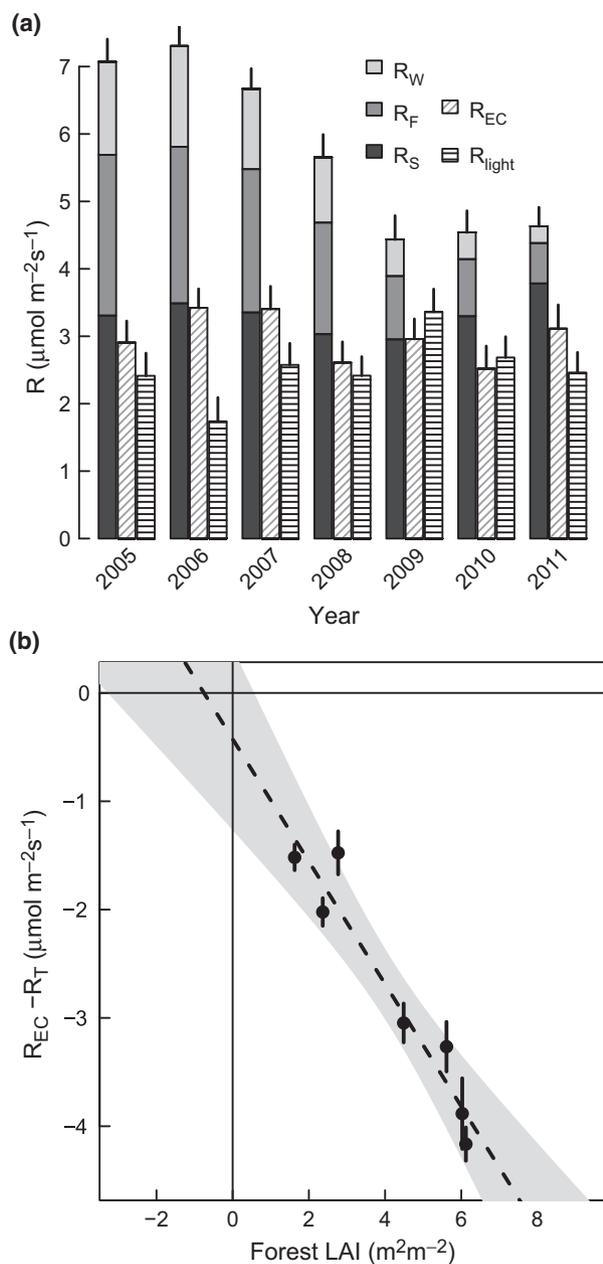
Fig. 6 (a) The difference between various estimation of R_e: chamber (R_T), nighttime EC (R_{EC}) and intercept of daytime EC light response curves (R_{light}) with SE. EC estimates of R_e (R_{EC} and R_{light}) remained constant throughout the bark beetle epidemic, and are lower than chamber estimates of soil respiration (R_S). Chamber estimates of R_e declined 35% with the beetle epidemic, a loss closely correlated with the loss of tree leaf area (LAI) (b). R_T and R_{EC} would converge at a forest LAI of -0.43 m^2 m^{-2} (±0.33). Points are the annual mean difference ($\pm$SE) between R_T and R_{EC} ($R_{EC} - R_T = -0.42 - 0.56$ LAI, shaded region is the 95% confidence interval, $r^2 = 0.92$).

bark beetle tree mortality (Morehouse *et al.*, 2008), with tree girdling in a piñon-juniper woodland (Berryman *et al.*, 2013) and in a eucalyptus plantation (Binkley

et al., 2006), but it differed from girdling studies in which soil respiration rapidly declined after girdling (50% decline, e.g. Högberg *et al.*, 2001). A lack of soil respiration response to bark beetle attack in this and other studies could be caused by (i) roots respiring stored carbohydrates for several years after beetle attack or (ii) the decline of autotrophic respiration is off-set by an increase in heterotrophic respiration from decomposition of newly fallen foliage and dead roots (Morehouse *et al.*, 2008; Berryman *et al.*, 2013). Resampling forest floor in 2011 showed that the litter fall from dead trees increased forest floor mass by 40% between 2005 and 2011 and increased litter quality as the C:N ratio dropped from 71 to 50 (H.N. Speckman, M.G. Ryan, unpublished data). In a nearby lodgepole pine ecosystem with similar tree mortality from mountain pine beetle, nitrogen in the increased litter from dead trees did not appear in streams (Rhoades *et al.*, 2013). In our study, at least some of the N from the dead foliage and needles remained within the forest ecosystem, as N was 68% more abundant in the forest floor after the epidemic (H.N. Speckman, M.G. Ryan, unpublished data). In the lodgepole pine study, the increased nitrogen increased decomposition (Rhoades *et al.*, 2013).

Exploration of uncertainty in R_{EC} (u filtering, an alternative technique for estimating R_e and energy balance) does not explain the discrepancy between R_{EC} and R_T*

Eddy covariance requires turbulence to be above a certain threshold to properly function (Goulden *et al.*, 1996; Baldocchi, 2003). At least a portion of the discrepancy between EC and chamber estimates of R_e may result from insufficient turbulence (Van Gorsel *et al.*, 2007; Aubinet *et al.*, 2010), even though most of the studies in Table 2 filtered R_{EC} values to exclude those with low u*. We investigated the possibility that the threshold empirically calculated for this study (0.2 m s^{-1}) was insufficient for estimating R_e by comparing R_{EC} under different u* filters, and R_{EC} vs. R_T with R_{EC} selected under u* filters as high as 0.7 m s^{-1} with an additional requirement that storage 'flux' be <0.4 μmol m^{-2} s^{-1}. R_{EC} proved robust to these filters, maintaining roughly the same absolute difference and correlation between the two datasets (see Table 4). While increased turbulence bought R_{EC} and R_T slightly closer, the two datasets still do not converge, providing strong evidence that insufficient turbulence above the canopy and selection of a u* filter were not responsible for the discrepancy R_{EC} and R_T.

We also explored the use of two alternatives to the u* filtering technique for estimating R_e, one that worked

Table 4 Comparison between EC and chambers insensitive to changes in u* filter

2005	
	$R_T = 0.96\ R_{EC} + 4.3$
Filter u* > 0.2 m s^{-1}	
	$R_T = 0.97\ R_{EC} + 3.6$
Filter u* > 0.7 m s^{-1}	
2011	
	$R_T = 0.79\ R_{EC} + 2.2$
Filter u* > 0.2 m s^{-1}	
	$R_T = 1.02\ R_{EC} + 0.9$
Filter u* > 0.7 m s^{-1}	

Where: R_T = Chamber estimate of R_e. Calculated from Eqn (4).
R_{EC} = Eddy covariance estimates of R_e using u* filtered nighttime data.

well in a Eucalypt forest and elsewhere (Van Gorsel *et al.*, 2007; van Gorsel *et al.*, 2008, 2009), and a light-curve method that matched R_T in a wet tropical forest (Hutyra *et al.*, 2008). The Van Gorsel *et al.* (2007) technique assumes that immediately after sunset the atmosphere is stable and advection is small compared to storage and vertical turbulent fluxes, and develops a relationship between the maximum respiration measured after sunset (R_{max}) and soil temperature for a monthly window. This relationship is used with measured soil temperature to derive a continuous estimate of R_{EC} for the ecosystem. R_{max} estimates of respiration were generally higher than u*-filtered R_{EC} values and much closer to chamber estimates of R_e (van Gorsel *et al.*, 2009). The R_{max} technique failed at this study site because (i) variability in NEE at night frequently obscured selection of a R_{max} (perhaps because the site *was* so turbulent at night); and (ii) when R_{max} values could be estimated, R_{max} had no relationship with soil temperature. The intercept of a light response curve (R_{Light}) to estimate R_e with EC flux in the day was similar to R_{EC}, did not decline with tree mortality, and did not match R_T in this study ($P > 0.1$ for all tests; Fig 6a) (Frank *et al.*, 2014).

Energy balance closure (comparison of measured net radiation with the sum of sensible + latent heat flux plus heat storage change) is frequently used as an indicator of EC data quality (Foken, 2008). Energy balance closure at this study site averaged 82% from 2005 to 2011 (Frank *et al.*, 2014), did not vary significantly from year to year or with bark beetle mortality ($t > 0.1$), and is similar to that reported in other studies (Aubinet *et al.*, 2000; Wilson *et al.*, 2002). The comparison during nighttime 30 minute periods was similar to periods in the day, but noisier ($r^2 = 0.38$ night vs. 0.72 day).

Exploration of uncertainty in R_T (chamber placement, sampling bias, model bias, and literature values for component fluxes) does not explain the discrepancy between R_{EC} and R_T

The first potential error for chamber measurements is a bias caused by physical placement of the chamber, which can alter temperature, air pressure, and diffusion gradients (Baldocchi, 2003), particularly for soil respiration (Bain *et al.*, 2005). Because the foliage measurements were taken at night, the wood measurements were on the large thermal mass of the stem, and the chambers were scrubbed with air at ambient CO_2 concentration prior to measurement, chamber bias is unlikely for these. The soil pore space can hold about a day's flux in easily disrupted storage (Ryan & Law, 2005), and CO_2 can be pulled from storage by wind and measured by EC (Bowling & Massman, 2011), and chambers might alter this wind-driven flux (Bain *et al.*, 2005). We have not directly tested this potential bias, but the chamber top included tubing to equilibrate pressure between the inside and outside of the chamber, making this bias for soil respiration less likely.

A second difficulty with chamber measurements is the difficulty in obtaining an unbiased sample for foliar respiration and wood CO_2 efflux for extrapolation on large trees. Foliar respiration varies with foliar age and throughout the canopy (Ryan *et al.*, 1996; Cavaleri *et al.*, 2008) and likely varied after the onset of mortality. We considered foliage age and light environment in our samples by measuring flux for a large sample (the distal ~15 cm of a branch) that usually included the full complement of foliage ages (older foliage receives less light as foliage develops distal to it, Schoettle, 1990). Our samples included foliage from a few beetle-infested trees (possibly attacked between the 2nd and 3rd foliage sample), but we did not analyze that factor separately. Wood CO_2 efflux can be greater at higher locations in the canopy and for smaller branches and trees (Ryan *et al.*, 1996; Cavaleri *et al.*, 2006). If so, our estimates of wood CO_2 efflux may be underestimates, particularly because we did not estimate efflux for trees <10 cm DBH. Our 84 soil respiration collars were established with a systematic sampling design and their locations should be unbiased.

CO_2 efflux rates at the tissue level for foliage and wood were comparable with other studies in boreal and subalpine forests. For example, wood CO_2 efflux per unit bark surface area was 0.4–4.2 μmol m^{-2} s^{-1} for spruce and 0.5–2.1 μmol m^{-2} s^{-1} for fir in this study, compared with 0.4–1.4 μmol m^{-2} s^{-1} for Engelmann spruce about 250 km south of these measurements (Ryan, 1990), 0.4–1.0 μmol m^{-2} s^{-1} for black spruce in boreal forests (Lavigne & Ryan, 1997; Ryan

et al., 1997), and 0.5 μmol m^{-2} s^{-1}; for Scots pine in Finland (Zha et al., 2007). Foliar respiration per leaf area was 0.3–0.5 μmol m^{-2} s^{-1} for spruce and fir in this study, compared with 0.3–0.7 μmol m^{-2} s^{-1} for boreal black spruce (Ryan et al., 1997) and 1.3 μmol m^{-2} s^{-1} for boreal Scots pine (Zha et al., 2007). Soil respiration was higher for this study (summer average of 3–3.8 μmol m^{-2} s^{-1}) than in boreal spruce (~2.5 μmol m^{-2} s^{-1}, Lavigne et al., 1997; Wang et al., 2003), but comparable for spruce-fir in Newfoundland, Canada (4 μmol m^{-2} s^{-1}, Moroni et al., 2009). R_{EC} averaged 3.0 μmol m^{-2} s^{-1}) for this study, higher than the 2.5 μmol m^{-2} s^{-1}) found in boreal spruce (Lavigne et al., 1997), but was comparable to that for Scots pine in Finland (Zha et al., 2007). The spruce-fir forest at GLEES had three times more tree biomass (150 Mg ha^{-1}) than the black spruce forests in the Lavigne et al. (1997) study (Gower et al., 1997). The greater biomass would yield larger wood, foliage, and root respiration at the GLEES site, perhaps explaining the higher R_T in this study compared to the boreal sites.

A third source of error is that the models extrapolated between measurements that were infrequent (~monthly) relative to the continuous R_{EC} record. To investigate if the difference between R_T and R_{EC} resulted from modeling error, we compared CO_2 efflux from wood, foliage, and soil taken over a 4 day period (August 7th–10th, 2011) to both R_{EC} and the chamber models [Eqns (1–3)]. The mean u* value for the three studied nights (August 7th, 9–10th) was 0.61 m s^{-1} (August 8 had u* <0.2 m s^{-1}). R_{EC} values during this time were 40% lower than observed R_T and 33% lower than modeled R_T (Figure S1), suggesting that at least for this point in time, modeling error did not cause the difference R_{EC} and R_T.

To estimate R_T for foliage and wood for trees attacked by bark beetles but not yet killed, we assumed that foliage and wood respiration rate was half that of healthy trees. We tested the impact of this assumption by comparing the R_T calculated with the 50% rate assumption with R_T estimated assuming infested trees have either zero foliage respiration or wood CO_2 efflux, or the same rate as healthy trees. R_T varied <1.0 μmol m^{-2} s^{-1} between the 0% and 100% rates for a given year, and the regression coefficients between R_T and R_{EC} values remained within one standard error of the original. We also note that soil respiration, the only chamber flux measured throughout the entire study, and with a large sample size and unbiased sample design, was larger or equal to R_{EC} throughout the study (Fig. 6a).

Potential explanation for EC-chamber discrepancy

The difference between R_{EC} and R_T estimates of R_e declined with the progression of tree mortality for bark

beetles and $R_{EC} - R_T$ was strongly correlated with tree leaf area (Fig. 6b), suggesting that the origin of this discrepancy is linked to the amount of canopy. Thick forest canopy can impede the mechanical mixing of air above the canopy and air within and below the canopy at night. If this occurs, flux measurements on top of the tower become decoupled from ground and canopy sources of CO_2, even with high u* values being recorded above the canopy (Amiro, 1990; Loescher et al., 2003; Kutsch et al., 2008; van Gorsel et al., 2011; Serafimovich et al., 2011; Thomas et al., 2013). This phenomena may be prevalent in tall forest canopies, with high leaf area, where a recent study in a tall Douglas-fir forest showed 88% of night measurements were decoupled from the tower flux measurement (Thomas et al., 2013).

Before the tree mortality from bark beetles, the site's thick canopy (effective projected LAI 6.1 m^2 m^{-2}, ±1.7 95% confidence interval) might have inhibited the mixing of air above and below the canopy, despite the site's high winds (Fig. 7). If low or intermittent mixing occurred, CO_2 from soil respiration (the largest source) and foliage and wood efflux would have moved off site without being observed by the tower-mounted EC system and profile. As the bark beetle mortality progressed and the canopy thinned (to 0.9 ± 0.3 m^2 m^{-2} in 2011), more turbulence could have penetrated through the canopy, allowing the EC system to observe proportionally more of the CO_2 sources. The lack of change in R_{EC} as tree mortality increased might be explained by the offsetting effects of a reduction in ecosystem respiration (from tree mortality) and the increase in the EC tower's ability to observe the true ecosystem respiration (because of better mixing in the thinning of canopy). Better mixing would also result in the observed convergence of chamber and EC estimates with a thinner canopy.

Turbulence during the day is also generated from convection, mostly derived from heating of the forest canopy, in addition to wind from above the canopy; with convection, air can be mixed even with a thick canopy (Fig. 7). This could explain why daytime EC estimates of A_{max} and quantum yield of photosynthesis (Φ) changed during the epidemic (Frank et al., 2014), but not nighttime R_{EC} measurements. It is uncertain why the intercept of EC light response curves (R_{light}) would not be affected by a change in forest LAI. These ideas could be explored through the installation of second EC system located below the canopy to identify coupling between subcanopy and above-canopy flux. At another site, such a system greatly improved the quality of EC measurements, and generated R_{EC} and R_T estimates of R_e within 3% of each other (Thomas et al., 2013).
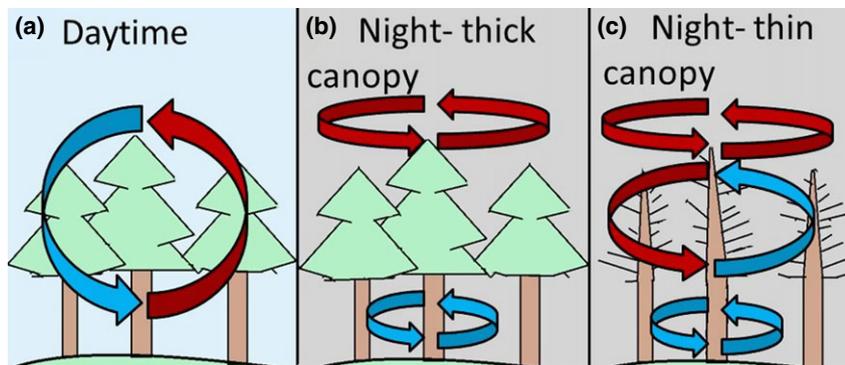
Fig. 7 Turbulence is generated by a different mechanism during the day vs. night. Blue arrows represent relatively colder carbon-rich air, and red arrows warmer carbon-poor air. During the day, (a) convective heating connects air below and above canopy. At night, turbulence is generated by above-canopy wind shear and requires mechanical mixing. A thick forest canopy (b) prevents this turbulence from mixing with the air below, decoupling flows, and much of the respiration flux can flow away via advection. A thinner canopy (c) allows some above-canopy turbulence to penetrate, resulting in partial coupling and allowing proportionally more respiration flux to be measured by the eddy covariance tower (see text for references).

A bias in chamber measurements could explain a portion of the relationship in Fig. 6b. For example, if the bias yielded an overestimate of foliar and wood respiration, then $R_T > R_{EC}$ and this inequality would widen with increasing forest LAI.

Need to quantify measurement uncertainty

Both chambers and eddy covariance are subject to many sources of error, ranging from instrument calibration to uncertainty in calculation coefficients. Error sources for chambers include IRGA calibration, chamber volume, estimation leaf and sapwood volume, and allometerics used for upscaling (Lavigne *et al.*, 1997; Davidson *et al.*, 2002; Loescher *et al.*, 2006). In addition to advection and lack of nighttime turbulence, eddy covariance error sources include IRGA calibration, measurements of wind speed, turbulence sampling error, and footprint spatial variability (Hollinger & Richardson, 2005; Oren *et al.*, 2006; Aubinet *et al.*, 2012). Formal analysis of all these errors is seldom performed and is difficult using traditional statistical techniques. New Bayesian statistical techniques have enabled the successful quantification of these errors (Hollinger & Richardson, 2005; Lasslop *et al.*, 2010) and is recommended for EC and chamber estimates of R_e.

Implications

EC is a powerful and widely adopted technique for measuring ecosystem fluxes, and has generated a substantial improvement in understanding of the response of carbon and waster fluxes to the environment and to disturbance. However, many findings have relied on the u* filtering and gap-filling techniques for estimates

of R_e used to estimate seasonal or annual sums of carbon flux, to make inferences about the environmental and vegetation controls over R_e, and to derive estimates of ecosystem photosynthesis. The discrepancy between chamber and EC estimates of R_e should be resolved before confidence can be attained in the true measurement of ecosystem carbon flux and its components. Knowledge of the true ecosystem fluxes will greatly advance scientific understanding of local carbon cycling, allow for more accurate carbon budgets, and improve the development of global ecological models.

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