THESIS

FOREST RESPIRATION FROM EDDY COVARIANCE AND CHAMBER MEASUREMENTS UNDER HIGH TURBULENCE AND A BARK BEETLE EPIDEMIC

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ABSTRACT

FOREST RESPIRATION FROM EDDY COVARIANCE AND CHAMBER MEASUREMENTS UNDER HIGH TURBULENCE AND A BARK BEETLE EPIDEMIC

Eddy covariance (EC) enables continuous estimates of carbon, water, and energy fluxes, and a global network of >500 sites (www.fluxnet.ornl.gov) has resulted in major advances in understanding ecosystem-scale biogeochemical cycling. However, long-term sums of net ecosystem exchange, photosynthesis and respiration fluxes have uncertainties because of potential measurement biases in respiration fluxes at night. Many studies have demonstrated that EC estimations of flux during the night are lower than chamber measurements—with low turbulence at night potentially causing the difference. A bark beetle outbreak at the GLEES Ameriflux site provided a unique opportunity to compare chamber and EC estimates of ecosystem respiration (R) under conditions of high turbulence (summer night mean u* = 0.7 m s^{-1}) and 85% mortality of the aboveground respiring biomass due to a bark beetle epidemic.

Chamber-based estimates of R were developed from periodic foliage, wood and soil CO_2 efflux measurements fit to models of phenological seasonal change and diurnal temperature response. These models estimated ecosystem mean nightly respiration to have declined 32% after the bark beetle epidemic (7.0 ±0.22 μmol m^{-2} s^{-1} in 2005 to 4.8 ±0.16 μmol m^{-2} s^{-1} in 2011). The decrease was entirely due to the loss of aboveground respiration, soil efflux remained constant throughout the epidemic.

Unlike chamber estimates, nighttime EC measurements did not decline after 85% of the forest basal area had been infested or killed by bark beetles, mean nighttime NEE of 3.0 μmol

m^{-2} s^{-1} for 2005 and 2011. These EC values were significantly lower than chamber estimates of respiration for the same time periods (58% lower in 2005, and 34% in 2011). Despite the large difference in values, the two estimates of R were correlated (yearly r^2 ranging from 0.18-0.60).

This study suggests that the traditional discrepancy of nighttime EC and chamber estimates of ecosystem respiration are not caused by insufficient turbulence (results proved robust to extreme u* filter > 0.7 m s^{-1}). Other sources of error are investigated for both techniques. To further explore this discrepancy, we suggest the installation of a second EC system below the canopy to improve understanding of air flows and fluxes throughout the ecosystem. This discrepancy must be resolved before scientific confidence can be attained in the true value of ecosystem carbon flux.

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TABLE OF CONTENTS

Contents

List of Tables vii

List of Figures viii

Introduction 1

Study area and methods 4

Study area 4

EC data collection and processing 5

EC footprint and forest mortality 6

Overview of chamber measurements 7

Chamber measurements of efflux from woody tissues 8

Chamber measurements of foliar respiration 9

Chamber measurements of soil efflux 10

Modeling observed chamber fluxes 11

Results 13

Bark beetle forest mortality 13

Chamber respiration measurements 14

EC and comparison to chambers 16

Discussion 16

Ecological implications of chamber measurements 16

Comparison of chamber and EC estimates of R 17

Possible source of errors in measurements 19

Potential explanation for EC-chamber discrepancy 21

Implications and future directions 22

References 37

Appendix A: Approximation EC Footprint and Mortality Survey 45

LIST OF TABLES

List of Tables

Table 1: List of studies documenting EC estimates of R being lower than chamber estimates.31

Table 2: Summary chamber measurements 32

LIST OF FIGURES

Figure 1: Repeat photography from the GLEES EC 33

Figure 2: Forest basal area at GLEES. 34

Figure 3: Observed and modeled efflux from woody tissues (r_W) 35

Figure 4: Observed and modeled foliar respiration (r_F) 36

Figure 5: Observed and modeled soil efflux rates (R_S). 37

Figure 6: Modeled respiration from chambers 38

Figure 7: Time series of nightly R as estimated by EC and chambers 39

Figure 8: Comparison of mean nightly R, as estimated by chambers and EC 40

Figure 9: Energy balance closure 41

Figure 10: Comparison of methods 42

Figure 11: Forest LAI vs. the difference between chamber and EC estimates of R 43

Figure 12: Air flow within a forest in daytime versus night 44

Figure 13: A map of GLEES: mortality plots, prevailing Winds, and suggested footprint 46

Figure 14: Comparing Mortality Surveys. 48

Figure 15: Forest biometrics specific to 'Ryan in Footprint' over time 50

Introduction

Each year, global terrestrial ecosystems sequester 2.3 GT of carbon, roughly 26% of annual anthropogenic global carbon emissions (Le Quere *et al.*, 2009). The net gain of carbon by an ecosystem is determined by two opposing processes: photosynthesis, which assimilates carbon into plant tissues, and respiration, which releases carbon back into the atmosphere. Whether an ecosystem is a net sink or source of carbon is primarily determined by respiration. (Valentini *et al.*, 2000). Despite this importance, respiration is less studied than photosynthesis and there are numerous uncertainties in its measurements (Valentini *et al.*, 2000). Two techniques are commonly used to estimate ecosystem respiration (R): eddy covariance (EC) and chamber measurements. Estimates from these two techniques can be directly compared at night, when both techniques should provide similar values and mutual validation (Goulden *et al.*, 1996). But, across the globe such comparisons have consistently observed that EC estimates of R are ~30% lower than values reported by chambers (see Table 1).

Eddy covariance is a micrometeorological technique that relies on turbulent air flows to measure the net ecosystem exchange (NEE) over a large area (>1 km^2) by quantifying three dimensional turbulent fluxes in rapid succession (10-20 Hz, Massman and Lee, 2002). This flux data is collected on top of a tower above the canopy, is highly variable over short time periods, and is generally assessed over 30 minute intervals for study. EC has gained popularity over the last 20 years due to its ability to measure total ecosystem fluxes nearly continuously (Goulden, 1996; Baldocchi, 2003). Currently there are >500 EC towers established across the globe, providing information from a wide variety of ecosystems (www.fluxnet.ornl.gov). This network has improved scientific understanding of the response of ecosystem carbon fluxes to the environment and disturbance (Law *et al.*, 2002; Baldochhi *et al.*, 2003; Amiro *et al.*, 2010).

Chambers measure fluxes over small areas (< 1 m^2) and then extrapolate to a larger area (Lavigne *et al.,* 1997). For a measurement, a chamber encloses or is attached to a biological substrate (such as a leaf), then a flux is calculated from the change in carbon dioxide concentration within the chamber over time. Through repeatedly measuring the major sources of carbon flux and how flux varies within an ecosystem, R can be estimated. Major sources of respiration in a forest are from live woody tissues (such as tree boles, branches, and roots), live foliage, and from the soil (live roots, mycorrhizae, and heterotrophic decomposers, Lavigne *et al.,* 1997). By studying these components separately, chamber measurements provide spatial resolution of fluxes and attribute changes in these fluxes to drivers such as soil temperature and moisture, as well as light quality and quantity. Disadvantages of chambers are their high labor demands, limited spatial/temporal sampling scales, and issues in extrapolation to ecosystem scale (Baldochhi *et al.,* 2003).

EC and chamber measurements should generate similar numbers, but studies in a variety of ecosystems reported u* filtered EC estimates of R that were significantly lower than R estimated by chambers. For example, EC estimates of respiration with u* > 0.2 m s^{-1} 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 EC and chamber respiration estimates (r^2 = 0.62, Bolstad *et al.,* 2004). Similar results were described in Chinese temperate forests (Wang *et al.,* 2010), eucalyptus forest in the Australian highlands (Keith *et al.,* 2009), managed meadows in the European Alps (Wohlfahrt *et al.,* 2005), North American semi-arid grasslands (Myklebust *et al.,* 2008) and Brazil's Amazon rainforest (Chambers *et al.,* 2004).

Numerous studies worldwide have documented EC estimates of R being systematically lower than chamber estimates, even after u* (friction velocity) filtering (Table 1).

A suspected cause of the disagreement between the chamber and EC measurements may occur when EC data is collected during calm nights (Goulden *et al.,* 1996; Baldocchi, 2003). EC only measures fluxes at one point (the tower) which is assumed to be representative of an entire ecosystem, and is based on the theory that in a well-mixed atmosphere any two points in space are similar. During the daytime the atmosphere is better mixed than during the night: the land is heated, causing the surface air (and fluxes) to mix constantly with the air above and be recorded by the tower's EC instrumentation (Masssman and Lee, 2002). However, at night there is no convective heating from the surface and in the absence of mechanical mixing, CO_2 produced near the ground may flow downhill via advection. 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 *et al.,* 2008).

The traditional method for dealing with a lack of turbulence in EC is a procedure known as u* filtering, in which all measurements taken below a certain friction velocity threshold are removed and then replaced via gapfilling (Goulden *et al.,* 1996). Limitations of u* filtering are heavily discussed in the literature (Ruppert *et al.* 2006; van Gorsel *et al.,* 2007; Audient *et al.,* 2008). Selection of the u* threshold is empirical (Gu *et al.,* 2005) and a small variation in u* can change the measurements from registering as a carbon sink to a carbon source (Miller *et al.,* 2004; Ruppert *et al.,* 2006). By u* filtering, most sites lose ~50% of their nighttime EC values, causing further uncertainty of the true nighttime flux (Feigenwinter *et al.,* 2004; Misson *et al.,* 2007; Gockede *et al.,* 2008).

This study compared EC and chamber measurements at the windiest EC site in North America (annual mean u* value of 0.9 m s^{-1}) to determine if the two data sets would converge under highly turbulent conditions (www.fluxnet.ornl.gov). If advection and a lack of turbulence is the cause of the discrepancy between EC and chambers, then the two measurement types should be roughly equal in this highly turbulent environment. In addition, fluxes were studied before, during, and after a bark beetle epidemic killed majority of the tree basal area (Figure 1), generating a major shift in R, and also likely changed the coupling between turbulence at night and the air surrounding respiration sources.

Study area and methods

Study area

Glacier Lake Ecosystem Experimental Site (GLEES) is a sub-alpine 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) is maintained by the Rocky Mountain Research Station, a branch of the US Forest Service (Musselman, 1994). GLEES has a mean annual temperature of -2 °C and a mean annual precipitation of 1000 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).

EC data collection and processing

The GLEES Ameriflux EC tower was constructed in 2004 to record micrometeorological data and estimate ecosystem fluxes (Frank *et al.*, in prep.). The tower is 28 m tall, with 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). Wind speed and direction were measured using a sonic anemometer (model SATI/3Vx, Applied Technologies, Inc., Longmont, CO, USA). Mean annual u* is 0.94 m s^{-1}, higher than any other North American tower (www.fluxnet.ornl.gov). 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.*, in prep.).

At GLEES, net ecosystem exchange (NEE) of carbon, water, and energy are calculated from the sum of vertical flux (eddy covariance) and changes in 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). Canopy storage of CO_2 was measured with a vertical profile of CO_2 concentration, measured at 8 different heights using a closed path IRGA (LI-6262, Li-Cor Biosciences, until August 2008, then a LI-7000, Li-Cor Biosciences). Data from the Li-Cor 7500 were collected at a frequency of 20 Hz and compiled into 30 minute statistics for study (Frank *et al.*, in prep). Each location on the profile was measured once a minute.

EC becomes unreliable during conditions of low-turbulence, (Goulden *et al.*, 1996), hence this study only used data collected while the atmospheric friction velocity (u*) was >0.2 m s^{-1} (Gu *et al.*, 2005). For comparison of EC and chamber estimates of R, nightly (PAR < 2 μmol m^{-2} s^{-1}) averages of NEE collected during the snow-free summer nights (July 1st to October 1st) from 2004 to 2011when mean u* was >0.2 m s^{-1} 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

Eddy covariance assumes that the fluxes observed by the tower originate from the ecosystem upwind of the tower, known as the EC footprint (Massman and Lee, 2002). Since the majority of the winds observed by the tower originate from the west, I assumed that the footprint was within a pie-shaped wedge extending 1 km to the west. Derivation of the probable eddy covariance footprint is given in Appendix A.

The forest within the footprint was surveyed to estimate stand basal area, leaf area, and bark beetle mortality. In 2004, 36 circular survey plots (each 201 m^2) and arranged into 9 clusters were established (Bradford *et al.*, 2008). Carbon pools and fluxes were quantified, accounting for carbon in live vegetation, dead wood, and soil to a depth of 30 cm, and the fluxes annual litter fall and wood net primary production. Trees with a diameter >10 cm at height of 1.37 m were tagged and each tree's species, height, diameter at 1.37 m, and health were measured (Bradford *et al.*, 2008).

Of the 36 plots established in 2004, 24 of them are found within the probable eddy covariance footprint and contribute to the fluxes observed by the tower. From these 24 plots, forest basal area, species composition, and biometrics were calculated. Allometric equations were used to compute tree leaf area, live and tree biomass, standing dead tree biomass, sapwood volume, and growth increment (Kaufmann and Troendle, 1981; Kaufmann and Troendle, 1982; Ryan, 1990).

Mortality from the epidemic was documented by repeating the original 2004 forest survey annually from 2009 to 2011. Bark beetles are endemic to the study site, but in 2008 their populations rose to epidemic levels, and killed majority of the overstory trees (85% of tree basal area, Figure 2; Frank *et al.*, in prep.). Trees with a DBH >10 cm as 'infected' 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 2006-2008, dendrochronology data (Frank et al., in prep.) was used to estimate mortality for those years (Appendix A).

Overview of chamber measurements

Nearly all chamber measurements were taken using a closed-system approach (Field *et al.*, 1991). For each measurement, a chamber was attached to a biological substrate (such as a leaf), tubing connected the chamber to a portable infrared gas analyzer (IRGA) which measured the increase in CO_2 over time. For woody and foliage measurements, air was pumped throughout system prior to measurement to check chamber-substrate seal integrity. 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, 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 outlet air tubing with many small holes to mix the chamber air).

Fluxes were calculated from the linear change in CO_2 concentration over time (~60 secs) in a known volume of air (Field *et al.*, 1991). Linear regression was almost always used for this

calculation, but on rare occasions an exponential curve better fit the data and was used. All regressions were required to have an r^2>0.98 for the fluxes to be included in this study. A few measurements of wood CO_2 efflux used an open-system configuration to estimate flux (Field *et al.*, 1991).

Chamber measurements of efflux from woody tissues

Chamber measurements of CO_2 efflux from living wood were taken three times during the summer 2010, and five times summer 2011. In spring 2010, twenty live tree stems were selected for repeated measurements, equally divided between Engelmann spruce and subalpine fir, and representing a variety of ages, diameters, position within the canopy, and beetle infestation. In 2011, five of these tree stems were replaced because the trees died. Wood CO_2 efflux from dead trees was measured on four boles (two fir and two spruce) in 2010 and 2011. All trees were located within 100 m of the EC tower.

To measure CO_2 efflux from wood, a portion of the dead outer bark that would be under the chamber plate was removed, and a 7x10 cm aluminum plate attached with putty to the smoothed inner bark at ~1.3 m height. These plates remained attached to the tree from summer 2010 through autumn 2011. For a measurement, a 250 mL clear polycarbonate chamber was temporarily strapped to the neoprene gasket on the surface of the aluminum plate and checked for leaks. 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 ($\mu mol\ m^{-3}$ of sapwood s^{-1}), and the sapwood volume underneath each gasket was calculated using allometeric equations and geometric formulas for a cylinder and wedge (Kaufmann and Troendle, 1982; Ryan, 1990).

Chamber measurements of foliar respiration

Foliar respiration was measured on ten intact branches at night once during the summer of 2010, and of sixteen branches three times during the summer of 2011 (repeated measurements on same branches). Measured branches included a range of foliage ages including new growth, were ~30 cm long, ~1 cm diameter, with about ~350 cm^2 of projected leaf area, and equally divided between fir and spruce. Branches represented a diverse range of tree sizes, health statuses, and light positions, even for trees sampled near the ground. In 2010, five branches were located at a height of 5-15 m and accessed from the EC tower. The remaining 5 branches in 2010 and all of the 2011 branches were located at a height of 2-3 m on trees within 100 m of the EC tower.

Foliar respiration of each branch was measured at night over a 60 sec interval after the increase in measured CO_2 concentration was linear. Foliage chambers were constructed of clear polycarbonate, rectangular in shape, and split length-wise into two equally sized halves. Studied branches were placed into a small semi-circle indentation (2 cm diameter) built into one end of the chamber (with putty creating an air-tight seal around the branch base), and the two halves were clamped together with a neoprene gasket to fully enclose and seal the branch. In 2010, 5 L chambers were used (each half 30 x 15 x 7.5 cm), and in 2011 these chambers were replaced by smaller 3 L chambers (each half 30 x 15 x 2 cm), yielding less system volume for a greater change in CO_2 concentration. Leaf temperatures were measured with an infrared thermometer and air temperature were measured at the top of the EC tower for extrapolation. Measurements were taken over a ~60 second period and fluxes expressed by leaf area (flux μmol m^{-2} of projected LAI s^{-1}).

At the end of each summer, branches were harvested and leaf area measured using a volume displacement method (Chen, 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 hours of cutting, foliar respiration was again measured in the laboratory at 22°C. Temperature curves response were tested on a subset of 5 branches (3 spruce and 2 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 minutes prior to each measurement.

Chamber measurements of soil efflux

Soil efflux was measured before, during, and after the peak bark beetle induced mortality using survey chambers throughout the footprint and long-term chambers located near the EC tower. For survey measurements, in 2004, 108 collars were permanently installed in the 36 plots located west of the eddy covariance tower (previously described in section "EC footprint and forest mortality"). However, only 84 of these collars were found to be within the probable EC footprint and were used for soil efflux model construction. 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 a 60 second measurements. Soil efflux at each collar was measured ~3 times per summer in 2004-2006 and 2009-2011 using a Li-Cor L1-820 (Li-Cor Biosciences, Lincoln, Nebraska). Soil temperature was measured at 10 cm depth using a Tee Style Penetration Probe (Omega Engineering, Stamford, CT, USA) and soil moisture was measured at 10 cm depth in 3 different spots near the collar (HydroSense, Campbell Scientific, Logan, UT, USA). Volume within each collar was calculated as the sum of

the chamber volume and space between the top of collar and soil's surface (a space measured 2-3 times per season to account for soil shifting). Fluxes were expressed as μmol m^{-2} of ground area s^{-1}. Soil efflux was not measured from collars containing standing water.

Modeling observed chamber fluxes

After repeated chamber measurements, fluxes for each ecosystem component (woody tissues, foliage, and soils) were modeled using linear regression of log-transformed fluxes. Model quality was evaluated using AIC and r^2, investigating the effects of substrate temperature, moisture, time of year, tree species, and health status.

Efflux from woody tissues displayed strong seasonal variability was modeled with linear regression on a log scale:

$$r_W = \exp(w_A + w_B D + w_C D^2 + w_D S) \quad \text{(Equation 1)}$$

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 specific variable, and w_A- w_D are model coefficients. To convert r_w to units of flux per ground area:

$$R_W = V r_W \quad \text{(Equation 2)}$$

where is R_W woody respiration per ground area (μmol m^{-2} s^{-1}), V is the average living sapwood volume per ground area (cm^3 m^{-2}), and r_W is woody respiration per sapwood volume (μmol m^{-3} of sapwood volume s^{-1}) (Ryan, 1990; Sprugel, 1990; Lavigne *et al.*, 1997). R_W was estimated on a continuous time scale for the entire footprint using Equations 1-2, estimates of forest species composition (S) and average sapwood volume (V) as provided by the annual forest inventory survey (see section "EC and Forest Mortality"), and sapwood temperature was measured using a thermocouple inserted ~3 cm into the tree outside the chamber plate. As bark beetles infect

sapwood with blue-stain fungus, this study estimated that wood CO_2 efflux from beetle infested trees to be 50% of uninfected trees (likely an overestimate).

Foliar respiration was related to air temperature and modeled using linear regression of log transformed flux values:

$$r_F = \exp(f_A + f_B T_A) \quad \text{(Equation 3)}$$

where r_F is foliar respiration per project leaf area (μmol m^{-2} of LAI s^{-1}), T_A is air temperature (°C) as observed by the EC tower, and f_A- f_B are model coefficients. Equation 3 is a mathematically equivalent to the commonly used Q_{10} equation (Lloyd and Taylor, 1994). To convert r_f to units of flux per ground area:

$$R_F = LAI\ r_F \quad \text{(Equation 4)}$$

where is R_F foliage respiration per ground area (μmol m^{-2} s^{-1}), LAI s the average projected leaf area (m^2 m^{-2}), and r_F is foliar respiration per project leaf area (μmol m^{-2} of LAI s^{-1}) (Lavigne *et al.*, 1997). R_F was estimated on a continuous time scale for the entire footprint using Equations 3-4, and continuous measurements of T_A were provided by the EC tower. Forest LAI was estimated from the annual forest inventory survey. Bark-beetle infested trees retain needles for ~2 years after infection, but with greatly impaired physiology (Frank *et al.*, in prep.). To capture this effect, foliar respiration for beetle infested trees were modeled to have 50% of the rate of uninfested trees.

Soil respiration was modeled to capture the effects of soil temperature and moisture using linear regression:

$$R_A = s_A + s_B T_S + s_C \theta \quad \text{(Equation 5)}$$

where R_A is soil respiration per ground area (μmol m^{-2} s^{-1}), T_S is soil temperature (°C), θ is percent volumetric water content, and s_A- s_C are model coefficients. To represent the entire EC

footprint, Equation 5 was fit using mean values of R_S, T_S, and θ observed during each field session from the 84 soil collars. Soil respiration (R_S) is already in units of flux per ground area ($\mu mol\ m^{-2}\ s^{-1}$) thus requires no unit conversion. To estimated R_S on a continuous time scale, Equation 5 was used with continuous measurements of soil temperature (T_S) and moisture (θ) from probes buried at 10 cm depth near the EC tower.

After fluxes from woody tissues, foliage, and soils were individually modeled, standardized to units of $\mu mol\ m^{-2}\ s^{-1}$, and estimated on continuous time scale, they can be summed together to estimate total ecosystem respiration according to chambers (R_T):

$$R_T = R_W + LAI\ R_F + R_S \qquad \text{(Equation 6)}$$

Chamber estimates of R_T were compared u*-filtered EC estimates (R_{EC}). Statistical analysis included an assessment of the absolute difference, and linear regression between the two data sets to search for trends.

Results

Bark beetle forest mortality

From 2008 to 2011, the spruce beetle and other mortality resulted in the death of 61% of the forest basal area (40 $m^2\ ha^{-1}$, Figures 1 and 2). An additional 24% of forest basal area (15 $m^2\ ha^{-1}$) was infested by bark beetles but still retained their needles; these trees have severely impaired physiology (Frank *et al.* in prep.), likely respire little, and will die completely in 1-2 years.

In 2011, only 15% of the forest basal area (10 of 65 $m^2\ ha^{-1}$) remained alive or uninfested by bark beetles. Trees which survived the bark beetle epidemic are smaller than their predecessors (mean stand DBH in 2005 was 24.5 cm, versus 18.2 cm in 2011). Healthy

sapwood volume decreased from 340 cm^3 ha^{-2} in 2005 to 22 cm^3 ha^{-2} in 2011 (7% of the original). Healthy projected leaf area similarly decreased from 9.7 m^2 m^{-2} in 2005 to 1.4 m^2 m^{-2} in 2011 (14% of the 2005 values). These estimates of forest mortality within the footprint were confirmed by two other independent surveys in the same area, described in Appendix A.

Chamber respiration measurements

Observed efflux rates from woody tissues (r_W) increased until the end of July and decreased afterwards (Figure 3), a pattern attributed to seasonal changes in tree growth and photosynthetic activity (Ryan, 1990). This trend was similar in 2010 and 2011, and modeled using Equation 1 (r^2 =0.68, *n*=146; see Table 2). Firs were observed respire more per unit sapwood volume than Engelmann, but had less sapwood per tree basal area. For this study, I did not measure diurnal variation of CO_2 flux with sapwood temperatures, however seasonal changes in sapwood temperature were not a significant predictor of r_W after accounting for seasonal trends. Respiration from dead tree boles was found to be zero (39 measurements on 4 trees).

Foliar respiration (r_F) varied with temperature, but temperature corrected foliage respiration did not vary across season (Equation 2, r^2 = 0.64, n=85, Figure 4). For every 10°C increase in air temperature, r_F is multiplied by 2.7 (i.e. Q_{10} = 2.7, ± 0.2). Observed foliar respiration per leaf area did not differ between firs and spruces.

Observed soil efflux (R_S) was influenced both by responses to temperature and soil moisture (Figure 5), as modeled by Equation 3 (r^2 = 0.85, n=1282). Model fit was substantially better using this linear temperature response instead of exponential Q_{10}. Observed 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.

Equation 6 combined the component fluxes (woody tissues, foliage, and soils) to estimate mean summer nightly respiration (R_T). R_T was modeled all years (2005-2011), however the paper's discussion focuses on the comparison on 2005 and 2011, as representative years of pre-beetle and post-beetle forest conditions.

The total ecosystem mean summer nightly respiration (R_T) was estimated to have declined 32% following the bark beetle epidemic; from 7.0 μmol m^{-2} s^{-1} (±0.22) in 2005 to 4.8 μmol m^{-2} s^{-1} (±0.16) in 2011. This decrease was entirely due to the loss of aboveground biomass; efflux from woody tissues (R_W) declined 72% after the epidemic (4.8 ±0.16 μmol m^{-2} s^{-1} in to 2005 to 4.8 ±0.16 μmol m^{-2} s^{-1} in 2011). Foliage respiration (R_F) similarly declined 74% (4.8 ±0.16 μmol m^{-2} s^{-1} in to 2005 to 4.8 ±0.16 μmol m^{-2} s^{-1} in 2011).

In contrast to the aboveground ecosystem components, soil efflux rates (R_S) did not decrease due to the bark beetle epidemic. Modeled mean R_S for 2011 was higher than 2005's values (3.3 μmol m^{-2} s^{-1} in 2005 vs 3.8 μmol m^{-2} s^{-1} in 2011). This increase was not the result of bark-beetle mortality, but rather record-breaking amounts of precipitation during the 2011 water year (250 cm, 4.5 standard deviations greater than the mean of 135 cm). A normal precipitation year after bark beetles (2010), displayed R_S was similar to pre-beetle years (summer nighttime mean 3.3 μmol m^{-2} s^{-1} for both years).

In the 2005 healthy forest, 20% (±0.5 standard error) of R_T was estimated to originate from woody tissue efflux, 32% (±0.6) from foliage respiration, and 48% (±0.5) from soils. These proportions are similar to those found in other studies (Lavigne *et al.*, 1997). In 2011, only 8% (±0.3) of R_T came from woody tissues, 12% (±0.4) from foliage, and the remaining 80% (±0.5) from soils.

EC and comparison to chambers

Unlike chamber estimates, nighttime EC measurements did not decline after 85% of the forest basal area had been infested or killed by bark beetles (F-test, $p > 0.5$), with a mean nighttime NEE of 3.0 μmol m^{-2} s^{-1} for both 2005 and 2011. However, the daytime EC values did reflect the epidemic: analysis of light-response curves reveals a 50% decline in maximum CO_2 assimilation rates (A_{max}) and quantum yield of photosynthesis (Φ) (Frank *et al.*, in prep.). Using Bayesian analysis, daytime EC data was able to correctly approximate the degree of bark beetle mortality independent of actual forest inventories (Frank *et al.*, in prep.).

Our EC tower consistently estimated R values much lower than those estimated by chambers (Figures 7 and 8). In 2005, before the bark beetle epidemic, EC estimated R to be on average 58% lower than chamber estimates (±0.10 standard error; summer nighttime means of 2.9 ±0.17 and 7.0 ±0.22 μmol m^{-2} s^{-1}, respectively). In 2011, EC estimates were only 34% lower than chambers (±0.02 standard error; summer nightly means of 3.1 ±0.15 and 4.7 ±0.18 μmol m^{-2} s^{-1}, respectively).

Despite the large difference in absolute values, the two estimates of R were correlated (yearly r^2 ranging from 0.18-0.60) with a slope ~0.9. After 85% of the aboveground biomass was killed or infected by bark beetles, R estimated from chamber measurements decreased by 32%, with no change in EC estimates of R (Figures 7 and 8).

Discussion

Ecological implications of chamber measurements

Chamber measurements enable scientists to see how individual ecosystem components react to environmental factors and disturbances. Following the bark beetle outbreak, respiration

from woody tissues and foliage declined an estimated 72% and 74% due to loss of healthy sapwood and foliage. Standing dead tree boles had no measurable efflux; decomposition of standing aboveground dead wood will likely remain negligible until the trees fall (Harmon *et al.*, 2011).

Unlike the aboveground components, observed soil efflux did not decline after the bark beetle epidemic. This result was consistent with another study of soil efflux after a bark beetle outbreak (Morehouse *et al.,* 2008), but different than girdling studies in which soil efflux declined 50% after tree death (Hogberg *et al.*, 2001). It is hypothesized that soil efflux remained steady because respiration loss from autotrophic sources (lack of new photosynthate) was compensated by the increase in respiration from heterotrophic sources (decomposition) (Morehouse *et al.*, 2008; Berryman, 2012). Forest mortality provided soil heterotrophs with an abundance of high quality litter and dead roots for decomposition. During the epidemic, litter fall from dying trees increased forest floor mass by 40%. Litter quality also increased with the influx of fresh needles as the C:N ratio dropped from 60 to 49. Nitrogen from this litter has not appeared in streams (Rhoades *et al.,* 2013), but remains within the forest ecosystem: N was 20% more abundant in the forest floor after the epidemic. The boost of nitrogen facilitated both forest regrowth and decomposition (Rhoades *et al*., 2013).

Comparison of chamber and EC estimates of R

Chambers and EC are two methods for estimating the true ecosystem respiration (R) and should generate similar numbers. However, this study yielded EC estimates of R significantly lower than chambers (Figure 7 and 8). Despite the large difference in absolute values, R estimates from chambers and EC were well correlated within each year (Figure 8). This

correlation suggests that both methods detect a similar response to environmental and phenological changes, despite the absolute difference in measurement values. This study sought to determine the origin of this difference.

It has been hypothesized that the discrepancy between EC and chambers estimates of ecosystem respiration is the product of insufficient turbulence. Eddy covariance requires turbulence to be above a certain threshold to properly function (Goulden *et al.,* 1996; Baldocchi, 2003). The threshold empirically calculated for this study was 0.2 m s^{-1}. However, to investigate the possibility of this threshold being insufficient, u* filters as high as 0.7 m s^{-1} were used in conjunction with filters requiring CO_2 canopy storage to be < 0.4 µmol m^{-2} s^{-1}. Initial results proved robust to such filters, maintaining roughly the same absolute difference and correlation between the two data sets (in 2005, u*>0.2 m^{-2} s^{-1}: Chambers = 0.94 EC + 4.2; u*>0.7 m^{-2} s^{-1}: Chambers = 0.94 EC + 3.5. In 2011, u*>0.2 m^{-2} s^{-1}: Chambers = 0.82 EC + 2.2; u*>0.7 m^{-2} s^{-1}: Chambers = 0.99 EC + 1.0). This suggests that insufficient turbulence above the canopy and u* filtering are not responsible for the discrepancy between EC and chamber estimates of ecosystem respiration.

An alternative to u* filtering technique (van Gorsel *et al.,* 2007) was attempted for this study but failed to reconcile EC and chamber estimates. This technique assumes that during early evenings the atmosphere is stable and advection is relatively small compared to storage and vertical turbulent fluxes. A relationship between early evening respiration maximum (R_{max}) and soil temperature is used to derive a temperature response function for the ecosystem. These estimates of respiration are generally higher than u*-filtered EC values and much better correlated to chamber estimates of respiration (van Gorsel *et al.,* 2009). This technique failed at this study site because 1) the noise in the nightly NEE frequently obscured selection of a R_{max}

and 2) when R_{max} values could be estimated, R_{max} had no relationship with soil temperature, so that ecosystem respiration could not be estimated.

Energy balance closure is frequently used as an indicator of EC data quality (Foken, 2008). Energy balance closure at this study site averaged 75% from 2005 to 2011 (Figure 9), did not vary significantly from year to year, and did not change with bark beetle mortality. Closure during nighttime 30 minute periods were similar to daytime periods, but had a much lower r^2 than during the day (0.38 night vs 0.72 day). This uncertainty is due to the smaller energy terms observed at night, resulting in a high noise-to-signal ratio.

Possible source of errors in measurements

This study's estimates of ecosystem respiration are higher than those typically reported for a subalpine forest (compare to Lavigne *et al.*, 1997; Ryan *et al.*, 1997; Zha *et al.*, 2007). How could a healthy forest be releasing so much carbon during the night and still manage to be a net carbon sink? Other studies have attempted to close the carbon budget and demonstrated chamber estimates of photosynthesis to be higher than daytime EC. Such measurements and modeling were not done with this study.

The first possible source of error in chamber measurements is a bias caused by physical placement of a chamber on a substrate, which can alter local variables such as temperature, air pressure, and diffusion gradients (Baldochi *et al.*, 2003). This study attempted to minimize these effects (see methods section), however it is still possible that the chambers' presence were affecting the measurements, both in this study and in others.

The second difficulty with chamber measurements is the inherent uncertainty of modeling between measurement sessions and possible model deviation from the true value.

Numerous things were not included in the simple respiration models described here (Equations 1-6), including variation of foliar respiration throughout the canopy (Ryan *et al.,* 1996), the difference in foliar respiration before versus after the epidemic (Brown *et al.*, 2010), or the respiration from trees <10 cm DBH.

To investigate if the difference between chambers and EC was a product of modeling error, respiration measurements of woody tissues, foliage, and soils were taken over a narrow 4 day period (Aug 7th-10, 2011). After extrapolating to ecosystem scale (Equations 2 and 4) and adjusting soil respiration (R_S) to colder nighttime soils, these chamber observations were directly compared to EC data and modeled chamber values (R_T). Comparison of observed and modeled chamber rates showed similar values (Figure 10), demonstrating the relative accuracy of the modeling process. Mean EC values were calculated from nights where u* was greater than 0.2 (which excluded the night of August 8th). The mean u* value for the three studied nights (Aug 7th, 9-10th) was 0.61 m s^{-1}. Mean nighttime EC values during this time were ~33% lower than observed and modeled chamber numbers, suggesting that the difference between chamber and EC estimates was not the product of faulty modeling.

An assumption made in this study was that trees infested with bark beetles respire 50% less than healthy trees. A sensitivity analysis was performed on this assumption. The model was run assuming that infested trees don't respire at all, and then run again assuming that infested trees respire at the same rate as healthy trees. Modeled ecosystem respiration (R_T) was insensitive to such changes: R_T values varied <1.0 μmol m^{-2} s^{-1} between the two extremes. The regression coefficients between chamber R_T and EC values remained within one standard error between the two extremes.

Potential explanation for EC-chamber discrepancy

The difference between EC and chamber estimates of ecosystem respiration cannot be easily be explained by u* filtering or modeling uncertainties. However, the difference was related to forest LAI (Figure 11), suggesting the origin of this discrepancy is linked to the amount of canopy. The presence of thick forest canopy can limit the mechanical mixing of air above and below the canopy at night. Instrumentation on top of the tower then becomes decoupled from ground-based sources of carbon during 88% of nighttime measurements (Thomas *et al.*, 2013), even with high u* values being recorded above the canopy (Amiro *et al.*, 1990; Loescher *et al.*, 2003; Kutsch *et al.*, 2008; Serafimovich *et al.*, 2011; Thomas *et al.*, 2013).

Before the bark beetle epidemic, the site's thick canopy (LAI 9.7 m^2 m^{-2}) could theoretically have inhibited the mixing of air mass above and below the canopy, despite the site's high winds (Figure 12). Soil-derived CO_2 would have advected off site without ever being observed by the tower-mount EC system. As the bark beetle epidemic progressed and the canopy thinned (1.4 m^2 m^{-2} in 2011), more turbulence could have penetrated through the canopy, allowing the EC system to observe proportionally more of the true ecosystem respiration. The apparent consistency of EC nighttime values could be explained by the balancing effects of a reduction in ecosystem respiration (due to the bark beetle epidemic) and the increase of the EC tower's ability to observe the true ecosystem respiration (due to the thinning of canopy). This would also result in observed convergence of chamber and EC estimates with a thinner canopy.

Daytime turbulence is not derived from above-canopy mechanical mixing, but rather surface-originating convection, resulting in above and below canopy air masses to be mixed even with a thick canopy (Figure 12). This could explain why the daytime NEE values decreased with forest mortality (Frank *et al.*, in prep.).

The above theory could be tested through the installation of second EC system located below the canopy. At other sites, such a system greatly improved the quality of EC measurements, and caused EC and chamber estimates of R to converge within 3% of each other (Thomas *et al.*, 2013).

Implications and future directions

This study suggests that the traditional discrepancy of nighttime EC and chamber estimates of ecosystem respiration are not caused by insufficient turbulence. At this time it is uncertain as to the origin of this discrepancy and if either method is reporting the true ecosystem flux. Chambers measurements could be biased due to the effects of placing a chamber on a substrate and modeling uncertainty. Sources of error in EC include advection caused by turbulence failing to through a thick canopy.

To further explore this unexplained divergence in estimates of ecosystem respiration, the installation of a second EC system below the canopy could improve understanding of air flows throughout the ecosystem, and generate more accurate carbon fluxes.

The discrepancy between chamber and EC estimates of R must be resolved before confidence can be attained in the true measurement of ecosystem carbon flux. Knowledge of the true ecosystem fluxes will greatly advance scientific understanding of local nutrient cycling, allow for more accurate carbon budgets, and improve the development of global ecological models.

Tables

Table 1: **List of studies documenting EC estimates of R being lower than chamber estimates.**

Reference	Ecosystem Type	Site Location	Comparison
Barford *et al.*, 2001	Deciduous hardwoods	Massachusetts, USA	EC < Chambers
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 *et al.*, 2005	Mixed grassland	Alberta, Canada	EC < chambers, but within uncertainty
Goulden *et al.*, 1996	Deciduous hardwoods	Massachusetts, USA	EC < chambers
Grunwald *et al.*, 2007	Subalpine spruce forest	Tharandt, Germany	EC < chambers*
Hermle *et al.*, 2010	Boreal Forest, black spruce	Quebec, Canada	EC < chambers
Keith *et al.*, 2009	Temperate eucalyptus forest	New South Wales, Australia	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	Semi-arid 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 *et al.*, 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
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

Table 2: Summary chamber measurements

Type	Measurements Taken	Time Frame	IRGA Used	Manufacturer
Woody Tissues	146 on 25 live boles 39 on 4 dead boles	2010 2010 2011	LCA-4 (open path) LI-820 (closed path) Ciras-2 (closed path)	ADC, Hoddeston, England Li-Cor Biosciences, Lincoln, NE, USA PP Systems, Amesbury, MA, USA
Foliage	85 on 24 branches	2010 2011	LI-820 (closed path) Ciras-2 (closed path)	Li-Cor Biosciences, Lincoln, NE, USA PP Systems, Amesbury, MA, USA
Soil	1282 on 84 collars	2004-2006, 2009-2011	LI-820 (closed path)	Li-Cor Biosciences, Lincoln, NE, USA

Figures

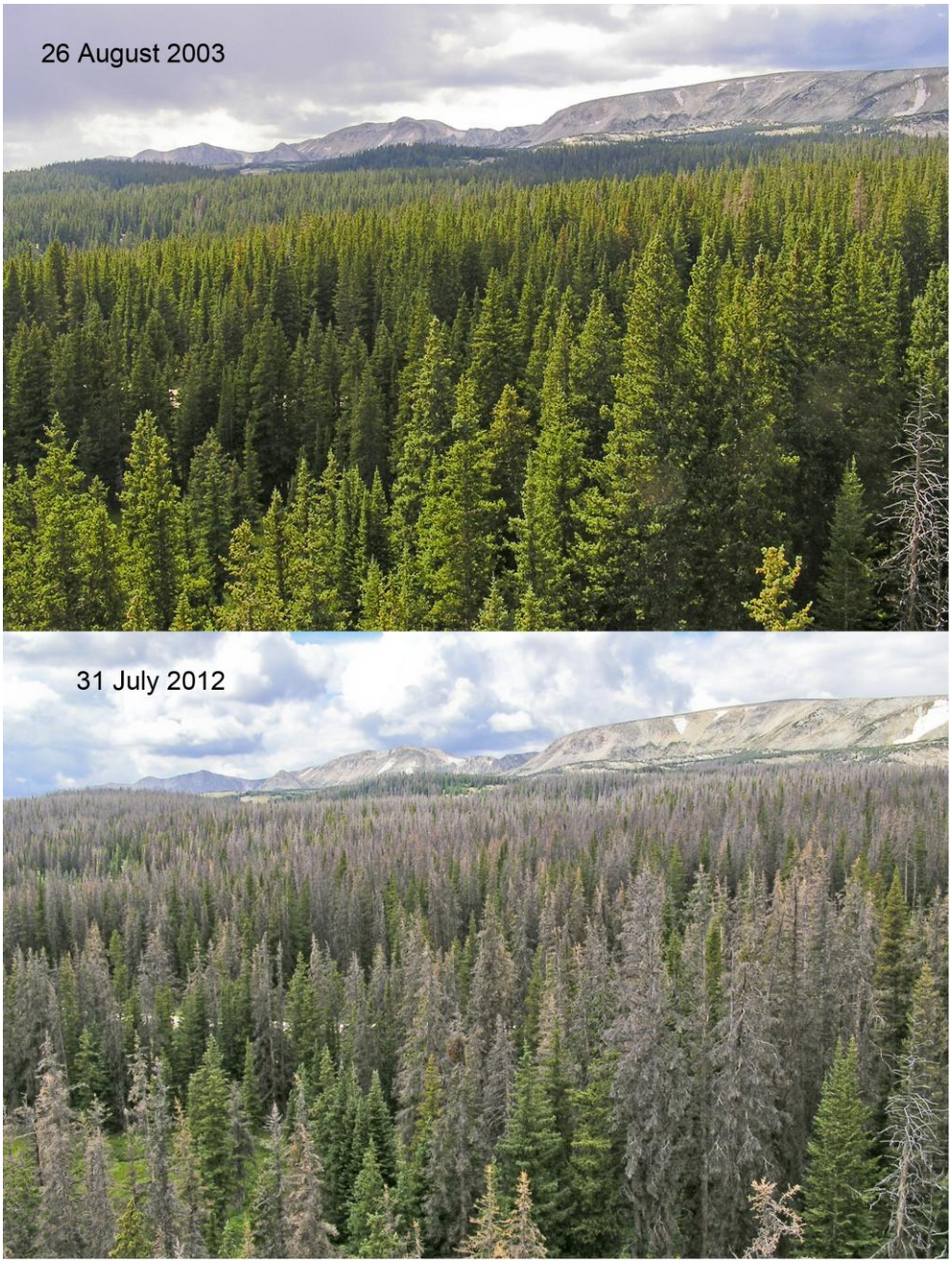

Figure 1: Repeat photography from the GLEES EC tower contrasting the forest pre- and post-bark beetle outbreak.

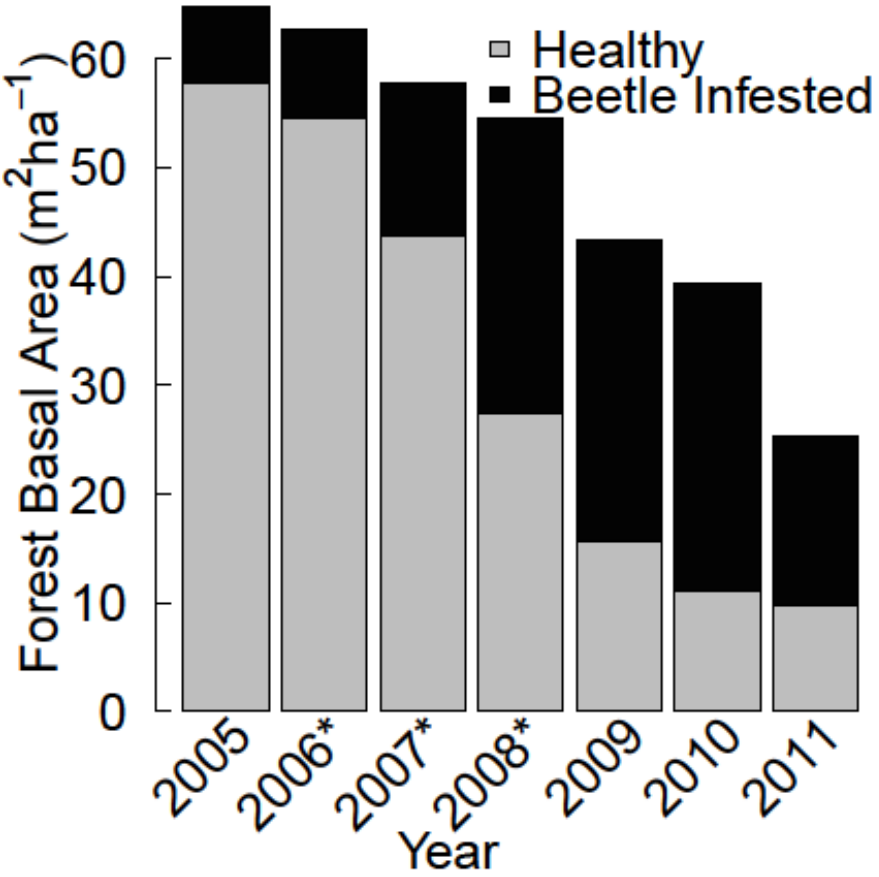

Figure 2: Forest basal area at GLEES. From 2008-2011, the bark beetle epidemic greatly reduced live basal area. In 2011, only 15% (10 of 65 m^2 ha^{-1}) of the original forest basal area remained alive and uninfected by bark beetles. An additional 24% (15 of 65 m^2 ha^{-1}) is alive, but infested by bark beetles, have severely impaired physiology, and likely respire little (Frank et al., in prep). Mortality survey not conducted 2006-2008 (marked *), numbers presented are estimations years the mortality survey was conducted.

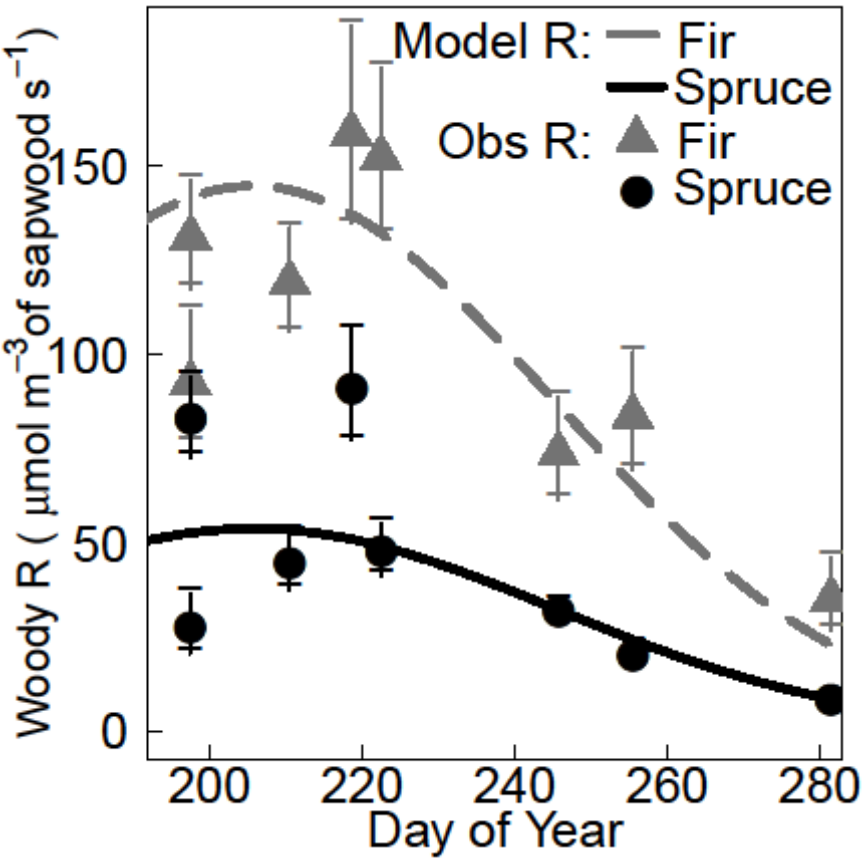

Figure 3: Observed and modeled efflux from woody tissues (r_W) as measured on live boles summers 2010 and 2011. Efflux from woody tissues is highly seasonal and scaled according to live sapwood volume. Subalpine fir has significantly higher respiration rates than Engelmann spruce. Data points represent the observed mean efflux for each species during each field session (~10 measurements taken over one day), and the associated standard error. Curved lines illustrate modeled mean efflux for each species (Equation 1):

$r_W = \exp(-9.57 + 0.13\ D - 0.00032\ D^2 + 0.99\ S)$. $r^2=0.68$

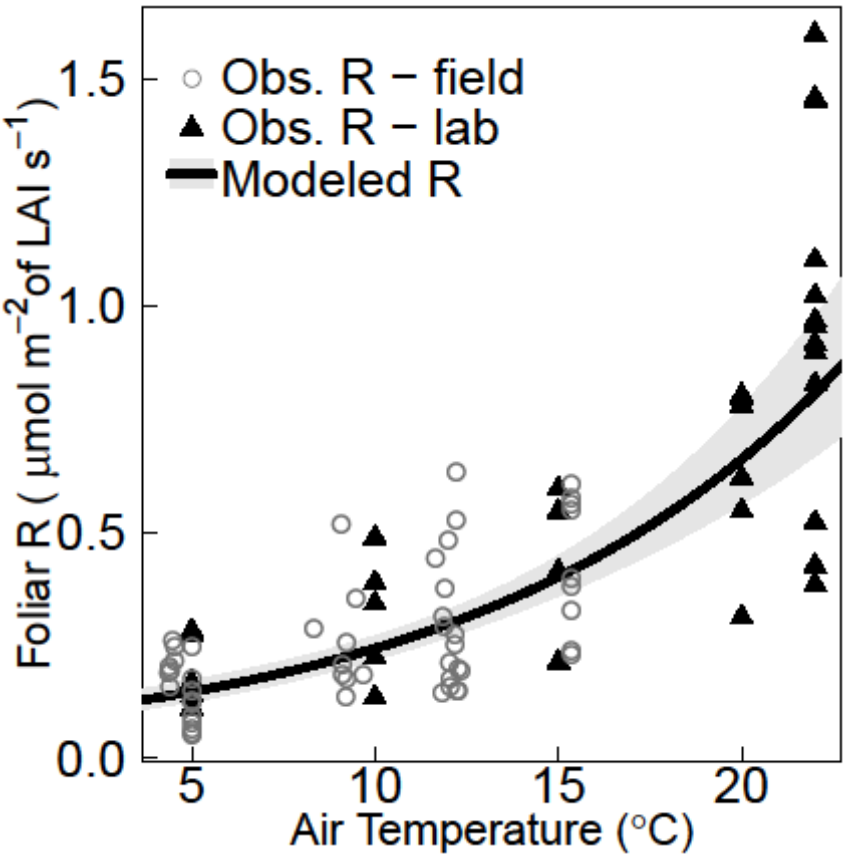

Figure 4: Observed and modeled foliar respiration (r_F). Foliar respiration is scaled according to leaf area (LAI) and dependent upon temperature. Data points represent foliage respiration rates observed in the field (circles) and lab (triangles). The solid line and shaded area represent the modeled mean and 95% confidence interval. Model formula (Equation 3):

$r_F = \exp(-2.42 + 0.10\ T_A)$. $r^2 = 0.64$.

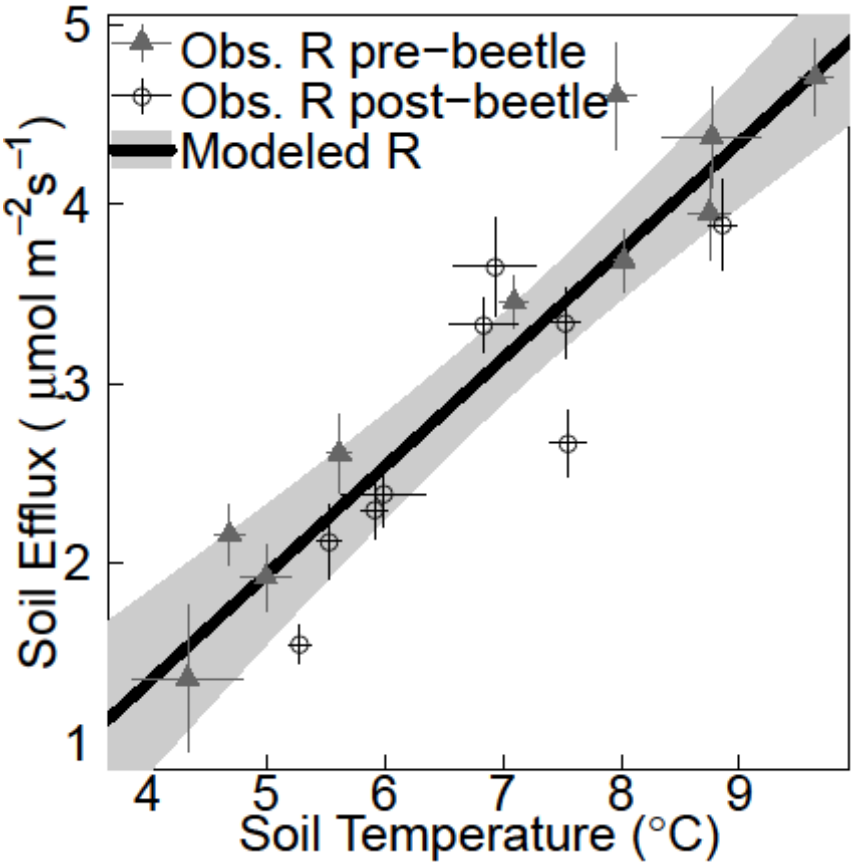

Figure 5: Observed and modeled soil efflux rates (R_S). Soil efflux is dependent upon both soil temperature and moisture. There was no difference in efflux rates from pre-beetle years (observed 2004-2006) to post-beetle years (2009-2011). Data points represent the mean observed soil efflux for each field session (~84 measurements taken over 2-3 days) and associated standard error. The solid line illustrates the modeled mean efflux and the shaded area represents the 95% confidence interval. Graphed points and trends were standardized to 20% volumetric soil moisture. Soil efflux was modeled as (Equation 5):

$R_S = -1.98 + 0.60\ T_S + 0.044\ \theta.$ $r^2=0.85$

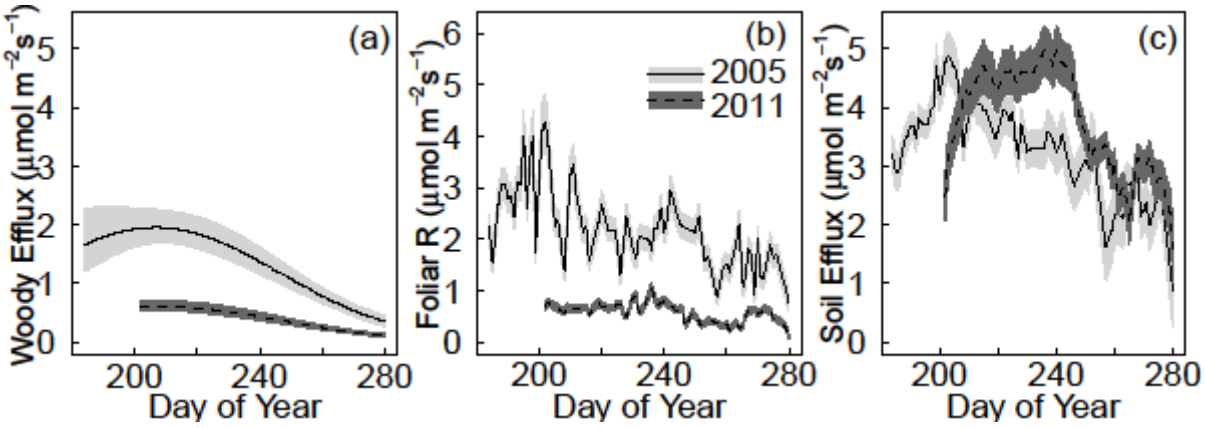

Figure 6: Modeled respiration from chambers for woody tissues (a), foliage (b), and soils (c). Respiration rates from woody tissues and foliage both declined 72% and 74% (respectively) from 2005 to 2011 due to bark beetle mortality. Soil efflux did not decrease due to the bark beetle epidemic. Shaded areas represent 95% confidence intervals of the predicted mean flux (solid line). Y-axis units are standardized as µmol m^{-2} s^{-1}.

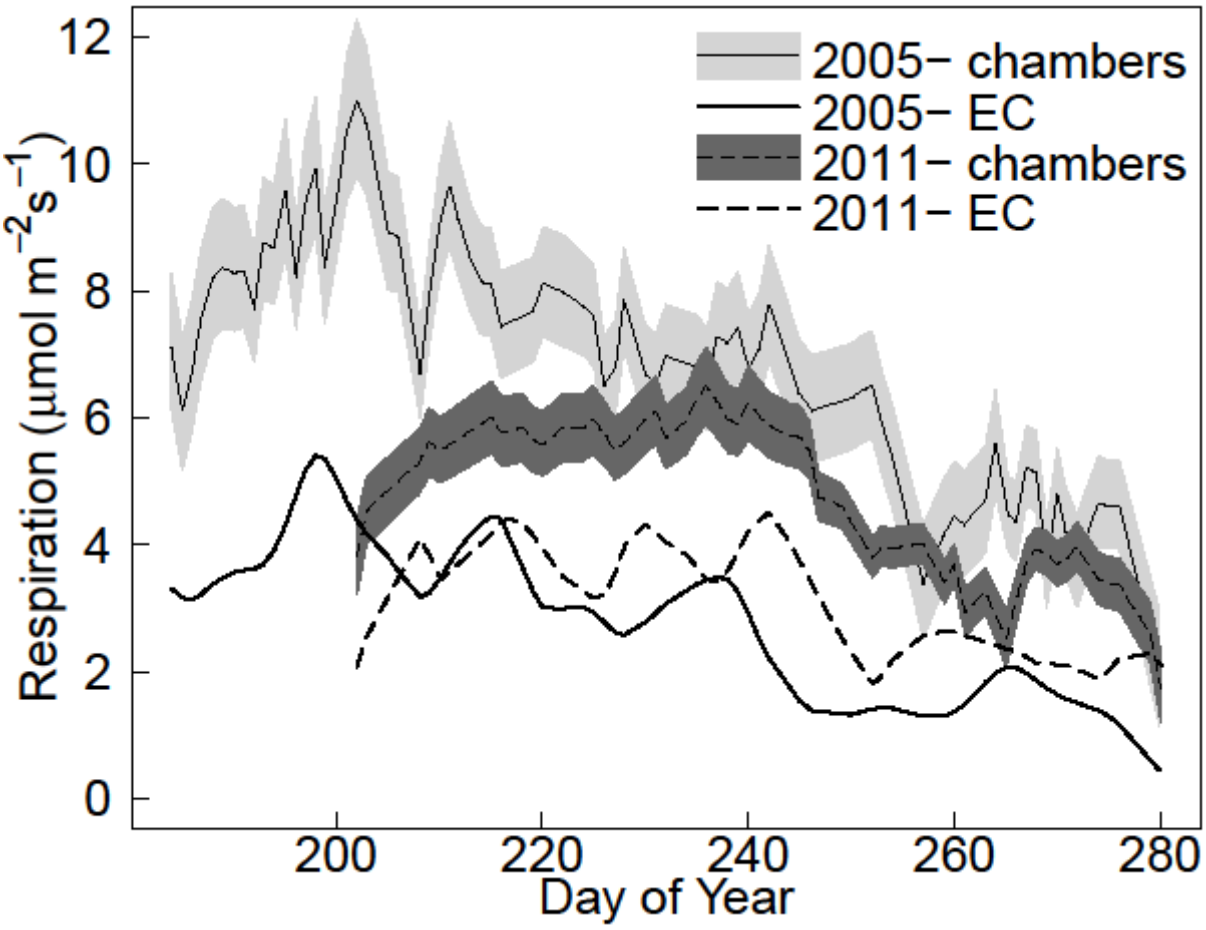

Figure 7: Time series of nightly R as estimated by EC and chambers. EC estimates of R are significantly lower than chambers estimates, but the data sets are well correlated. After the bark beetle epidemic, chambers estimated total ecosystem respiration (R_T) to decrease 32% from 2005 to 2011, whereas EC exhibits no decline after the epidemic. The shaded region represents the 95% confidence intervals around modeled chamber R_T (shaded line). EC values are the smoothed splines of nightly mean NEE measurements where u*> 0.2 m s^{-1}.

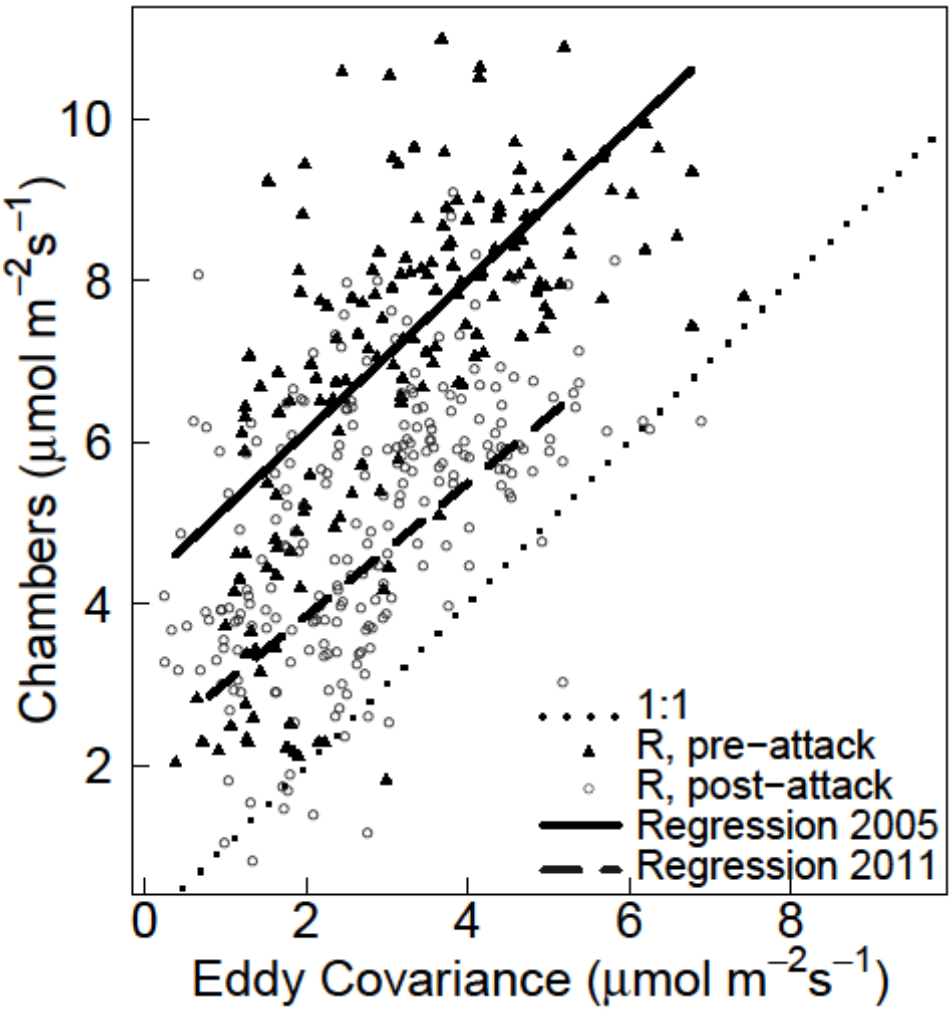

Figure 8: Comparison of mean nightly R, as estimated by chambers and EC. The two data sets are well correlated (yearly r^2 ranging from 0.18-0.60) for years 2005-2011. Absolute values of R estimated by chambers (R_T) are higher than nighttime EC NEE measurements. The data sets become closer after the bark beetle epidemic killed 85% of the forest basal area. Years before the beetle epidemic (pre-2008) are graphed in gray, years after the epidemic (2008 and after) are graphed in black.

Regression formula for 2005: Chambers = 0.94 EC + 4.2 (r^2 = 0.53).

Regression formula for 2011: Chambers = 0.82 EC + 2.2 (r^2 = 0.50)

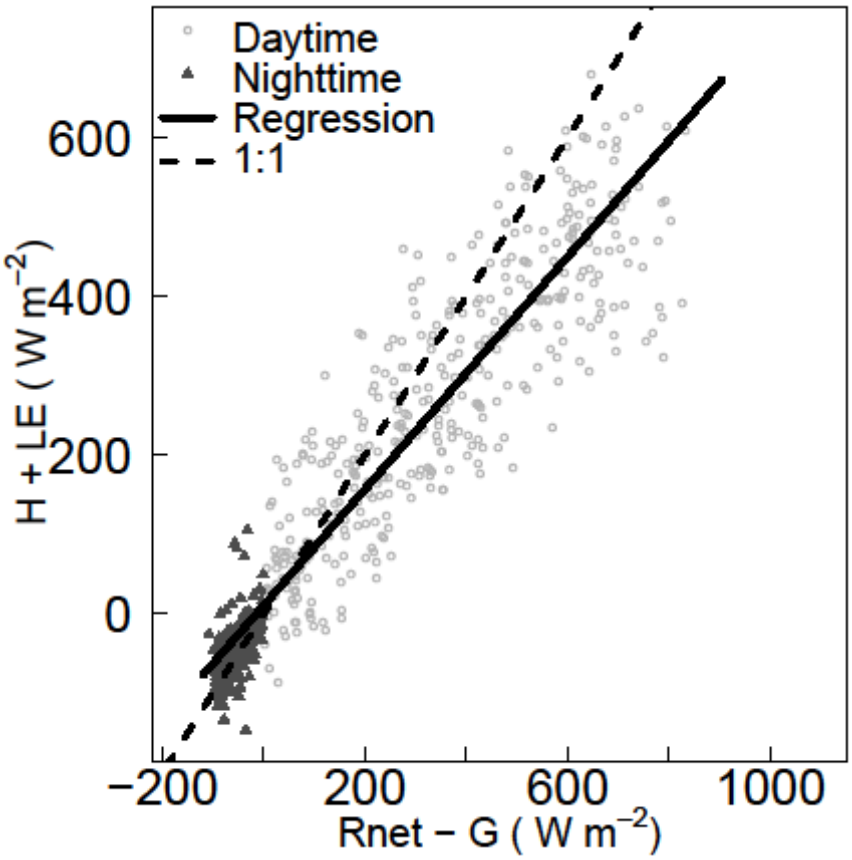

Figure 9: Energy balance closure slightly improved over the course of the bark beetle epidemic; summertime 2005 closure was 70% vs 79% in 2011. Regression of 30 minute data from all years: $(H + LE) = 0.73 (Rnet – G) + 10.4$ ($r^2 = 0.88$). Analysis of nighttime-only data produced a similar regression line, but with a much lower r^2 (0.31). Daytime-only regression had an r^2 of 0.75. Plotted data points are a random selection of 30 minute averages from day and night.

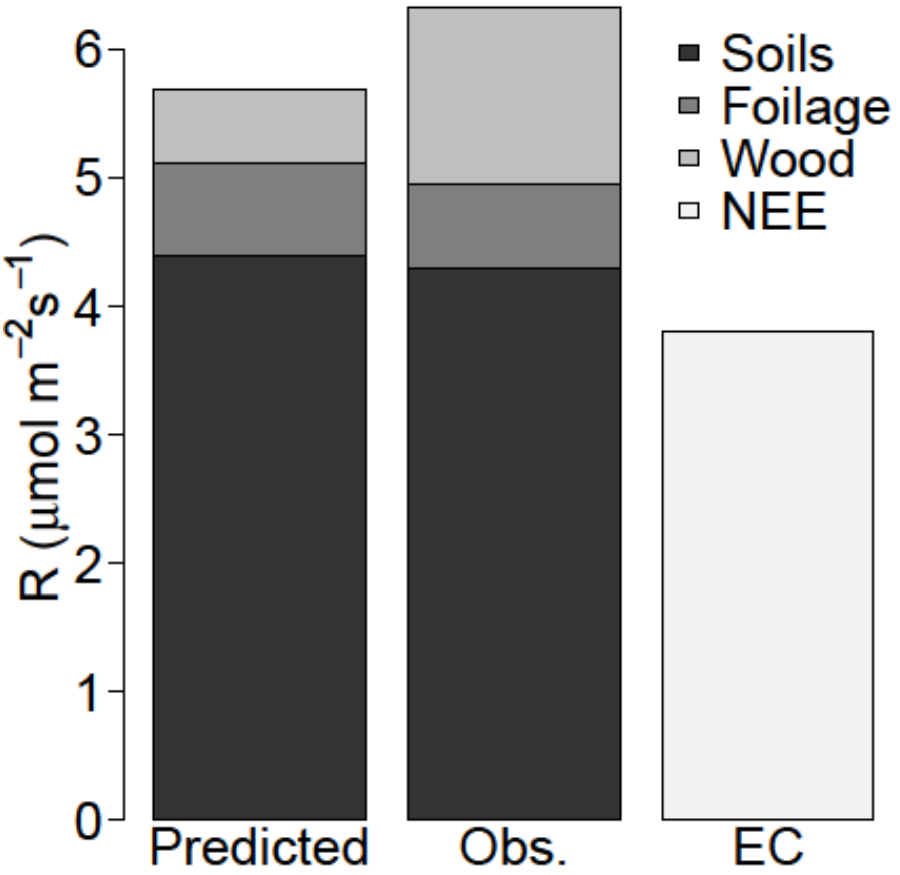

Figure 10: Comparison of chamber respiration using the seasonal chamber models (R_T, Equ. 6), chamber respiration measured August 7th-10th 2011 extrapolated to ecosystem scale (Equ. 2 & 4), and nighttime eddy covariance from the same time period. Modeled chamber values (R_T) were compared to observed respiration from woody tissues, foliage, and soils (n=174), generating similar results. Mean nighttime EC values during the time were ~33% lower than observed and modeled chamber numbers. EC values were also lower than observed soil respiration alone. These results suggest that the difference between chambers and EC is not the result of faulty modeling. Reported EC values were u* filtered (details in text).

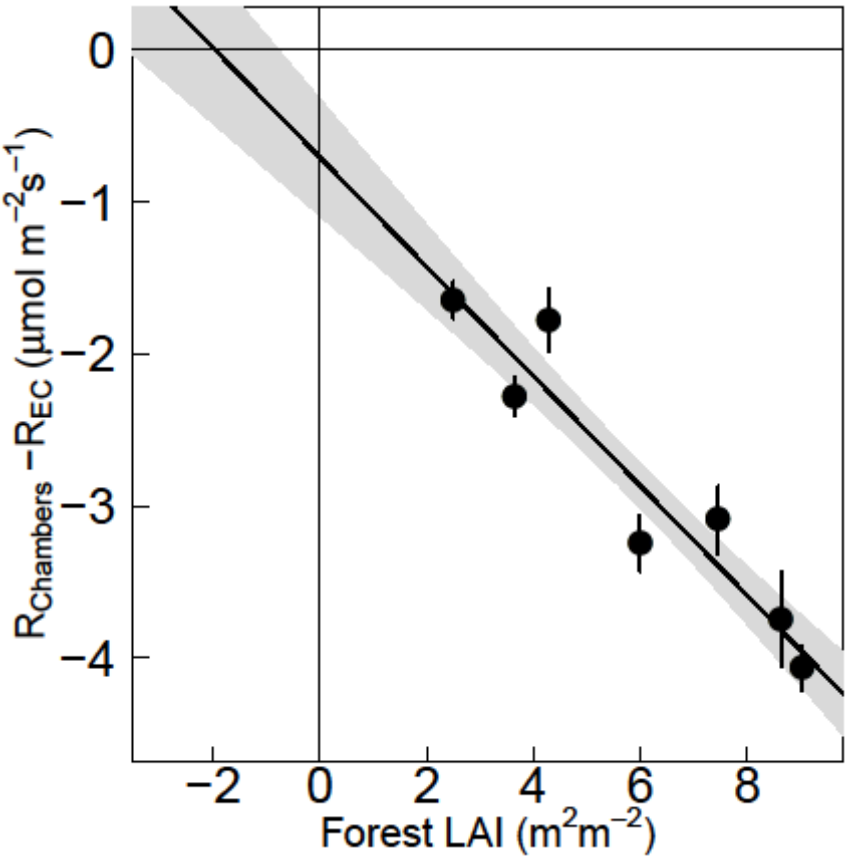

Figure 11: As forest leaf area index (LAI) declined, the difference between chamber and EC estimates of R became smaller. Hypothetically, chambers and EC would converge with a forest LAI of –2 m^2 m^{-2} (± 1.6 m^2 m^{-2}, 95% confidence interval). Plotted points represent the annual mean difference between $R_{chambers}$ and EC, with associated standard error. The regression line represents the regression between this difference and LAI, and the shaded region represents the associated 95% confidence interval.

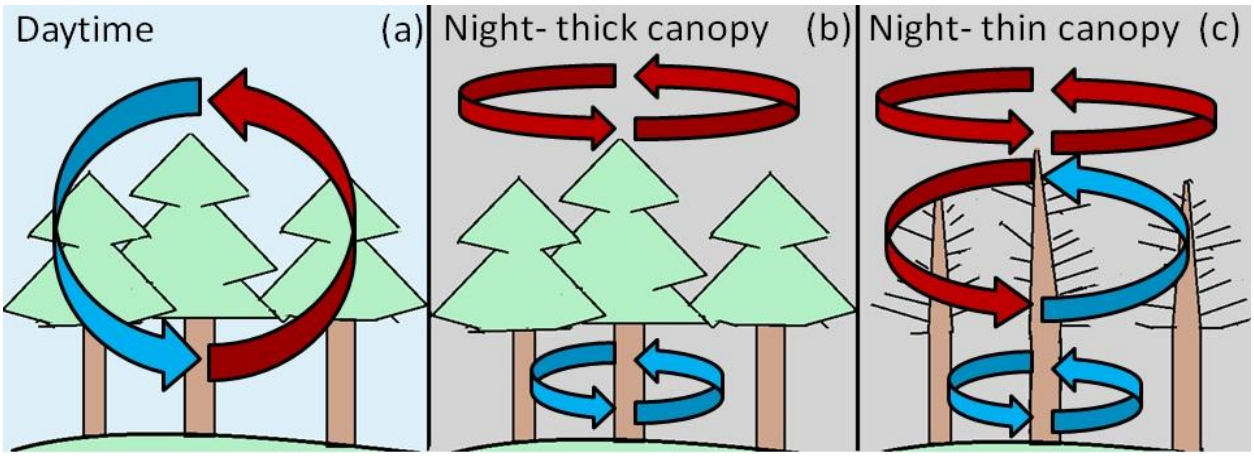

Figure 12: Air flow within a forest in daytime versus night. Blue arrows represent relatively colder carbon-rich air, and red arrows warmer carbon-poor air. During the day (a) convective heating connects air below and above canopy. At night, turbulence is generated by above-canopy wind shear and requires mechanical mixing. A thick forest canopy (b) prevents this turbulence from mixing with the air below, decoupling flows, and most of the soil efflux flows away via advection. A thinner canopy (c) allows some turbulence to penetrate through, resulting in partial coupling and allowing proportionally more soil efflux to be quantified by the eddy covariance tower (see text for references).

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Appendix A: Approximation EC Footprint and Mortality Survey

In the summer of 2010, three mortality surveys were conducted at the study site, GLEES Wyoming. Each survey sought to quantify the extent of the bark beetle mortality and had plots located within the presumed EC footprint. In autumn 2012, data was consolidated from these surveys for a more complete picture of the bark beetle mortality and its impact on the forest, particularly within the EC footprint.

Approximating the EC footprint

An EC footprint is defined as the land area upwind of the tower which has the largest impact on measurements and trends observed by the EC tower. This footprint was approximated by calculating the distance and direction from which 90% of the fluxes originate. To located the footprint and describe its features, a GIS map of GLEES was created of the EC tower and the three mortality survey plots (Figure A1).

We needed to know the direction in which the footprint is located and the distance from the tower. To estimate direction, we mapped the area from which the wind originates 50%, 75%, and 90% of the time. Over 50% of the time, the GLEES winds are blowing from a narrow area due west of the tower (250-300°), suggesting that the tower is influenced most by the plots located between these lines. To estimate the length of the footprint, we mapped circles of radiuses of 250, 500, and 1000 meters away from the tower. Because the tower is 23 meters tall (with most of the instruments located at a height of 23 meters), we assumed that the tower is unlikely to be affected by areas more than 750 m away (~30x tower height).

Knowing footprint directionality and distance, we hypothesized the land area which is our tower's footprint (Figure 13). This area was selected because it is within the prominent wind

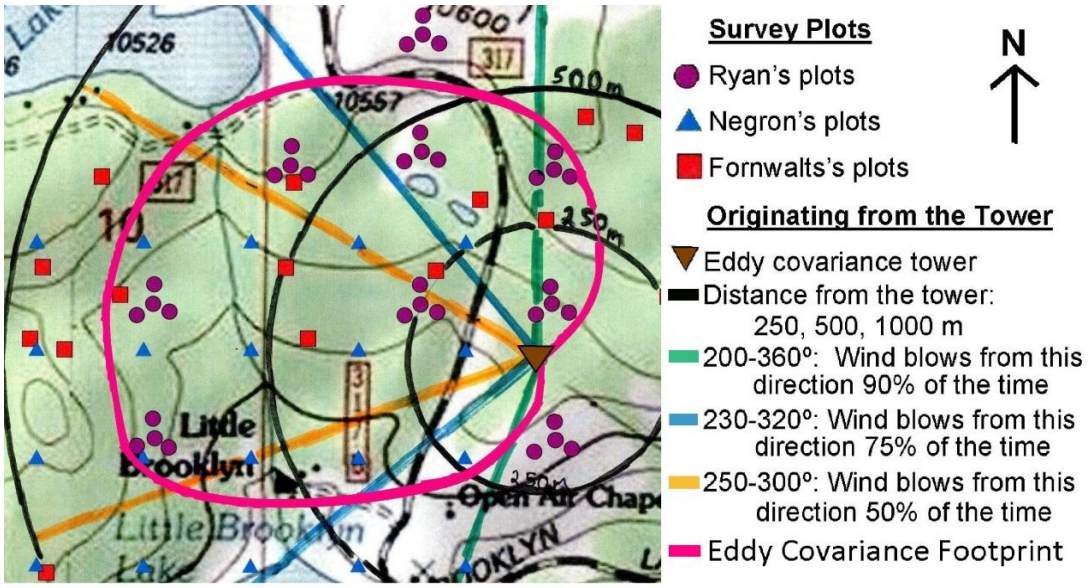

Figure 13: A map of GLEES: mortality plots, prevailing Winds, and suggested footprint

direction and within a reasonable distance. In the most predominate wind direction we extended the length of the footprint. We admit that this methodology was somewhat empirical, so we experimented with a variety of different footprint selections, including a much stricter footprint only extending 250 m from the tower (~10x tower heights). Forest statistics, such as stand basal area and bark beetle prevalence, proved similar in a strict footprint (~10x tower height) as a more liberal interpretation (~30x tower height). As no benefit was gained from the restrictive footprint, we opted to define the footprint as the larger area (drawn on Figure 13), which preserved the characteristics of the smaller footprint, but included many more plots.

Processing the mortality surveys

While documenting forest mortality at GLEES, We studied data from five different collections of plots. Three of these (Ryan, Negrón, and Fornwalt) were mortality surveys conducted at GLEES in summer 2010. The remaining two plot selections (EC Footprint and

Ryan in Footprint) were based upon the plot locations within the EC footprint. Details on the five plot collections are as follows:

Ryan – A survey led by Michael G. Ryan consisting of 36 plots, each 201 m^2, and arranged in clusters. All of Ryan's plots are mapped in Figure A1. This survey only included trees with a DBH>10 cm. Ryan's survey was initially conducted in 2004 (Bradford *et al.,* 2008) and repeated in 2009, 2010, and 2011.

Negrón – Led by José Negrón, this survey consisted of 35 plots, each 201 m^2, and arranged in grid, with a few plots located beyond the boundaries of the Figure A1 map. Negrón's survey included stems with a DBH>2.5 cm, and was conducted in the summer of 2010. Data is not yet published.

Fornwalt – Paula Fornwalt sampled 60 plots of 100 m^2, spaced quasi-randomly, with the majority of the plots located outside the Figure A1 map. Fornwalt conducted her survey in the summer of 2010 and included all trees of DBH height (DBH>0). Data is not yet published.

EC Footprint – A collection of plots found in the EC footprint and includes plots surveyed by Ryan, Negrón, and Fornwalt.

Ryan in Footprint – A collection of 28 plots surveyed by Ryan and found within the footprint. This is the selection of plots utilized in Speckman *et al.,* in prep.

In autumn 2012, we consolidated the information from the three 2010 surveys (Ryan, Negrón, and Fornwalt) and processed the raw data using a single standardized method. Trees were classified into four different health statuses: green, infected, beetle killed, and non-beetle dead. "Green" was defined as trees alive and showing no signs of beetle infestation (pitch tubes, beetle entrance holes, boring dust, or galleries). "Infected" trees displayed signs of beetle infestation but still retained their needles. "Beetle Killed" were dead trees showing evidence of

beetles and lacking >90% of their needles. "Non-Beetle Dead" were dead trees, lacking both needles and evidence of bark beetles, including trees whose deaths obviously pre-dated the 2008 beetle epidemic.

We calculated stand characteristics and the degree of bark beetle mortality for all five collections of plots (the three initial 2010 surveys and two selections within the EC footprint). LAI and sapwood volume for trees were calculated using allometric equations (Kaufmann and Troendle, 1981; Kaufmann and Troendle, 1982; Ryan, 1990). To conform to Ryan's survey, stems with a DBH < 10 cm were excluded from all data sets. This did not greatly affect forest statistics, as trees with a DBH <10 cm accounted for <5% of forest basal area in Negrón's and Fornwalt's surveys.

Results of survey comparisons

All surveys found similar forest biometrics and mortality, displayed in Figure 14. Total forest basal area for all surveys was ~78 m^2 ha^{-1} subdivided into ~15 m^2 ha^{-1} (20%) healthy trees, ~23 m^2 ha^{-1} (30%) infected, ~40 m^2 ha^{-1} (40%) dead from beetles and other causes. Projected LAI displayed a similar break down between healthy, infected, and dead trees.

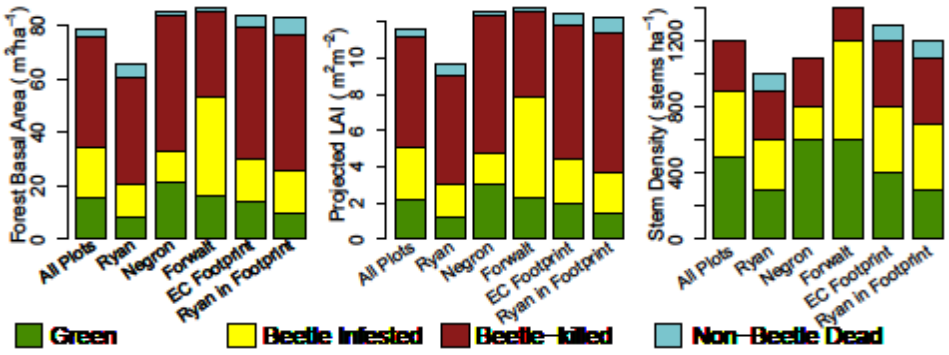

Figure 14: Comparing Mortality Surveys. A comparison of the different mortality surveys: their basal area, projected LAI, and stem density

There were a few minor differences between the various surveys. Ryan's plots have a disproportionally high amount of meadow area surveyed, resulting in a lower basal area, projected LAI, and stem density than the other surveys. A larger proportion of Fornwalt's plots were located in high elevations and remote locations, delaying their infection by beetles relative to other plots, hence a higher proportion of 'infected' versus 'beetle-killed' cases.

To examine the effects of the bark beetle mortality, we examined the size of trees attacked by beetles. Healthy trees unaffected by bark beetles tended to have the smallest median diameter at breast height (1.37 m) of ~15 cm. The largest trees were typically infested and killed by bark beetles (median DBH ~31 cm). Trees infested by bark beetles but not yet killed tended to have more intermediate DBH (median of ~22 cm). Trees not killed by things other than bark beetles also tended to have more intermediate DBH values (median ~16 cm). All of these values were consistent across each of the different surveys.

Implications for Speckman et al. paper (in prep)

For the analysis conducted by Speckman *et al.* (in prep), we utilized data from Ryan's plots found within the footprint (category 'Ryan in Footprint). We focused on Ryan's survey due to its repeated assessments in 2005, 2009, 2010, and 2011. This provided us with a time series of the epidemic's progression and was critical to chamber modeling of respiration rates. 'Ryan In Footprint' data generated similar values compared to other collections (Figure 14). Figure 15 displays forest biometrics specific to 'Ryan in Footprint' over time.

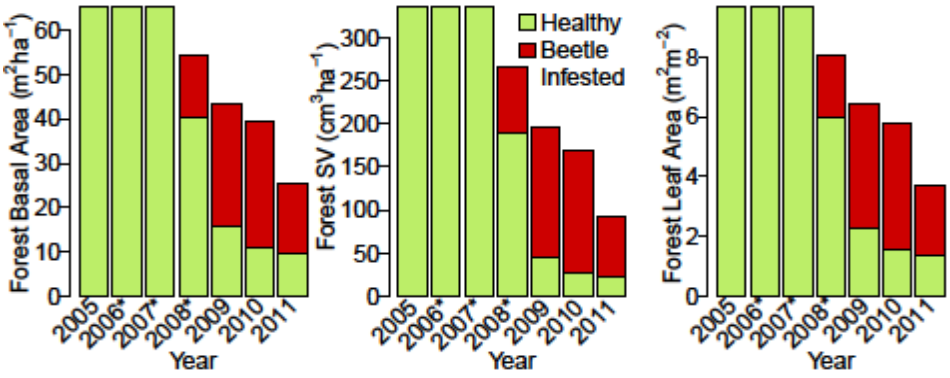

*Figure 15 displays forest biometrics specific to 'Ryan in Footprint' over time. These were the values used in Speckman et al 2013. *Mortality survey not conducted in 2006-2008, values displayed for these years are estimations*