

## RESEARCH ARTICLE

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### Key Points:

- Subalpine soil respiration was estimated across the Southern Rocky Mountains using 396 point measurements, Landsat Enhanced Vegetation Index, climate, and terrain
- Predicted soil respiration compared reasonably well to eddy covariance nocturnal respiration and MODIS GPP
- This method shows promise for large-scale estimates of soil respiration, a large component of the terrestrial carbon cycle

### Supporting Information:

- Table S1

### Correspondence to:

E. M. Berryman,  
eberryman@fs.fed.us

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## Estimating Soil Respiration in a Subalpine Landscape Using Point, Terrain, Climate, and Greenness Data

Erin M. Berryman<sup>1</sup> , Melanie K. Vanderhoof<sup>2</sup> , John B. Bradford<sup>3</sup> , Todd J. Hawbaker<sup>2</sup> , Paul D. Henne<sup>2</sup> , Sean P. Burns<sup>4,5</sup> , John M. Frank<sup>6</sup> , Richard A. Birdsey<sup>7</sup> , and Michael G. Ryan<sup>8,6</sup> 

<sup>1</sup>Cherokee Nation Technologies. Contractor to: U.S. Department of Agriculture, Forest Service, Forest Health Assessment and Applied Sciences Team, Fort Collins, CO, USA, <sup>2</sup>Geosciences and Environmental Change Science Center, U.S. Geological Survey, Denver, CO, USA, <sup>3</sup>Southwest Biological Science Center, U.S. Geological Survey, Flagstaff, AZ, USA, <sup>4</sup>Department of Geography, University of Colorado Boulder, Boulder, CO, USA, <sup>5</sup>National Center for Atmospheric Research, Boulder, CO, USA, <sup>6</sup>Rocky Mountain Research Station, U.S. Department of Agriculture, Forest Service, Fort Collins, CO, USA, <sup>7</sup>Woods Hole Research Center, Falmouth, MA, USA, <sup>8</sup>Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO, USA

**Abstract** Landscape carbon (C) flux estimates help assess the ability of terrestrial ecosystems to buffer further increases in anthropogenic carbon dioxide (CO<sub>2</sub>) emissions. Advances in remote sensing have led to coarse-scale estimates of gross primary productivity (GPP; e.g., MODIS 17), yet efforts to develop spatial respiration products are lacking. Here we demonstrate a method to predict growing season soil respiration at a regional scale in a mixed subalpine ecosystem. We related field measurements ( $n = 396$ ) of growing season soil respiration mostly from subalpine forests in the Southern Rocky Mountains ecoregion to a suite of biophysical predictors using a Random Forest model (30-m pixel size). We found that Landsat Enhanced Vegetation Index, growing season aridity index, temperature, precipitation, elevation, and slope aspect explained spatiotemporal variability in soil respiration. Our model had a pseudo- $r^2$  of 0.45 and root-mean-square error of roughly one quarter of the mean value of respiration. Predicted growing season soil respiration across the region was remarkably consistent across 2004, 2005, and 2006 (150-day sums of 542.8, 544.3, and 536.5 g C/m<sup>2</sup>, respectively). Yet we observed substantial variability in spatial patterns of soil respiration predictions that varied among years, suggesting that our method is sensitive to changes in respiration drivers. Mean predicted growing season soil respiration was 73% of MODIS GPP, while predicted soil respiration was generally within 20% of nocturnal net ecosystem exchange from nearby eddy covariance towers. Thus, geospatial and remotely sensed data sets can be used to estimate soil respiration at landscape scales.

**Plain Language Summary** Soil respiration returns carbon dioxide back to the atmosphere and is an important part of the carbon cycle, but estimates of soil respiration across large landscapes are difficult to come by. Soil respiration is sensitive to changes in climate and vegetation, which are available as mapped data products, thanks to remote sensing and geospatial technology. We developed a statistical model that mapped soil respiration across three forests and an entire region based on climate and vegetation spatial data. While this work was limited to subalpine forests in the Southern Rocky Mountains, our method can be used in other ecosystems to better understand how ecosystems interact with atmospheric carbon dioxide.

## 1. Introduction

Reporting requirements for national carbon budgets rely on accurate estimates of ecosystem C fluxes across multiple regions. This need for large-scale data cannot be fulfilled by field measurements alone due to methodological limitations; field measurements are usually conducted at small spatial scales with low areal coverage that may not represent the diversity and relative proportions of ecosystem condition. For example, eddy covariance (EC) studies that estimate net ecosystem C exchange capture areas up to 1 km<sup>2</sup> but relatively few exist due to the high cost of constructing and maintaining EC towers (Schuepp et al., 1990), whereas individual chamber-based measurements are <1 m<sup>2</sup> and must be repeated across the landscape to increase spatial coverage. This disconnect between information provided by ground-based measurements and large-scale data needs can be addressed with remote sensing and geospatial modeling. Advances over the past several decades have allowed for spatially continuous, large-scale estimates of gross and net primary productivity using MODIS satellite imagery (Running et al., 2004). However, ecosystem C sequestration depends upon

net balance of carbon gain and loss (Chapin et al., 2006), which requires accurate estimates of not only productivity but also respiration by both plants and heterotrophs.

Respiration can be predicted across space or time based on values of known controls, using two general approaches: employing ecosystem models to represent processes involved in respiration, or using field measurements to construct empirical (statistical) models. Biome-BGC, DayCent, LANDIS-II/Century, Community Land Model (CLM) 4.5, and FöBAAR are examples of process-based models that have been used to calculate productivity and respiration spatially (Carbone et al., 2016; Duarte et al., 2017; Hibbard et al., 2005; Parton et al., 1994; Scheller et al., 2007, 2011). However, process-based models are limited in how they handle landscape-level heterogeneity of respiration. For example, their accuracy is sensitive to parameters such as soil C pool turnover times, which are rarely measured and instead are assigned constant values over space (Bonan et al., 2013; Keenan et al., 2013). In addition, they can be time intensive to parameterize and calibrate. Finally, applying them across large areas at high spatial resolution is computationally expensive due to their substantial processing and data requirements. Alternatively, simple statistical models have lower computational costs and therefore are more feasible for application across large spatial extents, provided adequate representation of field measurements to inform model development. In fact, such models have already been utilized as surrogates for calibrating process-based models (Xu et al., 2018).

Measuring respiration from the whole ecosystem is technically challenging, requiring either EC towers or stem/foliar respiration chamber measurements that must be converted to projected ground area; thus, data are limited (Cavaleri et al., 2008; Speckman et al., 2015). However, soil respiration is more widely measured than aboveground respiration, due to its simple and scalable soil chamber methodology (unlike aboveground respiration). Soil respiration makes up much of forest ecosystem respiration, resulting primarily from root and mycorrhizal respiration and soil heterotrophic metabolism of root exudates and soil organic matter (Bond-Lamberty et al., 2004; Davidson et al., 2006; Gaudinski et al., 2000; Jian et al., 2018). Soil respiration is the largest natural flux of CO<sub>2</sub> to the atmosphere (Bond-Lamberty & Thomson, 2010b) and is sensitive to weather (Davidson et al., 1998), nutrient supply (Butnor et al., 2003), and carbon substrate supply (Cleveland et al., 2007) and, as with ecosystem respiration, is related to productivity at global scales (Reichstein et al., 2003). In addition to productivity, C substrate, microbial biomass and fine roots in soil and forest floor relate to characteristics identifiable via remote sensing, such as leaf area index (LAI; Bradford et al., 2009). Thus, soil respiration, even over broad, heterogeneous landscapes, has the potential to be accurately predicted given enough spatial information about variables related to forest productivity, soil properties, and climate.

The availability of spatially continuous data sets of ecosystem properties and environmental variables important for respiration provides an opportunity to predict soil respiration across large areas. Previously, annual soil respiration was predicted in northern latitudes using MODIS Normalized Difference Vegetation Index (NDVI), air temperature and precipitation (Bond-Lamberty et al., 2012). Wu et al. (2014) used MODIS-derived NDVI, LAI, and surface temperature to predict daily and 8-day summed soil respiration for forests in Saskatchewan, Canada. These studies had good predictive ability ( $r^2 > 0.6$ ) yet covered large areas at coarse spatial resolution (1 km) across relatively homogenous forest types and topography. Estimating soil respiration across complex terrain is complicated by steep gradients in climate and forest biomass over short distances (Swetnam et al., 2017). Thus, combining greenness measures with other spatial data sets on topography and climate (e.g., PRISM Climate Group, 2017) may allow for accurate predictions of forest soil respiration across mountainous regions.

In the Rocky Mountains, subalpine forests are a regionally important ecosystem for C sequestration and sensitive to future changes in snowpack amount and duration (Schimel et al., 2002; Sextstone et al., 2018; Winchell et al., 2016). Previous efforts within subalpine forests have focused on characterizing C pools and fluxes across individual sites (Bradford et al., 2008; Liang et al., 2016; Scott-Denton et al., 2013). Larger landscape-scale assessments are lacking, but they would improve our understanding of how C flux-environmental relationships gleaned at individual sites drive variability in regional C cycling. Mountainous regions provide additional challenges over past respiration modeling efforts because complex topography can create high spatial heterogeneity in climate, soil properties, and vegetation, all factors that influence soil respiration. For this reason, Landsat imagery may be better suited for modeling soil respiration over complex terrain because its 30-m resolution may better capture fine-scale heterogeneity in patterns of greenness than

MODIS imagery (250-m to 1-km resolution). Here we combine Landsat imagery with spatial data sets on topography and climate in a statistical framework to predict growing season soil respiration across subalpine forests in the Southern Rocky Mountains. This work has three objectives:

1. Relate site-level measurements of growing season soil respiration to geospatial and remotely sensed data for 2004–2006 in a statistical model;
2. Apply the predictive model to a subalpine forested area in the Southern Rocky Mountains to assess patterns of spatial and interannual variability;
3. Compare interannual trends in site- and regional-scale predicted growing season soil respiration with coincident EC respiration and MODIS-derived GPP.

## 2. Materials and Methods

### 2.1. Study Area

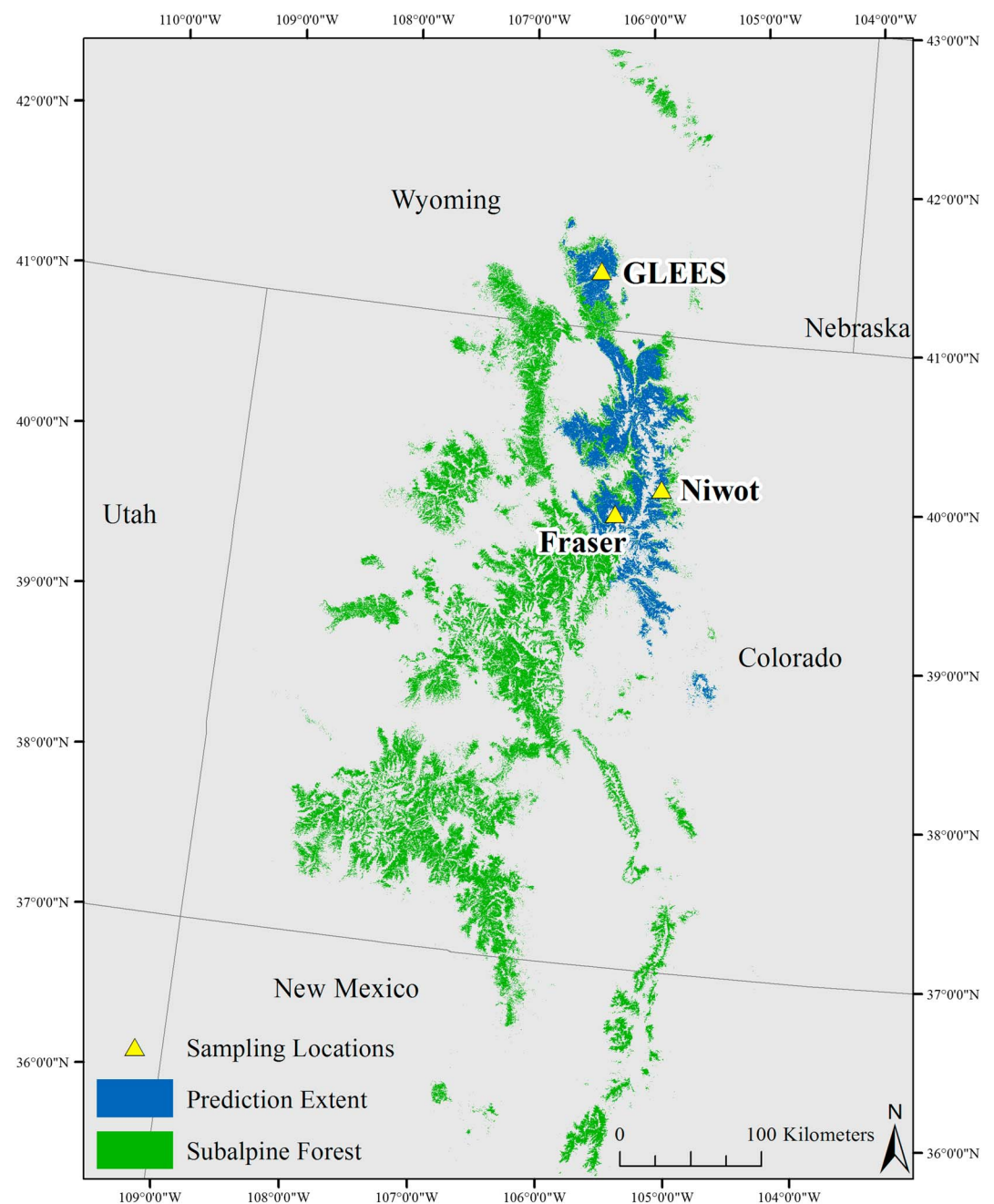
Field data came from 144 forest monitoring plots at three subalpine forest sites in the Southern Rocky Mountains: the Glacier Lakes Ecosystem Experiments Site (GLEES), the Niwot Ridge Long-Term Ecological Research site (Niwot), and the Fraser Experimental Forest (Fraser; Figure 1). GLEES (41°22'N, 106°15'W) is located in the Snowy Range of southeastern Wyoming at 3,190-m elevation and has a mean annual temperature of 0.0 °C, with a mean January air temperature of −9.3 °C and mean July air temperature of 13.0 °C, and mean annual precipitation of 1,200 mm with ~80% falling as snow. Niwot (40°2'N, 105°33'W) is located at 3,050-m elevation in the Front Range of Colorado just east of the Continental Divide and has a mean annual temperature of 1.5 °C, with mean January air temperature of −6.4 °C and mean July air temperature of 14.0 °C, and mean annual precipitation of 800 mm with ~60% falling as snow (Burns et al., 2015). Fraser (39°4'N, 105°52'W) is located at ~3,000-m elevation in the Front Range of Colorado just west of the Continental Divide; it has a mean annual air temperature of 0.6 °C, with mean January air temperature of −10 °C and mean July air temperature of 12.2 °C, and mean annual precipitation of about 750 mm, with 75% as snow (Rhoades et al., 2017).

Soils at Niwot are mapped as a mixed Typic Humicryept formed on colluvium, eolian material, and glacial till (Soil Survey Staff, NRCS). At Fraser, soils are mapped as loamy-skeletal, mixed, superactive Typic Dystrocryept formed on till, slope alluvium, or colluvium (Soil Survey Staff, NRCS). Soils at GLEES are mapped as loamy-skeletal, mixed, superactive Eutric Haplocryalfs developed on glacial till (Hopper & Walthall, 1992).

Plots were arranged in clusters of four following the plot design of the U.S. Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis Program, found to be statistically independent in a previous study at the site (Bechtold & Patterson, 2005; Bradford et al., 2010). Twelve clusters were located at each of the three sites, with nine located along a 250-m grid covering a 1-km<sup>2</sup> area and three randomly located outside of the 1-km<sup>2</sup> area (Figure 2). Most of these plots typified subalpine mixed conifer forest, with young stands dominated by lodgepole pine (*Pinus contorta* Douglas ex Loudon) with a subalpine fir [*Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa*] and Engelmann spruce (*Picea engelmannii* Parry ex Engelm. var. *engelmannii*) understory; mature stands were dominated by Engelmann spruce and subalpine fir. Eight of the 144 plots were located in subalpine meadow, eight were located in subalpine wetland, and five were located in aspen (*Populus tremuloides* Michx.) stands. The measurements at GLEES and Niwot were made at plots near and surrounding AmeriFlux EC towers (US-GLE and US-NR1).

### 2.2. Field Data Collection

For each year of the study (2004–2006), soil respiration was measured at three permanent collars (78.5-cm<sup>2</sup> area per collar) per plot, evenly spaced 7 m from plot center, during the peak of the snow-free season (*growing season*). The growing season sampling period varied by year and site depending on snowmelt and snow accumulation timing but typically began in late June and ended in September. Plots were sampled three to four times each growing season sometime between 7 a.m. to 4 p.m. Respiration measurements used an opaque static survey chamber connected to an infrared gas analyzer (LI-820; Li-Cor Biosciences, Lincoln, NE, USA) to measure the flux of CO<sub>2</sub> from the soil surface at near-ambient CO<sub>2</sub> concentrations (±20 ppm). Two consecutive respiration cycles (each lasting from 30 to 60 s) were run and subsequent fluxes were averaged together. Further details of flux measurements and respiration system can be found in Speckman et al. (2015). Because the objective was to predict growing season respiration at an annual time step, for



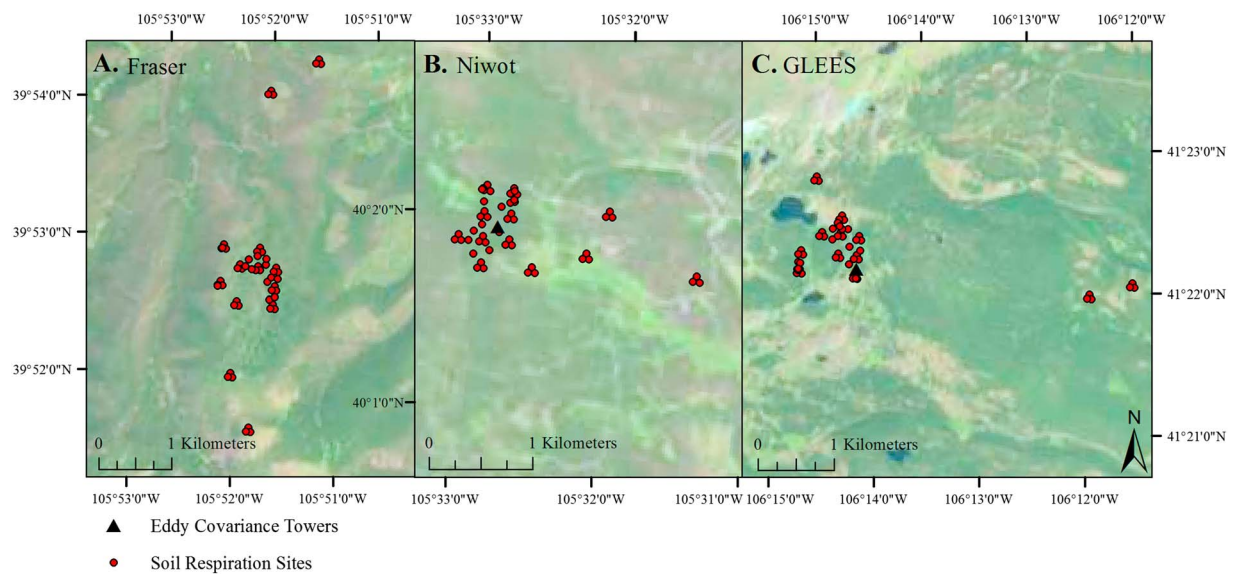
**Figure 1.** Distribution of soil respiration sampling locations (black triangles), the extent over which soil respiration was predicted, and the extent of subalpine forest type in the southern Rocky Mountain ecoregion.

statistical models, mean plot respiration ( $R_s$ ) was averaged across all sampling dates per year. Further details of field sampling, including study design, can be found in Bradford et al. (2008) and Berryman et al. (2016).

### 2.3. Spatial Data

Based on previous research, we expected that soil respiration would vary spatially and from year-to-year based on both coincident and time-lagged satellite greenness, air temperature, and precipitation, and topography (Table 1; Bond-Lamberty et al., 2012; Wu et al., 2014). Lagged (1 year) and current year peak growing season greenness were defined using the Enhanced Vegetation Index (EVI; Huete et al., 2002). The NDVI (Tucker, 1979) was also tested; however, EVI was found to improve model performance compared to NDVI.





**Figure 2.** Landscape sampling design of plots within clusters at (a) Fraser, (b) Niwot, and (c) GLEES. Background imagery is Landsat thematic mapper images from summer 2006 (path 34 row 32 and path 35 row 31).

EVI is based on the algorithm for NDVI, except EVI better optimizes the vegetation signal and accounts for the canopy background signal and distortions in the atmosphere (Huete et al., 2002). The Southern Rockies subalpine forest types extend across 13 Landsat path/rows. Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images for these path/rows were collected during the growing season (June–September) for 2003–2006. The Landsat images were atmospherically corrected and converted to surface reflectance values using the Landsat Ecosystem Disturbance Adaptive Processing System (Masek et al., 2006). EVI was calculated from the visible blue (Band 1), green (Band 3), and near-infrared (Band 4) reflectance in the absence of cloud cover:

$$\text{EVI} = 2.5^* (\text{Band 4} - \text{Band 3}) / (\text{Band 4} + 6^* \text{Band 3} - 7.5^* \text{Band 1} + 1) \quad (1)$$

The *function of mask* (FMask) algorithm was used to mask out clouds, cloud shadows, and snow (Zhu & Woodcock, 2014). For Landsat 7 ETM+ images, scan line corrector off pixels were also masked out. For each Landsat path/row, images representing the peak growing season (July or August) EVI were selected. Additional Landsat EVI images were mosaicked with the original image to fill in data gaps. Clouds are common in mountainous areas in the summer months necessitating the use of a relatively large number of Landsat images (41, 54, 55, and 54 images in 2003, 2004, 2005, and 2006, respectively, across the 13 path/rows) across the study area. Our compilation of maximum EVI was slightly varied across space and time, because cloud cover necessitated the intermittent usage of images outside of the expected peak in EVI (e.g., June or September). A list of the Landsat images and dates used is in Table S1 in the supporting information.

Minimum and maximum monthly air temperature and monthly precipitation were obtained from PRISM (PRISM Climate Group, 2017) at 4-km resolution for the years 2004–2006. Mean temperature was determined by averaging the minimum and the maximum temperature. From these data, mean growing season temperature for each year was calculated over the

**Table 1**

*Annual (2004–2006) Mean Growing Season (June–September) Rates of Observed and Predicted Soil Respiration, MODIS GPP, MODIS Maintenance Respiration, and Key Parameters Selected for in the Random Forest Model Across the Entire Prediction Region*

Data	Year	Minimum	Maximum	Mean	Standard deviation
Observed mean soil respiration	2004	1.76	6.60	3.49	0.93
	2005	1.16	4.54	2.72	0.74
	2006	1.46	8.14	3.93	1.13
Predicted mean soil respiration	2004	1.81	5.29	3.49	0.37
	2005	1.75	6.17	3.50	0.54
	2006	2.27	5.30	3.45	0.38
MODIS GPP	2004	0.78	6.59	4.75	0.89
	2005	0.90	6.51	4.85	0.93
	2006	0.76	6.27	4.60	0.85
AI	2004	0.00	0.55	0.01	0.02
	2005	0.00	0.57	0.15	0.10
	2006	0.00	0.60	0.14	0.09
EVI	2003	0.12	0.61	0.22	0.07
	2004	0.06	0.59	0.23	0.11
	2005	0.11	0.66	0.23	0.09
	2006	0.11	0.67	0.22	0.06
Summer temperature (May–Sep) (°C)	2004	2.59	13.42	8.10	1.32
	2005	3.26	14.40	9.00	1.21
	2006	3.20	14.80	9.27	1.23
Total precipitation (Jan–Mar) (mm)	2004	28.14	273.98	140.09	44.79
	2005	40.13	367.15	167.16	56.34
	2006	23.66	427.43	178.18	76.00

*Note.* MODIS = moderate resolution imaging spectroradiometer; GPP = gross primary productivity; AI = aridity index; EVI = Enhanced Vegetation Index.

time period from day of water year 210 (April 28/29) through 365/366 (September 30). The start and end dates were intentionally broader than a *normal* growing season of the region to account for abnormal early- and/or late-season warmth which may influence productivity and respiration. Monthly precipitation was summed for the months of January, February, and March for each year to approximate trends in winter snowfall.

Slope, elevation, and aspect were determined from a 10-m resolution digital elevation model (DEM) from the U.S. Geological Survey (USGS) National Elevation Dataset (30-m spatial resolution). Aspect was transformed into *folded aspect* (so higher values indicated more southerly slopes) to better relate to radiation load using the following calculation (McCune & Keon, 2002):

$$\text{Aspect}_{\text{folded}} = \text{abs}(180 - \text{abs}(\text{aspect} - 225)) \quad (2)$$

Annual evapotranspiration (AET) and potential evapotranspiration (PET) were calculated and integrated into a simple aridity index (AI):  $1 = \text{AET}/\text{PET}$ . AI quantifies evaporative demand unmet by soil water, with higher values indicating drier conditions. AET and PET were calculated using a monthly water balance that applied a modified Thornthwaite approach in R (Lutz et al., 2010; Redmond, 2015; Redmond et al., 2017). The water balance model required inputs of mean monthly temperature and precipitation, slope, aspect, latitude, and soil available water capacity (AWC). AWC was derived from the Soil Survey Geographic database (SSURGO; Soil Survey Staff, Natural Resources Conservation Service, NRCS, 2017). To quantify summer moisture stress, we averaged AI for July, August, and September for each year. Other variables were also tested but not found to improve model performance and therefore were not included in the final analysis. These variables included nitrogen deposition (National Atmospheric Deposition Program, 2017), slope (USGS DEM), soil and drainage characteristics collected from SSURGO (Soil Survey Staff, NRCS, 2017), and wetland presence/absence, as mapped by the National Wetland Inventory dataset (United States Fish and Wildlife Service, 2010).

Data sources coarser than 30 m in resolution (e.g., PRISM precipitation and temperature and AI) were resampled to 30 m to match the resolution of the Landsat and DEM data using a two-step cubic convolution, from 4 km to 1 km, then 1 km to 30 m. We recognize that differences in the spatial resolution of the input data sets can introduce uncertainty in the landscape predictions of soil respiration, particularly in areas that can be expected to experience rapid changes in climate (e.g., sharp elevation changes). However, as greenness and topography play a major role in influencing fine-scale patterns in soil respiration in mountainous regions (Berryman et al., 2015; Riveros-Iregui et al., 2012) and both data sets were available at 30 m, our analysis was run at 30-m resolution to maximize our ability to capture fine-scale spatial heterogeneity.

## 2.4. Statistical Modeling

We used a Random Forest model to estimate mean growing season soil respiration at each of the 144 plots from each of the predictor variables discussed above (Breiman, 2001). This approach has previously been used to model soil respiration across large regions (Bond-Lamberty et al., 2012). Random Forest models use bootstrapping to employ hundreds or thousands of regression trees, each using a different random subset of the full data set and a subset of all available predictors. The resulting predicted value represents the mean of all the trees that were sampled. We chose to use a Random Forest model because it can generate more accurate predictions than single classification and regression tree (CART) models (Breiman, 2001) and it makes no prior assumptions about cause and effect relationships or correlations among variables that are likely present with our data set (Hastie et al., 2009). For our model, 500 regression trees were generated and we did not restrict the maximum number of nodes nor minimum sample size per node. Random Forest models were run in R statistical software using the *randomForest* package, and the *rfUtilities* package was used for variable selection, variable collinearity, and overfitting ratio tests (Murphy et al., 2010).

Our models were developed on annual time scales, similar to previous work (Bond-Lamberty et al., 2012), because the influence of short-term variation in weather and phenology on subannual temporal patterns of soil respiration could not be captured by the temporal resolution of the available spatial data sources (e.g., EVI was only available at best once every 16 days and typically less often than that due to cloud cover). Further, growing season soil respiration was previously found at these sites to be related to leaf area index (Berryman et al., 2016), to which EVI is correlated (Gao et al., 2000; Huete et al., 2002).

All possible predictor variables were included in initial Random Forest simulations, but only the most important, nonredundant variables were included in the final version of the models. Variable selection (using row standardization and multicollinearity tests), variable importance, model significance, and the overfitting ratio were determined using the *rfUtilities* package in R (Murphy et al., 2010). Model fit was assessed by the out-of-bag (i.e., not part of the bootstrap sample) pseudo- $r^2$  and root-mean-square error (RMSE) of all the trees. This approach to model performance was taken instead of splitting the data into independent training and validation data sets because of the limited number of observations (396). Model performance was also assessed by comparing Random Forest RMSE to RMSE from a null model, wherein soil respiration was modeled as the mean growing season soil respiration across all sites for each year from 2004 to 2006.

After model selection was complete, the Random Forest model was then used with continuous spatial data to predict mean growing season soil respiration across the subalpine forest extent within the Southern Rocky Mountains and the three sites contained within (Figure 1). Subalpine forest was defined using the USDA Forest Service forest type map and limited to 120-Spruce/fir group and 280-Lodgepole pine group (Ruefenacht et al., 2008). To ensure consistency with training data, only areas  $>2,800$  m in elevation were predicted. Predictions were further limited to the northern and eastern extent of the Southern Rocky Mountains to avoid projecting to an area far from the geographical coverage of our training data (Figure 1).

### 2.5. Comparison Data Sets

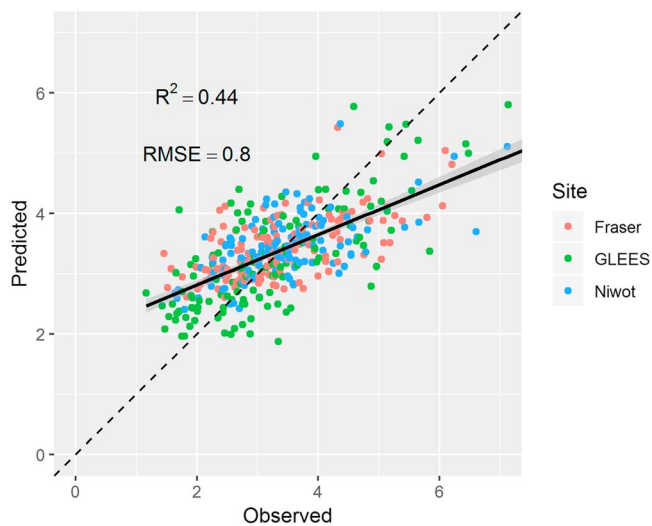
Site-level mean observed and predicted growing season soil respiration were compared to colocated EC towers at GLEES and Niwot (US-NR1 and US-GLE). Although there is currently an EC tower at Fraser, only US-NR1 and US-GLE were active during the prediction years (2004–2006). We used nocturnal net ecosystem exchange (NEE) measured by EC as a proxy for ecosystem respiration for comparison to predicted soil respiration as previously done at GLEES (Speckman et al., 2015). (Note that EC nocturnal respiration was lower than ecosystem respiration estimated by chambers in a study at GLEES; Speckman et al., 2015). Data collected at low turbulence ( $u^* < 0.2$  m/s) were filtered out (Monson et al., 2002; Speckman et al., 2015). Nocturnal NEE (from 19:30 to 5:30 MDT) was averaged at each site over a time period that aligned with soil respiration sampling season which differed slightly from year to year and from site to site. No gap-filling algorithms were performed on the data. Additional details regarding the preprocessing of EC data from Niwot and GLEES can be found in Burns et al. (2015) and Frank et al. (2014).

The predicted growing season soil respiration for the entire study region was compared to MODIS GPP. The MODIS GPP/NPP (MOD17) data are available every 8 days from 2001 to present (Zhao et al., 2005) at 1-km resolution. We downloaded data for all available dates between June 1 and September 30 for 2004 through 2006 (16 dates per year) for the three image extents covering our study area (H10V04, H09V04, and H09V05). Null values were excluded and values were averaged across the 16 dates and mosaicked across the three image extents to create a GPP raster per year.

### 2.6. Analysis Summary

A number of analyses were made to address the research objectives for this study. First, summaries of soil respiration measurements at the site level were made, including means and 95% confidence intervals of the growing season soil respiration from all plots. Next, model fit statistics and accuracy metrics of the Random Forest model were calculated and compared to the null model. From the Random Forest model, predictions of growing season soil respiration were generated for 2004–2006 for the subalpine zone of the Southern Rocky Mountains. Additionally, uncertainty of pixel-level means was assessed by calculating the Random Forest model 95% confidence intervals at each pixel using *ModelMap* in R (version 3.3.5; Freeman, 2009). We visually assessed the overall spatial and temporal patterns of the Random Forest model predictions to determine how the patterns varied in relation to the predictor variables.

Finally, we compared summaries of soil respiration from the observed data and Random Forest predictions to the EC tower nocturnal NEE and MODIS GPP data. Average predicted respiration for each site and growing season was compared to average nocturnal NEE from each year and site (for GLEES and Niwot only; Fraser was excluded because of lack of EC tower). Average predicted respiration for the subalpine forested region for each year was compared to MODIS GPP for each year from the same area. From the entire predicted region, we randomly selected 1,000 points in each of the 3 years and tested for significant linear correlations between MODIS GPP and predicted soil respiration resampled to 1-km resolution using a nearest-neighbor



**Figure 3.** Predicted versus observed growing season soil respiration ( $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) from random Forest model. Regression line between predicted and observed values is shown, with the 95% confidence interval (gray band). Dotted line is 1:1.

algorithm ( $\alpha = 0.05$ ). Points were at least 1 km from the edge of the study area to ensure that the MODIS pixel adequately represented the appropriate forest type.

### 3. Results

Mean measured growing season soil respiration across all sites and years was  $3.37 (\pm 0.11)$  95% confidence interval (CI)  $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Across all sites, mean measured growing season soil respiration was  $3.49 (\pm 0.18)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in 2004,  $2.72 (\pm 0.12)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in 2005, and  $3.93 (\pm 0.19)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in 2006. Across all years, mean measured growing season soil respiration was  $3.41 (\pm 0.17)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at Fraser,  $3.28 (\pm 0.22)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at GLEES, and  $3.43 (\pm 0.16)$   $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at Niwot.

The Random Forest model of growing season soil respiration had an out-of-bag pseudo  $r^2$  of 0.45 and RMSE of  $0.80 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or 24% of the mean measured soil respiration (Figure 3). For comparison, the null model (using the mean across all sites for each year) had a RMSE of  $1.51 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or 45% of the mean measured soil respiration.

Average predicted growing season soil respiration for our prediction region was  $3.49 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $\pm 0.37$  standard deviation of all pixels) in 2004,  $3.50 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $\pm 0.54$ ) in 2005, and  $3.45 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $\pm 0.38$ ) in 2006. Predicted soil respiration varied spatially at both the site level (Figure 4) and across the region of interest (Figure 5). Spatial patterns of respiration were different from year to year, especially in the northern extent of the predictive region near GLEES in 2005 (Figure 6). Large changes in predicted soil respiration across this area follow spatial changes in AI, winter precipitation, and elevation, whereas EVI and GPP (for comparison) varied less (Figure 6). Uncertainty of the predictions at the pixel level (95% confidence intervals) ranged from  $0.04$  to  $0.20 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ .

Model input variables varied widely across sites and the region; however, the mean values of model inputs at the site scale were similar to the mean values at the regional scale, with the exception of folded aspect, which was more E and NW facing (i.e., wetter) at the sites than across the region. Across the extent of our prediction region, EVI varied little from year to year. The other important predictors of soil respiration varied interannually. AI was low in 2004 compared to 2005 and 2006. Winter precipitation and summer temperatures were lowest in 2004 and highest in 2006 (Table 1). These patterns, however, were not always consistent across the entire study area.

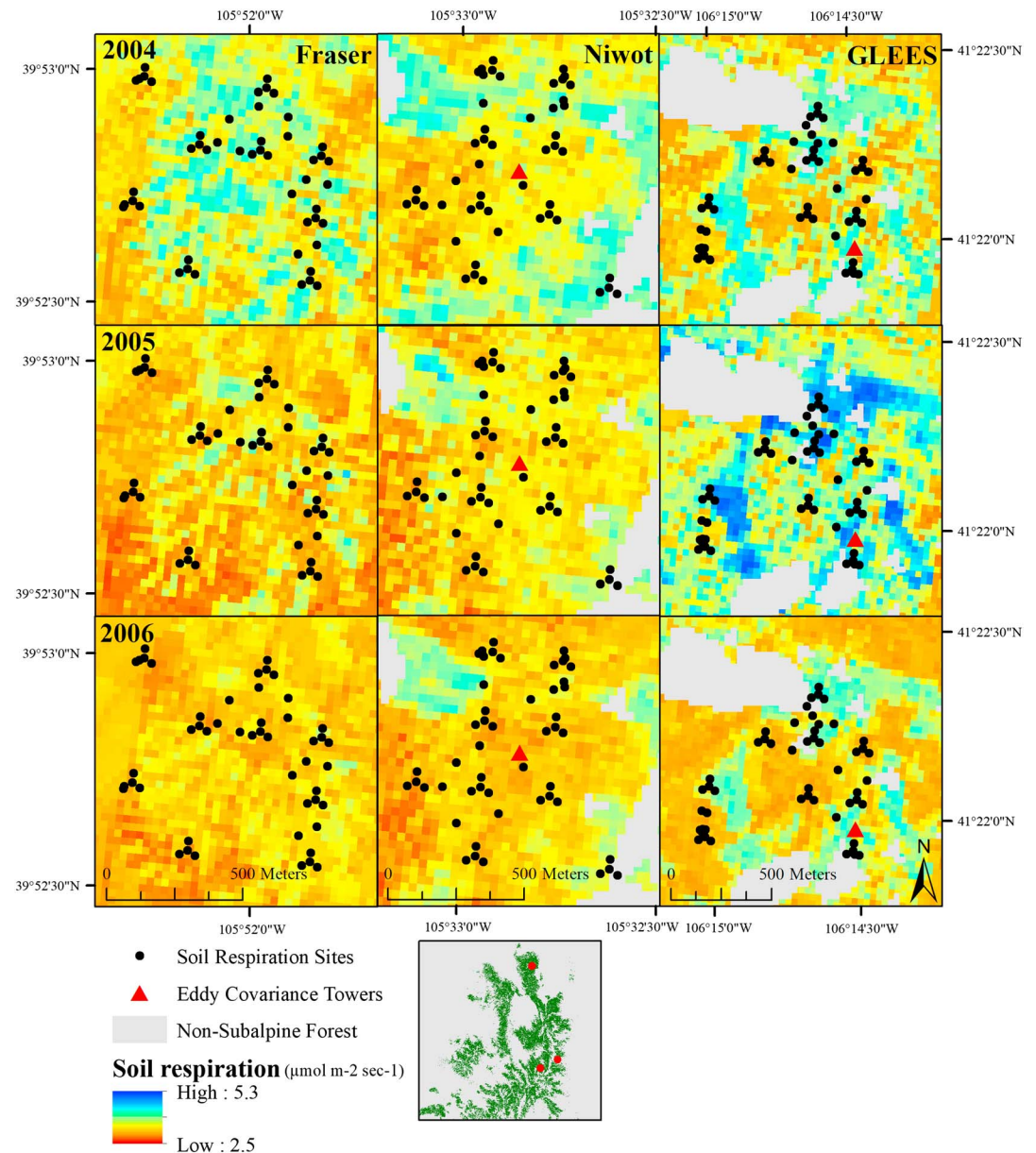
Of the original 10 variables examined (see section 2), seven variables emerged as the most important for predicting soil respiration (Tables 1 and 2). Previous years' mean growing season EVI and the mean growing season AI were the most important variables selected in the Random Forest model (Table 2). Higher EVI and winter precipitation tended to increase soil respiration, whereas soil respiration tended to be lower during higher AI, on drier aspects, and at higher elevations (Figure 7).

#### 3.1. Comparison to Eddy Covariance Respiration and MODIS GPP

At Niwot, observed and predicted values for soil respiration within the EC footprint were similar to each other for all years; however, at GLEES, the observed values were lower than the predicted respiration values in 2004 and 2005 (Figure 8). Predicted soil respiration from the EC tower footprints at GLEES and Niwot was within 20% of nocturnal NEE measured by EC towers in all cases except at GLEES in 2005 (Figure 8). Predicted soil respiration at GLEES was 143% of nocturnal NEE in 2005 compared to 84% in 2006. Predicted soil respiration at Niwot was 117% of nocturnal NEE in 2004, 120% in 2005, and 113% in 2006.

Mean predicted soil respiration across the study region was 73%, 72%, and 75% of mean MODIS GPP for the growing season (1 June to 30 September) in 2004, 2005, and 2006, respectively (Table 1). Interannual trends in predicted soil respiration when averaged across the study area were similar to those of MODIS GPP, with the lowest values for both occurring in 2006. However, there was no significant correlation between MODIS GPP and predicted soil respiration.

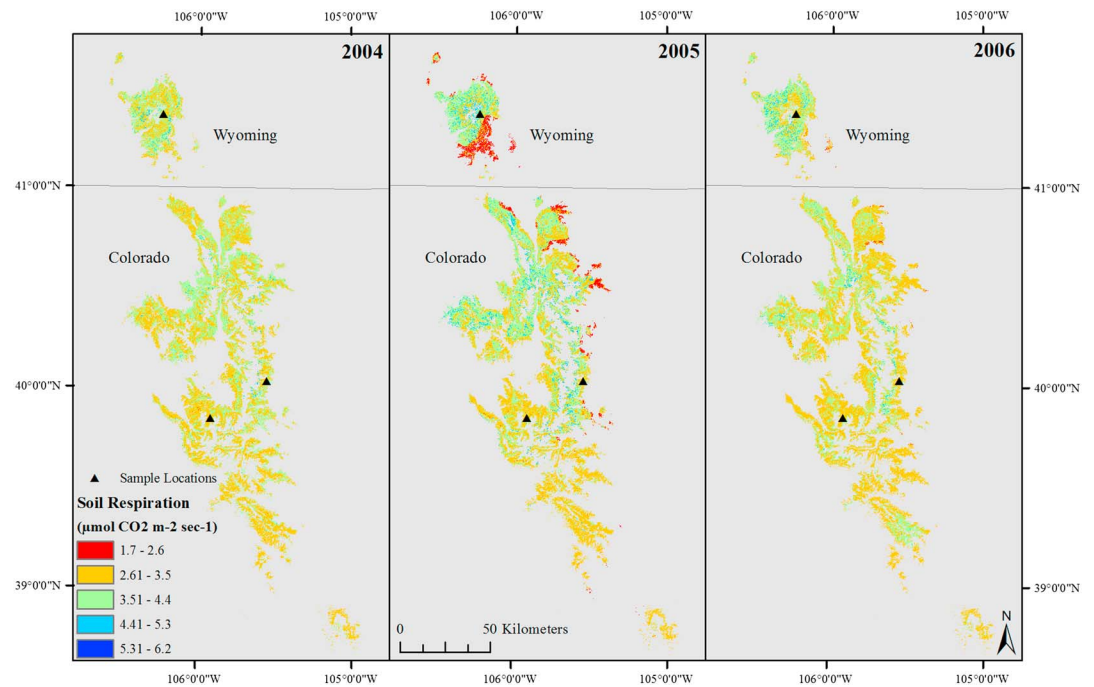




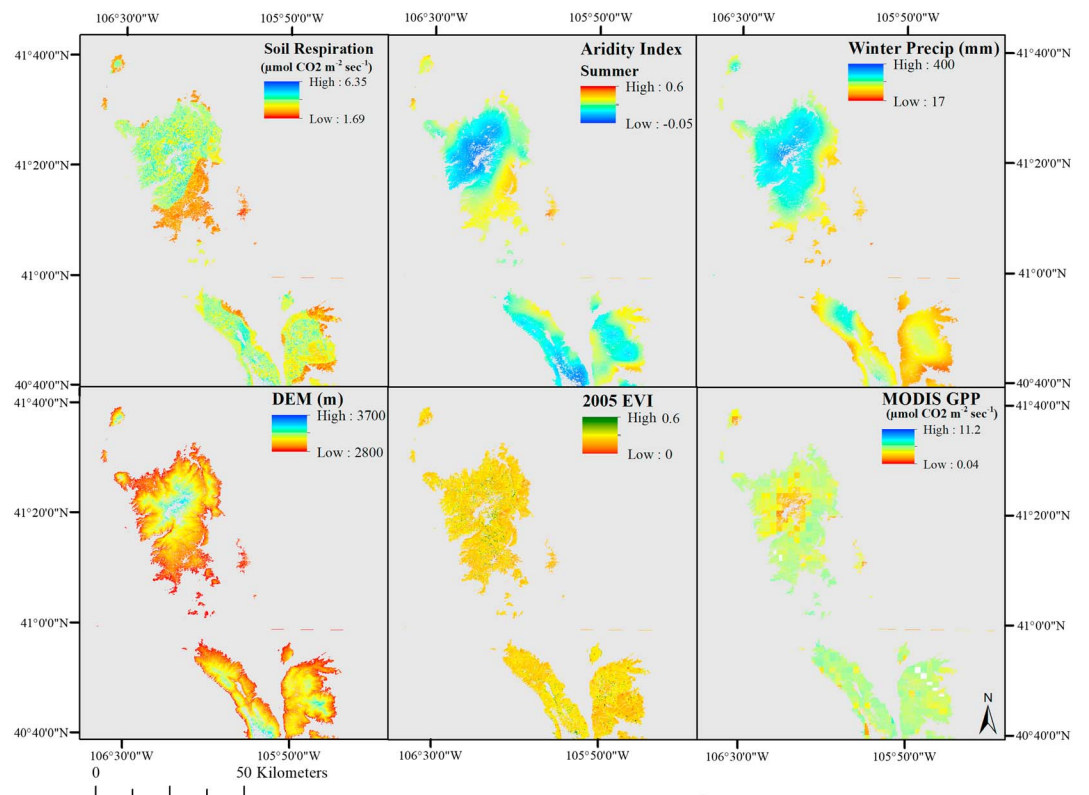
**Figure 4.** Distribution of predicted growing season soil respiration across the three sample locations and from 2004 to 2006. Minimap shows the location of sites within the extent of subalpine forest in the southern Rocky Mountains.

#### 4. Discussion

For regional carbon assessments, there is a need for landscape-scale estimates of respiration that reflect spatiotemporal variability in biophysical and climatic drivers. Using field data, we modeled soil respiration rates for 3 years across our study area at 30-m resolution, revealing spatial variability across mountainous terrain where soil and vegetation characteristics reflect fine-scale changes in elevation, slope, and aspect. Our work demonstrates that statistical models based on field measurements and remotely sensed data sets can be used to map soil respiration. This approach takes advantage of a growing availability of geospatial data that can represent drivers of soil respiration. Further expansion of these data sets, covering a wider range of environmental conditions (e.g., Soil Respiration Database; Bond-Lamberty & Thomson, 2010a), could increase the applicability of this method.



**Figure 5.** The spatial distribution of the predicted growing season (June–September) soil respiration for 2004 through 2006 across the subalpine forests of the front range in the southern Rocky Mountains.



**Figure 6.** For 2005, a visual comparison between a spatial subset of the predicted soil respiration, corresponding independent variables and MODIS gross primary productivity (GPP). DEM = digital elevation model; EVI = enhanced vegetation index; MODIS = moderate resolution imaging spectroradiometer.

**Table 2**

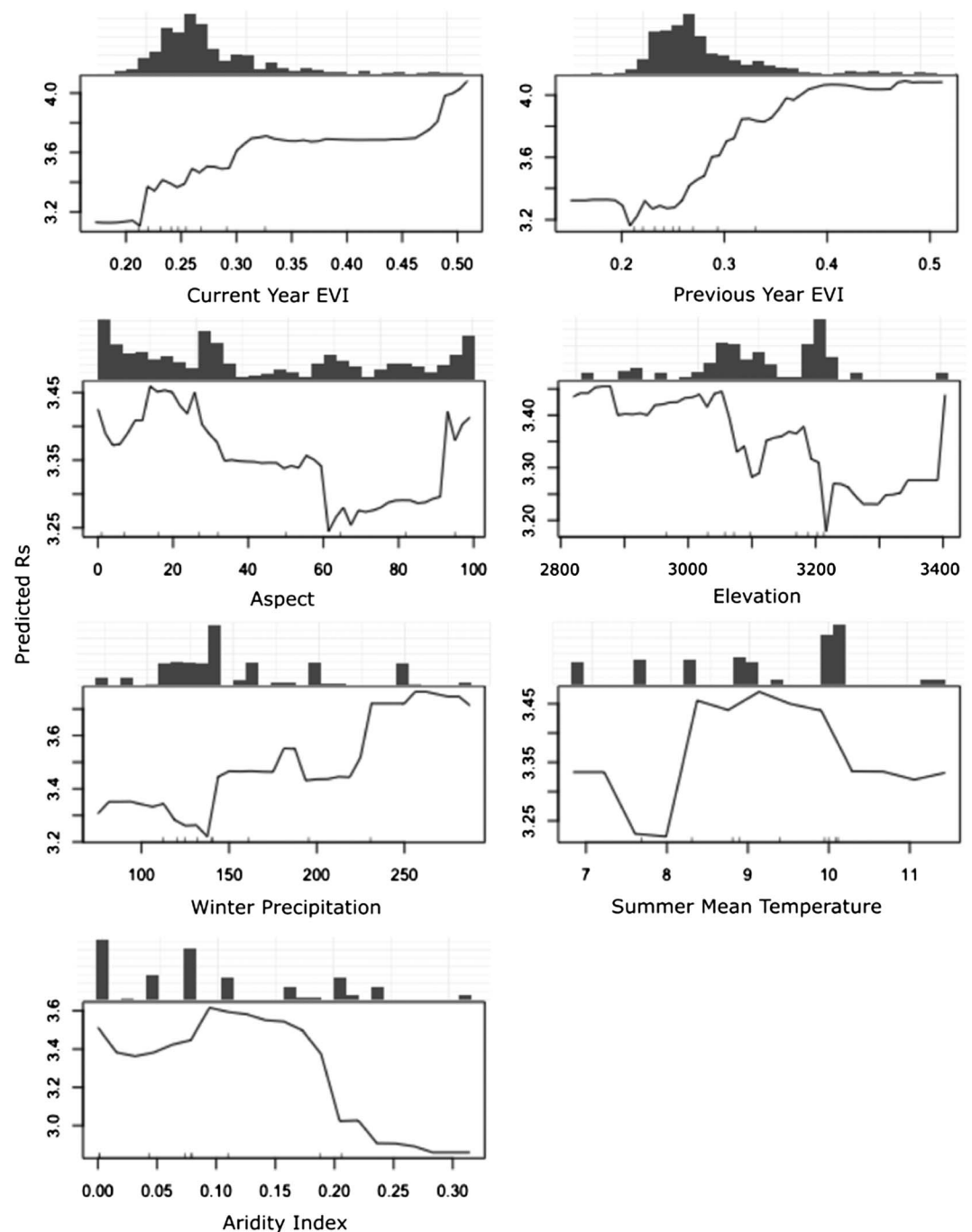
*Variables Selected for in Random Forest Model, Their Units of Measure, the Mean, Minimum, and Maximum Values Across the Training Plots, the Pixel Size of the Original Data Sources, Original Temporal Resolution, and Variable Importance*

Variable	Units	Mean (min, max) across plots	Mean (min, max) across subalpine forest extent	Pixel size	Temporal resolution	Variable importance
Mean AI (Jun–Sep)	relative scale of cool/wet (0) to hot/dry (1)	0.094 (0, 0.31)	0.10 (0, 0.60)	4 km	monthly	0.99
Total PRISM precipitation from January to March	mm	150 (75, 287)	162 (24, 427)	4 km	monthly	0.86
Current year mean EVI (Jul–Sep)		0.26 (0.17, 0.51)	0.23 (0.06, 0.67)	30 m	once every 16 days	0.84
Previous year mean EVI (Jul–Sep)		0.26 (0.15, 0.51)	0.23 (0.04, 0.69)	30 m	once every 16 days	1.0
Mean PRISM air temperature (May 1 to Sep 30)	°C	9.2 (6.8, 11.4)	8.8 (2.6, 14.8)	4 km	daily	0.73
Elevation	m	3,105 (2,819, 3,403)	3,089 (2,754, 4,122)	10 m	NA	0.47
Aspect (folded)	relative scale of NE-facing (0) to SW facing (180)	42 (0, 99)	90 (0, 180)	10 m	NA	0.26

*Note.* EVI = Enhanced Vegetation Index from Landsat; PRISM = predicted precipitation from PRISM climate group (PRISM Climate Group, Oregon State University, 2017). Variable importance is a relative measure of the degree of influence over the predicted value and should not be confused with effect size.

We found that soil respiration was predicted with reasonable uncertainty by canopy greenness (EVI), topography, and climate, in support of previous findings (Reichstein et al., 2003; Riveros-Iregui et al., 2012). This is consistent with canopy-driven controls of soil respiration via photosynthesis and litter production (Butnor et al., 2003; Hibbard et al., 2005; Reichstein et al., 2003). EVI is related to canopy seasonality and leaf area index, so it was selected for use in our model as a proxy for substrate fueling respiration (Huete et al., 2002). Canopy-correlated substrates are expected to represent both recently fixed photosynthates via root respiration/exudates that are respired within days or months and canopy and root litter that is consumed over several years (Högberg et al., 2007; Sulzman et al., 2005). The selection of previous-year's EVI in our model is supported by findings of multiyear time lags between reductions in canopy greenness and lower soil respiration in boreal forests (Bond-Lamberty et al., 2012). In addition to influencing canopy variables, climate and topography are important drivers of decomposition rates and microbial activity that contribute to soil respiration (Du et al., 2015). Thus, informed selection of predictor variables that represent known drivers of ecosystem processes allowed us to build a model that reasonably predicted annual soil respiration across a large area. In addition, the relatively small-scale Landsat EVI may have been more likely to capture microsite-scale heterogeneity of biophysical drivers of soil respiration than MODIS. Yet we acknowledge that even at 30 m resolution, predictions are unlikely to capture fine-scale gradients in soil moisture, microclimate conditions, and soil nutrients. Advancements in the availability of remotely sensed data sets that reflect soil condition and canopy structure, as well as high-resolution DEMs, could help improve our ability to predict fine-scale variability in soil respiration.

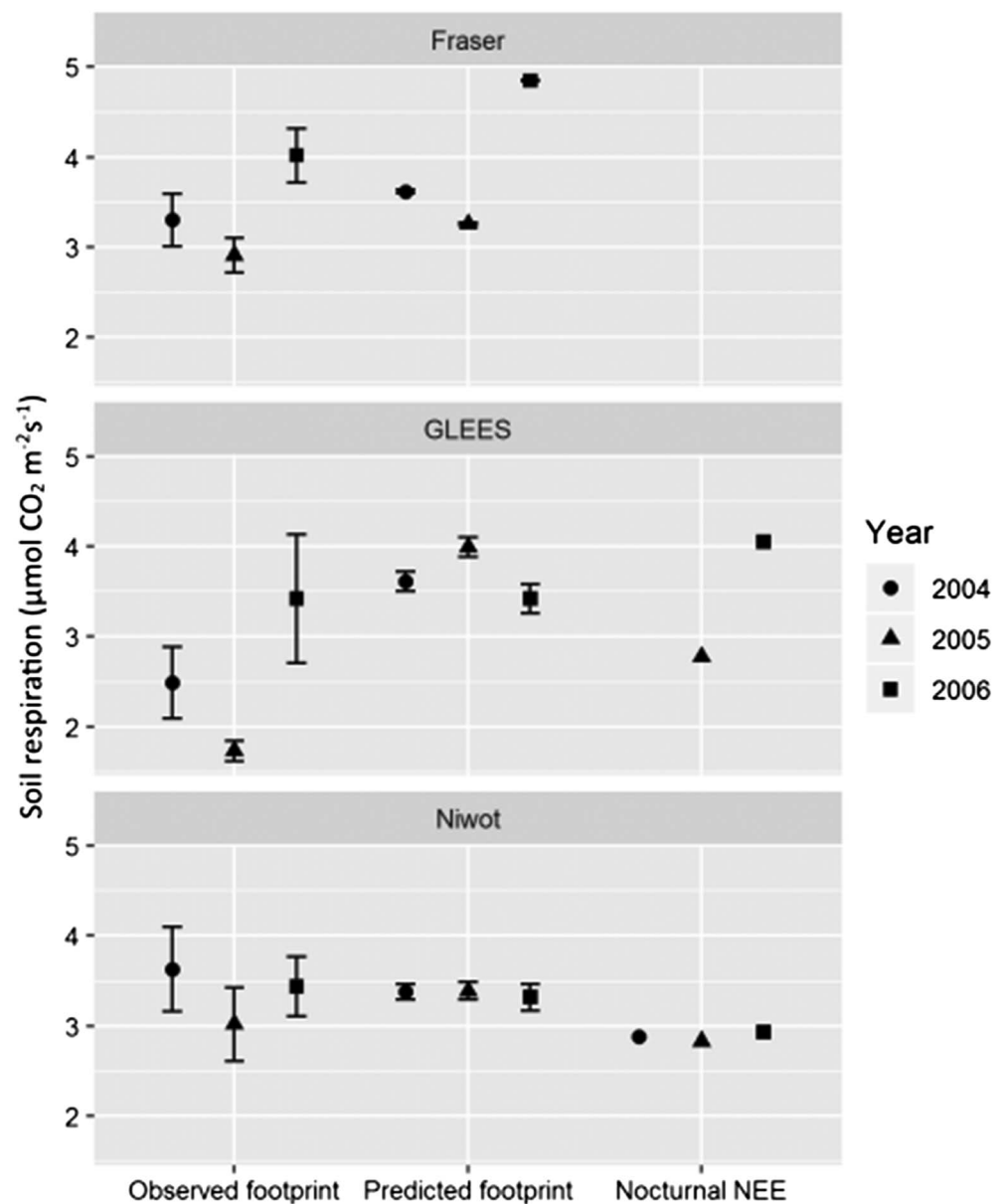
In addition to the utility of this approach for estimating regional-scale respiration, our paper also compared two approaches to characterizing site-level soil respiration: by averaging measurements made by field sampling and by using a model to spatially interpolate across each site. Consistent with previous estimates of soil and forest floor decomposition at the three sites using the same sampling scheme, soil respiration measurements were not significantly different across sites when averaged across all years (Bradford et al., 2008). However, both observed and predicted respiration at the site level varied from year to year. Furthermore, observed values were significantly lower than predicted for 2004 and 2005 at GLEES, a highly heterogeneous site (Figure 8). The field sampling scheme used for these sites follows that of a national forest inventory program and represents a systematic, moderate density (four plots per 6 ha) approach for characterizing landscapes. These results suggest that this scheme may inadequately capture the true distribution of soil respiration rates across a highly heterogeneous landscape. This has important



**Figure 7.** Partial dependence of growing season soil respiration on the selected variables for the random Forest model (Table 1), with histograms of each predictor variable indicated. The plots demonstrate how the model prediction is affected by the value of a given variable after accounting for the influence of all other variables in the model. Note that units for *elevation* are  $100 \times$  meters.

implications for C budgets that use the mean value from landscape sampling. Mean values may be inaccurate at worst, and at best smooth over spatial and interannual heterogeneity in C fluxes. Such patterns can be captured by accounting for spatial heterogeneity in respiration drivers using models, perhaps leading to better informed landscape-scale estimates of soil respiration.





**Figure 8.** Comparison of observed and predicted respiration in the eddy covariance (EC) footprint with nocturnal NEE (net ecosystem exchange) for the two sites with EC towers. EC data do not exist from 2004 at GLEES. Error bars for observations indicate 95% confidence interval calculated using the standard error of spatial replicates (i.e., plots;  $n = 36$  for Fraser,  $n = 8$  for GLEES, and  $n = 12$  for Niwot). Error bars for predictions indicate 95% confidence interval calculated using the standard error of spatial replicates (i.e., pixels;  $n = 1,111$  for Fraser,  $n = 348$  for GLEES, and  $n = 142$  for Niwot). Note that  $n$  is higher for Fraser because the entire site area was averaged due to lack of EC tower, whereas only area that fell within the EC tower footprint were included in Niwot and GLEES observed and predicted values.

#### 4.1. Limitations of Modeling Approach

Our model predicted soil respiration at annual time steps. Even more informative would be models that can predict soil respiration at subannual or seasonal time scales. The time step of our models was largely determined by soil respiration sampling intervals and Landsat data quality and availability, which were often out of sync with each other (thus the growing season averaging approach). MODIS imagery could be used to provide near-daily predictions, but would sacrifice spatial resolution. Alternatively, new satellites, such as Sentinel-2, could be used alone or in conjunction with Landsat 8 to predict monthly or even weekly respiration provided the availability of training data at adequate temporal resolutions and response times between

drivers and respiration rates exists. Such models could better take into account seasonal variation in drivers and different time scales of influence between drivers and soil respiration.

A common challenge of spatial modeling efforts is potential for transferability errors by using data constrained to distinct field sites to predict across a geographic extent not represented by the field sites (Wenger & Olden, 2012). We took measures to avoid projecting beyond the conditions represented by the data used to fit the model by limiting our predicted area to the same forest type, elevation range, and orographic climatic influences (near and on either side of the continental divide) represented by our sites. Due to a lack of validation data from areas outside the range of our sites, we could not assess error associated with model transferability. Thus, predictions from outside the range of our sites should be interpreted with caution.

Even considering that out-of-bag  $r^2$  can underestimate model performance, our model fit was not as high as those reported in similar studies (Bond-Lamberty et al., 2012; Wu et al., 2014). This could have been due to a number of reasons: a more heterogeneous landscape that is not as fully represented by sampled plot locations, higher spatial resolution of our predictions, a smaller range of variability in respiration (due to both seasonal averaging and restricting sampling to a single forest type) compared to past efforts, lack of high-resolution climate data, or timing of soil respiration sampling (Cueva et al., 2017). Soil respiration is highly variable over time, both seasonally and diurnally. Because only one survey unit was used to sample all plots, some measurements were collected earlier and later in the day than others. Additionally, soil respiration varies seasonally, making sampling more difficult. These issues, however, are common to most studies involving landscape soil respiration measurements. Despite these limitations, the confidence interval around our predictions was reasonable across the predictive range, and confidence intervals of site-level estimates were lower than those from observations alone (Figure 8). Given the large investment in time and resources required to collect soil respiration measurements across multiple sites for fully characterizing a region, our modeling approach provides an acceptable level of uncertainty for large-scale assessments of soil respiration.

#### 4.2. Comparison to Independent C Cycle Measures

Soil respiration measurements independent of those used to train our Random Forest model were limited in number and spatial extent. Therefore, performing a thorough validation of our model results was not possible. Instead, we compared our predicted results to other C flux measures, to which our soil respiration predictions compared well for our study area and time period of interest. We found predicted regional summertime soil respiration to be 72–75% of MODIS GPP, a reasonable value given previous findings. A few independent measurements exist of both soil respiration and GPP at the same temperate forested site; they report annual soil respiration as 43–60% (Wang et al., 2010; Zha et al., 2007), 65% (Tang et al., 2008), 80% (Thomas et al., 2013), and 85% (Hermle et al., 2010) of GPP. Across the predictive region, we expected to see a positive correlation between MODIS GPP and predicted soil respiration, reflecting that seen at global and hemispheric scales (Hibbard et al., 2005; Litton et al., 2007; Raich & Schlesinger, 1992). However, a random sample of 100 one-kilometer pixels showed no significant correlation between MODIS GPP and our predicted respiration rates. Further, macroscale comparison between soil respiration and MODIS GPP showed opposite spatial trends in 2005 in the northern extent of the region (Figure 7). In this area, MODIS showed lower GPP at high elevations than low elevations. In contrast, predicted soil respiration responded to spatial variability in aridity and winter precipitation, resulting in greater respiration at higher elevations in this area. This analysis was not intended, and is unable, to assess the accuracy of either MODIS GPP or our modeled respiration rates. It does, however, highlight the differences between these two products and emphasizes a need for a product that is more relevant at the regional scale, grounded in within-forest-type relationships between canopy greenness and soil respiration that may not emerge at the global scale.

Several factors could explain the lack of correlation with MODIS. The soil respiration measurements used to inform our model were made during the daytime; because soil respiration can have lower values at night compared to day, this could bias our estimates high compared to a 24-hr averaged value such as MODIS GPP. Ecosystem respiration, of which soil respiration is a component, is often correlated with vegetation productivity—which MODIS GPP estimates. However, these can easily decouple due to forest disturbance (Kurz et al., 2008; Running, 2008) or when drought differentially affects productivity versus heterotrophic respiration, for example (Jassal et al., 2008). In addition, carbon use efficiency of forest primary productivity (NPP divided by GPP) ranges from 23% to 83% across different forest types and stand ages (DeLucia et al., 2007;

Litton et al., 2007); therefore, heterogeneity in disturbance history (for which we could not account) could lead to differences in the ratio of respiration to productivity. MODIS GPP can also have high uncertainty at the regional level, especially over complex terrain, because the algorithm is informed by coarse-resolution climate and land cover data and a simplistic water use model (Hwang et al., 2008; Kimball et al., 2017). Finally, scaling our values to the entire region assumes our spatial layer delineating forest from other ecosystems is accurate, whereas this likely introduces uncertainty.

Our predicted soil respiration was 84% to 143% of nocturnal ecosystem respiration as estimated by EC towers at two of the sites, Niwot and GLEES. During the growing season, soil respiration in forests is expected to be between 45% and 80% of ecosystem respiration (Bolstad et al., 2004; Davidson et al., 2006; Tang et al., 2008), so our predictions were biased high compared to nocturnal NEE. Mismatches between tower- and chamber-based estimates of respiration are common (Bolstad et al., 2004; Speckman et al., 2015; Wang et al., 2017). Soil respiration sampling bias as discussed above could have contributed to this (Cueva et al., 2017). Another cause of mismatch could be errors in the estimated EC footprint shape and size that are not taken into account by our predicted estimates. Flux tower footprints are not constant over time, because they shift with the prevailing wind direction and speed, often expanding at night compared to the daytime, and thus are a large source of uncertainty (Wehr & Saleska, 2015). Our estimate of each tower's footprint over which predicted soil respiration was summed were based on general tendencies of the prevailing wind direction at night. We would expect footprint motion to be more of an issue for flux comparison at GLEES than Niwot; GLEES is highly heterogeneous in measured and predicted soil respiration rates whereas Niwot has a more homogenous landscape. In addition, underestimation of ecosystem respiration by nocturnal NEE could have been a factor. Nocturnal NEE from EC towers is considered a proxy for ecosystem respiration due to the lack of photosynthesis at night; however, there are several widely recognized problems with interpreting nocturnal NEE (Massman & Lee, 2002; Wohlfahrt & Galvagno, 2017). First, EC is vulnerable to errors from lack of turbulence and mixing below the canopy, conditions which are more prevalent at night. This would result in an underestimation of ecosystem respiration, even when using a turbulence filter (Goulden et al., 2011; Thomas et al., 2013). Respiration often shows a diurnal pattern becoming lower at night than during the day in subalpine forests (Bowling et al., 2015). However, there was often nighttime turbulence at these sites (GLEES and Niwot are the first and third most turbulent flux sites in the Ameriflux network; <http://ameriflux.lbl.gov/>), so this may not have been a sizeable source of error in the flux tower-derived ecosystem respiration.

### 4.3. Spatial Patterns of Predicted Respiration

Modeling spatial patterns in soil respiration across the three sites yielded some unique insights compared to site-level averages of point measurements. First, we discovered high spatial heterogeneity in predicted respiration at GLEES compared to the other two sites. GLEES is a mosaic of wetlands, upland forests, meadows, and lakes, likely reflected by increased variability in EVI and topography leading to the resulting predicted pattern of respiration. This may have led to a greater mismatch between observed and predicted EC footprint soil respiration at GLEES in 2005 (Figure 8). Our model predictions of soil respiration in the tower footprint had lower uncertainty than observations and, at GLEES, were closer to nocturnal NEE trends than observed soil respiration. Therefore, our modeling approach shows potential for improving upscaling of chamber-based soil respiration measurements for comparison to EC (Phillips et al., 2016). By taking into account spatial heterogeneity of drivers within the EC footprint area, our modeling approach could be a useful tool to generate annual soil respiration values under a range of footprint scenarios that may compare better to EC fluxes for purposes of closing forest C budgets in heterogeneous landscapes (Wehr & Saleska, 2015).

Despite high spatiotemporal variability observed in predicted respiration and its drivers, we found remarkable consistency in average predicted respiration for the region across all 3 years of the study. Climate variability at seasonal and annual time scales can create substantial variability in patterns of soil respiration. However, climate pressures (e.g., hotter, drier) are not necessarily consistent when considered at larger spatial scales, meaning that local temporal variability in soil respiration does not necessarily translate into regional temporal variability in soil respiration. For example, the potential for higher respiration in wetter areas (e.g., high elevations and shaded hillslopes) to compensate for reduced respiration in drier areas (e.g., lower elevations and Sun-facing aspects) should be taken into account when designing field-monitoring programs intended to be representative of a mountainous region.

## 5. Conclusions

Soil respiration is an important component of the C cycle, yet because the rate of respiration can vary rapidly over fine spatial and temporal scales (i.e., diurnal, daily, and seasonally), it can be challenging to characterize rates of soil respiration at a landscape scale. One significant challenge in this endeavor is that spatial data sets are not yet available at appropriate spatial resolution for many drivers known to induce spatiotemporal variability in soil respiration such as C substrate, soil moisture, nutrient availability, and microbial and fine root activity (Kelsey et al., 2012; Martin & Bolstad, 2009; Scott-Denton et al., 2003; Stielstra et al., 2015). Despite these challenges, we found that we could predict the mean rate of growing season soil respiration using the current year and 1-year lagged EVI, winter precipitation, growing season temperature and aridity, elevation, and aspect. When the model was extrapolated across subalpine forests in the Southern Rocky Mountains, we observed spatial and temporal variability in the predicted rates of growing season soil respiration. Our predictions were similar in magnitude to MODIS GPP and EC nocturnal respiration. If accurate C accounting is a priority, then improvements in regional to national predictions of ecosystem and soil respiration are needed. A statistical modeling approach using field-based data to train a model based on geospatial and remotely sensed data sets provides a simple framework that can be applied to diverse regions and ecosystem types.

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## References

- Bechtold, W. A., & Patterson, P. L. (2005). The enhanced forest inventory and analysis program: National sampling design and estimation procedures.
- Berryman, E., Ryan, M. G., Bradford, J. B., Hawbaker, T. J., & Birdsey, R. (2016). Total belowground carbon flux in subalpine forests is related to leaf area index, soil nitrogen, and tree height. *Ecosphere*, 7(8). <https://doi.org/10.1002/ecs2.1418>
- Berryman, E. M., Barnard, H. R., Adams, H. R., Burns, M. A., Gallo, E., & Brooks, P. D. (2015). Complex terrain alters temperature and moisture limitations of forest soil respiration across a semiarid to subalpine gradient. *Journal of Geophysical Research: Biogeosciences*, 120, 707–723. <https://doi.org/10.1002/2014JG002802>
- Bolstad, P. V., Davis, K. J., Martin, J., Cook, B. D., & Wang, W. (2004). Component and whole-system respiration fluxes in northern deciduous forests. *Tree Physiology*, 24(5), 493–504. <https://doi.org/10.1093/treephys/24.5.493>
- Bonan, G. B., Hartman, M. D., Parton, W. J., & Wieder, W. R. (2013). Evaluating litter decomposition in earth system models with long-term litterbag experiments: An example using the Community Land Model version 4 (CLM4). *Global Change Biology*, 19(3), 957–974. <https://doi.org/10.1111/gcb.12031>
- Bond-Lamberty, B., Bunn, A. G., & Thomson, A. M. (2012). Multi-year lags between forest browning and soil respiration at high northern latitudes. *PLoS One*, 7(11), e50441. <https://doi.org/10.1371/journal.pone.0050441>
- Bond-Lamberty, B., & Thomson, A. (2010a). A global database of soil respiration data. *Biogeosciences*, 7(6), 1915–1926. <https://doi.org/10.5194/bg-7-1915-2010>
- Bond-Lamberty, B., & Thomson, A. (2010b). Temperature-associated increases in the global soil respiration record. *Nature*, 464(7288), 579–582. <https://doi.org/10.1038/nature08930>
- Bond-Lamberty, B., Wang, C., & Gower, S. T. (2004). Contribution of root respiration to soil surface CO<sub>2</sub> flux in a boreal black spruce chronosequence. *Tree Physiology*, 24(12), 1387–1395. <https://doi.org/10.1093/treephys/24.12.1387>
- Bowling, D. R., Egan, J. E., Hall, S. J., & Risk, D. A. (2015). Environmental forcing does not induce diel or synoptic variation in the carbon isotope content of forest soil respiration. *Biogeosciences*, 12(16), 5143–5160. <https://doi.org/10.5194/bg-12-5143-2015>
- Bradford, J., Weishampel, P., Smith, M.-L., Kolka, R., Birdsey, R. A., Ollinger, S. V., & Ryan, M. G. (2009). Detrital carbon pools in temperate forests: Magnitude and potential for landscape-scale assessment. *Canadian Journal of Forest Research. Journal Canadien de La Recherche Forestiere*, 39(4), 802–813. <https://doi.org/10.1139/X09-010>
- Bradford, J. B., Birdsey, R. A., Joyce, L. A., & Ryan, M. G. (2008). Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. *Global Change Biology*, 14(12), 2882–2897. <https://doi.org/10.1111/j.1365-2486.2008.01686.x>
- Bradford, J. B., Weishampel, P., Smith, M.-L., Kolka, R., Birdsey, R. A., Ollinger, S. V., & Ryan, M. G. (2010). Carbon pools and fluxes in small temperate forest landscapes: Variability and implications for sampling design. *Forest Ecology and Management*, 259(7), 1245–1254. <https://doi.org/10.1016/j.foreco.2009.04.009>
- Breiman, L. (2001). Random forests. *Machine Learning*, 45(1), 5–32.
- Burns, S. P., Blanken, P. D., Turnipseed, A. A., Hu, J., & Monson, R. K. (2015). The influence of warm-season precipitation on the diel cycle of the surface energy balance and carbon dioxide at a Colorado subalpine forest site. *Biogeosciences*, 12(23), 7349–7377. <https://doi.org/10.5194/bg-12-7349-2015>
- Butnor, J. R., Johnsen, K. H., Oren, R., & Katul, G. G. (2003). Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. *Global Change Biology*, 9(6), 849–861. <https://doi.org/10.1046/j.1365-2486.2003.00630.x>
- Carbone, M. S., Richardson, A. D., Chen, M., Davidson, E. A., Hughes, H., Savage, K. E., & Hollinger, D. Y. (2016). Constrained partitioning of autotrophic and heterotrophic respiration reduces model uncertainties of forest ecosystem carbon fluxes but not stocks. *Journal of Geophysical Research: Biogeosciences*, 121, 2476–2492. <https://doi.org/10.1002/2016JG003386>
- Cavaleri, M. A., Oberbauer, S. F., & Ryan, M. G. (2008). Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell & Environment*, 31(4), 473–483. <https://doi.org/10.1111/j.1365-3040.2008.01775.x>
- Chapin, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., et al. (2006). Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9(7), 1041–1050. <https://doi.org/10.1007/s10021-005-0105-7>
- Cleveland, C. C., Nemergut, D. R., Schmidt, S. K., & Townsend, A. R. (2007). Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. *Biogeochemistry*, 82(3), 229–240. <https://doi.org/10.1007/s10533-006-9065-z>



- Cole, J. A., Johnson, K. D., Birdsey, R. A., Pan, Y., Wayson, C. A., McCullough, K., et al. (2015). North American Carbon Program biometric database. 2nd edition. USDA Forest Service, Northern Research Station. <https://doi.org/10.2737/RDS-2013-0008-2>
- Cueva, A., Bullock, S. H., López-Reyes, E., & Vargas, R. (2017). Potential bias of daily soil CO<sub>2</sub> efflux estimates due to sampling time. *Scientific Reports*, 7(1), 11925. <https://doi.org/10.1038/s41598-017-11849-y>
- Davidson, E. A., Belk, E., & Boone, R. D. (1998). Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, 4(2), 217–227. <https://doi.org/10.1046/j.1365-2486.1998.00128.x>
- Davidson, E. A., Richardson, A. D., Savage, K. E., & Hollinger, D. Y. (2006). A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. *Global Change Biology*, 12(2), 230–239. <https://doi.org/10.1111/j.1365-2486.2005.01062.x>
- DeLucia, E., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6), 1157–1167. <https://doi.org/10.1111/j.1365-2486.2007.01365.x>
- Du, Z., Riveros-Iregui, D. A., Jones, R. T., McDermott, T. R., Dore, J. E., McGlynn, B. L., et al. (2015). Landscape position influences microbial composition and function via redistribution of soil water across a watershed. *Applied and Environmental Microbiology*. <https://doi.org/10.1128/AEM.02643-15>
- Duarte, H. F., Raczka, B. M., Ricciuto, D. M., Lin, J. C., Koven, C. D., Thornton, P. E., et al. (2017). Evaluating the community land model (CLM4.5) at a coniferous forest site in northwestern United States using flux and carbon-isotope measurements. *Biogeosciences*, 14(18), 4315–4340. <https://doi.org/10.5194/bg-14-4315-2017>
- Frank, J. M., Massman, W. J., Ewers, B. E., Huckaby, L. S., & Negrón, J. F. (2014). Ecosystem CO<sub>2</sub>/H<sub>2</sub>O fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce bark beetles. *Journal of Geophysical Research: Biogeosciences*, 119, 1195–1215. <https://doi.org/10.1002/2013JG002597>
- Freeman, E. (2009). ModelMap: An R package for modeling and map production using random forest and stochastic gradient boosting. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, USA. Retrieved from <http://CRAN.R-project.org/~eafreeman@fs.fed.us>
- Gao, X., Huete, A. R., Ni, W., & Miura, T. (2000). Optical–biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment*, 74(3), 609–620. [https://doi.org/10.1016/S0034-4257\(00\)00150-4](https://doi.org/10.1016/S0034-4257(00)00150-4)
- Gaudinski, J. B., Trumbore, S. E., Davidson, E. A., & Zheng, S. (2000). Soil carbon cycling in a temperate forest: Radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*, 51(1), 33–69. <https://doi.org/10.1023/A:1006301010014>
- Goulden, M. L., Mcmillan, A. M. S., Winston, G. C., Rocha, A. V., Manies, K. L., Harden, J. W., & Bond-Lamberty, B. P. (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, 17(2), 855–871. <https://doi.org/10.1111/j.1365-2486.2010.02274.x>
- Hastie, T., Tibshirani, R., & Friedman, J. (2009). Chapter 15. Random forests. In *The elements of statistical learning: data mining, inference, and prediction* (pp. 587–604). New York: Springer-Verlag.
- Hermle, S., Lavigne, M. B., Bernier, P. Y., Bergeron, O., & Paré, D. (2010). Component respiration, ecosystem respiration and net primary production of a mature black spruce forest in northern Quebec. *Tree Physiology*, 30(4), 527–540. <https://doi.org/10.1093/treephys/tpq002>
- Hibbard, K. A., Law, B. E., Reichstein, M., & Sulzman, J. (2005). An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry*, 73(1), 29–70. <https://doi.org/10.1007/s10533-004-2946-0>
- Högberg, P., Höglberg, M. N., Göttlicher, S. G., Betson, N. R., Keel, S. G., Metcalfe, D. B., et al. (2007). High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. *The New Phytologist*, 177, 220–228.
- Hopper, R. W. E., & Walthall, P. M. (1992). The Soil. In R. C. Musselman (Ed.), *The Glacier Lakes Ecosystem Experiments Site* (Vol. RM-249, pp. 23–29). Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83(1–2), 195–213. [https://doi.org/10.1016/S0034-4257\(02\)00096-2](https://doi.org/10.1016/S0034-4257(02)00096-2)
- Hwang, T., Kang, S., Kim, J., Kim, Y., Lee, D., & Band, L. (2008). Evaluating drought effect on MODIS gross primary production (GPP) with an eco-hydrological model in the mountainous forest, East Asia. *Global Change Biology*, 14(5), 1037–1056. <https://doi.org/10.1111/j.1365-2486.2008.01556.x>
- Jassal, R. S., Black, T. A., Novak, M. D., Gaumont-Guay, D., & Nesic, Z. (2008). Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. *14*, 1–14.
- Jian, J., Steele, M. K., Thomas, R. Q., Day, S. D., & Hodges, S. C. (2018). Constraining estimates of global soil respiration by quantifying sources of variability. *Global Change Biology*, 24(9), 4143–4159. <https://doi.org/10.1111/gcb.14301>
- Keenan, T. F., Davidson, E. A., Munger, J. W., & Richardson, A. D. (2013). Rate my data: Quantifying the value of ecological data for the development of models of the terrestrial carbon cycle. *Ecological Applications*, 23(1), 273–286. <https://doi.org/10.1890/12-0747.1>
- Kelsey, K. C., Wickland, K. P., Striegl, R. G., & Neff, J. C. (2012). Variation in soil carbon dioxide efflux at two spatial scales in a topographically complex boreal forest. *Arctic, Antarctic, and Alpine Research*, 44(4), 457–468. <https://doi.org/10.1657/1938-4246-44.4.457>
- Kimball, H. L., Selmants, P. C., Moreno, A., Running, S. W., & Giardina, C. P. (2017). Evaluating the role of land cover and climate uncertainties in computing gross primary production in Hawaiian Island ecosystems. *PLoS One*, 12(9), e0184466.
- Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., et al. (2008). Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452(7190), 987–990. <https://doi.org/10.1038/nature06777>
- Liang, L. L., Riveros-Iregui, D. A., & Risk, D. A. (2016). Spatial and seasonal variability of the stable carbon isotope composition of soil CO<sub>2</sub> and flux in complex terrain. *Journal of Geophysical Research: Biogeosciences*, 121, 2328–2339. <https://doi.org/10.1002/2015JG003193>
- Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, 13(10), 2089–2109. <https://doi.org/10.1111/j.1365-2486.2007.01420.x>
- Lutz, J. A., van Wagtenonk, J. W., & Franklin, J. F. (2010). Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *Journal of Biogeography*, 37(5), 936–950. <https://doi.org/10.1111/j.1365-2699.2009.02268.x>
- Martin, J. G., & Bolstad, P. V. (2009). Variation of soil respiration at three spatial scales: Components within measurements, intra-site variation and patterns on the landscape. *Soil Biology & Biochemistry*, 41(3), 530–543. <https://doi.org/10.1016/j.soilbio.2008.12.012>
- Masek, J. G., Vermote, E. F., Saleous, N. E., Wolfe, R., Hall, F. G., Huemmrich, K. F., et al. (2006). A Landsat surface reflectance dataset for North America, 1990–2000. *IEEE Geoscience and Remote Sensing Letters*, 3(1), 68–72. <https://doi.org/10.1109/LGRS.2005.857030>
- Massman, W. J., & Lee, X. (2002). Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agricultural and Forest Meteorology*, 113(1–4), 121–144. [https://doi.org/10.1016/S0168-1923\(02\)00105-3](https://doi.org/10.1016/S0168-1923(02)00105-3)
- McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, 13(4), 603–606. <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>

- Monson, R. K., Turnipseed, A. A., Sparks, J. P., Harley, P. C., Scott-Denton, L. E., Sparks, K., & Huxman, T. E. (2002). Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, 8(5), 459–478. <https://doi.org/10.1046/j.1365-2486.2002.00480.x>
- Murphy, M. A., Evans, J. S., & Storer, A. (2010). Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology*, 91(1), 252–261. <https://doi.org/10.1890/08-0879.1>
- National Atmospheric Deposition Program. (2017). NADP Program Office, Illinois State Water Survey. *University of Illinois, Champaign, IL 61820*. <http://nadp.sws.uiuc.edu/data/ntn/>
- Parton, W. J., Ojima, D. S., Cole, C. V., & Schimel, D. S. (1994). A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture and management. In R. B. Bryant & R. W. Arnold (Eds.), *Quantitative Modeling of Soil Forming Processes* (pp. 147–167). Madison, WI: Soil Science Society of America.
- Phillips, C. L., Bond-Lamberty, B., Desai, A. R., Lavoie, M., Risk, D., Tang, J., & Vargas, R. (2016). The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling. *Plant and Soil*, 431, 1–25.
- PRISM Climate Group, Oregon State University, Descriptions of PRISM spatial climate datasets for the Conterminous United States (2017). Retrieved from [http://www.prism.oregonstate.edu/documents/PRISM\\_datasets.pdf](http://www.prism.oregonstate.edu/documents/PRISM_datasets.pdf)
- Raich, J. W., & Schlesinger, W. H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, 44B, 81–99.
- Redmond, M. (2015). Climatic water deficit scripts for R. Retrieved from [https://naes.unr.edu/weisberg/old\\_site/downloads/cwd\\_function.zip](https://naes.unr.edu/weisberg/old_site/downloads/cwd_function.zip)
- Redmond, M. D., Kelsey, K. C., Urza, A. K., & Barger, N. N. (2017). Interacting effects of climate and landscape physiography on piñon pine growth using an individual-based approach. *Ecosphere*, 8(3). Retrieved from <https://doi.org/10.1002/ecs2.1681/full>
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banz, J., et al. (2003). Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochemical Cycles*, 17(4), 1104. <https://doi.org/10.1029/2003GB002035>
- Rhoades, C. C., Hubbard, R. M., & Elder, K. (2017). A decade of streamwater nitrogen and forest dynamics after a mountain pine beetle outbreak at the Fraser Experimental Forest, Colorado. *Ecosystems*, 20(2), 380–392. <https://doi.org/10.1007/s10021-016-0027-6>
- Riveros-Iregui, D. A., McGlynn, B. L., Emanuel, R. E., & Epstein, H. E. (2012). Complex terrain leads to bidirectional responses of soil respiration to inter-annual water availability. *Global Change Biology*, 18(2), 749–756. <https://doi.org/10.1111/j.1365-2486.2011.02556.x>
- Ruefenacht, B., Finco, M. V., Nelson, M. D., Czaplewski, R., & Helmer, E. H. (2008). Conterminous U.S. and Alaska forest type mapping using Forest Inventory and Analysis data. *Photogrammetric Engineering & Remote Sensing*, 74(11), 1379–1388. <https://doi.org/10.14358/PERS.74.11.1379>
- Running, S. W. (2008). Ecosystem disturbance, carbon, and climate. *Science*, 321(5889), 652–653. <https://doi.org/10.1126/science.1159607>
- Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *Bioscience*, 54(6), 547–560. [https://doi.org/10.1641/0006-3568\(2004\)054\[0547:ACSMOG\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2)
- Scheller, R. M., Domingo, J. B., Sturtevant, B. R., Williams, J. S., Rudy, A., Gustafson, E. J., & Mladenoff, D. J. (2007). Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, 201(3–4), 409–419. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>
- Scheller, R. M., Van Tuyl, S., Clark, K. L., Hom, J., & La Puma, I. (2011). Carbon sequestration in the New Jersey pine barrens under different scenarios of fire management. *Ecosystems*, 14(6), 987–987–1004. <https://doi.org/10.1007/s10021-011-9462-6>
- Schimel, D., Kittel, T. G. F., Running, S., Monson, R., Turnipseed, A., & Anderson, D. (2002). Carbon sequestration studied in western US mountains. *Eos, Transactions of the American Geophysical Union*, 83(40), 445–449. <https://doi.org/10.1029/2002EO000314>
- Schuepp, P. H., Leclerc, M. Y., MacPherson, J. I., & Desjardins, R. L. (1990). Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. *Boundary-Layer Meteorology*, 50(1–4), 355–373. <https://doi.org/10.1007/BF00120530>
- Scott-Denton, L. E., Moore, D. J. P., Rosenbloom, N. A., Kittel, T. G. F., Burns, S. P., Schimel, D. S., & Monson, R. K. (2013). Forecasting net ecosystem CO<sub>2</sub> exchange in a subalpine forest using model data assimilation combined with simulated climate and weather generation. *Journal of Geophysical Research: Biogeosciences*, 118, 549–565. <https://doi.org/10.1002/jgrg.20039>
- Scott-Denton, L. E., Sparks, K. L., & Monson, R. K. (2003). Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest. *Soil Biology & Biochemistry*, 35(4), 525–534. [https://doi.org/10.1016/S0038-0717\(03\)00007-5](https://doi.org/10.1016/S0038-0717(03)00007-5)
- Sexstone, G. A., Clow, D. W., Fassnacht, S. R., Liston, G. E., Hiemstra, C. A., Knowles, J. F., & Penn, C. A. (2018). Snow sublimation in mountain environments and its sensitivity to forest disturbance and climate warming. *Water Resources Research*, 54, 1191–1211. <https://doi.org/10.1002/2017WR021172>
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. 2017. Web soil survey. Retrieved October 31, 2017, from <https://websoilsurvey.sc.egov.usda.gov/>
- Speckman, H. N., Frank, J. M., Bradford, J. B., Miles, B. L., Massman, W. J., Parton, W. J., & Ryan, M. G. (2015). Forest ecosystem respiration estimated from eddy covariance and chamber measurements under high turbulence and substantial tree mortality from bark beetles. *Global Change Biology*, 21(2), 708–721. <https://doi.org/10.1111/gcb.12731>
- Stielstra, C. M., Lohse, K. A., Chorover, J., McIntosh, J. C., Barron-Gafford, G. A., Perdrial, J. N., et al. (2015). Climatic and landscape influences on soil moisture are primary determinants of soil carbon fluxes in seasonally snow-covered forest ecosystems. *Biogeochemistry*, 123(3), 447–465. <https://doi.org/10.1007/s10533-015-0078-3>
- Sulzman, E. W., Brant, J. B., Bowden, R. D., & Lajtha, K. (2005). Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO<sub>2</sub> efflux in an old growth coniferous forest. *Biogeochemistry*, 73(1), 231–256. <https://doi.org/10.1007/s10533-004-7314-6>
- Swetnam, T. L., Brooks, P. D., Barnard, H. R., Harpold, A. A., & Gallo, E. L. (2017). Topographically driven differences in energy and water constrain climatic control on forest carbon sequestration. *Ecosphere*, 8(4), e01797. <https://doi.org/10.1002/ecs2.1797>
- Tang, J., Bolstad, P. V., Desai, A. R., Martin, J. G., Cook, B. D., Davis, K. J., & Carey, E. V. (2008). Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States. *Agricultural and Forest Meteorology*, 148(2), 171–185. <https://doi.org/10.1016/j.agrformet.2007.08.008>
- Thomas, C. K., Martin, J. G., Law, B. E., & Davis, K. (2013). Toward biologically meaningful net carbon exchange estimates for tall, dense canopies: Multi-level eddy covariance observations and canopy coupling regimes in a mature Douglas-fir forest in Oregon. *Agricultural and Forest Meteorology*, 173, 14–27. <https://doi.org/10.1016/j.agrformet.2013.01.001>
- Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, 8(2), 127–150. [https://doi.org/10.1016/0034-4257\(79\)90013-0](https://doi.org/10.1016/0034-4257(79)90013-0)
- US Fish and Wildlife Service (2010). National Wetlands Inventory Website. US Department of the Interior, Washington, DC. <https://www.fws.gov/wetlands/Data/Data-Download.html>

- Wang, M., Guan, D.-X., Han, S.-J., & Wu, J.-L. (2010). Comparison of eddy covariance and chamber-based methods for measuring CO<sub>2</sub> flux in a temperate mixed forest. *Tree Physiology*, 30(1), 149–163. <https://doi.org/10.1093/treephys/tpp098>
- Wang, X., Wang, C., & Bond-Lamberty, B. (2017). Quantifying and reducing the differences in forest CO<sub>2</sub>-fluxes estimated by eddy covariance, biometric and chamber methods: A global synthesis. *Agricultural and Forest Meteorology*, 247, 93–103. <https://doi.org/10.1016/j.agrformet.2017.07.023>
- Wehr, R., & Saleska, S. R. (2015). An improved isotopic method for partitioning net ecosystem–atmosphere CO<sub>2</sub> exchange. *Agricultural and Forest Meteorology*, 214–215, 515–531.
- Wenger, S. J., & Olden, J. D. (2012). Assessing transferability of ecological models: An underappreciated aspect of statistical validation. *Methods in Ecology and Evolution / British Ecological Society*, 3(2), 260–267. <https://doi.org/10.1111/j.2041-210X.2011.00170.x>
- Winchell, T. S., Barnard, D. M., Monson, R. K., Burns, S. P., & Molotch, N. P. (2016). Earlier snowmelt reduces atmospheric carbon uptake in midlatitude subalpine forests. *Geophysical Research Letters*, 43, 8160–8168. <https://doi.org/10.1002/2016GL069769>
- Wohlfahrt, G., & Galvagno, M. (2017). Revisiting the choice of the driving temperature for eddy covariance CO<sub>2</sub> flux partitioning. *Agricultural and Forest Meteorology*, 237–238, 135–142. <https://doi.org/10.1016/j.agrformet.2017.02.012>
- Wu, C., Gaumont-Guay, D., Black, T. A., Jassal, R. S., Xu, S., Chen, J. M., & Gonsamo, A. (2014). Soil respiration mapped by exclusive use of MODIS data for forest landscapes of Saskatchewan, Canada. *ISPRS Journal of Photogrammetry and Remote Sensing: Official Publication of the International Society for Photogrammetry and Remote Sensing*, 94, 80–90.
- Xu, H., Zhang, T., Luo, Y., Huang, X., & Xue, W. (2018). Parameter calibration in global soil carbon models using surrogate-based optimization. *Geoscientific Model Development*, 11(7), 3027–3044. <https://doi.org/10.5194/gmd-11-3027-2018>
- Zha, T., Niinisto, S., Xing, Z., Wang, K.-Y., Kellomäki, S., & Barr, A. G. (2007). Total and component carbon fluxes of a scots pine ecosystem from chamber measurements and eddy covariance. *Annals of Botany*, 99(2), 345–353. <https://doi.org/10.1093/aob/mcl266>
- Zhao, M., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment*, 95(2), 164–176. <https://doi.org/10.1016/j.rse.2004.12.011>
- Zhu, Z., & Woodcock, C. E. (2014). Automated cloud, cloud shadow, and snow detection in multitemporal Landsat data: An algorithm designed specifically for monitoring land cover change. *Remote Sensing of Environment*, 152, 217–234. <https://doi.org/10.1016/j.rse.2014.06.012>