

Autotrophic respiration dominates ecosystem respiration at Canadian boreal forest

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Key Points:

- A newly developed, mechanistic, hydro-biogeochemical model for simulating ecosystem respiration (R_{eco}) at the subarctic regions
- Regional-scale modelling of R_{eco} and its partitioning to Autotrophic respiration (R_a) and heterotrophic respiration (R_h)
- R_a dominate R_{eco} at Canadian boreal forests

Abstract

Most of the Earth System Models (ESMs) rely on empirical functions for decomposition of litter with multiple soil carbon pools decaying at different rates to estimate R_{eco} variations and its partitioning into autotrophic (R_a) and heterotrophic respiration (R_h) in relation to variation in temperature and soil water content. However, microbially-mediated litter decomposition schemes are very scarce in ESMs. Microbial enzymatic processes are integral parts in litter as well as soil organic matter (SOM) decomposition. Here we developed a mechanistic model comprising of multiple hydro-biogeochemical modules to explicitly incorporate microbially-enzymatic litter decomposition and decomposition of SOM for estimating regional-scale R_a , R_h and R_{eco} . Modeled annual mean R_{eco} values are found varying from 1000 to 8000 kg C ha⁻¹ yr⁻¹ in 2000-2013 within the boreal forest covered sub-basins of the Athabasca River Basin (ARB), Canada. While, for the 2000-2013 period, the annual mean R_a and R_h are varying within 800-6000 kg C ha⁻¹ yr⁻¹ and 500-3500 kg C ha⁻¹ yr⁻¹, respectively. R_a generally dominates R_{eco} with nearly 30-80% contribution in most of the sub-basins in ARB. The model estimates corroborate well with the site-scale and satellite-based estimates reported at similar land use and climatic regions. Modeling the partitioning of R_{eco} to R_a , and R_h are critical to understanding future climate change feedbacks and to help reduce uncertainties in ESMs in the boreal and subarctic regions.

Plain language summary

Estimating ecosystem respiration (R_{eco}) is becoming a major topic in global climate change studies. Our new integrated hydro-biogeochemical modeling can successfully estimate regional-scale R_{eco} and its subsequent partitioning into autotrophic (R_a) and heterotrophic respiration (R_h) at the boreal forest covered Athabasca river basin (ARB), Canada. R_a generally dominates R_{eco} with nearly 30-80% contribution in most of the sub-basins in ARB. The proposed modeling approach does represents a step forward to improve global respiration modeling in widely used earth system models (ESMs) as it is well capturing both, the site-scale measurements and satellite-based estimates. These more realistic respiration estimates are achieved after shifting from purely empirical representation of ecosystem respiration and its partitioning pathway to microbial enzymatic kinetics-based approach. The approach presented in this paper would directly improve ESM estimates or indicate where in existing ESM improvement should be sought.

1 Introduction

Ecosystem respiration (R_{eco}) is the primary natural source of atmospheric carbon dioxide (CO₂) throughout the globe (Ciais *et al.*, 2014). There is an urgent need to completely understand the soil carbon conversion processes and the associated land-surface gas exchange in estimating climate change feedback, which ultimately lead to the release of soil carbon as CO₂ to the atmosphere (Mitchard, 2018). In natural ecosystems, R_{eco} can be partitioned into the soil heterotrophic respiration (R_h) resulting from soil microorganisms and autotrophic respiration (R_a) resulting from plant species (both from aboveground components and roots) (Hicks Pries *et al.*, 2013; 2016). Globally, R_a is the predominant component of the terrestrial carbon budget with photosynthetic carbon consumption rate of 54-71% (Ryan *et al.*, 1997). In permafrost regions, R_a accounts for 40 to 70% of the total ecosystem respiration (Hicks Pries *et al.*, 2013). The R_a , and R_h have different adaptation mechanisms in response to climate change. For example, rising temperature can accelerate microbial enzymatic activities and thus enhance R_h and thus facilitate

nutrient dynamics based on substrate availability (Davidson and Janssens, 2006; Manzoni et al., 2008). On the other hand, rising temperature has different influence in plant growth (aboveground component showing positive response while root showing near neutral response) and also on R_a (Hick Pries et al., 2013). For example, 2.3 °C warming of soil lead to 20% increase in aboveground productivity at an Alaskan site (Natali et al., 2009). With an increase of 2 °C, root respiration was not showing any significant changes, while heterotrophic respiration showed 21% increase linked with increased microbial activities (Wang et al., 2014). Therefore, quantifying the distinct contributions of R_{eco} , R_a , and R_h is necessary to estimate climate feedbacks and sensitivity in the rapidly changing subarctic regions but state of the art monitoring techniques, such as eddy covariance and remote sensing techniques, are still unable to directly partition R_a and R_h from R_{eco} (Davidson and Janssens, 2006; Konings et al., 2019). In addition to the distinct characteristics and feedbacks to climate change processes by R_a and R_h , respiration partitioning is particularly important as it has been reported that global land carbon sink has been increasing in recent years (Ciais et al., 2019).

Climate change-linked future projections of ecosystem respiration are challenging because estimating litter and SOM decomposition rates and anticipated soil derived CO₂ feedbacks resulting from anthropogenic warming are both seen as being highly uncertain (Collins et al., 2013; Crowther et al., 2016). Many experimental and modelling studies have been performed to determine the R_{eco} and its partitioning and gross primary production (GPP) at different land use types (Hardie et al., 2009; Hicks Pries et al., 2013; Senapati et al., 2018). On the other hand, predicting the net ecosystem exchange (NEE), and R_{eco} require the development of sophisticated land-surface models. These modeling approaches can be categorized into: 1) agroecosystem models, and 2) the Earth System Models (ESMs). Both modelling approaches commonly use empirical formula of multiple soil C pools decaying at different rates to calculate R_{eco} (Oleson et al., 2010; Clark et al., 2011; Davison and Janssens, 2006; Del Grosso et al., 2005). The CENTURY model used simplified functions of soil temperature and moisture for estimating soil respiration and its partition to autotrophic and heterotrophic components (Del Gorsso et al., 2005). The decaying module of multiple soil C pools in DayCent has also been incorporated into ORCHIDEE (Qiu et al., 2018) and CLMs (Lawrence et al., 2019). The microbial processes in ESMs are simplified into linear, empirical equations (Crowther et al., 2014; 2019). It is found that most ESMs cannot reproduce grid-scale variation in soil C due to missing key processes and the predicted global carbon stocks in the fifth Coupled Model Intercomparison Project (CMIP) led to 6-fold difference in predicted data (Todd-Brown et al., 2013). Microbial activity responses (as reflected in soil heterotrophic respiration) are expected to increase with warming (Karhu et al., 2014; Walker et al., 2018). However, the relationship between warming and soil carbon loss, as well as overall ecosystem respiration, is not straightforward as the microbially mediated litter and SOM decomposition processes are not linearly correlated with temperature (Melillo et al., 2017). Additionally, microbially-mediated decomposition of SOM is not only an important biological-driven process for carbon conversion but also play a major role in overall global nutrient dynamics (Manzoni et al., 2008).

Despite importance, both site-scale agroecosystem models and ESMs have also not yet explicitly considered: (i) microbially-mediated decomposition of litter and SOM, (ii) redox processes and (iii) hydrological processes coupled with soil microbial processes (Wieder et al., 2013; Bhanja et al., 2019a; Crowther et al., 2019). Apart from the environmental variables, the turnover of organic material is directly controlled by soil microbes (Crowther et al., 2019). As a result, there is a need to improve microbial processes for global carbon modeling estimates

(Wieder et al., 2013; Crowther et al., 2019). Microbial abundances are relatively larger in arctic and subarctic regions (Serna-Chavez et al., 2013; Xu et al., 2013). They are also responsible for biogeochemical cycling of nutrients (Crowther et al., 2019). However, different types of microbes require favorable soil redox conditions for their growth (deAngelis et al., 2010). Thus, soil redox condition is an essential measure for the dynamics of nutrients as well as soil organic matter, which microbes used as a substrate (Bhanja et al., 2019a; 2019b). It has been found that nutrient availability directly controls soil organic matter stock and terrestrial carbon sink (Wieder et al., 2015). Alteration of hydrological processes has profound impact in soil carbon mineralization (Anthony et al., 2018). Therefore, integration of hydrological processes along with redox/biogeochemical and microbial processes would definitely improve model estimates (Bhanja et al., 2019a; 2019b). Based on the present structure of the contemporary ESMs, it is very difficult to improve further accuracy and generality of the litter and SOM decomposition modules (Wieder et al., 2015; Luo et al., 2016). Particularly, while the ecosystem respiration is calculated using the application of Q_{10} in the remote sensing and eddy covariance (Reichstein et al., 2007; Zhao and Running, 2010), the techniques are also used extensively for verification and calibration of ESMs and agroecosystem models. This is an open loop verification, which is unreasonable according to scientific principles. Therefore, global-scale respiration studies continue to be sought for further improving the modeling processes and soil respiration estimates (Todd-Brown et al., 2013; Luo et al., 2016; Wang et al., 2020). For closed loop feedback, a decomposition feedback to warming requires accounting explicitly for not only temperature but also nutrient availability and microbial activities (Davidson et al., 2012).

Substantial amount of soil organic carbon can be released due to enhanced microbial activities associated with climate warming in arctic, subarctic regions (Schuur et al., 2015). The arctic and subarctic regions are the most sensitive regions to the combined climate change impacts due to declining permafrost, glacial retreat and change in freeze-thaw cycles on its ecosystems (Bates et al., 2008). An abrupt thawing in lakes due to global warming can lead to faster mobilization of deeper stored carbon (Anthony et al., 2018). Therefore, in these regions, modeling the carbon mobilization processes and their feedbacks are much sought after (Schuur et al., 2009). The present study describes the development of a mechanistic model to simulate regional-scale, autotrophic, heterotrophic and total ecosystem respirations at the boreal forest covered Athabasca River Basin (ARB), Canada (Figure S1). This being achieved through an explicitly integrated inclusion of microbially-mediated decomposition of litter as well as SOM, redox processes and hydrological processes. Model output validation at regional-scale was achieved using both site-scale, as well as remote-sensing data. Importantly, our approach can also provide a new way for improving accurate carbon emission estimates of the litter and SOM decomposition modules, which so far are simply using linear carbon pool transformation concepts in all of the ESMs (Wieder et al., 2015; Luo et al., 2016).

2 Materials and Methods

2.1 Model introduction

The Soil and Water Assessment Tool (SWAT) is widely used for its capacity to simulate regional-scale hydrology in a detailed way (Arnold et al., 1998). Integrated hydro-biogeochemical modeling was performed using our microbial kinetics and thermodynamics (MKT) model integrated within SWAT, known as SWAT-MKT (Bhanja et al., 2019a; 2019b;

Bhanja and Wang, 2020). New carbon cycle capabilities are incorporated into SWAT to simulate ecosystem respiration components from litter decomposition, root respiration, above ground respiration and respiration component from the dissolved organic carbon transformation by enzymatic processes (Figure S2; S3). The entire chemical processes considered in the new version of SWAT-MKT are shown in Figure S3. Major oxidation-reduction reactions considered in this approach were given in Table S1 and their reaction quotient values are provided in Table S2.

2.2 Soil mineralization and litter decomposition

Soil mineralization module is modeled considering two carbon pools such as, active and passive. The active pool represent fraction of active litter including microbial biomass (Fujita et al., 2014). We used microbial enzymatic litter transformation approach that is an advancement of the CENTURY model's simple, first order kinetics-based litter decomposition approach (Parton et al., 1987; 1994; Fujita et al., 2014):

$$R_{d_{i,C}} = k_{i,C} \times C_i \quad (1)$$

Where, litter decomposition rate originally adopted in CENTURY model: $R_{d_{i,C}}$ (gC kg^{-1} soil d^{-1}). i represents the substrate type i.e. active and passive. C_i (gC kg^{-1} soil) is the carbon content within active or passive substrate. $k_{i,C}$ (d^{-1}) is the first-order decomposition coefficient of C_i .

Litter decomposition can also be modeled through microbial enzymatic approach following one-substrate Michaelis-Menten kinetics (Fujita et al., 2014), the new decomposition rate becomes:

$$R_{d_{i,M}} = k_{i,M} \times \frac{C_i}{K_{m_i} + C_i} \quad (2)$$

Where, K_{m_i} is the half-saturation constant or Michaelis-Menten constant. $k_{i,M}$ is the decomposition coefficient of C_i and can be estimated separately for the active (AC) and passive (PA) substrates as:

$$k_{AC,M} = \frac{k_{AC,C} \times (K_{m_{AC}} + 2 C_b)}{C_b} \quad (3)$$

$$k_{PA,M} = \frac{k_{PA,C} \times (K_{m_{PA}} + C_T)}{C_b} \quad (4)$$

Where, $k_{AC,C}$ and $k_{PA,C}$ are decomposition coefficients used in CENTURY model for the active and passive substrates, respectively. $K_{m_{AC}}$ is the half-saturation constant for active substrate and it is approximated as 0.3 g C kg^{-1} soil (Allison et al., 2010). $K_{m_{PA}}$ is the half-saturation constant for the passive substrate and its value is taken as 600 g C kg^{-1} soil (Allison et al., 2010). C_b (g C kg^{-1} soil) represents microbial biomass; the value is approximated as the median microbial biomass (0.87 g C kg^{-1} soil) from a global-scale study of Cleveland and Liptzin (2007). C_T represents total carbon stock of soil; its value is approximated as the global total soil carbon (46 g C kg^{-1} soil; Cleveland and Liptzin, 2007).

Consideration of microbial biomass being an active component of the litter and assuming microbial biomass decomposition is directly proportional to the litter decomposition, the new litter decomposition rate ($R_{d,MM}$) becomes (Fujita et al., 2014):

$$R_{d,MM} = k_{i,M} \times \frac{C_i}{Km_i + C_i} \times C_b \quad (5)$$

Actual soil respiration rates (R_{LD}) from litter transformation is estimated following Fujita et al. (2014).

$$R_{LD} = \sum_{i=AC}^{PA} (1 - e_{i,m}) \times I_{m,c} \times R_{d,MM} + O_{m,c} \quad (6)$$

Where, $e_{i,m}$ represents the growth efficiency of microbes during assimilation of either active or passive substrates; its value is estimated as 0.45 (Fujita et al., 2014). $I_{m,c}$ is an decomposition inhibition factor (its value varies from 0 for full to 1 for no inhibition); at present its value taken as 1 also resembles the CENTURY model parameterization (Fujita et al., 2014). $O_{m,c}$ is the overflow of carbon due to limiting nitrogen concentration; its value is taken as 0 now without proper data to represent the processes.

2.3 Root respiration

Root respiration (R_r) is an essential component of soil respiration, however, SWAT does not have the ability to simulate root respiration. To simulate root respiration, we have developed a new sub-module within SWAT following Li et al. (1994):

$$R_r = (R_n \times U_n + R_{rg} \times BG_r + R_{rm} \times B_{lr}) \quad (7)$$

Where, CO₂ produced by roots for nitrogen uptake: R_n (13.8 mg C meq⁻¹ N; Veen, 1981; Li et al., 1994). Nitrogen uptake rates of plant is represented as U_n (kg N ha⁻¹ d⁻¹). CO₂ produced by roots due to their growth: R_{rg} (19.19 mg C g⁻¹ dry matter; Veen, 1981; Li et al., 1994). Root biomass growth at a day: BG_r (g dry matter ha⁻¹). CO₂ produced as a function of root maintenance: R_{rm} (0.288 mg C g⁻¹ dry matter d⁻¹; Veen, 1981; Li et al., 1994). B_{lr} is the living root biomass (g dry matter ha⁻¹).

2.4 Aboveground autotrophic respiration

Above ground respiration (R_{abv}) is estimated following the equation (Ryan et al., 1994):

$$R_{abv} = (R_{abvf} \times BG_{abvf} + R_{abvw} \times BG_{abvw}) \quad (8)$$

Where, aboveground foliar biomass growth at a day: BG_{abvf} (g dry matter ha⁻¹ d⁻¹). CO₂ produced as a function of aboveground foliar biomass growth: R_{abvf} (1.767 mgC g⁻¹ dry matter d⁻¹; Ryan et al., 1994). Aboveground woody biomass growth at a day: BG_{abvw} (g dry matter ha⁻¹ d⁻¹). CO₂ produced as a function of aboveground woody biomass growth: R_{abvw} (0.12 mgC g⁻¹ dry matter d⁻¹; Ryan et al., 1994).

2.5 Satellite-based estimates of autotrophic respiration

We used gross primary productivity (GPP) and net primary productivity (NPP) data from the observation of the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors (Zhao et al., 2005; 2006; Zhao and Running, 2010). Annual mean MOD17 products are used at a spatial resolution of 30 arcsec. MOD17 is the first satellite derived continuous data product for vegetation productivity at the global-scale (Zhao et al., 2006). The algorithm includes several satellite derived parameters such as the land cover, fractional photosynthetically active radiation and leaf area index along with the meteorological variables (Zhao et al., 2006). NCEP/DOE reanalysis II outputs are used for meteorological parameters (Zhao and Running, 2010). Detailed descriptions of the MOD17 products can be found in Zhao et al. (2005; 2006). Satellite-based R_a is estimated by subtracting NPP from the GPP data (Bond-Lamberty et al., 2018).

$$R_a = GPP - NPP \quad (9)$$

2.6 Assumptions and limitations

In order to compute the total soil respiration, we only used the heterotrophic and autotrophic components. Here, we have not considered the geological CO_2 emission (Andrews and Schlesinger, 2001). Ecosystem respiration also includes animal respiration. However, due to the cold climatic conditions and presence of very low number of animals at the ARB (Weber et al., 2015), respiration from animals are not considered at present in our approach. Other assumptions and limitations associated with the basic version of the model can be obtained from Bhanja et al. (2019a; 2019b) and Bhanja and Wang (2020). In natural conditions all of the soil microbes present are not producing enzymes or even producing at a slower rate and taking part in the decomposition activities; these type of microbes restrict/slow down the decomposition process (Kaiser et al., 2015).

3 Results, or a descriptive heading about the results

3.1 Heterotrophic, autotrophic and total ecosystem respiration

Annual mean ecosystem respiration (R_{eco}) did show spatial variability, however, most of the predicted values for the 2000-2013 period are in the range of $1000\text{--}8000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ (Figure 1). The R_{eco} estimates were compared with the available site-scale measurements from the Canadian boreal forest locations data retrieved from FLUXNET2015 (Pastorello et al., 2017). Most of the site-scale R_{eco} values vary within $4000\text{--}10000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$, but with values on three exceeding $12000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ (Table S3). The modeled R_{eco} estimates were in lower range compared to the other boreal forest R_{eco} observations shown in Table S3. These reported sites are however located either at more southern or the same latitude as our study area. Therefore, overall the prevailing climatic conditions at the ARB are more nudging towards a arctic-like climate, with more limited respiration rates. In general, the respiration values were lower during winter months, both climatic factors and the presence of deciduous trees do account for these lower rates (Cumming, 2001). The mean heterotrophic respiration (R_h) values did mostly vary from $500\text{--}3500 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ in 2000-2013 at the ARB (Figure 1). The data showed strong seasonality with highest R_h values occurring during the summer months. Although, no actual measurements are available within Athabasca River basin (ARB), our results match those of other Canadian boreal forests site-scale estimates (Table S4) retrieved from the SRDB archives (Bond-Lamberty and Thomson, 2010b). Most of these site-scale values varied between 1700--

5900 kg C ha⁻¹ yr⁻¹, but on few occasions with values of >10000 kg C ha⁻¹ yr⁻¹ were recorded (Table S4). Mean root respiration (R_r) values (400-2700 kg C ha⁻¹ yr⁻¹) were however found to be lower than the mean R_h values in our study at ARB (Figure 1). In general, R_h is found to be higher than R_r in global boreal sites (Bond-Lamberty and Thomson, 2010b) and at an Alaskan site (Hicks Pries et al., 2013). R_h is not only contributing higher toward R_s , the contribution rate has been increased from 54% to 63% over the years during 1990 to 2014 at a global study (Bond-Lamberty et al., 2018). Annual mean autotrophic respiration from above-ground vegetation components (R_{abv}) did vary from 500 to 2500 kg C ha⁻¹ yr⁻¹, and were comparable with the site-scale estimates from the other Canadian boreal sites (Table S4). In general, the combination of R_r and R_{abv} that is the mean autotrophic respiration (R_a) is estimated to be higher than the mean R_h (Figure 1). Annual mean R_a varies within 800-6000 kg C ha⁻¹ yr⁻¹ (Figure 1). Most of the ARB is covered by forests (Bhanja et al., 2018), which may account for the higher magnitude of autotrophic respiration compared to its heterotrophic counterpart. Contribution of above-ground canopy respiration to R_{eco} is significant at boreal forests (Ryan et al., 1997) and at arctic climates (Hick Pries et al., 2013). Thus R_{abv} along with the R_r , makes R_a dominant over R_h in forest. The R_a dominancy was also observed in savanna and grasslands (Ma et al., 2007), and in peatland ecosystems (Hardie et al., 2009). The autotrophic and heterotrophic respiration estimates are well in line with the data reported in Goulden et al. (2011) from Canadian boreal forests with values reported for R_a was estimated at 2000-4500 kg C ha⁻¹ yr⁻¹ and R_h at ~2000 kg C ha⁻¹ yr⁻¹. Similar R_a was reported by Ryan et al. (1997) at eight Canadian boreal forest sites with values between 3120 and 6110 kg C ha⁻¹ yr⁻¹. Bond-Lamberty et al. (2010b) reported R_h within 200-6000 kg C ha⁻¹ yr⁻¹ at boreal locations and 100-900 kg C ha⁻¹ yr⁻¹ at arctic locations across the globe. In general, mean soil respiration (R_s) also show spatial patterns with values from 1000 to 5000 kg C ha⁻¹ yr⁻¹ at the ARB (Figure 1). The lower values of R_s were mainly found at the Southern ARB sub-basins dominated by mountains. The R_s values do also well comparable with the site-scale estimates (3000-10000 kg C ha⁻¹ yr⁻¹) from other Canadian boreal sites (Table S4).

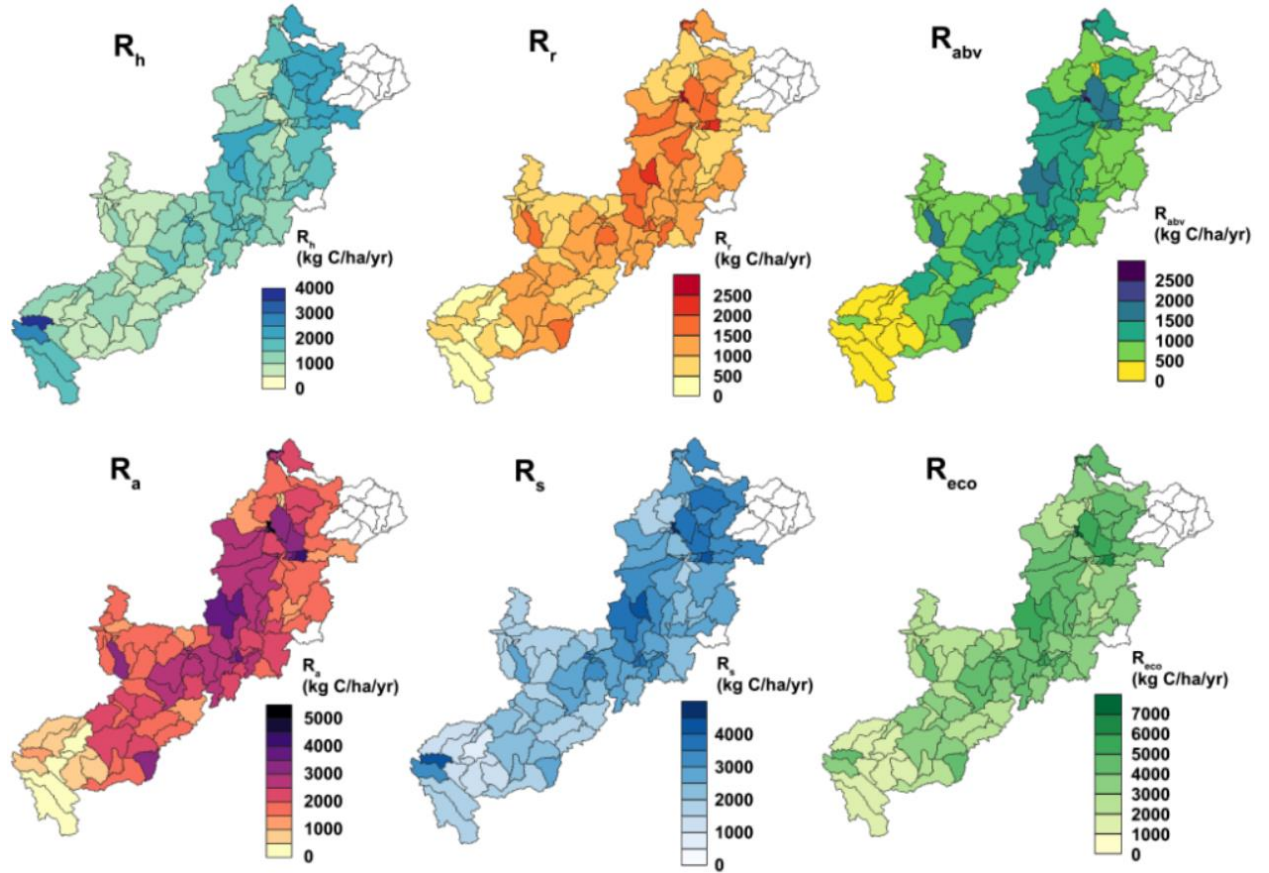


Figure 1. Subbasin-wise, long-term modeled (2000-2013) annual average maps of soil heterotrophic respiration (R_h), root respiration (R_r), autotrophic respiration from above-ground autotrophic respiration (R_{abv}), autotrophic respiration (R_a), soil respiration (R_s), ecosystem respiration (R_{eco}) in $\text{kg C ha}^{-1} \text{yr}^{-1}$. The northernmost regions are not modelled and are shown blank.

3.2 Relationships between the respiration components

Relationship between R_h and R_s shows near equal contribution of soil autotrophic and heterotrophic respiration to total soil respiration in most of the sub-basins (Figure 2). Root contribution to total soil respiration (R_c) values did varies from 0.1 to 0.6 (occasionally 0.7). This generally matches the field-scale estimates (Table S4). The R_a to R_{eco} ratio did show varying contribution of R_a to R_{eco} from 30 to 80% in most of the sub-basins (Figure 2). The estimates are well within the ranges reported in previous studies (40-80% in Nowinski et al., 2010; 40-70% in Hicks Pries et al., 2013) at similar eco-climatic regions. R_s contributes nearly 60-85% of R_{eco} in most parts of the study area (Figure 2). Contribution of R_r to R_{eco} lies within 10-45%. Results are consistent with the observation of Hicks Pries et al. (2013) at arctic climate (15-35% contribution reported).

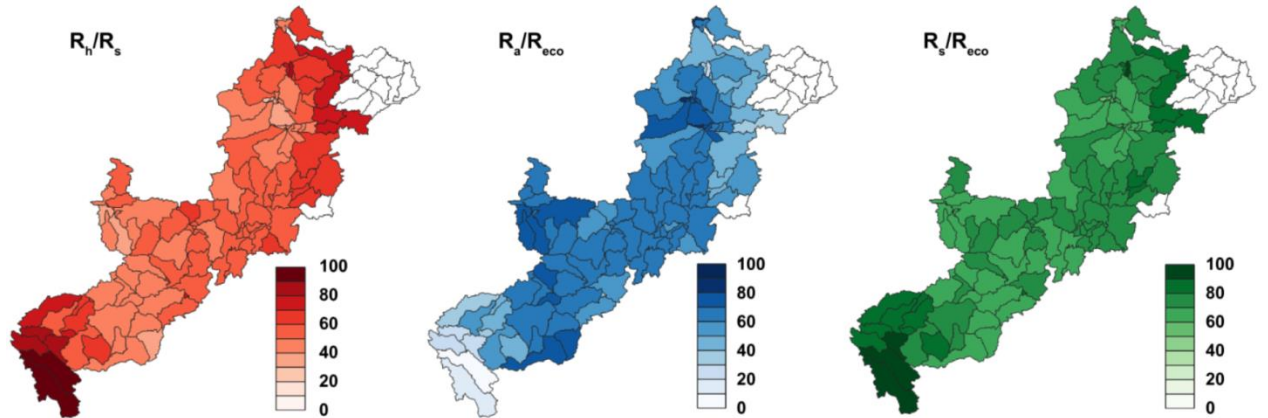


Figure 2. Maps of the average percentage (%) ratios of soil respiration (R_s) and heterotrophic respiration (R_h), autotrophic respiration (R_a) and ecosystem respiration (R_{eco}), R_s and R_{eco} , respectively in 2000-2013. The northernmost regions are not modelled and are shown blank.

ARB is mostly covered by forest (Figure S4) and occurrence of comparatively lower annual mean soil temperature ($<2^\circ\text{C}$, Figure S5) are the two main reasons for the dominance of autotrophic respiration toward the total ecosystem respiration (Ryan et al., 1997; Hicks Pries et al., 2013; Crowther et al., 2016). The relative proportions of R_h to R_{eco} were also found to be consistent with the values reported in previous studies (Hardie et al., 2009; Schuur et al., 2009; Hicks Pries et al., 2013).

The respiration partitioning and their ratio show some interesting facts. Our work showed that the relationships between R_s and R_{eco} and R_a and R_{eco} follow linear relationship ($r^2 > 0.79$, $p < 0.001$, Figure 3b, 3c). Relationship between R_h and R_s follow non-linear pattern (Figure 3a). Similar relationships are also observed by Bond-Lamberty et al. (2004) in different locations across the globe.

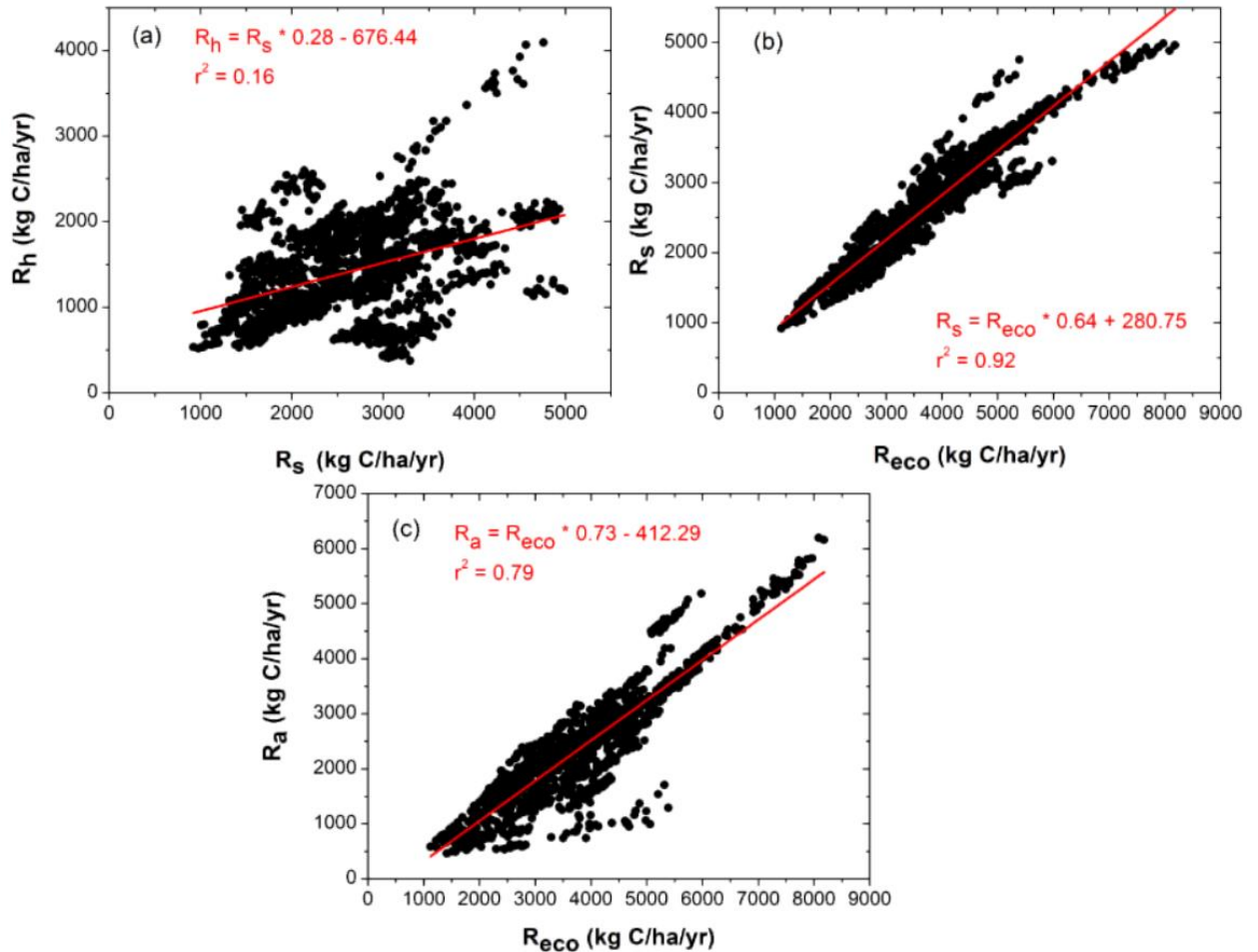


Figure 3. Relationships between (a) annual mean soil heterotrophic respiration (R_h) and total soil respiration (R_s); (b) R_s and ecosystem respiration (R_{eco}); (c) autotrophic respiration (R_a) and R_{eco} , respectively. The linear regression results are shown in red color and polynomial regression results are shown in blue color in (b).

Global anthropogenic CO_2 emissions (combination of fossil fuel and land use change) has been increased from 4.5 to 11 Gt C yr^{-1} from 1960-1969 to 2009-2018 (Friedlingstein et al., 2019). Global terrestrial ecosystem carbon sink has increased from 1.3 to 3.2 Gt C yr^{-1} from 1960-1969 to 2009-2018 and subsequently slowing down the atmospheric CO_2 concentration increase (Friedlingstein et al., 2019). Terrestrial ecosystems are acting as a carbon sink for approximately 29% annual anthropogenic CO_2 emissions during the last decade (2009-2018) and the magnitude is higher than the ocean sink rates ($\sim 23\%$) (Friedlingstein et al., 2019). Although the direct link is unclear, it has been reported that atmospheric CO_2 concentration is also sensitive to terrestrial water storage change at global-scale with declining values associated with rapid increase of CO_2 concentration (Humphrey et al., 2018).

3.3 Modelled estimates comparison with remote sensing data

Satellite-based estimates of R_a (Figure 4a) show similar spatial patterns on comparing with the modeled R_a (Figure 1). Satellite-based R_a varies from 800 $\text{kg C ha}^{-1} \text{ yr}^{-1}$ to as high as

3943 kg C ha⁻¹ yr⁻¹ across the sub-basins of ARB. In general, modeled R_a is aligned with the satellite-based R_a in the mid- R_a region (1500-4000 kg C ha⁻¹ yr⁻¹; Figure 4b). The dissimilarity, in lower and higher R_a ranges are result of various well known issues with the satellite-based approach. Several studies have reported erroneous satellite-based NPP estimates (~15% less estimates comparing the observations). These were found to be associated with the interference from the autotrophic respiration estimation from the neighboring areas (Ito, 2011). This make the satellite-based R_a value smaller than its real value. The GPP and NPP database developed using different available meteorological datasets are also showing an overestimation of the indices when comparing with the GPP (~30% higher GPP reported using NCEP data) and NPP (15-20% higher NPP using NCEP data) developed using observed meteorological data (Zhao et al., 2006). The NCEP/DOE reanalysis II meteorological data were used to develop the global-scale GPP and NPP products (Zhao and Running, 2010) – this can also be a further reason for the overestimation. Turner et al. (2006) reported overestimation of MODIS NPP and GPP products at regions with comparatively lower productivity e.g. Boreal forest regions.

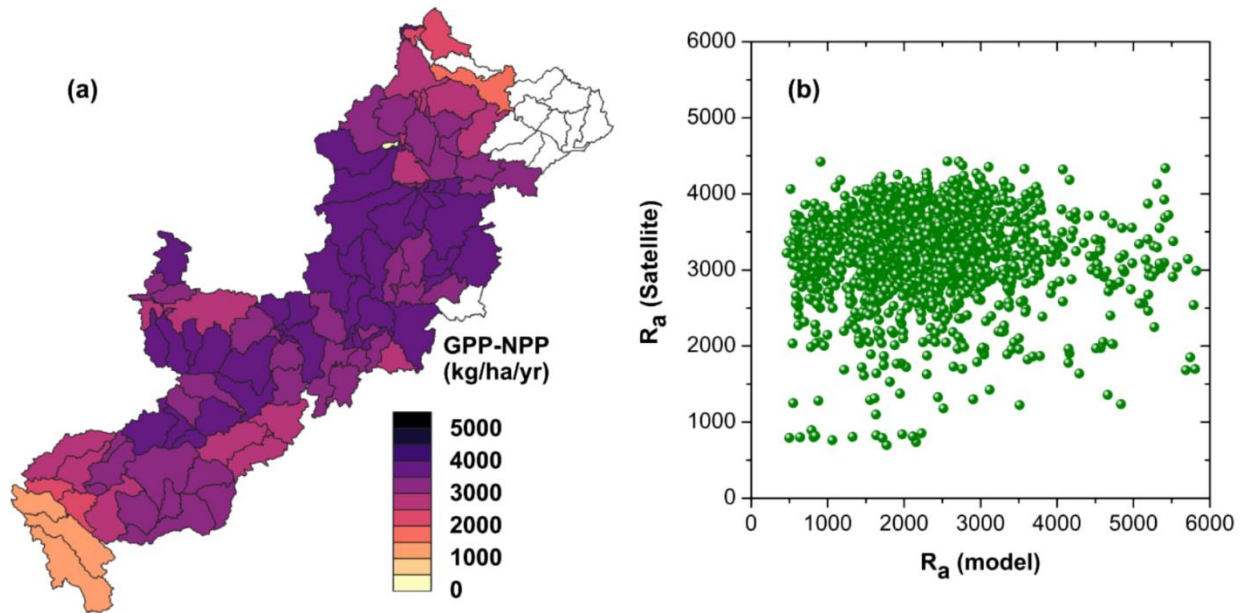


Figure 4. (a) Mean annual total autotrophic respiration (root and above ground biomass) from satellite-based estimates [R_a (Satellite)] in 2000-2013. (b) Relationship between autotrophic respirations from satellite and modeled estimates in kg C ha⁻¹ yr⁻¹ at ARB during 2000-2013.

4 Conclusions

Although the terrestrial ecosystem respiration is one of main components of climate change feedbacks, the sign and magnitude of this feedback is highly uncertain in future. Our new integrated hydro-biogeochemical modeling can successfully estimate regional-scale R_{eco} and its subsequent partitioning into R_a and R_h at the boreal forest covered Athabasca river basin, Canada. Annual mean R_{eco} ranging between 1000 and 8000 kg C ha⁻¹ yr⁻¹ in 2000-2013. Interestingly, the R_a dominated and contributed 30-80% toward R_{eco} . The model estimates are in line with the site-scale measurements reported at similar land use and climatic regions. Satellite-based estimates of R_a also show similar patterns as of the modeled estimates. We believe that the

proposed modeling approach does represents a step forward to improve global respiration modeling in widely used ESMs as it is well capturing both, the site-scale measurements and satellite-based estimates. These more realistic respiration estimates are achieved after shifting from purely empirical representation of ecosystem respiration and its partitioning pathway to microbial enzymatic kinetics-based approach. Therefore, our process-based modeling approach can also in future be coupled with widely used ESMs as a core module of soil greenhouse gas emission.

Acknowledgments and Data

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The authors use open source data in this manuscript. SRDB and FLUXNET data were obtained from https://daac.ornl.gov/SOILS/guides/SRDB_V4.html and <https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>, respectively. MOD17 data were obtained from <https://modis.gsfc.nasa.gov/data/dataproduct/mod17.php>.

References

- Allison, S.D., Wallenstein, M.D. & Bradford, M.A. Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience* **3**, 336-340 (2010).
- Andrews, J.A., Schlesinger, W.H. Soil CO₂ dynamics, acidification, and chemical weathering in a temperate forest with experimental CO₂ enrichment. *Global Biogeochem. Cy.* **15**, 149–162 (2001).
- Anthony, K.W. et al. 21st-century modeled permafrost carbon emissions accelerated by abrupt thaw beneath lakes. *Nature communications* **9**, 1-11 (2018).
- Arnold, J.G., Srinivasan, R., Muttiah, R.S. & Williams, J.R. Large area hydrologic modeling and assessment part I: model development. *Journal of American Water Resource Association* **34**, 73–89 (1998).
- Bates, B., Kundzewicz, Z. & Wu, S. *Climate change and water*. Intergovernmental Panel on Climate Change Secretariat (2008).
- Bhanja, S.N., Zhang, X. & Wang, J. Estimating long-term groundwater storage and its controlling factors in Alberta, Canada. *Hydrology and Earth System Sciences* **22**, 6241-6255 (2018).
- Bhanja, S.N., Wang, J., Shrestha, N.K. & Zhang, X. Microbial kinetics and thermodynamic (MKT) processes for soil organic matter decomposition and dynamic oxidation-reduction potential: Model descriptions and applications to soil N₂O emissions. *Environmental Pollution* **247**, 812-823 (2019a).

- Bhanja, S.N., Wang, J., Shrestha, N.K. & Zhang, X. Modeling microbial kinetics and thermodynamic processes for quantifying soil CO₂ emission. *Atmospheric Environment* **209**, 125-135 (2019b).
- Bhanja, S.N. & Wang, J. Estimating influences of environmental drivers on soil heterotrophic respiration in the Athabasca River Basin, Canada. *Environmental Pollution* **257**, 113630 (2020).
- Bond-Lamberty, B., Wang, C. & Gower, S.T. A global relationship between the heterotrophic and autotrophic components of soil respiration?. *Global Change Biology* **10**, 1756-1766 (2004).
- Bond-Lamberty, B. & Thomson A.M. A global database of soil respiration measurements. *Biogeosciences* **7**, 1321-1344 (2010).
- Bond-Lamberty B, Bailey VL, Chen M, Gough CM & Vargas R. Globally rising soil heterotrophic respiration over recent decades. *Nature* **560**, 80 (2018).
- Ciais, P. et al. Carbon and other biogeochemical cycles. In *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, 465-570 (2014).
- Ciais, P. et al. Five decades of northern land carbon uptake revealed by the interhemispheric CO₂ gradient. *Nature* **568**, 221-225 (2019).
- Clark DB, et al. (2011) The Joint UK Land Environment Simulator (JULES), model description—Part 2: Carbon fluxes and vegetation dynamics. *Geosci. Model Dev.*, **4**, 701–722.
- Cleveland, C. C., & Liptzin, D. C:N:P stoichiometry in soil: Is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry* **85**(3), 235–252 (2007).
- Collins, M. et al. Long-term Climate Change: Projections, Commitments and Irreversibility. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA (2013).
- Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R. and Bradford, M.A. Untangling the fungal niche: the trait-based approach. *Frontiers in microbiology*, **5**, 579 (2014).
- Crowther, T.W. et al. Quantifying global soil carbon losses in response to warming. *Nature* **540**, 104-108 (2016).
- Crowther, T.W., Van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C. and Maynard, D.S. The global soil community and its influence on biogeochemistry. *Science* **365**(6455), p.eaav0550 (2019).
- Cumming, S.G. Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological applications* **11**, 97-110 (2001).

- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165.
- Davidson EA, Samanta S, Caramori SS, Savage K (2012) The Dual Arrhenius and Michaelis–Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, **18**, 371–384.
- DeAngelis, K.M., Silver, W.L., Thompson, A.W. & Firestone, M.K.. Microbial communities acclimate to recurring changes in soil redox potential status. *Environmental Microbiology* **12**, 3137–3149 (2010).
- Del Grosso, S. J., Parton, W. J., Mosier, A. R., Holland, E. A., Pendall, E., Schimel, D. S., & Ojima, D. S. (2005). Modeling soil CO₂ emissions from ecosystems. *Biogeochemistry*, 73(1), 71–91.
- Friedlingstein, P. et al. Global carbon budget 2019. *Earth System Science Data* **11**, 1783–1838 (2019).
- Fujita, Y., Witte, J.P.M. & van Bodegom, P.M. Incorporating microbial ecology concepts into global soil mineralization models to improve predictions of carbon and nitrogen fluxes. *Global biogeochemical cycles* **28**, 223–238 (2014).
- Goulden, M.L. et al. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology* **17**, 855–871 (2011).
- Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Ostle, N.J. & Rowland, A.P. Bomb-C-14 analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon. *Geoderma* **153**, 393–401 (2009).
- Hicks Pries, C.E., Schuur, E.A. & Crummer, K.G. Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$. *Global Change Biology* **19**, 649–661(2013).
- Hicks Pries, C.E., Schuur, E.A., Natali, S.M. & Crummer, K.G. Old soil carbon losses increase with ecosystem respiration in experimentally thawed tundra. *Nature Climate Change* **6**, 214 (2016).
- Humphrey, V., Zscheischler, J., Ciais, P., Gudmundsson, L., Sitch, S. & Seneviratne, S.I.. Sensitivity of atmospheric CO₂ growth rate to observed changes in terrestrial water storage. *Nature* **560**, 628–631 (2018).
- Ito, A. A historical meta-analysis of global terrestrial net primary productivity: are estimates converging? *Global Change Biology* **17**, 3161–3175 (2011).
- Kaiser, C., Franklin, O., Richter, A., & Dieckmann, U. Social dynamics within decomposer communities lead to nitrogen retention and organic matter build-up in soils. *Nature communications* **6**, 1–10 (2015).
- Karhu, K. et al. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* **513**, 81 (2014).
- Konings, A.G., Bloom, A.A., Liu, J., Parazoo, N.C., Schimel, D.S. and Bowman, K.W., 2019. Global satellite-driven estimates of heterotrophic respiration. *Biogeosciences*, 16(11), pp.2269–2284.

- Lawrence, D., et al. Technical Description of version 5.0 of the Community Land Model (CLM). http://www.cesm.ucar.edu/models/cesm2/land/CLM50_Tech_Note.pdf (2019).
- Li, C., Frolking, S. & Harriss, R. Modeling carbon biogeochemistry in agricultural soils. *Global biogeochemical cycles* **8**, 237-254 (1994).
- Luo, Y. et al. Toward more realistic projections of soil carbon dynamics by Earth system models. *Global Biogeochemical Cycles* **30**, 40-56 (2016).
- Ma, S., Baldocchi, D.D., Xu, L. and Hehn, T. Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California. *Agricultural and Forest Meteorology* **147**, 157-171 (2007).
- Manzoni, S., Jackson, R.B., Trofymow, J.A. & Porporato, A. The global stoichiometry of litter nitrogen mineralization. *Science* **321**, 684-686 (2008).
- Melillo, J.M. et al. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* **358**, 101-105 (2017).
- Mitchard, E. T. The tropical forest carbon cycle and climate change. *Nature* **559**, 527-534 (2018).
- Natali, S.M., Schuur, E.A. & Rubin, R.L.. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of ecology* **100**, 488-498 (2012).
- Nowinski NS, Taneva L, Trumbore SE, Welker JM (2010) Decomposition of old organic matter as a result of deeper active layers in a snow depth manipulation experiment. *Oecologia*, **163**, 785–792.
- Oleson KW, et al. (2010) Technical description of version 4.0 of the Community Land Model (CLM), NCAR Tech. Note NCAR/TN-478+STR, doi:10.5065/D6FB50WZ.
- Parton, W.J., Schimel, D.S., Cole, C.V. & Ojima, D.S. Analysis of factors controlling soil organic matter levels in Great Plains Grasslands 1. *Soil Science Society of America Journal* **51**, 1173-1179 (1987).
- Parton, W.J., Ojima, D.S., Cole, C.V. & Schimel, D.S. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. *Quantitative modeling of soil forming processes*, 147-167 (1994).
- Pastorello, G. et al. A new data set to keep a sharper eye on land-air exchanges. *Eos, Transactions American Geophysical Union (Online)* **98** (2017).
- Qiu, C. et al. ORCHIDEE-PEAT (revision 4596), a model for northern peatland CO₂, water, and energy fluxes on daily to annual scales. *Geosci. Model Dev.* **11**, 497–519 (2018).
- Reichstein M, Papale D, Valentini R et al. (2007) Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophysical Research Letters*, **34**, L01402.01262
- Ryan, M.G., Linder, S., Vose, J.M. & Hubbard, R.M. Dark respiration of pines. *Ecological Bulletins*, 50-63 (1994).

- Ryan, M.G., Lavigne, M.B. & Gower, S.T. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research: Atmospheres* **102**, 28871-28883 (1997).
- Schuur, E.A.G. et al. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* **459**, 556–559 (2009).
- Schuur, E.A., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M. & Natali, S.M., 2015. Climate change and the permafrost carbon feedback. *Nature*, **520**, 171-179.
- Senapati N, Chabbi A, Smith P (2018) Modeling daily to seasonal carbon fluxes and annual net ecosystem carbon balance of cereal grain-cropland using DailyDayCent: A model data comparison. *Agriculture, Ecosystems & Environment*, **252**, 159-177
- Serna-Chavez, H.M., Fierer, N. and Van Bodegom, P.M. Global drivers and patterns of microbial abundance in soil. *Global Ecology and Biogeography* **22**, 1162-1172 (2013).
- Todd-Brown KEO, Randerson JT, Post WM, Hoffman FM, Tarnocai C, Schuur EAG, Allison SD. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations, *Biogeosciences*, **10**, 1717-1736 (2013).
- Turner, D.P. et al. Evaluation of MODIS NPP and GPP products across multiple biomes. *Remote Sensing of Environment* **102**, 282-292 (2006).
- Veen, B.W. Relation between root respiration and root activity. In *Structure and Function of Plant Roots* (pp. 277-280). Springer, Dordrecht (1981).
- Walker, T.W. et al. Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. *Nature Climate Change* **8**, 885 (2018).
- Wang, X. et al. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. *Global change biology* **20**, 3229-3237 (2014).
- Wang, J., Li, Y., Bork, E.W., Richter, G.M., Eum, H.I., Chen, C., Shah, S.H.H. & Mezbahuddin, S., 2020. Modelling spatio-temporal patterns of soil carbon and greenhouse gas emissions in grazing lands: Current status and future prospects. *Science of The Total Environment*, 139092.
- Weber, M., Hauer, G. & Farr, D. Economic-ecological evaluation of temporary biodiversity offsets in Alberta's boreal forest. *Environmental conservation* **42**, 315-324 (2015).
- Wieder, W.R., Bonan, G.B. & Allison, S.D. Global soil carbon projections are improved by modeling microbial processes. *Nature Climate Change* **3**, 909 (2013).
- Wieder, W.R., Cleveland, C.C., Smith, W.K. & Todd-Brown, K. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience* **8**, 441 (2015).
- Zhao, M., Running, S.W. & Nemani, R.R. Sensitivity of Moderate Resolution Imaging Spectroradiometer (MODIS) terrestrial primary production to the accuracy of meteorological reanalyses. *Journal of Geophysical Research* **111**, G01002 (2006).
- Zhao, M., Heinsch, F.A., Nemani, R.R. & Running S.W. Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment* **95**, 164-176 (2005).

559 Zhao, M. & Running, S.W. Drought-induced reduction in global terrestrial net primary
560 production from 2000 through 2009. *Science* **329**, 940-943 (2010).