

Modeling the implications of post-fire alternative successional trajectory for boreal carbon and permafrost dynamics in Interior Alaska

Elchin E. Jafarov¹, Valeria Briones¹, Aiza Kabeer¹, Brendan M. Rogers¹, Susan Natali¹, H       Genet², Ruth M. Rutter² & Tobey B. Carman²

¹*Woodwell Climate Research Center, Falmouth, Massachusetts, United States*

²*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, United States*



ABSTRACT

Spruce forests have dominated Interior Alaska for millennia, generally self-replacing after wildfires. However, contemporary climate change has been linked to an increase in fire severity and frequency, promoting alternative successional trajectories and conversion to permanent deciduous forests. Because wildfire is the primary recent disturbance in interior Alaska, intensifying fire regimes have the potential to convert evergreen to deciduous-dominated landscapes. Compared to evergreen forests, deciduous forests exhibit large differences in carbon and nitrogen storage and turnover. The absence of moss cover in deciduous forests is also associated with an increase in soil temperature and deepening of the active layer compared to evergreen forests, which provide a microclimate and biochemical setting conducive to thick moss development. It is therefore critical for biosphere models to represent the biochemical and structural differences associated with boreal evergreen and deciduous forests to represent the long-term implications of climate warming and increasing fires on successional trajectories, regional carbon balance, and permafrost dynamics. In this study, we use a biosphere model developed for high latitude ecosystems to conduct a sensitivity analysis to (1) investigate the capacity of biosphere models to represent the differences in ecosystem structure and functions characterizing spruce and birch forests, (2) evaluate the differences in responses of ecosystem carbon balance and permafrost dynamics to projected climate change between these two ecosystems, and (3) evaluate the important ecological processes driving carbon and permafrost dynamics at two neighboring experimental sites representing typical black spruce dominated and birch dominated mid-successional stands. Findings will further our understanding of the impact of Arctic warming on long-term permafrost dynamics, over the next several decades.

1 INTRODUCTION

Across much of Alaska and Canada, boreal forests are dominated primarily by a mix of deciduous and spruce forests (Calef et al. 2005). For Interior Alaska, spruce forests dominated the landscape for millennia and would self-replace following wildfires (Chapin et al. 2006). However, contemporary climate change is linked to an increase in fire severity (Turetsky et al. 2011), promoting alternative successional trajectories, and the establishment of deciduous forests (Johnstone et al. 2011). With wildfire being the primary disturbance in Interior Alaska, an increase in fire severity has the potential to shift evergreen to deciduous-dominated landscapes (Pastick et al. 2016). Field investigations revealed differences in carbon and nitrogen distribution and turnover between deciduous forests and evergreen forests (Melvin et al. 2015). The absence of moss cover in many deciduous forests leads to increased soil temperature and a deeper active layer compared to evergreen forests, where a thick moss layer thrives (Jean et al. 2018). The northern boreal region contains large carbon reserves and fire disturbances dominate the distribution of plant and soil carbon (Harden et al. 2000). Predicted increases in the area burned in the boreal forest and its interactions with vegetation distribution suggest significant feedback to the climate system and potentially substantial impacts on the carbon budget, with the potential to convert vast regions of forests from sinks to carbon sources (Dieleman et al. 2020; Kasischke et al. 1999; Van Wagner 1988; Flannigan and Van Wagner 1991). Although boreal forests act as a net carbon sink over

long time periods, severe fire activity can disrupt the net carbon balance thus resulting in forests turning into net carbon sources (Harden et al., 2000, Mack et al 2021, Walker et al 2019).

Understanding how terrestrial ecosystems will respond to future climate change is challenging due to complex interactions among ecosystem structure and function, soil and permafrost processes, disturbance dynamics, and regional climate (Rupp et al. 2002). Additional research is needed to simulate realistic ecosystem responses to climate change accurately, especially to evaluate the sensitivity of boreal vegetation communities to these changes (Miquelajauregui et al. 2019).

Here, we investigate how interactions among forest soils, fire characteristics, and stand characteristics influence biogeochemical dynamics under varying fire return intervals. We use a biosphere model developed for high latitude ecosystems to (1) investigate the capacity of this biosphere model to represent the differences in ecosystem structure and functions characterizing spruce and birch forests and (2) evaluate the differences in responses of ecosystem carbon balance and permafrost dynamics to varying fire return intervals. Our study aims to highlight the key processes at stand and landscape scales that require further investigation to improve our ability to predict the future dynamics of Alaskan boreal forests under future change in climate.

2 MATERIALS AND METHODS

2.1 Site Description

We use two sites at Murphy Dome, near Fairbanks, Alaska, that have measured vegetation and stock carbon and nitrogen data. The sites represent evergreen (black spruce) and deciduous plant functional types. The evergreen and deciduous plant functional types are members of the boreal forest community types MD1 and MD3 correspondingly, where MD stands for Murphy Dome. Throughout the paper MD1 will be referred to as the evergreen stand, while MD3 will be referred to as the deciduous stand. The community type in the DVM-DOS-TEM includes multiple plant functional types, where each plant functional type stores carbon and nitrogen in stems, leaves, and roots.

The study site of Murphy Dome is located within the Tanana Valley State Forest located outside of Fairbanks, Alaska (64°53'N, 148°23'W). In 1958, the Murphy Dome fire destroyed the sites, which covered an area of 8,930 hectares. As a result, the area has regrown with a uniformly aged upper layer consisting of paper birch trees and a patchy lower layer of white spruce trees (Sullivan et al. 2021). The two most common forest types, across interior Alaska, are made up of evergreen stands of black spruce and deciduous broadleaf forests. Within this region, roughly 39% of the area is made up of evergreen forest and 24% deciduous forest stands (Calef et al. 2005; Jean et al. 2020). The average organic layer thickness is roughly 16.4 cm at the black spruce site, and 7.6 cm at the birch site, which subsequently results in larger carbon (C) stocks of the organic layer within the black spruce site (4.8 kg C m⁻²) compared to the birch (2.4 kg C m⁻²) as reported by Melvin et al. (2015).

2.2 Model Description

The Terrestrial Ecosystem Model with Dynamic Vegetation and Dynamic Organic Soil Layers (DVM-DOS-TEM) is a process-based biosphere model designed to simulate biophysical and biogeochemical processes between the soil, the vegetation and the atmosphere. DVM-DOS-TEM v0.6.1 is the latest version of the Terrestrial Ecosystem Model (McGuire et al. 1992; Raich et al. 1991) that focuses on representing carbon and nitrogen cycles in high latitude ecosystems and how they are affected at monthly-to-centennial scales by climate, disturbances and biophysical processes such as soil thermal and hydrological dynamics (Yi et al. 2009; Zhuang et al. 2002), snow cover (Euskirchen et al. 2006) and vegetation (Euskirchen et al. 2016). DVM-DOS-TEM has been used extensively in arctic and boreal permafrost regions with applications to the soil environment (Yi et al. 2009; Zhuang et al. 2002; Zhuang et al. 2001), tundra vegetation dynamics (Euskirchen et al. 2016; Euskirchen et al. 2009), carbon storage (Genet et al. 2018; Lyu et al. 2018), ecological impacts of wildfire (Balshi et al. 2007; Genet et al. 2013; Yi et al. 2010) and feedback to climate (Euskirchen et al. 2016). The ecological processes represented in DVM-DOS-TEM include carbon and nitrogen dynamics for every plant functional type of the vegetation community and every layer of the soil column. Carbon and nitrogen dynamics are driven by climate,

atmospheric chemistry, soil and canopy environment, and wildfire occurrence and severity. Carbon and nitrogen from the litterfall are divided into aboveground and belowground. Aboveground litterfall is assigned only to the top layer of the soil column, while belowground litterfall is assigned to different layers of the three soil horizons based on the fractional distribution of fine roots with depth.

Before conducting the historical simulations, a typical spin-up procedure was conducted for each site in which the model was driven by averaged modern forcings for that location and this process was repeated continuously until a dynamic equilibrium was achieved (i.e., constant pools and fluxes). The resulting modeled ecosystem state for each site then served as the starting point for the historical simulation. The DVM-DOS-TEM model inputs include annual time series of atmospheric CO₂ concentration, monthly mean air temperature, total precipitation, net incoming shortwave radiation, and vapor pressure (McGuire et al. 2016).

2.3 Model Simulations

We ran experimental site simulations at a single pixel, 1 km x 1 km resolution for both the black spruce and deciduous community types at Murphy Dome with soil drainage conditions set to well-drained to simulate upland soils at the site. Historical climate data (1901–2015) for use in DVM-DOS-TEM were extracted from the Climatic Research Unit time series version 4.0 (CRU TS4.0; Harris et al. 2014) downscaled at 1 km × 1 km spatial resolution on a monthly time step, prepared by the Scenario Network for Alaska Planning (<https://uaf-snap.org/>; Pastick et al. 2017).

To compare baseline site characteristics, we ran simulations at each site without the occurrence of fire, by turning the fire module (DSBM) off. This allows us to first assess stand characteristics at two semi-mature forest stands without the presence of fire as well as a baseline to compare our fire disturbance simulations. We used site data from Melvin et al. (2015), which took measurements from both aboveground stand characteristics and soil characterization at the black spruce and paper birch dominated stands throughout the period between 2012–13. We compared our baseline model outputs to those of Melvin et al. (2015) to validate our results as well as ensure the model was representing the key differences between the two successional stands. To compare the effects of increased fire frequency we ran simulations forced with a fire (DSB) module turned on, to compare the effects of varying fire return intervals (FRI) on stand components such as carbon stocks. We ran a total of 5 fire simulations with FRI ranging from 50–250 at 50-year increments under a moderate severity which equates to approximately 69% of the organic soil depth combusted (Yi et al. 2010). The occurrence and severity of the fire during simulations was set up to simulate the Murphy Dome fire which occurred in 1958. A lower FRI corresponds to shorter time period between fires, while a larger FRI corresponds to a longer period of time between fire disturbance. Each simulation was run at the evergreen site to simulate the effects of fire on spruce dominants forest stands to assess how increased FRI effects stand characteristics especially if we are able to observe changes in plant composition. Each FRI was

simulated during the month of July and ran at a fire severity of 3 (moderate severity), and the entire pixel (1x1 km) was burned. We ran simulations consisting of a spin-up for 250 years, equilibrium for 6,000 years, and transient for 115 years, which represented the historical period of (1901–2015).

We focused on assessing a subset of model variables for both aboveground and belowground variables, e.g., soil carbon and nitrogen stocks grouped by layer (fibric, humic, mineral), vegetation carbon for the dominant tree species (spruce, birch) also grouped by plant compartment (leaf, stem), as well as emission from vegetation and soil which are only output when a fire has occurred. In addition, we looked at fire specific model outputs to assess the impacts of each FRI. Such variables are only produced after a fire has been simulated and includes emissions outputs including burned carbon from both the vegetation and soil to the atmosphere.

3 RESULTS

3.1 Baseline Comparisons

Baseline model outputs run without the occurrence of fire showed generally good agreement to site observations from (Melvin et al. 2015) and were able to capture major stand characteristic differences. The birch stand had aboveground carbon stocks (leaf, stem) at a total aboveground 13,033.26 g C-m²-yr compared to evergreen site at 2,271 g C m² yr (Figure 1) compared to observed total aboveground C at 5308.92 and 2281.70 2,271 g C m² yr at the deciduous and evergreen sites respectively. Similarly, the deciduous site exhibited higher stem nitrogen (N) stocks compared to the evergreen site, at 228.92 and 38.33 g N m² yr respectively.

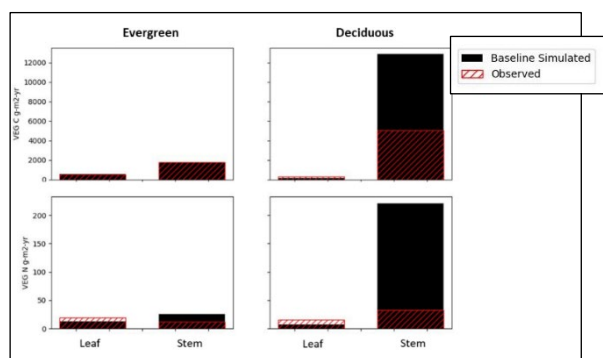


Figure 1. Comparison of simulated aboveground carbon and nitrogen stocks g m²yr at the spruce dominated (MD1) and deciduous birch dominated site (MD3) grouped by leaf and stem measured during 2012 to observations derived from Melvin et al. 2015.

Similarly, DVM-DOS-TEM was able to capture stand differences belowground. Model estimates of organic layer thickness (OLT) accurately simulated differences between evergreen and deciduous site. Our model estimated OLT at the evergreen site to be 18.3 cm while OLT at the deciduous site was 11.6 cm compared to observed OLT of 16.4 and 7.6 respectively, thus slightly overestimating for MD3. Deeper organic soils at the evergreen site also results in greater soil carbon stocks in the organic layer compared to that of soil carbon at the deciduous site as shown in Figure 2. While observed data show larger soil carbon stocks within the top 10 cm at the evergreen site than the deciduous, our baseline data show an opposite trend where we are overestimating soil carbon in the mineral layer at the deciduous site than the evergreen.

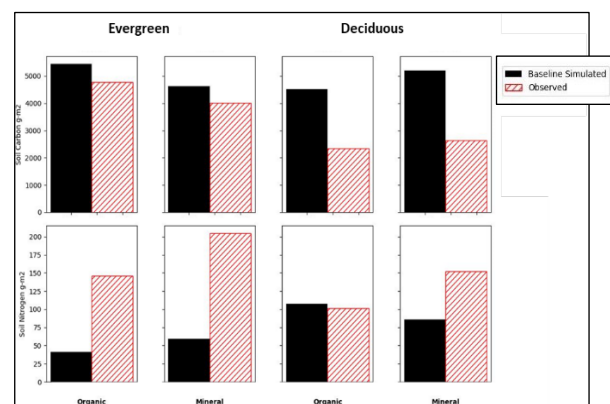


Figure 2. Soil carbon and nitrogen stocks for the Murphy Dome evergreen (MD1) and deciduous (MD3) sites. Soil carbon and nitrogen stocks are depicted for both the organic and mineral layers. Soil carbon and nitrogen were measured at the top 10 cm of the mineral layer for both sites and observations derived from Melvin et al. 2015.

A deeper OLT at the evergreen site results in slightly cooler soil temperatures at 10 cm depth particularly during the Fall and Spring shoulder months as shown in Figure 3, which the model was better able to capture at the evergreen site than at the deciduous. The baseline model run at MD3 shows an average soil temperature of -0.95 °C while observed average soil temperature is 0.95 °C during the study period at the 10 cm depth.

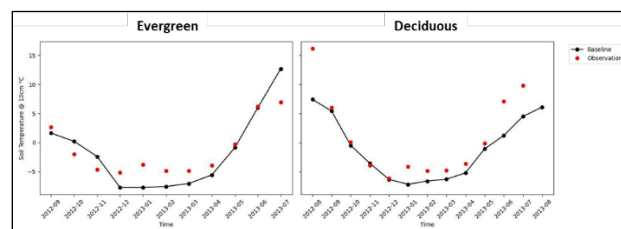


Figure 3. Soil temperature (°C) measured at 10 cm depth below soil surface for both sites at Murphy Dome: Spruce (MD1) and Deciduous (MD3) for baseline simulations and observations derived from Melvin et al. 2015. Average soil temperature at MD1 was -1.3 °C for the baseline run, and -1.25 °C for observations.

3.2 Fire Simulations

Simulated aboveground carbon stocks for simulations across varying FRI at the deciduous site shows a general increase in total aboveground biomass as FRI increases (Figure 4e). Looking at the change in carbon stocks per dominant plant functional type (PFT), we see a decrease in total aboveground biomass of evergreen trees at the shorten FRI of 50 years from baseline of 2171.12 to 1598.12 g C m², with a switch to an increase in biomass from the baseline on FRI 100 to 2444.19 g C m² (Figure 4a). A minimal decrease in the carbon stocks of deciduous trees (Figure 4c) also is apparent at FRIs 50 from baseline 346.47 to 284.65 g C m² with a net increase on FRI 150–250 to 446.59 g C m², showing more pronounced decrease in PFT evergreen trees with more frequent FRI compared to deciduous trees.

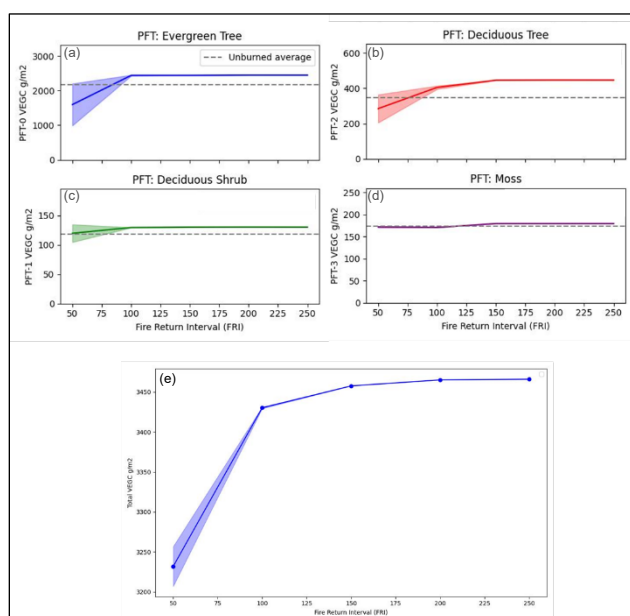


Figure 4. Comparison of the main plant function types found at spruce dominated evergreen site (MD1): (a) evergreen trees, (b) deciduous shrubs, (c) deciduous trees, and (d) moss and their respective aboveground vegetation stocks (g/m²) in relation to their baseline values (unburned, dotted lines) and varying fire return intervals (FRI) (e).

Similar to aboveground vegetation stocks, less frequent FRI results in an increase in total organic carbon (g m² yr) for both organic layer and mineral soil carbon (Figure 5). Simulations with more frequent fire greatly reduce total organic carbon (TOC), with a decrease in TOC with shortening FRI to an average of 13,807.33 for FRI-50 with an increase in TOC starting at FRI-100 for both organic and mineral soil layers resulting in a TOC of 16261.21 g/m² and a peak in TOC at FRI-150 before TOC begins to gradually plateau (Figure 5).

Simulations show that as the FRI becomes more frequent, fire emissions released from the soil matter increases until a threshold is reached where emissions begin to gradually decrease at FRI-150 (Figure 6). At FRI-50 carbon

emissions from the soil averaged 327.89 g/m² and carbon emissions from vegetation to the atmosphere averaged 856.78 g/m². Both carbon emissions peaked at FRI-150 averaging 416.05 and 892.84 g/m² for soil and vegetation to the atmosphere, respectively.

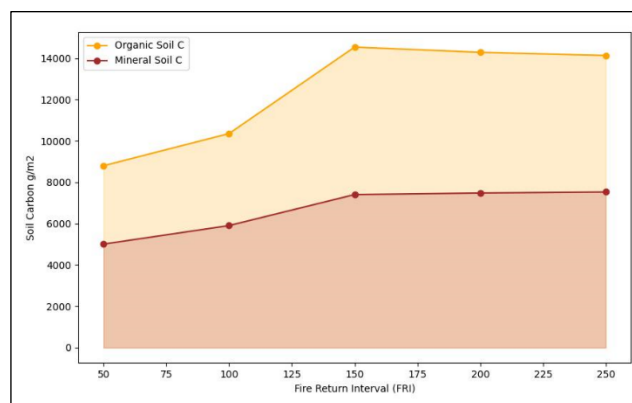


Figure 5: Relationship between soil carbon stocks (g/m²) broken up by organic and mineral layers for the spruce dominated evergreen site to variance in fire return interval (FRI).

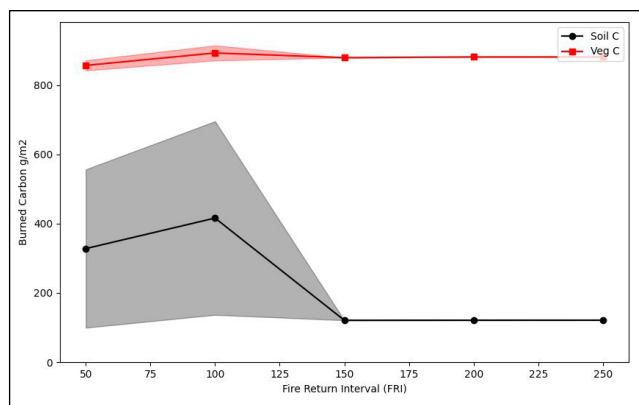


Figure 6 Change in carbon emissions from soil and vegetation burned compared across varying fire return intervals (FRI). The mean (solid lines) and standard deviation (shadow) are shown for each variable.

4 DISCUSSION

Representing large-scale fire events in ecosystem models is critical because wildfires significantly impact ecosystem processes and carbon dynamics at landscape and regional scales (McKenzie et al. 1996; Kasischke et al. 1995; Alvarado et al. 1998). Based on our findings, the occurrence of fire disturbances play an important role in determining the abundance of different ecosystem types at a plant functional level, leading to distinct patterns and changes in carbon cycling across our sites (Rupp et al. 2000, 2002). Our results show that vegetation carbon of all dominant plant functional types in the black spruce dominant site decreased post-fire. In addition, we observe

a gradual increase in the total amount of vegetation carbon as the time between each fire occurrence increases, thus allowing more time for the vegetation community to recover post disturbance.

Our simulations suggest that changes to the frequency of fire occurrence can cause distinct changes to vegetation and soil carbon stocks, thus causing additional changes to stand characteristics of a semi-mature black spruce forest stand. Under the longer FRI of 250 years, our simulations showed an increase in total aboveground C for PFT evergreen trees at the evergreen site, deciduous trees, and an increase of moss. In comparison under the shorter FRI of 50 years, simulations showed an increase in total aboveground C for PFT evergreen trees at the evergreen site, and an increase in total aboveground C for PFT deciduous trees signifying a shift to greater biomass of deciduous trees under more frequent fire disturbance. The observed gradual increase in spruce evergreen plant functional types may be due to moderate burns which are allowing for a rapid regeneration of spruce (Kurkowski et al. 2008). These connections enable us to predict the potential shifts in landscape forest cover that could occur in response to increased severity or frequency of fires under future climate change scenarios (Gillett et al. 2004; Flannigan et al. 2005; Balshi et al. 2009).

The absence of moss can lead to warmer and drier soils, thus exposing areas underlain by permafrost to accelerated loss, contributing to a feedback of permafrost carbon loss to the atmosphere (Kasischke et al. 1995). By quantifying carbon and nutrient pools and examining potential shifts in their distribution, this research can contribute to improved predictions regarding the impact of changes in the wildfire regime on boreal ecosystems. However, it's important to acknowledge that uncertainties in model formulation and parameterization can significantly influence the results (Euskirchen et al. 2016; Genet et al. 2018). While our model validation suggests that DVM-DOS-TEM can generally simulate carbon stocks of boreal forest vegetation and soil dynamics, there remains substantial uncertainty in representing critical ecosystem processes in response to wildfires, such as changes in forest successions such as shifts in forest type from spruce dominated to deciduous, which is currently unrepresented in our model (Klupar et al. 2021; Parker et al. 2016).

Another finding is that the possibility of fire influencing changes in successional trajectories depends on landscape variables like site moisture. As a result, we should anticipate that the resilience of black spruce forests to climate and fire regime changes will vary across the landscape, and drier spruce forests might have the highest potential to transition into deciduous-dominated forests under future environmental changes.

5 CONCLUSIONS

Our study highlights the critical role of fire disturbances in shaping the composition and carbon dynamics of these ecosystems. Notably, it reveals that the frequency of fire occurrences can significantly impact vegetation and soil carbon stocks, influencing the recovery and composition of forest stands. The findings suggest that under certain conditions, prolonged fire return intervals may lead to an increase in evergreen tree abundance and a transition to deciduous-dominated forests. Moreover, the absence of moss in deciduous forests can have implications for soil temperature, permafrost dynamics, and carbon feedback to the atmosphere.

While our study enhances our understanding of boreal forest dynamics, it also underscores the complexities and uncertainties inherent in modeling such ecosystems. The need for further research to improve the accuracy of ecosystem models in predicting responses to climate change and fire disturbances is needed such as the ability for models to simulate shifts in vegetation community types and the dynamic feedbacks to soil thermal and hydrological properties. Overall, this research contributes valuable insights into the potential impacts of climate change on Alaskan boreal forests, emphasizing the importance of considering landscape variations and moisture levels in assessing forest resilience and future trajectories.

6 ACKNOWLEDGEMENTS

This project was made possible with funding through the Audacious Project and Quadrature Climate Foundation Prime Grant Number 01-21-000094 (to SMN and BR).

7 REFERENCES

- Alvarado, E., Sandberg, D., and Pickford, S.G. 1998. 'Modeling large forest fires as extreme events', *Northwest Science* 72, pp. 66–75.
- Balshi, M., McGuire, A., Zhuang, Q., Melillo, J., Kicklighter, D., Kasischke, E., et al. 2007. 'The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: A process-based analysis', *Journal of Geophysical Research* 112. doi:10.1029/2006JG000380.
- Balshi, M.S., McGuire, A.D., Duffy, P., Flannigan, M., Kicklighter, D.W., and Melillo, J. 2009. 'Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century', *Global Change Biology* 15(6), pp. 1491–1510. doi:10.1111/j.1365-2486.2009.01877.x.
- Calef, M.P., David McGuire, A., Epstein, H.E., Scott Rupp, T., and Shugart, H.H. 2005. 'Analysis of vegetation distribution in Interior Alaska and sensitivity to climate change using a logistic regression approach', *Journal of Biogeography* 32(5), pp. 863–878. doi:10.1111/j.1365-2699.2004.01185.x.

- Chapin, F.S., Trainor, S.F., Huntington, O., Lovcraft, A.L., Zavaleta, E., Natcher, D.C., et al. 2008. 'Increasing Wildfire in Alaska's Boreal Forest: Pathways to Potential Solutions of a Wicked Problem', *BioScience* 58(6), pp. 531–540. doi:10.1641/B580609.
- Dieleman, C.M., Rogers, B.M., Potter, S., Veraverbeke, S., Johnstone, J.F., Laflamme, J., Solvik, K., Walker, X.J., Mack, M.C., and Turetsky, M.R. 2020. 'Wildfire combustion and carbon stocks in the southern Canadian boreal forest: Implications for a warming world', *Global Change Biology* 26(11), pp. 6062–6079. doi:10.1111/gcb.15158.
- Euskirchen, E.S., Edgar, C.W., Turetsky, M.R., Waldrop, M.P., and Harden, J.W. 2016. Differential response of carbon fluxes to climate in three peatland ecosystems that vary in the presence and stability of permafrost, *Journal of Geophysical Research: Biogeosciences* 119(8), pp. 1576–1595. Available at: <https://doi.org/10.1002/2014JG002683>.
- Euskirchen, E.S., McGuire, A.D., Chapin III, F.S., Yi, S., and Thompson, C.C. 2009. 'Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks', *Ecological Applications* 19(4), pp. 1022–1043. doi:10.1890/08-0806.1.
- Euskirchen, E.S., McGuire, A.D., Kicklighter, D.W., Zhuang, Q., Clein, J.S., Dargaville, R.J., et al. 2006. 'Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems', *Global Change Biology*, 12(4), pp. 731–750. doi:10.1111/j.1365-2486.2006.01113.x.
- Flannigan, M. and Wagner, C.E. 1991. 'Climate change and wildfire in Canada', *Canadian Journal of Forest Research* 21, pp. 66–72. doi:10.1139/x91-010.
- Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., and Stocks, B.J. 2005. 'Future Area Burned in Canada', *Climatic Change* 72(1), pp. 1–16. doi:10.1007/s10584-005-5935-y.
- Genet, H., He, Y., Lyu, Z., McGuire, A.D., Zhuang, Q., Clein, J., et al. 2018. 'The role of driving factors in historical and projected carbon dynamics of upland ecosystems in Alaska', *Ecological Applications* 28(1), pp. 5–27. doi:10.1002/eap.1641.
- Genet, H., McGuire, A.D., Barrett, K., Breen, A., Euskirchen, E.S., Johnstone, J.F., et al. 2013. 'Modeling the effects of fire severity and climate warming on active layer thickness and soil carbon storage of black spruce forests across the landscape in interior Alaska', *Environmental Research Letters* 8(4), 045016. doi:10.1088/1748-9326/8/4/045016.
- Gillett, N.P., Weaver, A.J., Zwiers, F.W., and Flannigan, M.D. 2004. 'Detecting the effect of climate change on Canadian forest fires', *Geophysical Research Letters* 31(18). doi:10.1029/2004GL020876.
- Harden, J., Trumbore, S., Stocks, B., Hirsch, A., Gower, S., O'Neill, K., and Kasischke, E. 2000. 'The role of fire in the boreal carbon budget', *Global Change Biology* 6(S1), pp. 174–184. doi:10.1046/j.1365-2486.2000.06019.x.
- Harris, I., Jones, P., Osborn, T., and Lister, D. 2014. 'Updated high-resolution grids of monthly climatic observations—The CRU TS3.10 Dataset', *International Journal of Climatology* 34. doi:10.1002/joc.3711.
- Jean, M., Mack, M.C., and Johnstone, J.F. 2018. 'Spatial and temporal variation in moss-associated dinitrogen fixation in coniferous- and deciduous-dominated Alaskan boreal forests', *Plant Ecology* 219(7), pp. 837–851. doi:10.1007/s11258-018-0838-y.
- Johnstone, J.F., Rupp, T.S., Olson, M., and Verbyla, D. 2011. 'Modeling impacts of fire severity on successional trajectories and future fire behavior in Alaskan boreal forests', *Landscape Ecology* 26(4), pp. 487–500. doi:10.1007/s10980-011-9574-6.
- Kasischke, E.S., Bergen, K., Fennimore, R., Sotelo, F., Stephens, G., Janetos, A., and Shugart, H.H. 1999. 'Satellite imagery gives clear picture of Russia's boreal forest fires', *Eos, Transactions American Geophysical Union* 80(13), pp. 141–147. doi:10.1029/99EO00094.
- Kasischke, E.S., Christensen Jr, N.L., and Stocks, B.J. 1995. 'Fire, Global Warming, and the Carbon Balance of Boreal Forests', *Ecological Applications* 5(2), pp. 437–451. doi:10.2307/1942034.
- Klupar, I., Rocha, A.V., and Rastetter, E.B. 2021. 'Alleviation of nutrient co-limitation induces regime shifts in post-fire community composition and productivity in Arctic tundra', *Global Change Biology* 27(14), pp. 3324–3335. doi:10.1111/gcb.15646.
- Kurkowski, T.A., Mann, D.H., Rupp, T.S., and Verbyla, D.L. 2008. 'Relative importance of different secondary successional pathways in an Alaskan boreal forest', *Canadian Journal of Forest Research* 38(7), pp. 1911–1923. NRC Research Press. doi:10.1139/X08-039.
- Lyu, Z., Genet, H., He, Y., Zhuang, Q., McGuire, A.D., Bennett, A., et al. 2018. 'The role of environmental driving factors in historical and projected carbon dynamics of wetland ecosystems in Alaska', *Ecological Applications: A Publication of the Ecological Society of America* 28(6), pp. 1377–1395. doi:10.1002/eap.1755.
- Mack, M.C., Walker, X.J., Johnstone, J.F., Alexander, H.D., Melvin, A.M., Jean, M., and Miller, S.N. 2021 'Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees', *Science* 372, pp. 280–3.
- McGuire, A.D., Koven, C., Lawrence, D.M., Clein, J.S., Xia, J., Beer, C., et al. 2016. 'Variability in the sensitivity among model simulations of permafrost and carbon dynamics in the permafrost region between 1960 and 2009', *Global Biogeochemical Cycles* 30(7), pp. 1015–1037. doi:10.1002/2016GB005405.

- McGuire, A.D., Melillo, J.M., Joyce, L.A., Kicklighter, D.W., Grace, A.L., Moore III, B., and Vorosmarty, C.J. 1992. 'Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America', *Global Biogeochemical Cycles* 6(2), pp. 101–124. doi:10.1029/92GB00219.
- Mckenzie, D., Peterson, D.L., and Alvarado, E. 1996. 'Extrapolation Problems in Modeling Fire Effects at Large Spatial Scales: a Review', *International Journal of Wildland Fire* 6(4), pp. 165–176. doi:10.1071/wf9960165.
- Melvin, A.M., Mack, M.C., Johnstone, J.F., David McGuire, A., Genet, H., and Schuur, E.A.G. 2015. 'Differences in Ecosystem Carbon Distribution and Nutrient Cycling Linked to Forest Tree Species Composition in a Mid-Successional Boreal Forest', *Ecosystems* 18(8), pp. 1472–1488. doi:10.1007/s10021-015-9912-7.
- Miquelajaugui, Y., Cumming, S.G., and Gauthier, S. 2019. 'Short-term responses of boreal carbon stocks to climate change: A simulation study of black spruce forests', *Ecological Modelling* 409, 108754. doi:10.1016/j.ecolmodel.2019.108754.
- Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., et al. 2010. 'The next generation of scenarios for climate change research and assessment', *Nature* 463(7282), pp. 747–756. doi:10.1038/nature08823.
- Parker, R.J., Boesch, H., Wooster, M.J., Moore, D.P., Webb, A.J., Gaveau, D., and Murdiyarso, D. 2016. 'Atmospheric CH₄ and CO₂ enhancements and biomass burning emission ratios derived from satellite observations of the 2015 Indonesian fire plumes', *Atmospheric Chemistry and Physics* 16(15), pp. 10111–10131. doi:10.5194/acp-16-10111-2016.
- Pastick, N.J., Duffy, P., Genet, H., Rupp, T.S., Wylie, B.K., Johnson, K.D., Jorgenson, M.T., Bliss, N., McGuire, A.D., Jafarov, E.E., and Knight, J.F. 2017. 'Historical and projected trends in landscape drivers affecting carbon dynamics in Alaska', *Ecological Applications: A Publication of the Ecological Society of America* 27(5), pp. 1383–1402. doi:10.1002/eap.1538.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore, B., and Vorosmarty, C.J. 1991. 'Potential Net Primary Productivity in South America: Application of a Global Model', *Ecological Applications: A Publication of the Ecological Society of America* 1(4), pp. 399–429. doi:10.2307/1941899.
- Rupp, T.S., Chapin, F.S., and Starfield, A.M. 2000. 'Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska', *Global Change Biology* 6(5), pp. 541–555. doi:10.1046/j.1365-2486.2000.00337.x.
- Rupp, T.S., Starfield, A.M., Chapin, F.S., and Duffy, P. 2002. 'Modeling the Impact of Black Spruce on the Fire Regime of Alaskan Boreal Forest', *Climatic Change* 55(1), pp. 213–233. doi:10.1023/A:1020247405652.
- Sullivan, P.F., Brownlee, A.H., Ellison, S.B.Z., and Cahoon, S.M.P. 2021. 'Comparative drought sensitivity of co-occurring white spruce and paper birch in interior Alaska', *Journal of Ecology* 109(6), pp. 2448–2460. doi:10.1111/1365-2745.13654.
- Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D., and Tuittila, E.-S. 2012. 'The resilience and functional role of moss in boreal and arctic ecosystems', *New Phytologist* 196(1), pp. 49–67. doi:10.1111/j.1469-8137.2012.04254.x.
- Walker, X.J., Baltzer, J.L., Cumming, S.G., Day, N.J., Ebert, C., Goetz, S., et al. 2019. 'Increasing wildfires threaten historic carbon sink of boreal forest soils', *Nature* 572, pp. 520–523.
- Yi, S., McGuire, A.D., Harden, J., Kasischke, E., Manies, K., Hinzman, L., et al. 2009. 'Interactions between soil thermal and hydrological dynamics in the response of Alaska ecosystems to fire disturbance', *Journal of Geophysical Research: Biogeosciences* 114(G2). doi:10.1029/2008JG000841.
- Yi, S., McGuire, A.D., Kasischke, E., Harden, J., Manies, K., Mack, M., and Turetsky, M. 2010. 'A dynamic organic soil biogeochemical model for simulating the effects of wildfire on soil environmental conditions and carbon dynamics of black spruce forests', *Journal of Geophysical Research: Biogeosciences* 115(G4). doi:10.1029/2010JG001302.
- Zhuang, Q., McGuire, A.D., O'Neill, K.P., Harden, J.W., Romanovsky, V.E., and Yarie, J. 2002. 'Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska', *Journal of Geophysical Research: Atmospheres* 107(D1), pp. FFR 3-1–FFR 3-26. doi:10.1029/2001JD001244.
- Zhuang, Q., Romanovsky, V.E., and McGuire, A.D. 2001. 'Incorporation of a permafrost model into a large-scale ecosystem model: Evaluation of temporal and spatial scaling issues in simulating soil thermal dynamics', *Journal of Geophysical Research: Atmospheres* 106(D24), pp. 33649–33670. doi:10.1029/2001JD900151.