ARCTIC
VOL. 72, NO. 4 (DECEMBER 2019)

InfoNorth

How Do Disturbances across Spatial Scales Influence Treeline Range Dynamics?

by Lucas Brehaut

INTRODUCTION

The relationship between plants and disturbance regimes (i.e., frequency, severity, size, and location of a disturbance) ultimately shapes patterns and processes of ecosystems across spatial scales (Greene et al., 1999; Cairns and Moen, 2004; Turner, 2010; Brown and Vellend, 2014; Johnstone et al., 2016). Localized (e.g., herbivory) to large-scale (e.g., fire) disturbances are intimately connected to plant communities, their successional trajectory, and the geographic distributions of individual species. The boreal biome encompasses a mosaic of post-disturbance plant communities that are primarily driven by fire, insects, and anthropogenic influences.

Many plant species have evolved reproductive strategies in order to recover after disturbance regimes. Across the circumpolar boreal forest, some conifers (*Pinus* spp., *Picea mariana* [Mill.] B.S.P.) employ a serotinous regeneration strategy, where cones release their seeds after being exposed to the heat of a fire. This strategy results in a pulse of seed that is dispersed onto the landscape, potentially saturating any seed-predator pressures (Cairns and Moen, 2004). Several deciduous shrub and tree species common to boreal forests (*Betula* spp.; *Salix* spp.; *Populus* spp.) are able to re-sprout from roots after fire, which allows them to recolonize via vegetative reproduction. In some cases however, persistent or novel disturbances to a plant community can initiate a successional trajectory change (Johnstone et al., 2010; Brown and Johnstone, 2012). This change can occur when the dominant species historically present in that ecosystem has either lost its reproductive potential through a change in disturbance or has been out-competed by another species more fit to the new conditions (Buma et al., 2013). Determining a plant community's *ecological inertia* (i.e., ability to resist change; Westman, 1978) and subsequent *resilience* (i.e., ability to return to the previous state after a disturbance; Holling, 1973) are two important priorities that should be addressed under continued climate change (Johnstone et al., 2016). Fire regimes are changing rapidly across the Subarctic. Longer growing seasons paired with moisture-stressed forests and increased thunderstorms have resulted in fires that are burning more frequently, lasting longer, and covering a much larger spatial extent (Kasischke et al., 2010; Stevens-Rumann et al., 2018). Evidence of a shift in boreal forest succession with novel fire activity has already been observed in the Yukon, where more frequent and severe fires have resulted in the complete loss of boreal tree seed, shifting the landscape from conifer-dominated to deciduous-dominated stands and shrub-grassland vegetation (Johnstone and Chapin, 2006; Brown and Johnstone, 2012). Fires are also becoming more common in ecosystems otherwise unfamiliar to this type of disturbance (Hu et al., 2015). On the North Slope of Alaska, dry conditions have resulted in large areas of the tundra burning despite low levels of fuel (Mack et al., 2011).

While tundra fires still remain relatively infrequent, the burning of tundra vegetation begs the question of whether tundra plant communities have a high level of resilience after experiencing a novel disturbance (Fig. 1). Tundra ecosystems are assumed to have some ability to resist change (i.e., high ecological inertia), as the vegetation and soil characteristics are unsuitable growing conditions for most boreal tree and shrub seedlings (Johnstone et al., 2016). Additionally, tundra ecosystems are geographically isolated from other ecosystem types, meaning that potentially colonizing species, such as trees, have limited likelihood of dispersal. However, as fires continue to become more common at higher latitudes, a concerted scientific effort is required to determine whether fire has the ability to lower the tundra's ecological inertia, thereby facilitating successional trajectory change.

In addition to fire regimes changing, so too are biotic disturbances (Cairns and Moen, 2004). While vertebrate herbivores limit a seedling's ability to establish, either through trampling or consumption (Munier et al., 2010), recent evidence in Labrador (Jameson et al., 2015) and southern Yukon (Kambo and Danby, 2017) suggests that prior to seedling establishment, pre-dispersal insect herbivory results in a loss of viable seed for some boreal tree species (e.g., black and white spruce). Unfortunately, our geographic understanding of pre-dispersal insect herbivory is limited, despite viable seed production and dispersal capabilities representing two of the largest constraints to range expansion under continued climate warming (Brown et al., 1996; Viglas et al., 2013; Brown et al., 2019). An

FIG. 1. Will fire at the treeline ecotone break the tundra plant community's ecological inertia, thus facilitating the range expansion of boreal tree and shrub species? Photo depicts the effects of a northern Yukon fire that occurred in 2017, burning much of the lower elevation forest (to the right of image) and up into the treeline ecotone. Seeding experiments in the burned and unburned tundra substrate will help determine the possibility of boreal tree establishment.

accurate measure of pre-dispersal herbivory is required to better model successional vegetation dynamics under changing disturbance regimes.

The treeline ecotone, defined as the transition zone from forested to non-forested ecosystems (Körner, 1998), is an ideal location to study disturbance and successional trajectory change at northern latitudes. At the interface of boreal forest and tundra communities, latitudinal and altitudinal treelines have been considered a classic study system for boreal tree range expansion (Danby and Hik, 2007; Payette, 2007; Munier et al., 2010). Much of the previous literature has focused on the effects of climate because, at a global scale, climate is considered to be the dominant control of the spatial positioning of northern treelines (Körner, 1998). Yet, climate warming has not resulted in a ubiquitous upslope or northward advance of the treeline across the Subarctic, despite this region experiencing the most intense ongoing warming (Harsch et al., 2009). Furthermore, where there has been an advance, the rate has been much slower than what has been predicted by temperature-based models. These findings imply that explaining treeline range expansion exclusively by climatic conditions is overly reductive. A consistent rise in surface air temperature paired with a disturbance, in this case fire, may be what is required to disrupt the ecological inertia of the tundra ecosystems proximal to the treeline, potentially resulting in a surge establishment of the newly favoured boreal tree species beyond their current range (Buma et al., 2013). Our increasing understanding of the importance of biotic disturbances at the present edge warrants the investigation of how different disturbance types may positively or negatively influence range edge dynamics (Cairns and Moen, 2004).

Using the ecological inertia concept and the field of disturbance ecology, my research goal was to assess whether the inertia of the treeline ecotone vegetation community was affected by two disturbance types of different spatial scales. This research goal was achieved by first examining pre-dispersal insect herbivory of cones at the treeline, followed by a manipulative experiment detailing the effects of fire at the treeline on the germination of boreal tree species. Insect herbivory is a more localized disturbance, therefore sampling effort across their range was undertaken. In contrast, fire is a large-scale disturbance, but local effects at the treeline are poorly understood; thus, an intensive, more localized approach was completed. While the insect herbivory study took place at treelines across northern Canada, research on treeline fires was conducted in northern Yukon, where fires have occurred more frequently in recent decades.

RESEARCH APPROACH

To determine the extent of pre-dispersal cone and seed herbivory, cones from reproductive black and white spruce were collected during 2018 and 2019 at 10 different treeline sites across Canada. Working with a team of collaborators from Memorial University, Queen's University, University of Saskatchewan, and Université de Sherbrooke, data were collected from the Yukon (n = 4), Northwest Territories (n = 2), Manitoba (n = 1), Québec (n = 1), Nunatsiavut (n = 1), and the island of Newfoundland (n = 1). Treeline form varied between sites and included diffuse (i.e., gradual reduction in tree density up slope), abrupt (i.e., clear line of high tree density to tundra vegetation), and tree circle (i.e., patchy dense tree areas dispersed across landscape) types (sensu Harsch and Bader, 2011). Cones from individual trees were stored in separate paper bags and visually inspected for any sign of insect damage such as frass or exit holes created by cone borrowing insects. I was specifically interested in cone herbivory from species such as *Megastigmus* spp. and *Cecidomyiidae* spp., as cone

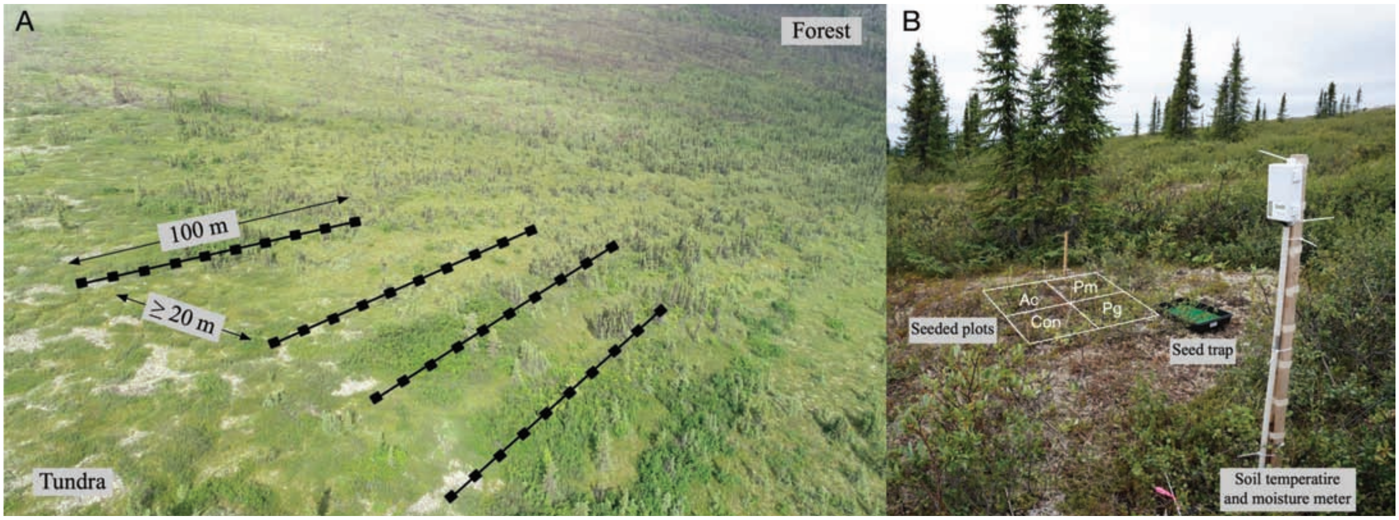

FIG. 2. Aerial photograph of my PhD research paired site design (A). Four 100 m transects running parallel with the treeline ecotone. Distance between transects is a minimum of 20 m. Black boxes located every 10 m represent randomized seeded plots (B) of black spruce (Picea mariana—Pm), white spruce (Picea glauca—Pg), green alder (Alnus viridis crispa—Ac), and a control plot (Con). Measurements of soil moisture, soil temperature, and natural seed dispersal (green garden tray) were recorded at each seeded plot.

damage is easily identifiable, and the destructive insect species could be found across northern latitudes. Seeds were extracted from cones and counted to establish average number of seeds per cone. A proportion of these seeds were then visually inspected for seed herbivory and physical damage (e.g., holes, cracks) and put through germination trials to assess seed viability.

Additional measurements were taken at each site to provide context for the pre-dispersal insect herbivory. Understory vegetation composition (percent cover) and tree stand density (number of stems per plot) were measured along a 75 m belt transect to determine whether any significant relationships with vegetation composition were evident. Cone herbivory and seed viability were also related to vegetation cover classes within a 500 m buffer around the transect using the 30 m land cover classification data derived from the North American Landcover Dataset (CEC, 2017). While I expected to find increased levels of herbivory at more dense treelines, preliminary results suggest a negative relationship between stand density and cone herbivory. This pattern suggests that treelines with fewer trees (i.e., diffuse treelines) may exhibit increased pressures of cone herbivory, potentially because there are fewer cones to be predated upon (e.g., less food). This preliminary finding provides some evidence of differential pressures of seed herbivory depending on the current plant community composition; however, further data analysis is required to examine the effects of interannual variability of herbivory.

My second objective was to identify how fires affect biotic and abiotic conditions across treeline ecotones. Despite there being a strong understanding of how fire alters site conditions within the boreal forest (Johnstone et al., 2004; Jayen et al., 2006), there is limited understanding of how a treeline ecotone may change after experiencing a wildfire. One difference I expected to observe is for treelines to have lower fire severity (i.e., biomass consumption) than continuous boreal forest stands, as there is less fuel to consume at the treeline. Lower severity fires result in charring rather than more substantial organic layer consumption, which is not ideal for seedling germination (Johnstone et al., 2004). High germination rates are much more likely to happen on soils when the organic layer has been completely combusted down to the mineral soils (Charron and Greene, 2002). Nevertheless, I anticipated that fire at the treeline would alter biotic and abiotic conditions enough to make the environment more suitable for tree seed germination when compared to conditions at an unburned treeline.

I established a natural field experiment to assess the impact of fire on treeline floral composition at three treeline ecotones in northern Yukon. These fires were heterogeneous in their consumptive path across the treeline, allowing for the direct comparison of burned and unburned treelines in close proximity (≤ 10 km in distance), henceforth referred to as treatments, either burned and unburned within a site. Two sites were located near Eagle Plains, Yukon, and burned in 2017 (65.80˚ N, −137.77˚ W) and 2007 (66.46˚ N, −136.59˚ W), respectively. The third site was located west of Dawson, Yukon, and burned in 2005 (64.21˚ N, −140.87˚ W). Within each treatment, I established four 100 m × 10 m transects running parallel with the treeline ecotone (Fig. 2A). In an attempt to disentangle climate from site-level conditions, measurements of maximum active layer depth, organic layer depth, soil temperature, soil moisture, soil pH, soil nitrogen, vegetation functional group percent cover, and natural seed dispersal were recorded every 10 m along each transect within each treatment

(Fig. 2B). In addition, daily measurements of soil moisture, soil temperature, near-surface air temperature (growing degree days), plant phenology (fall senescence and spring green-up), snow depth, and snow duration were recorded to establish any seasonal differences between treatments.

Using the data described above, my final objective was to determine whether post-fire treeline conditions promote boreal forest range expansion. As previously stated, seed limitation represents one of the largest and most effective bottlenecks to range expansion (Greene et al., 1999); therefore, using burned and unburned treelines in a paired manipulative seeding experiment, I examined which variables, if any, explain seedling establishment when seed limitation is removed as a constraining factor (Fig. 3). I anticipated that germination would be significantly different between treatments, with burned treelines predicted to have higher rates of germination as a result of post-fire increases in soil moisture, temperature, nutrient availability, and decreased substrate competition. During the summers of 2018 and 2019, I added 100 black spruce and white spruce seeds to separate 0.5 m × 0.5 m plots every 10 m along established transects within each treatment. Green alder was also added in a separate plot along each transect, because alder represents a primary colonizer, often in advance of tree species. Additionally, shrub expansion across altitudinal and latitudinal treeline ecotones has been documented across the circumpolar North regardless of disturbance (Myers-Smith et al., 2011).

Interestingly, after two years of seeding, there has been extremely limited, almost negligible, emergence across all experimental plots. There is also very little natural seedling regeneration, even at sites that burned more than 10 years ago, which is unexpected based on regeneration rates 10 years post-fire in neighbouring Alaska (Johnstone et al., 2004). While these findings are still preliminary, I hypothesize that in these model systems, fire did not create suitable conditions for boreal tree establishment. While germination from seeds of both tree and shrub species did not occur, increases in grasses and vegetative regrowth were evident at each burn treatment when compared to the unburned treeline. This finding, in conjunction with our understanding of seed herbivory at treeline, suggests that a tree range retraction at diffuse black spruce-dominated treelines may be occurring, while shrubs and grasses are becoming more expansive in their range (Brown and Johnstone, 2012; Aubin et al., 2018; Stevens-Rumann et al., 2018). This research is still ongoing; thus, further data analysis is required to determine the significance of these general conclusions.

FIG. 3. Photograph of Lucas Brehaut at a seeded plot in his 2017 burned treeline ecotone. Lucas is inserting a UniBest Nutrient Capsule (UniBest Company, Walla Walla, Washington, USA) at a soil depth of 5 cm to record annual inorganic soil nitrogen levels (Photo credit: Dr. Carissa Brown).

SIGNIFICANCE

Predicting consequences of and finding adaptations to climate change are two very important priorities across the North. As longer growing seasons facilitate greater insect herbivory pressures and record-breaking wildfire years continue across Canada, there is a general understanding that increases in disturbance frequency, severity, and extent will result in major changes to northern ecosystems. My PhD research represents an important step in understanding some of those changes in an ecologically sensitive area, where one major biome transitions into another. Whether pre-dispersal insect herbivory or fire facilitates an advance or recession in the treeline, any change to the successional trajectory of the ecotone will have notable consequences at both local and global scales. Less productive forest and treelines may allow for the establishment of alternate species (Turner et al., 1999), while a darker, lower albedo landscape after fire would make conditions drier, creating further moisture stress for vegetation (Chambers et al., 2005). Permafrost has a strong relationship with the above vegetation, which if altered, may result in increased permafrost thaw and a loss of carbon storage (Mack et al., 2011; Jones et al., 2015). Each of these ecosystem changes can further exacerbate the effects of climate change.

Changes to the vegetation across the treeline ecotone may also have implications for current and future conservation efforts aimed at identifying habitat for northern species. Much of northern Yukon is identified as important habitat for woodland and barren-ground caribou that are of ecological and socioeconomic importance to the region (Mallory and Boyce, 2018). Any persistent change to these landscapes may have prominent impacts on migratory routes and overwintering grounds. My research explicitly tests what biotic and abiotic conditions facilitate changes to the treeline ecotone, ultimately providing key contributions to management and conservation efforts through more accurate predictions of northern ecosystem change.

ACKNOWLEDGEMENTS

I am honoured to be the recipient of the Arctic Institute of North America's 2019 Jennifer Robinson Memorial Scholarship. I would like to thank the Tr'ondëk Hwëch'in and Vuntut Gwitchin First Nations for allowing me to complete my PhD research on their traditional lands. Additional funding and logistical support for this research was provided from NSERC (PGS-D to L. Brehaut and Discovery Grant to C. Brown); the Association of Canadian Universities for Northern Studies (Canadian Northern Studies Trust); the W. Garfield Weston Foundation Fellowship Program, a program of the Wildlife Conservation Society Canada funded by the W. Garfield Weston Foundation; Polar Knowledge Canada (Northern Scientific Training Program); Memorial University (Dr. Ian Brookes Graduate Award in Geography and the Dr. Joyce MacPherson Scholarship); the Royal Canadian Geographic Society; Yukon Energy Mines and Resources (Forestry Division); and Natural Resources Canada (National Tree Seed Center). This research was conducted under Vuntut Gwitchin Research Agreement and Yukon Scientists and Explorers Permits No. 17-36S&E, 18-30S&E, and 19-11S&E.

I am very fortunate to have Dr. Carissa Brown as my mentor and PhD supervisor. She has provided unwavering support and guidance throughout my degree. I also get to work with an incredible team of researchers, many of whom have supported me in the field and laboratory. Thank you to Daniel Brehaut, Anna Crofts, Dr. Ryan Danby, Frédéric Dwyer-Samuel, Piers Evans, Mike Grant, Katie Goodwin, Meghan Hamp, Emily Ko, Dr. Steven Mamet, Lauren Rees, Kirsten Reid, Gabby Riefesel, Brian Ronayne, Jennifer Sullivan, Leah Walker, and Yifeng Wang.

REFERENCES

Aubin, I., Boisvert-Marsh, L., Kebli, H., McKenney, D., Pedlar, J., Lawrence, K., Hogg, E.H., Boulanger, Y., Gauthier, S., and Ste-Marie, C. 2018. Tree vulnerability to climate change: Improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere 9(2): article e02108. https://doi.org/10.1002/ecs2.2108

Brown, C.D., and Johnstone, J.F. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. Forest Ecology and Management 266:34–41. https://doi.org/10.1016/j.foreco.2011.11.006

Brown, C.D., and Vellend, M. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B 281: 20141779. https://doi.org/10.1098/rspb.2014.1779

Brown, C.D., Dufour-Tremblay, G., Jameson, R.G., Mamet, S.D., Trant, A.J., Walker, X.J., Boudreau, S., et al. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography 42(1):137–147. https://doi.org/10.1111/ecog.03733

Brown, J.H., Stevens, G.C., and Kaufman, D.M. 1996. The geographic range: Size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., and Johnstone, J.F. 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience 63(11):866–876. https://doi.org/10.1525/bio.2013.63.11.5

Cairns, D.M., and Moen, J. 2004. Herbivory influences tree lines. Journal of Ecology 92(6):1019–1024. https://doi.org/10.1111/j.1365-2745.2004.00945.x

CEC (Commission for Environmental Cooperation). 2017. 2010 land cover of North America at 30 meters: Canada – TIFF file. Montreal, Québec: CEC. http://www.cec.org/tools-and-resources/map-files/land-cover-2010-landsat-30m

Chambers, S.D., Beringer, J., Randerson, J.T., and Chapin, F.S., III. 2005. Fire effects on net radiation and energy partitioning: Contrasting responses of tundra and boreal forest ecosystems. Journal of Geophysical Research 110, D09106. https://doi.org/10.1029/2004JD005299

Charron, I., and Greene, D.F. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research 32(9):1607–1615. https://doi.org/10.1139/X02-085

Danby, R.K., and Hik, D.S. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. Journal of Ecology 95(2):352–363. https://doi.org/10.1111/j.1365-2745.2006.01200.x

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29(6):824–839. https://doi.org/10.1139/x98-112

Harsch, M.A., and Bader, M.Y. 2011. Treeline form—a potential key to understanding treeline dynamics. Global Ecology and Biogeography 20(4):582–596. https://doi.org/10.1111/j.1466-8238.2010.00622.x

Harsch, M.A., Hulme, P.E., McGlone, M.S., and Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12(10):1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hu, F.S., Higuera, P.E., Duffy, P., Chipman, M.L., Rocha, A.V., Young, A.M., Kelly, R., and Dietze, M.C. 2015. Arctic tundra fires: Natural variability and responses to climate change. Frontiers in Ecology and the Environment 13(7):369–377. https://doi.org/10.1890/150063

Jameson, R.G., Trant, A.J., and Hermanutz, L. 2015. Insects can limit seed productivity at the treeline. Canadian Journal of Forest Research 45(3):286–296. https://doi.org/10.1139/cjfr-2014-0385

Jayen, K., Leduc, A., and Bergeron, Y. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. Écoscience 13(2):143–151. https://doi.org/10.2980/i1195-6860-13-2-143.1

Johnstone, J.F., and Chapin, F.S., III. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9(1):14–31. http://link.springer.com/10.1007/s10021-004-0042-x

Johnstone, J.F., Chapin, F.S., III, Foote, J., Kemmett, S., Price, K., and Viereck, L. 2004. Decadal observations of tree regeneration following fire in boreal forests. Canadian Journal of Forest Research 34(2):267–273. https://doi.org/10.1139/x03-183

Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S., III, and Mack, M.C. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16(4):1281–1295. https://doi.org/10.1111/j.1365-2486.2009.02051.x

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., et al., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14(7):369–378. https://doi.org/10.1002/fee.1311

Jones, B.M., Grosse, G., Arp, C.D., Miller, E., Liu, L., Hayes, D.J., and Larsen, C.F. 2015. Recent Arctic tundra fire initiates widespread thermokarst development. Scientific Reports 5: Article 15865. https://doi.org/10.1038/srep15865

Kambo, D., and Danby, R.K. 2017. Constraints on treeline advance in a warming climate: A test of the reproduction limitation hypothesis. Journal of Plant Ecology 11(3):411–422. https://doi.org/10.1093/jpe/rtx009

Kasischke, E.S., Verbyla, D.L., Rupp, T.S., McGuire, A.D., Murphy, K.A., Jandt, R., Barnes, J.L., et al. 2010. Alaska's changing fire regime—Implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40(7):1313–1324. https://doi.org/10.1139/X10-098

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115(4):445–459. https://doi.org/10.1007/s004420050540

Mack, M.C., Bret-Harte, M.S., Hollingsworth, T.N., Jandt, R.R., Schuur, E.A.G., Shaver, G.R., and Verbyla, D.L. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. Nature 475:489–492. https://doi.org/10.1038/nature10283

Mallory, C.D., and Boyce, M.S. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews 26(1):13–25. https://doi.org/10.1139/er-2017-0032

Munier, A., Hermanutz, L., Jacobs, J.D., and Lewis, K. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: Implications for treeline advance with climate warming. Plant Ecology 210(1):19–30. https://doi.org/10.1007/s11258-010-9724-y

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., et al. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. Environmental Research Letters 6(4): 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Payette, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. Ecology 88(3):770–780. https://doi.org/10.1890/06-0265

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P., and Veblen, T.T. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21(2):243–252. https://doi.org/10.1111/ele.12889

Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91(10):2833–2849. https://doi.org/10.1890/10-0097.1

Turner, M.G., Romme, W.H., and Gardner, R.H. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9(1):21–36. https://doi.org/10.1071/WF99003

Viglas, J.N., Brown, C.D., and Johnstone, J.F. 2013. Age and size effects on seed productivity of northern black spruce. Canadian Journal of Forest Research 43(6):534–543. https://doi.org/10.1139/cjfr-2013-0022

Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28(11):705–710. https://doi.org/10.2307/1307321

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