

Pre-fire forest type drives long-term changes in understory plant communities post-fire, Taiga Shield, Northwest Territories

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Executive Summary

This report summarises information about post-fire changes in understory plant species composition in relation to environmental variables and burn severity, following fires in 1996 and 1998 on the Taiga Shield in the Northwest Territories (NWT). In 1998 and 1999 ten, 55 m transects permanently-marked transects were established, six at Tibbitt Lake and four at Gordon Lake. Transects were established in different forest types, soil types, and burn severities, as measured by the composite burn index (CBI). On each transect, a 5 m by 1 m plot was established every 5 m, for a total of six plots per transect for the purpose of recording understory plants and lichens. Abundances of vascular plant species and non-vascular functional types, including lichens, were recorded annually for up to 12 years post-fire. Bare ground cover, rock cover, woody debris, burnt bare ground cover, and canopy openness were also recorded. We used this unique and fine-temporal scale dataset to ask the following questions: (1) Do areas in higher severity burns lead to different and sustained shifts in composition, or are other environmental variables more important for determining post-fire plant community composition?; (2) How do understory plant communities change over fine temporal scales and are there predictable shifts in composition over time?

Pre-fire forest type, and associated variables, was the most important factor explaining post-fire understory plant communities. Specifically, pre-fire forest type, soil type, rock cover, woody debris cover, and canopy openness were significantly correlated with plant species composition. Species composition was not related to either burn severity or time since fire. Changes in composition over time for up to 12 years post-fire were minimal and difficult to detect. Together, the importance of pre-fire forest type and lack of effect of CBI on species composition demonstrates high resilience of the understory plants to fire and the ability of understory plant communities to recover over a range of burn severities. These results suggest that forests in the NWT may not respond to fire in the same way as other areas of boreal forests in Northwestern North America. Recommendations are made on how forest monitoring in the NWT can be effective and targeted, based on the results from this high quality and long-term dataset.

Keywords

Plant species composition; Plant community dynamics; Boreal wildfire; Tibbitt Lake; Gordon Lake; Succession; Forests

Introduction

Boreal forest ecosystems are well-adapted and resilient to wildfires, evidenced by forests recovering to pre-fire species composition over time (Dyrness et al., 1986). However, extreme plant mortality and alterations to the environment may lead to shifts in composition in the early years after a fire, particularly in areas of high burn severity. For example, in Alaska, severe fires have been shown to result in removal of the entire organic layer, exposing mineral soil and leading to successional shifts towards deciduous-dominated forests (Beck et al., 2011; Kelly et al. 2013). This is largely due to enhanced competitive ability of deciduous species on exposed mineral soils (Johnstone et al., 2004, 2010). How understory plant communities assemble in the years post-fire is less clear, particularly at fine temporal scales (i.e., frequent, short-term time intervals between measurements; Hart and Chen, 2006). Most studies investigating changes in plant communities use a chronosequence approach, which involves measuring areas that have burned at different times based on historical records (e.g., Thomas and Kiliaan, 1998). While useful, these methods can only provide relatively coarse information about changes in species composition. This approach cannot provide information about the dynamics of early colonisation and species turnover within the communities, or the importance of previous composition in determining future changes in composition. Establishing permanent monitoring sites immediately post-fire and repeatedly measuring is a preferred way to truly understand the temporal dynamics of forest plant community assembly post-fire.

Fire severity has been shown to be a key driver of post-fire plant community composition in the understory in Alaska (Hollingsworth et al., 2013) and Québec (Purdon et al., 2004). This is due to reduced regeneration of species that rely on belowground tissues to grow post-fire in severely burned areas and a shift towards species regenerating from seed (Ryan, 2002; Mack et al., 2008; Hollingsworth et al., 2013). However, a study at the treeline in the Taiga Plains ecozone (Ecosystem Classification Group, 2009) in the Northwest Territories (NWT), found that fire had little impact on understory species composition (Black and Bliss, 1978), suggesting that this landscape may respond differently to fires. In addition, a large-scale study on the wintering grounds of the Beverly caribou herd in the Taiga Shield ecozone, south-eastern NWT (Ecosystem Classification Group 2008), also noted that total low-shrub biomass was unrelated to time since fire (Thomas and Kiliaan, 1998). They suggested that factors other than fire may be more important at determining shrub community composition and abundance. This previous work indicates that NWT forests may respond differently to fires than those in other areas of boreal forests in Northwestern North America. Microsite characteristics and factors that are little impacted by fires, such as soil type and moisture availability, may be more important drivers of

post-fire plant community assembly in the NWT. However, because these studies were based on chronosequences and did not encompass burn severity metrics to assess its relative importance. There is currently little information about post-fire plant community dynamics over the long term in the NWT, particularly in areas experiencing different burn severities, and relying on studies from other areas may not represent what will happen in the NWT or other understudied parts of the boreal.

The aim of the current study was to describe the first 11-12 years of post-fire understory plant community dynamics in the NWT at fine temporal scales. We used data collected from permanent vegetation plots that were established zero to three years post-fire in different forest types in the Taiga Shield (Ecosystem Classification Group 2008). These plots were re-measured annually for up to 12 years post-fire, providing a unique and high quality dataset to accurately investigate plant community dynamics during the first decade following fire. It is rare to gain information on vegetation regeneration at this fine temporal scale, particularly in relatively remote, high latitude systems. The Tibbitt Lake Fire was extensive (>100,000 ha) and created a mosaic of areas from intensely burned to unburned remnants of vegetation. We used these data to investigate the following questions: (1) Do areas in higher severity burns lead to different and sustained shifts in composition, as observed in Alaska, or are other environmental variables more important for determining post-fire plant community composition? Our hypothesis was that fire severity would be an important driver of understory plant community composition, based on previous work in Northwestern North America that has encompassed areas of different burn severity when assessing regeneration (e.g., Hollingsworth et al. 2013). However, underlying soil type or pre-fire vegetation may be more important determinants of post-fire vegetation in this region; (2) How do the understory plant communities change over the first 11-12 years after fire and are there predictable shifts in composition over time? We hypothesised that there would be detectable changes in plant species composition over time, because this is an important period for species sorting during the community assembly process. For example, different species may have different abundances depending on time since fire or as canopies close and shade-tolerant plants become more abundant by out-competing those that have higher light requirements.

Methods

Transect design

Plots were established in 1998 and 1999 across forest types on the Taiga Shield. Three transects were established near the northern end of a 1998 burn at the Gordon Lake study area (63.08°N, 113.15°W). An additional transect was established across Gordon Lake in a 1996 burn. Six transects were established near the southern end of the 1998 burn at the Tibbitt Lake study area (62.55°N, 113.34°W). Transects were established in different pre-fire forest types from zero to three years post-fire (Table 1; Fig. 1). Transects were categorised by pre-fire forest type (spruce, pine, or mixed) and underlying soil type (clay, muskeg, rock, or sand). Each transect was 55 m

long, with a 25 m² plot every 5 m (6 plots per transect; Fig. 1). Plots along transects were laid from unburned or low severity burned towards greater burn severity. Within each plot, a strip of five contiguous 1 m² patches were established specifically to measure vegetation, including understory species. Patches within each plot were measured annually until 2008, providing information for up to 12 years post-fire for a total of 624 data points (number of plots × number of years measured; Table S1). Other aspects of post-fire changes in forests were assessed in other areas of the plot and will be subjects of future reports.

TRANSECT design

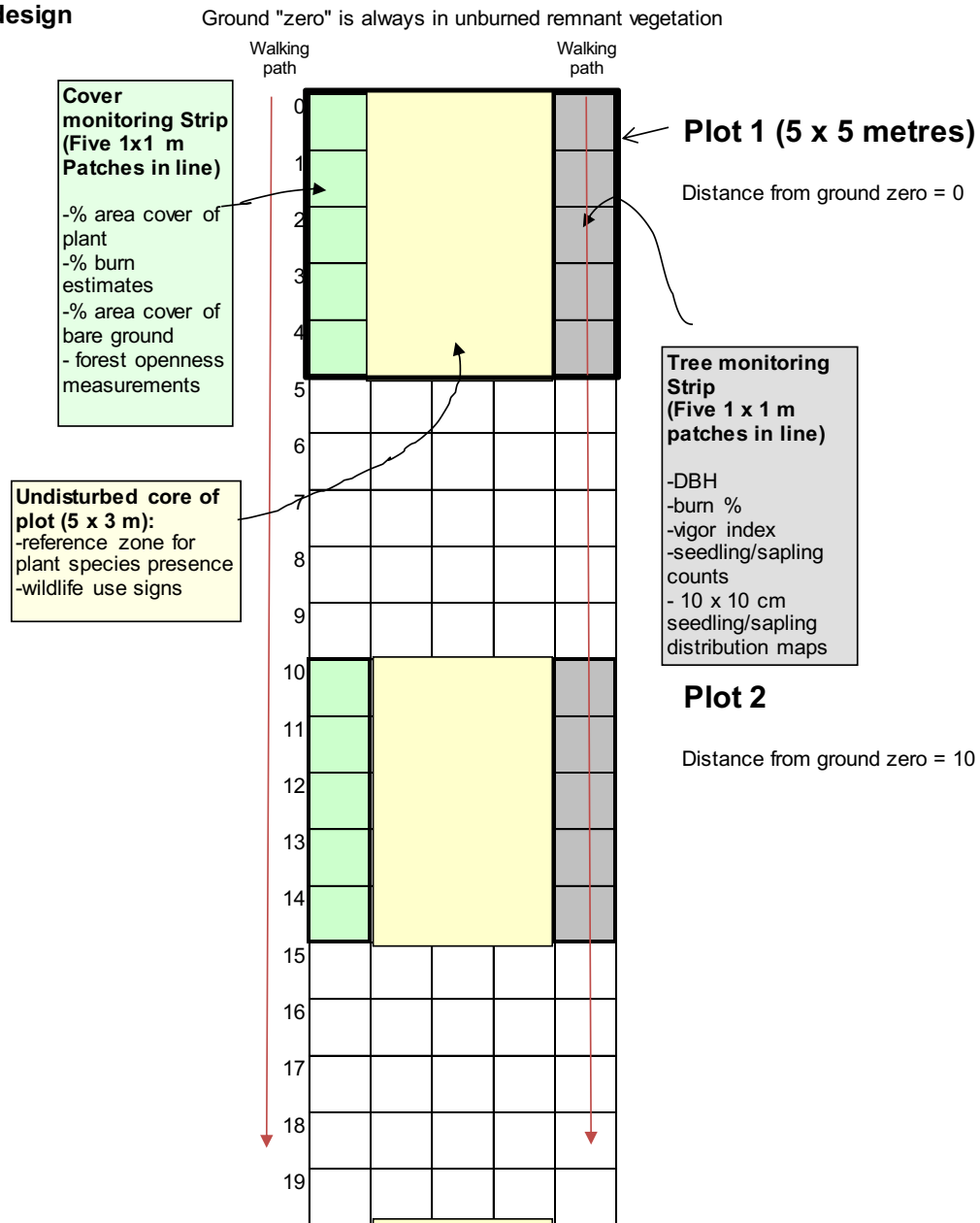


Fig. 1: Transect design, showing the first two of a total of six plots (5 x 5 m²) established from unburned forest remnant to burned area. Strips were used to measure different aspects of the same plot. Each strip is composed of five 1 m² patches adjacent and in line. The cover monitoring strips that are the focus of this report are represented in green. Other aspects of this study will be presented in future reports. To minimise disturbance to ground cover during annual visits, walking paths were strictly restricted.

Vegetation monitoring

In each cover monitoring 1 m² patch within each plot (Fig. 1), the percent cover of each vascular plant species and non-vascular functional types was recorded. Lichens were categorised only as caribou lichens or non-caribou lichens (Table S2). Percent cover and species identities were recorded by Dr. Suzanne Carrière each year to reduce observer bias. Patches were also measured at the same time of year: July to early September, ensuring consistency in plant biomass and cover estimates between plots within years. Percent covers of woody debris, bare rock, bare ground, and burned bare ground were also measured.

Other variables

Composite burn index (CBI) was assessed at each plot using data measured at the time of establishment. This is a standardised method allowing comparison of burn severity between sites, and assesses burn severity of ground substrates, understory, and overstory components (Key and Benson 2006). Canopy openness, as a percentage, was measured at each patch at each time using a spherical crown densitometer (Lemon 1956). Although canopy openness was measured most times, there are 115 instances of the 624 data points where it was not measured: canopy openness was not measured in 1998 and 1999, on 19 plots in 2002, 8 plots in 2005, two plots in 2003, and one plot in each of 2000, 2006, 2007, and 2008 (Table S3). Therefore, the importance of this variable could only be assessed at the times that it was recorded (see Statistical Analyses section).

Statistical Analyses

All analyses were performed in the open source statistical software program R, version 3.2.2, with packages where specified (R Core Development Team, 2015). The abundance of each plant species in each plot in each year was calculated by summing the number of patches it was in per plot (abundance range = 0 to 5). Large trees (taller than 2 m) were excluded from these analyses because our focus was on changes in understory vegetation. Dead plants were also excluded.

An ordination was used to visualise species composition in each plot at each time. This compresses multi-dimensional species data into fewer dimensions to allow relationships and temporal changes in species composition to be visualised graphically. Points that are closer together on the graph are more similar in species composition. Principal co-ordinates analysis (PCoA) ordination was calculated in six dimensions, specifying the square-root of the Bray-Curtis distance (Legendre and Legendre, 2012) and calculated using function “vegdist” in vegan

version 2.3-2 (Oksanen et al., 2015) and the PCoA was run using function “cmdscale” in base R. Correlations between species composition and environmental variables were assessed using function “envfit” in the vegan package, with 999 permutations to assess the significance of the correlations (Oksanen et al., 2015). The following variables were used: CBI, pre-fire forest type, soil texture, number of years post-fire, abundance of bare ground cover, burned bare ground cover, rock cover, and woody debris covers (N=623, referred to as the full dataset). This was re-run with a subset of the dataset where only the plots that had values for canopy openness to assess the significance of this variable (N=508, referred to as the restricted dataset). Correlations of species composition with the variables were visualised on the ordination diagram. Tibbitt transect 2, plot 6 contained no species in 1998, so it had to be eliminated it from all analyses (ordination scores cannot be calculated with zero values).

Table 1: Number of transects, showing year of establishment and distribution across pre-fire forest types.

Site	Year of fire	Year monitoring established	Pre-fire forest type			Number of transects	Number of plots
			Pine	Spruce	Mixed		
Tibbitt Lake	1998	1998	2	2	0	4	24
	1998	1999	1	1	0	2	12
Gordon Lake	1996	1999	0	1	0	1	6
	1998	1999	1	1	1	3	18
Total						6	60

Results

CBI in all plots ranged from 0 to 3 (mean 1.74 ± 0.15 ; Fig. 2). A species accumulation curve showed that most species established within the first 1-4 years in each forest type (Fig. 3). A total of 81 understory plant species were recorded across the sampling period (Table S2). The PCoA explained 44.19% of the variation in the understory species composition (Fig. 4). The first two axes explained 23.50% of the variation (axis 1: 14.49%; axis 2: 9.02%).

Pre-fire forest type, soil type, rock cover, and woody debris cover were all significantly correlated with species composition (Table 2). Under the restricted dataset, bare ground cover and canopy openness were also significantly correlated with species composition. Spruce forest had a more open canopy and greater rock cover (Figs. 4 and 6). Pine forest had greater abundance of woody debris and bare ground cover (Figs. 4 and 6). Both caribou and non-caribou lichens were more associated with bare ground and pine forest (Figs. 5 and 6). *Saxifraga* sp. and *Arctostaphylos uva-ursi* were also associated with pine forest, while spruce forest was more associated with *Salix* sp., *Sphagnum* sp., all the *Equisetum* species and *Ledum* species (Fig. 6).

Neither CBI nor the number of years post-fire were significantly correlated with plant community composition. The relatively few changes in composition within plots over time were accentuated by overlaying temporal changes in composition on to the ordination (Fig. 7). Trajectories following composition of each plot over time show that each plot moved very little in ordination space, indicating that there were few substantial changes in composition within each plot over time (Fig. 7).

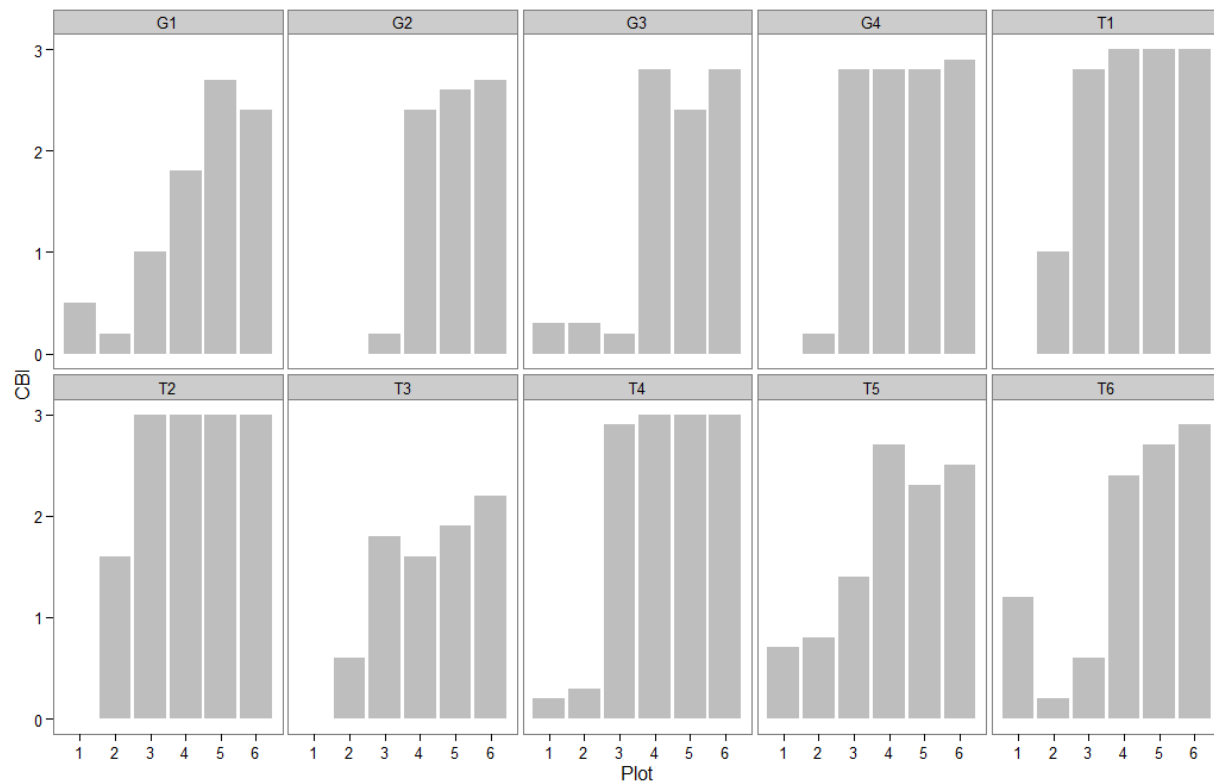


Fig 2: CBI for each plot on each transect. G=Gordon, T=Tibbitt. A low CBI indicates a low severity burn. Plots along transects were laid from unburned or low severity burned towards greater burn severity (Fig. 1). A value of zero indicates completely unburned.

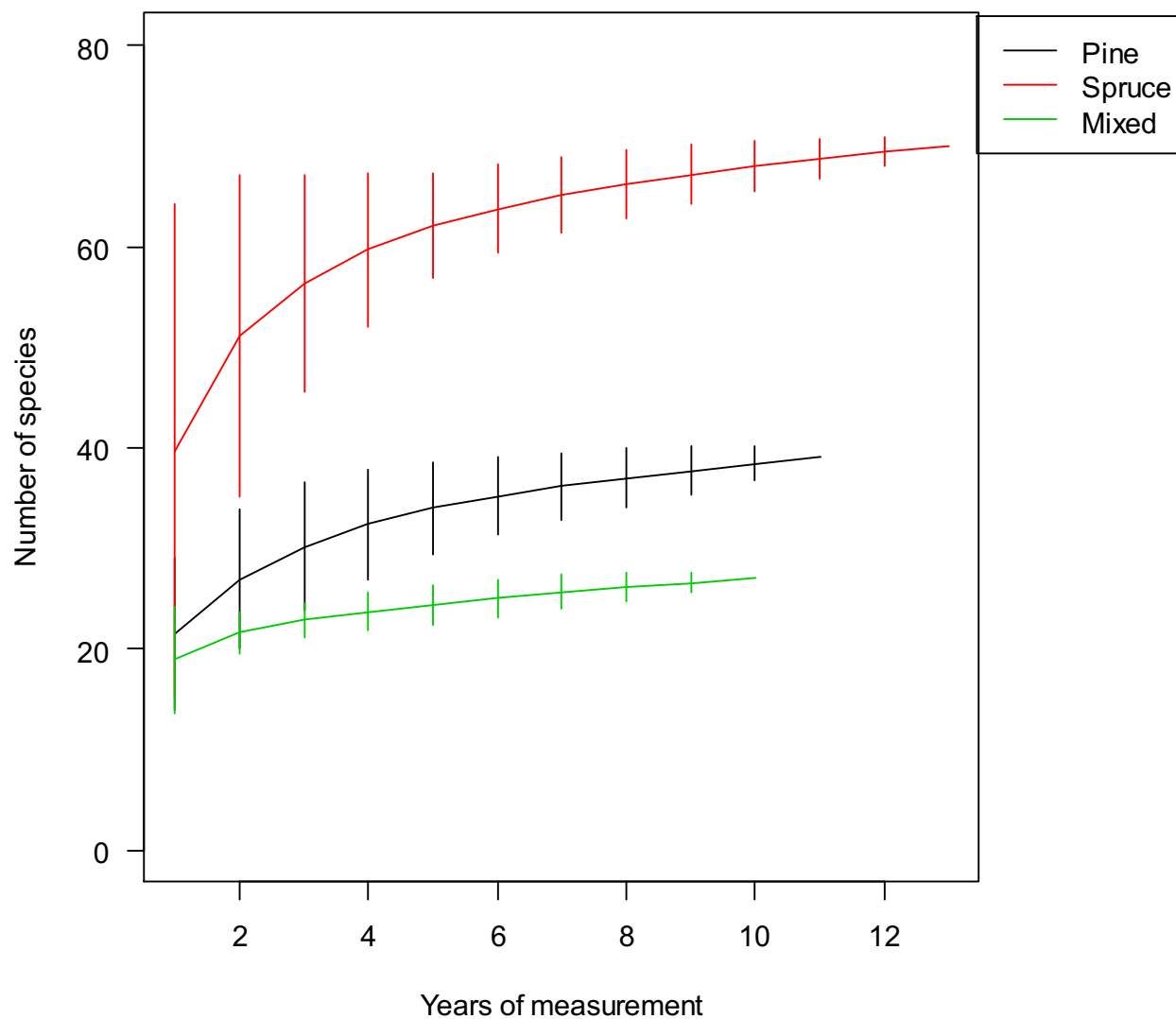


Fig. 3: Species accumulation curve over time for each pre-fire forest type, showing means and standard deviations based on 1000 permutations. Most species established within the first 1-4 years of measurement in each forest type. The flattening out of each curve indicates that adequate sampling was done to capture all species present in each forest type.

Table 2: Correlations between environmental variables and understory plant species composition. R^2 is the squared correlation coefficient. Statistically significant variables are those that explain significant amounts of variation in species composition: pre-fire forest type, soil type, rock ground cover, woody debris, bare ground cover, and canopy openness. *** indicates P -value <0.001 ; ** indicates P -value <0.01 ; * indicates P -value <0.05 , based on 999 permutations.

Variable	R^2	
	Without canopy openness (N=623)	With canopy openness (N=508)
Bare ground cover	0.003	0.017*
Rock cover	0.035***	0.032**
Woody debris	0.028***	0.029**
Burned bare ground cover	0.002	0.001
Number of years post-fire	0.001	0.004
CBI	0.005	0.006
Pre-fire forest type	0.027***	0.025***
Soil type	0.031***	0.028***
Canopy openness (%)	NA	0.020**

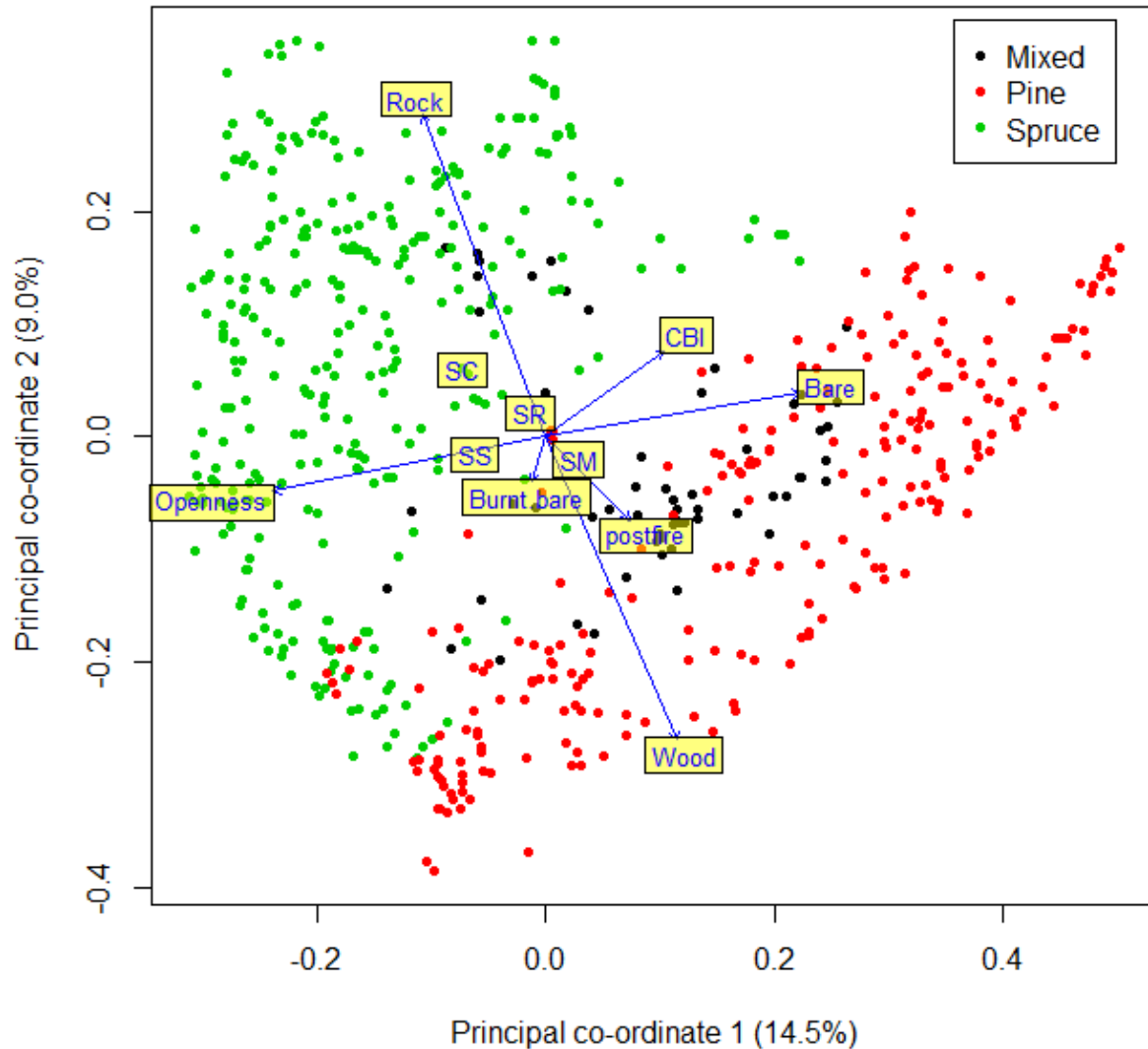


Fig. 4: Site scores for principal co-ordinates analysis (PCoA) ordination, with environmental variables overlaid for 508 data points, including canopy openness. Points that are close together are plots that are more similar in plant species composition than those further apart. Points are coloured according to pre-fire forest type; the clustering of points by pre-fire forest type indicates that this is an important variable determining species composition. Values in brackets on the axes represent the amount of variation in species composition explained by each axis. Long arrows for environmental variables indicate that these correlate with species composition; rock cover, woody debris, bare ground cover, and canopy openness were important variables, while CBI, time post-fire, and burnt bare ground cover were less important (Table 2). The labels for the environmental variables are: SC=soil clay; SM=soil muskeg; SR=soil rock; SS=soil sand; CBI=composite burn index; postfire=number of years post-fire; Bare=abundance of bare ground cover; Burnt.bare=abundance of burned bare ground cover; Rock=abundance of rock cover; Wood=abundance of woody debris cover; Openness = % canopy openness.

Fig. 5: Species scores for principal co-ordinates analysis (PCoA) ordination, with environmental variables overlaid for 508 data points, including canopy openness. Species points that were close together indicate those that are more likely to co-occur. Values in brackets on the axes represent the amount of variation in species composition explained by each axis. Abbreviations and explanations for environmental variables are the same as for Fig. 4. See Table S2 for full species names. Both caribou and non-caribou lichens were more abundant when there was high bare ground cover.

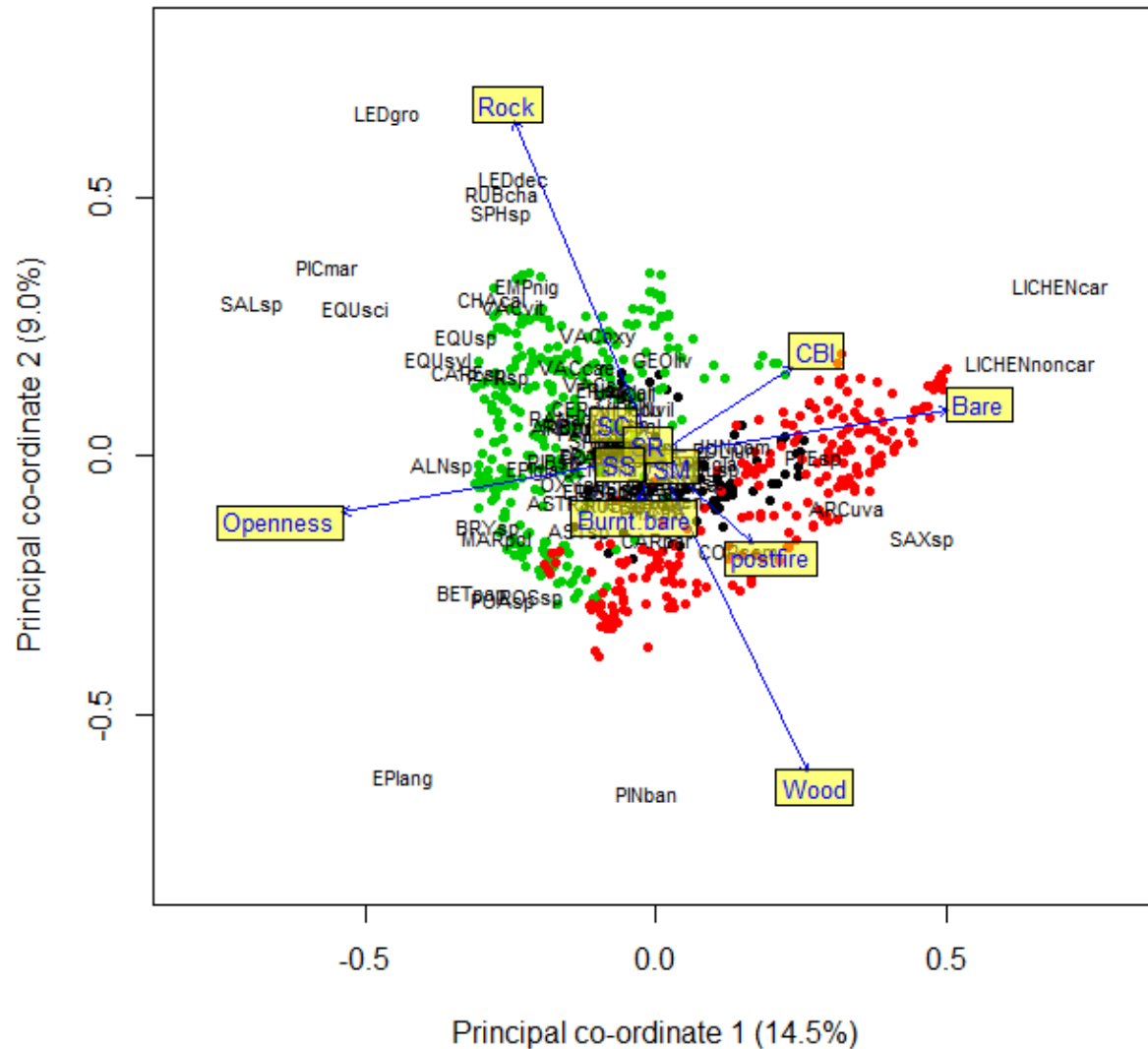


Fig. 6: Both site and species scores for principal co-ordinates analysis (PCoA) ordination, with environmental variables overlaid for 508 data points, including canopy openness. Points are coloured according to pre-fire forest type. Abbreviations for environmental variables are the same as for Fig. 4. See Table S2 for full species names. Both caribou and non-caribou lichens were more abundant when there was high bare ground cover and in pine forest.

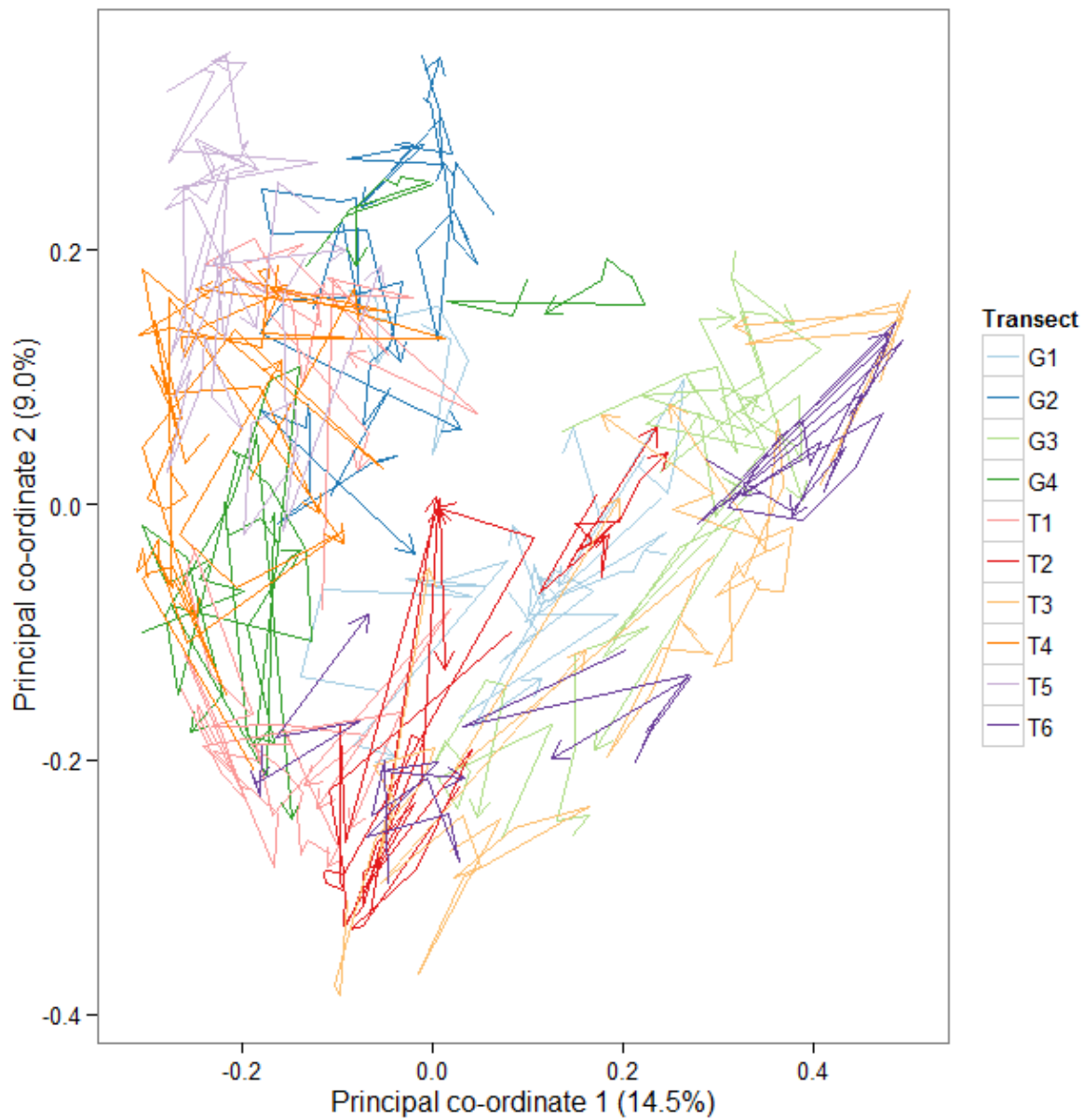


Fig. 7: Time overlaid on site scores from principal co-ordinates analysis (PCoA) ordination for all 623 data points, showing trajectories in plant species composition over time. Changes in species composition over time are shown by linking scores for each plot at each measurement with arrows. Plots are coloured according to site and transect: G=Gordon, T=Tibbitt. Individual plots did not move substantially in PCoA space, indicating that understory species composition did not change very much over time.

Discussion

Overall, we found that changes in post-fire understory species composition were related to environmental factors (Table 2). Specifically, pre-fire forest type, soil type, rock cover, woody debris, and canopy openness were significantly correlated with plant species composition over the for 11-12 years post-fire (Table 2). Changes in composition over time for up to 12 years post-fire were minimal and difficult to detect (Table 2; Fig. 7). In combination, the importance of pre-fire forest type and lack of effect of CBI shows that pre-fire vegetation was the most important factor determining post-fire species composition. This demonstrates high resilience of the understory plants to fire and the ability of understory plant communities to recover over a range of burn severities.

Pre-fire forest type was the most important environmental factor for understory species composition over the sampling period. This was correlated with soil type (Table S4), bare ground cover, and rock cover (Fig. S2). Pre-fire forest type is therefore probably related to other variables known to affect plant species composition, such as soil moisture and nutrient availability. For example, woody debris, which was more associated with pine forest, may provide a heterogeneous environment with microsites for understory plants and decaying wood as a substrate for some bryophytes (Hart and Chen, 2006). Canopy composition is thought to be a key driver of understory composition in post-fire boreal forests (Hart and Chen, 2006).

The lack of significant changes in species composition over time (Fig. 6) emphasises the importance of pre-fire forest type and vegetation for determining future species composition. Species that establish immediately post-fire are important for determining plant community structure for at least 12 years post-fire. The current work in the NWT supports the idea that there are particular periods after fires where there is high recruitment. For trees, the first 3-7 years post-fire are the most important times for recruitment in the Yukon and Alaska and mortality rates are generally low after this period (Johnstone et al., 2004). The few significant changes in species composition over time, and the establishment of most species within the first few years post-fire, are valuable results from a forest management perspective. These show that monitoring forests within the first 1-4 years after fire can provide critical information about how forests will recover over the longer term.

Results from this study support other work suggesting that light availability is an important determinant of understory plant communities in boreal forests (De Grandpré et al. 1993; Hart and Chen, 2006). Canopy openness was significantly correlated with understory species composition and spruce forests had more open canopies (Figs. 4 and 6). The increased light availability corresponded to increases in species such as *Alnus* sp., and non-vascular plants such as Bryophytes, and *Marchantia polymorpha* (Figs. 5 and 6). These non-vascular species are common in post-fire communities and are important for insulating the soil to mitigate permafrost thaw, which can negatively impact forest ecosystems and cause fragmentation (Nilsson and Wardle, 2005; Mack et al., 2008; Baltzer et al., 2014). These results indicate the importance of

abiotic factors for determining understory species composition in boreal regions, possibly by determining species interactions and competition (Marshall and Baltzer, 2015).

Lichen communities are considerably impacted by fire (e.g., Mack et al. 2008). We found that caribou and non-caribou lichens showed similar patterns to each other; they were more associated with pine forest and where bare ground was abundant (Figs. 5 and 6). This correlation between lichen functional types shows that their abundance and distributions may be driven by the same environmental variables. Because lichens were aggregated and not determined to genus or species level, it is difficult to know if there are distinctive species within these groups that were differentially influenced by the environmental factors. Black and Bliss (1978) described four stages of succession in lichens from a fire chronosequence near Inuvik. They estimated that the first stage of succession lasted 1-15 years post-fire.

It was surprising that burn severity had no effect on understory species composition, especially because the plots encompassed the full range of CBI measurements (Fig. 2; Table 2) and previous work in other regions has shown this is an important driver of change (Purdon et al., 2004; Mack et al., 2008; Hollingsworth et al., 2013). Similar to the present work, previous research in the NWT based on a fire chronosequence showed that vascular plants readily resprout after fire resulting in a resilient forest plant community (Black and Bliss 1978; Thomas and Kiliaan 1998). These results suggest that NWT may respond differently to fires compared to other boreal regions, pointing to the need for the NWT to use information from its own forests when making management decisions. The transects described in this report are in a relatively small area of the NWT landscape on the Taiga Shield, so it is possible that shifts in species composition could or have occurred in other regions of the NWT due to fire. In addition, changes in fire regimes towards more frequent fires (Kasischke and Turetsky, 2006) could affect this resilience of the understory community by repeatedly burning belowground structures and seedbanks, which could lead to mortality (Hollingsworth et al., 2013).

The CBI method for assessing burning has been criticised because it cannot give an accurate measure of the depth of burn or the amount of organic layer consumed (Key and Benson, 2006; Boby et al., 2010). Having a measure of the depth of burn can help explain regeneration patterns; the deeper the burn, the less likely belowground plant structures will be undamaged and able to regenerate. Boby et al. (2010) proposed a method to accurately measure depth of burn in the organic layer using adventitious roots on black spruce trees. These roots penetrate the bark above the root collar and grow into the organic layer. After fires, they are clearly visible and the height of the root from the organic layer surface can provide a quantitative estimate of how deep the organic layer was pre-fire (Boby et al., 2010). While this method was not available at the establishment of the present study, it should be considered in future monitoring. An effective method to measure depth of burn has yet to be developed for non-black spruce forests.

While it is possible that there may have been a relationship between burn severity and post-fire changes in understory vegetation if a different measure of burn severity was used, this is unlikely. Pre-forest type and its associated variables were clearly highly important at these sites

on the Taiga Shield. While this report focussed on understory plant species, tree species may have responded differently to fire severity and environmental variables. High severity fires can destroy seeds in the cones of conifer trees (aerial seedbanks) and reduce regeneration (Ryan, 2002), leading to dramatic and sustained changes in canopies post-fire compared to pre-fire (Johnstone et al., 2004). These dynamics will be investigated in further reports.

In conclusion, pre-fire forest type and associated environmental variables were the most important drivers of post-fire understory species composition. There was no evidence for areas experiencing different burn severity to change in species composition differently, or that this has led to successional shifts. In fact, most species that had established immediately post-fire were likely to remain in the community for at least 12 years post-fire, and there were few detectable changes in species composition over time.

Recommendations

The Gordon Lake study area is located in the Great Slave Lake Upland – low subarctic ecoregion and the Tibbitt Lake study area is location in the Great Slave Lake Lowland – high boreal ecoregion of the Taiga Shield in the NWT (Ecosystem Classification Group 2008). This dataset provides a snapshot of post-fire species composition dynamics in the entire range of soil types and moisture gradients in two ecoregions in the NWT (Ecosystem Classification Group 2008). The dataset is extremely valuable due to the fine temporal scale and long-term measurements for up to 12 years post-fire. Knowledge of these patterns in the NWT is indispensable for forest and wildlife managers, and ecologists. The following actions are recommended based on the present study from Tibbitt and Gordon Lakes fires:

- (1) The unique landscape of the NWT needs to be recognised, and using results from other boreal regions may not be applicable to the NWT. Therefore, establishment and maintenance of a network of permanent vegetation plots to assess impacts of fire on forest vegetation in the NWT is recommended. This network should encompass a range of environmental factors, including ecozones, forest types, and soil moisture gradients. Maintenance and management of the data is important to ensure high quality information is recorded and accessible.
- (2) Results from the present study suggest that annual re-measurements may not be necessary to understand post-fire changes in species composition because there were few changes over time. Therefore, measuring permanent plots one-to-three years post-fire and repeated re-measuring approximately every five years may provide enough information to detect potential shifts in forest species composition.
- (3) Metrics other than, or as well as, CBI should be used to accurately quantify measure burn severity. Metrics that include depth of burn, such as the measurement of adventitious roots proposed by Boby et al. (2010), are recommended.
- (4) Research into measurements of burn severity that apply to non-black spruce dominated forests would be valuable.

References

- Baltzer, J.L., Veness, T., Chasmer, L.E., Sniderhan, A.E., Quinton, W.L., 2014. Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. *Global Change Biology* 20, 824–834. doi:10.1111/gcb.12349
- Beck, P.S.A., Goetz, S.J., Mack, M.C., Alexander, H.D., Jin, Y., Randerson, J.T., Loranty, M.M., 2011. The impacts and implications of an intensifying fire regime on Alaskan boreal forest composition and albedo. *Global Change Biology* 17, 2853–2866. doi:10.1111/j.1365-2486.2011.02412.x
- Black, R.A., Bliss, L.C., 1978. Recovery sequence of *Picea mariana*-*Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Canadian Journal of Botany* 56, 2020–2030.
- Boby, L.A., Schuur, E.A., Mack, M.C., Verbyla, D., Johnstone, J.F., 2010. Quantifying fire severity, carbon, and nitrogen emissions in Alaska's boreal forest. *Ecological Applications* 20, 1633–1647.
- De Grandpré, L., Gagnon, D., Bergeron, Y., 1993. Changes in the understory of Canadian southern boreal forest after fire. *Journal of Vegetation Science* 4, 803–810.
- Dyrness, C.T., Viereck, L.A., Van Cleve, K., 1986. Fire in Taiga Communities of Interior Alaska, in: Van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function, Ecological Studies*. Springer-Verlag, New York, pp. 74–88.
- Ecosystem Classification Group. 2009. *Ecological Regions of the Northwest Territories – Taiga Plains*. Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NT, Canada. 173 p. Available at http://www.enr.gov.nt.ca/sites/default/files/reports/nwt_taiga_plains_enrdoc_full_report_ver9_revisions2009_2ndprintingerrata_corrected_april2013web.pdf
- Ecosystem Classification Group. 2008. *Ecological Regions of the Northwest Territories – Taiga Shield*. Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NT, Canada. 146 p. Available at http://www.enr.gov.nt.ca/sites/default/files/reports/nwt_taiga_shield_final_to_printererrata_corrected_april2013_webversion.pdf.
- Hart, S.A., Chen, H.Y.H., 2006. Understory vegetation dynamics of North American Boreal Forests. *Critical Reviews in Plant Sciences* 25, 381–397. doi:10.1080/07352680600819286
- Hollingsworth, T.N., Johnstone, J.F., Bernhardt, E.L., Chapin, F.S., 2013. Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. *PLoS ONE* 8, e56033. doi:10.1371/journal.pone.0056033
- Johnstone, J.F., Chapin, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V., Turetsky, M., 2010. Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research* 40, 1302–1312. doi:10.1139/X10-061
- Johnstone, J.F., Chapin III, F.S., Foote, J., Kemmett, S., Price, K., Viereck, L., 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research* 34, 267–273. doi:10.1139/x03-183
- Kasischke, E.S., Turetsky, M.R., 2006. Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters* 33, L09703. doi:10.1029/2006GL025677

- Kelly, R., Chipman, M. L., Higuera, P. E., Stefanova, I., Brubaker, L. B., Hu, F. S., 2013. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proceedings of the National Academy of Sciences of the United States of America* 10, 13055–13060.
- Key, C.H., Benson, N.C., 2006. Landscape assessment (LA). *FIREMON: Fire effects monitoring and inventory system*. Gen. Tech. Rep. RMRS-GTR-164-CD, Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Legendre, P., Legendre, L., 2012. *Numerical Ecology*, Third ed. Elsevier, Amsterdam.
- Lemon, P. E. 1956. A Spherical densiometer for estimating forest overstory density. *Forest Science* 2:314-320
- Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G., Vogel, J.G., Randerson, J.T., Chapin, F.S., 2008. Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems* 11, 209–225. doi:10.1007/s10021-007-9117-9
- Marshall, K. E., Baltzer, J. L., 2015. Decreased competitive interactions drive a reverse species richness latitudinal gradient in subarctic forests. *Ecology*, 96,461–470.
- Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* 3, 421–428.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. *vegan: Community Ecology Package*. R package version 2.3-2. <http://CRAN.R-project.org/package=vegan>.
- Purdon, M., Brais, S., Bergeron, Y., 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Applied Vegetation Science* 7, 49–60.
- R Core Development Team, 2015. *R: A language and environment for statistical computing v. 3.2.2*. R Foundation for Statistical Computing, Vienna.
- Ryan, K.C., 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* 36, 13–39.
- Thomas, D. C. and Kiliaan, H.P.L. 1998. Fire-caribou relationships: (IV) Recovery of habitat after fire on winter range of the Beverly herd. Tech, Rep. Series No. 312. Can. Wildl. Serc. Prairie and Northern Region. Edmonton, Canada. 115 p.

Table S1: Distributions of measurements across transects, showing when each transect was established and the total number of measurements they had since established.

Site	Transect number	Number of plots	Number of years measured	Total number of measurements (number of plots × number of years measured)
Tibbitt	1	6	11 (1998-2008)	66
	2	6	11 (1998-2008)	66*
	3	6	11 (1998-2008)	66
	4	6	11 (1998-2008)	66
	5	6	10 (1999-2008)	60
	6	6	10 (1999-2008)	60
Gordon	1	6	10 (1999-2008)	60
	2	6	10 (1999-2008)	60
	3	6	10 (1999-2008)	60
	4	6	10 (1999-2008)	60
Total				624

* Note Tibbitt transect 2, plot 6 was bare in 1998

Table S2: The 81 species recorded, their abbreviated codes, the number of plots they were recorded in in each year, and the number of years in which they were recorded over the study period. Species are ordered from those that occurred in all years to those that occurred in fewer years.

Species code	Latin name	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	No. years
ALNsp	<i>Alnus</i> sp.	4	10	8	9	12	14	14	16	17	19	20	11
ARCuva	<i>Arctostaphylos uva-ursi</i>	2	8	14	13	16	18	14	14	14	13	11	11
BETpap	<i>Betula papyrifera</i>	3	21	21	28	34	34	33	35	35	34	34	11
BRYsp	Bryophyte sp.	12	40	52	57	60	56	56	50	49	46	45	11
EMPnig	<i>Empetrum nigrum</i>	1	6	4	4	3	3	4	5	6	5	5	11
EPIang	<i>Epilobium angustifolium</i>	3	19	30	32	32	30	32	30	30	30	26	11
EQUsci	<i>Equisetum scirpoides</i>	1	5	6	13	15	14	15	15	17	18	18	11
LEDgro	<i>Ledum groenlandicum</i>	4	16	21	19	24	23	24	25	26	26	26	11
LINbor	<i>Linnaea borealis</i>	2	3	8	8	10	10	8	7	9	8	7	11
MARpol	<i>Marchantia polymorpha</i>	13	21	17	12	16	11	12	10	4	5	4	11
PICmar	<i>Picea mariana</i>	8	18	24	35	34	39	38	40	38	39	39	11
PINban	<i>Pinus banksiana</i>	1	16	20	17	20	21	23	22	24	23	23	11
POAasp	Poaceae sp.	14	35	44	44	48	46	53	44	43	42	39	11
PYRsp	<i>Pyrola</i> sp.	2	1	3	4	9	8	11	11	11	14	11	11
ROSsp	Rosaceae sp.	3	7	3	3	3	4	4	4	4	4	4	11
SALsp	<i>Salix</i> sp.	5	19	27	25	30	31	33	34	36	35	34	11
VACvit	<i>Vaccinium vitis-idaea</i>	7	40	40	42	41	44	42	44	44	47	45	11
CAREsp	<i>Carex</i> sp.	0	9	5	4	7	7	12	15	13	17	15	10
CHAcac	<i>Chamaedaphne calyculata</i>	0	1	6	5	6	6	6	2	6	6	7	10
EQUsp	<i>Equisetum</i> sp.	0	17	13	22	2	22	10	10	7	7	8	10
LEDdec	<i>Ledum decumbens</i>	0	15	12	12	8	12	12	11	12	12	13	10
RUBcha	<i>Rubus chamaemorus</i>	0	11	9	12	9	10	8	10	9	9	9	10
SAXsp	<i>Saxifraga</i> sp.	0	7	8	15	13	12	12	12	12	12	13	10

Species code	Latin name	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	No. years
SPHsp	<i>Sphagnum</i> sp.	0	6	8	8	8	8	8	8	7	7	8	10
VACcae	<i>Vaccinium caespitosum</i>	0	3	4	7	5	2	6	7	5	4	7	10
CORsem	<i>Corydalis sempervirens</i>	8	10	11	7	6	2	2	2	1	0	0	9
EPIgla	<i>Epilobium glandulosum</i>	0	0	6	9	8	7	4	3	2	3	4	9
GEOliv	<i>Geocaulon lividum</i>	0	0	1	2	2	3	3	2	2	3	2	9
JUNcom	<i>Juniperus communis</i>	0	0	1	2	1	1	1	2	2	2	2	9
OXYsp	<i>Oxytropis</i> sp.	0	0	2	1	2	3	2	2	1	2	2	9
PICgla	<i>Picea glauca</i>	0	0	1	1	1	1	1	1	1	1	1	9
ASTrame	<i>Astragalus americanus</i>	0	0	0	1	2	2	2	3	3	3	2	8
PTEsp	Pteridophyta sp.	0	0	1	3	4	2	0	2	2	1	2	8
RIBsp	<i>Ribes</i> sp.	0	2	2	3	3	0	0	3	3	2	3	8
ASTsp	<i>Aster</i> sp.	0	0	0	0	1	5	3	1	3	2	2	7
ERIs	<i>Eriophorum</i> sp.	0	0	2	0	1	1	1	2	2	2	0	7
POLjun	<i>Polytrichum juniperinum</i>	0	0	0	1	0	9	9	14	15	17	17	7
POPtr	<i>Populus tremuloides</i>	0	0	1	1	0	0	1	1	1	1	1	7
POTnor	<i>Potentilla norvegica</i>	0	0	0	0	3	6	3	2	1	1	1	7
RANaqu	<i>Ranunculus aquatilis</i>	0	0	0	0	1	2	2	1	3	2	4	7
RIBtri	<i>Ribes tristes</i>	0	1	0	2	1	0	0	2	3	3	3	7
RUBsp	<i>Rubus</i> sp.	0	0	4	0	0	1	8	5	4	2	4	7
STEsp	<i>Stellaria</i> sp.	0	0	0	1	0	1	1	2	2	2	1	7
VACsp	<i>Vaccinium</i> sp.	0	0	0	1	1	3	0	5	2	3	3	7
ARCrub	<i>Arctostaphylos rubra</i>	0	0	1	0	1	0	3	0	2	3	3	6
CARpar	<i>Cardamine parviflora</i>	2	3	7	4	1	2	0	0	0	0	0	6
CERpur	<i>Ceratodon purpureus</i>	0	0	0	0	0	4	4	7	7	8	8	6
EQUsyl	<i>Equisetum sylvaticum</i>	0	0	0	0	19	0	13	13	12	11	11	6
LARlar	<i>Larix laricina</i>	0	0	0	0	0	1	1	1	1	1	1	6

Species code	Latin name	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	No. years
DRAsp	<i>Draba</i> sp.	0	0	0	0	0	0	0	1	0	0	0	1
POLsp	Polypodiaceae sp.	0	0	0	0	0	0	3	0	0	0	0	1
POPsp	<i>Populus</i> sp.	0	0	0	0	0	1	0	0	0	0	0	1
RANlap	<i>Ranunculus lapponicus</i>	0	0	0	0	0	0	1	0	0	0	0	1
LICHENcar	Caribou lichens: <i>Cladina</i> , <i>Cladonia</i> & <i>Stereocaulon</i> sp..	8	9	28	33	30	36	39	35	35	32	33	11
LICHENnoncar	Non-caribou lichens: <i>Erioderma pedicellatum</i> , <i>Umbilicaria muhlenbergii</i> , Lichen	4	35	19	19	26	30	30	31	32	32	32	11

Table S3: Plots with missing values for canopy openness, according to measurement year.

Site	Transect	Plot	Measurement year
Tibbitt	1	1	1998
Tibbitt	1	2	1998
Tibbitt	1	3	1998
Tibbitt	1	4	1998
Tibbitt	1	5	1998
Tibbitt	1	6	1998
Tibbitt	2	1	1998
Tibbitt	2	2	1998
Tibbitt	2	3	1998
Tibbitt	2	4	1998
Tibbitt	2	5	1998
Tibbitt	2	6	1998
Tibbitt	3	1	1998
Tibbitt	3	2	1998
Tibbitt	3	3	1998
Tibbitt	3	4	1998
Tibbitt	3	5	1998
Tibbitt	3	6	1998
Tibbitt	4	1	1998
Tibbitt	4	2	1998
Tibbitt	4	3	1998
Tibbitt	4	4	1998
Tibbitt	4	5	1998
Tibbitt	4	6	1998
Gordon	1	1	1999
Gordon	1	2	1999
Gordon	1	3	1999
Gordon	1	4	1999
Gordon	1	5	1999
Gordon	1	6	1999
Gordon	2	1	1999
Gordon	2	2	1999
Gordon	2	3	1999
Gordon	2	4	1999
Gordon	2	5	1999
Gordon	2	6	1999
Gordon	3	1	1999

Gordon	3	2	1999
Gordon	3	3	1999
Gordon	3	4	1999
Gordon	3	5	1999
Gordon	3	6	1999
Gordon	4	1	1999
Gordon	4	2	1999
Gordon	4	3	1999
Gordon	4	4	1999
Gordon	4	5	1999
Gordon	4	6	1999
Tibbitt	1	1	1999
Tibbitt	1	2	1999
Tibbitt	1	3	1999
Tibbitt	1	4	1999
Tibbitt	1	5	1999
Tibbitt	1	6	1999
Tibbitt	2	1	1999
Tibbitt	2	2	1999
Tibbitt	2	3	1999
Tibbitt	2	4	1999
Tibbitt	2	5	1999
Tibbitt	2	6	1999
Tibbitt	3	1	1999
Tibbitt	3	2	1999
Tibbitt	3	3	1999
Tibbitt	3	4	1999
Tibbitt	3	5	1999
Tibbitt	3	6	1999
Tibbitt	4	1	1999
Tibbitt	4	2	1999
Tibbitt	4	3	1999
Tibbitt	4	4	1999
Tibbitt	4	5	1999
Tibbitt	4	6	1999
Tibbitt	5	1	1999
Tibbitt	5	2	1999
Tibbitt	5	3	1999
Tibbitt	5	4	1999
Tibbitt	5	5	1999

Tibbitt	5	6	1999
Tibbitt	6	1	1999
Tibbitt	6	2	1999
Tibbitt	6	3	1999
Tibbitt	6	4	1999
Tibbitt	6	5	1999
Tibbitt	6	6	1999
Tibbitt	6	2	2000
Gordon	1	3	2002
Tibbitt	1	1	2002
Tibbitt	1	2	2002
Tibbitt	1	3	2002
Tibbitt	1	4	2002
Tibbitt	1	5	2002
Tibbitt	1	6	2002
Tibbitt	2	1	2002
Tibbitt	2	2	2002
Tibbitt	2	3	2002
Tibbitt	2	4	2002
Tibbitt	2	5	2002
Tibbitt	2	6	2002
Tibbitt	6	1	2002
Tibbitt	6	2	2002
Tibbitt	6	3	2002
Tibbitt	6	4	2002
Tibbitt	6	5	2002
Tibbitt	6	6	2002
Gordon	3	4	2003
Tibbitt	2	6	2003
Gordon	4	1	2005
Gordon	4	3	2005
Gordon	4	4	2005
Gordon	4	5	2005
Gordon	4	6	2005
Tibbitt	3	3	2005
Tibbitt	3	4	2005
Tibbitt	3	5	2005
Tibbitt	2	2	2006
Tibbitt	4	4	2007
Gordon	4	4	2008

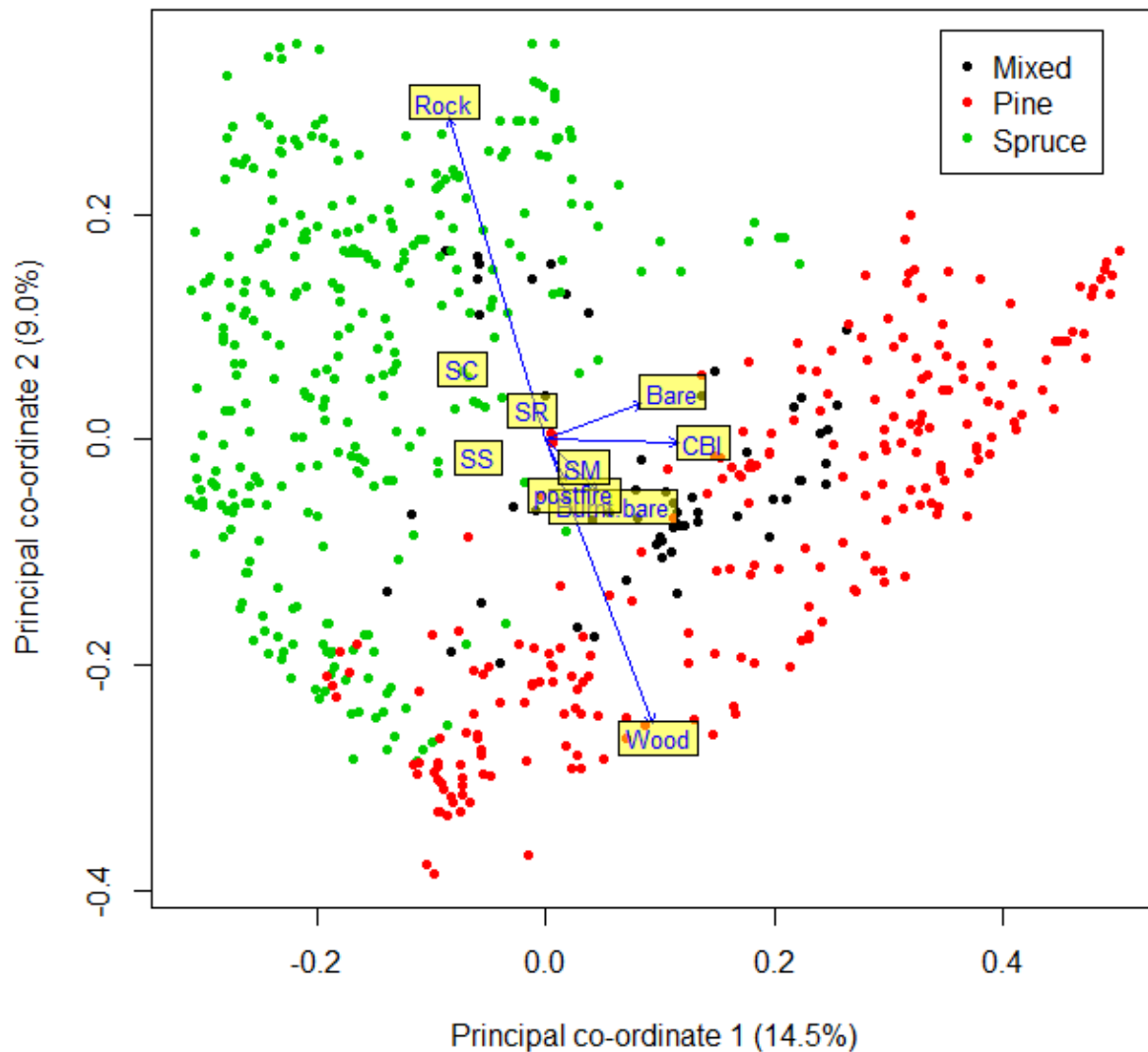


Fig. S1: Site scores for principal co-ordinates analysis ordination, with environmental variables overlaid, for all 623 data points, excluding canopy openness. Points are coloured according to forest type. Values in brackets on the axes represent the amount of variation in species composition explained by each axis. The labels for the environmental variables are: SC=soil clay; SM=soil muskeg; SR=soil rock; SS=soil sand; CBI=composite burn index; postfire=number of years since burned; Bare=abundance of bare ground cover; Burnt.bare=abundance of burned bare ground cover; Rock=abundance of rock cover; Wood=abundance of woody debris .

Table S4: Number of plots in each forest type with each soil type. NA = Not applicable, this combination is not present in the ecoregions studied.

Forest type	Soil type			
	Clay	Muskeg	Rock	Sand
Mixed	6	NA	NA	NA
Pine	NA	NA	18	6
Spruce	NA	30	NA	NA

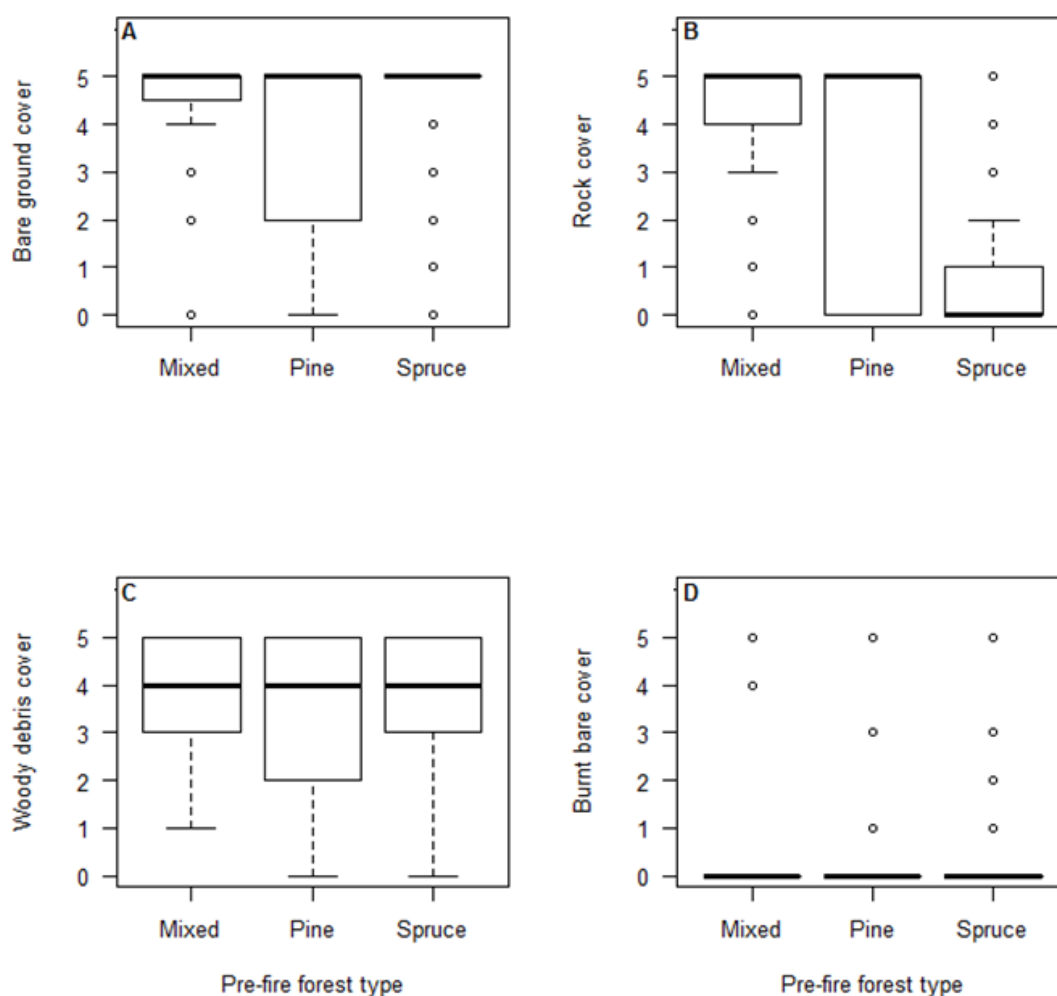


Fig. S2: Relationship between pre-fire forest type and A) bare ground cover, B) rock cover, C) woody debris cover, and D) burned bare ground cover.