Multiple factors influence plant richness and diversity in the cold and dry boreal forest of southwest Yukon, Canada

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Abstract The intermediate disturbance hypothesis (IDH) is regarded as an appropriate model for understanding plant diversity–disturbance relationships in the boreal region. However, concern has been raised over its applicability across such a broad region, in particular, in low productive areas of the region such as the cold, dry region of the southwest Yukon. We examined plant richness and diversity in relation to the IDH in the context of both disturbance and productivity

gradients. We then tested whether environmental variation and resource quantity interacted with development stage to shape richness patterns in the region. We found that richness and diversity did not conform to the IDH but that environmental variation and resource quantity influenced richness and diversity patterns. Overall richness and diversity patterns were not influenced by development stage though plant functional group patterns were. Richness patterns varied between plant functional groups suggesting that divergent processes shape inter functional group richness within the same stands. Our findings highlight the influence of multiple factors governing patterns of plant richness and diversity in the cold dry boreal forests of the southwest Yukon.

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Introduction

Disturbance events can drive change in plant diversity over time and space (Nilsson and Ericson 1997). These discrete events create a mosaic of structures and processes across landscapes that affect ecosystem structure and composition, which in turn influences the richness and diversity of species (Palik et al. 2002; Johnstone and Chapin 2006a). The fire driven nature of the boreal forest makes them a robust candidate for studying diversity–disturbance responses (Kershaw and Mallik 2013) as the frequency and severity of fire are known to affect diversity patterns (Wardle et al. 1997). This understanding underpins the coarse filter management of biodiversity within many forest management agencies across the boreal forests of Canada. Biodiversity management in landscapes across Canada’s boreal forest is strongly linked to diversity–disturbance relationships, in particular the intermediate disturbance hypothesis (IDH) (Kershaw and Mallik 2013). According to the IDH, local/regional diversity is maximized when disturbances are neither too frequent nor too rare (Connell 1978). In other words, higher diversity is maintained when the intensity and frequency of disturbances are intermediate (Grime 1973). In the boreal forests of Alberta, Mayor et al. (2012) found that the IDH was consistently supported across native tree, shrub, and grass species subjected to varying intensities and frequencies of anthropogenic disturbance. Other studies, however, have identified that a wide variety of diversity–disturbance relationships exist, particularly in response to natural disturbances (Hall et al. 2012; Kershaw and Mallik 2013). For example, in boreal forests, the IDH has been shown to be a broadly acceptable model for upland sites of moderate to high productivity; however, it typically does not apply on poorly drained or less productive sites (Kershaw and Mallik 2013).

The impact of different disturbances on plant communities in the SW Yukon has been studied to a limited extent (Turkington et al. 2002; Boonstra et al. 2008); however, diversity–disturbance relationships have not been explored. The combination of a varying fire history, historic, and recent spruce bark beetle (SBB) outbreaks [ca. 340,000 hectares (Waeber et al.

2013)], salvage harvesting and a changing climate (Frugal and Prowse 2008) in the SW Yukon represent an excellent opportunity to explore the role of environmental variation and disturbance on plant diversity. The objectives of this study were (1) to test the validity of the IDH in this cold, dry region of the boreal forest using stand age, productivity, and disturbance severity indicators; and (2) to examine the variation in plant diversity and richness along gradients of environmental and stand structural factors in interaction with stand age and disturbance history.

Methodology

Study area

The study was carried out in the Champagne and Aishihik Traditional Territory (CATT) within SW Yukon (Fig. 1). The mean annual temperature of the region is -1.65°C , and precipitation is 320 mm. Elevation ranges from 651 to 1158 m. Soils vary from sands to silty clays (Government of Yukon 2004). Permafrost is common but discontinuous (Lewkowicz et al. 2012). The region is dominated by fire origin stands of *Picea glauca* (86 % of area) and *Populus tremuloides* (13 % of area) (Government of Yukon 2004).

Data collection

A nested design consisting of 90 sample plots was located along topographically orientated transects within six geographically distinct locations in the summer of 2008 (Fig. 1). The design captured both topographic and geographic variability in the region. In each block, the starting point for each transect was a visible landmark. The first plot was established 100 m from the landmark along a randomly selected bearing; subsequent plots were systematically located every 100 m along the dominant topographic gradient.

At each location, data on slope, aspect, latitude, longitude, elevation, tree density, tree composition, basal area, and crown cover were collected in a 20×20 m plot. Aspect was transformed into cosine and sine of aspect to represent northness and eastness, respectively (Paudel et al. 2015). Within each 400 m^2 plot, three 5×5 m nested subplots were randomly selected to collect shrub cover and sapling density data. Seedling density, and shrub, herb, lichen, and bryophyte

Fig. 1 Study area showing research locations and plots. Site “A” ($n = 13$) was affected by wildfire <100 years ago and consists of remnant patches (15 % of plots >120 years old). Site “B” ($n = 20$) had past spruce bark beetle (SBB) mortality (10 % of plots) and was affected by multiple wildfires: <100 years ago in 25 % of plots, between 100 and 160 years ago in 50 % of the plots, and >200 years in 25 % of plots. Site “C” ($n = 10$) has recent SBB mortality (10 % of plots) and was affected by multiple wildfires: <100 years ago (40 % of plots) and >175 years ago (60 % of plots). Site “D” ($n = 25$) was affected by multiple wildfires: 32 % plots in 1998, 48 % of plots

between 100 and 200 years ago, and 20 % of plots >200 years ago. 48 % of plots had varying levels of recent SBB mortality and 8 % of plots had been partially harvested. Site “E” ($n = 13$) was affected by wildfire <100 years (90 %) and again in 1998 (10 % of plots) and had varying levels of recent SBB mortality in 85 % of plots along with partial harvesting (75 % of plots). Site “F” ($n = 9$) was affected by wildfire <100 years (33 % of plots) and again between 130 and 200 years ago (70 % of plots) with 100 % of plots that have varying levels of recent SBB mortality and partial harvesting

cover data were collected separately from three additional randomly selected 1×1 m micro-plots located within the 25 m^2 subplots. One soil pit was located in a randomly selected micro-plot for soil sampling and characterization. Soil variables measured at each plot were soil depth (cm), texture, organic layer thickness

(cm), and rooting zone depth (cm), and humus form characteristics were depth of the litter (L), fermented (F), and humus (H) layers. Finally, within each 20×20 m plot, a 21-m diagonal transect was established to sample coarse woody debris (≥ 7 cm in diameter) and fine woody debris (<7 cm diameter).

ClimateWNA (Wang et al. 2012) was used to estimate mean annual temperature, precipitation, maximum temperature, and minimum temperature, as well as the number of frost free days and number of growing degree days for each plot. The annual heat moisture index, hereafter known as aridity, was also calculated from mean annual temperature and precipitation following Wang et al. (2006). High indices result from warm temperatures and/or low precipitation and indicated sites of higher aridity. Disturbance history was recorded at each plot as indicated by evidence of fire (burnt snags and coarse woody debris), SBB attack (dead trees with pitch tubes and frass), and harvesting (cut stumps). Disturbance was included as a dummy variable in the form of presence and absence for the data analysis. In addition, at each plot, tree cores were collected from sample trees that represented the range of height and diameter classes for each species within a plot; a total of 416 trees were sampled. Cores between and within trees were cross-dated, cf. Chavardès et al. (2013) for details. The oldest aged tree was assumed to represent the time since last stand replacing disturbance as all trees in the region are fire intolerant.

Data analysis

Prior to analyzing, plant diversity and richness descriptive statistics on diversity and richness were calculated using the Vegan package (Oksanen et al. 2005) in R 3.2.1 (R Core Team 2015) to develop a species accumulation curve from the plot data. The curve indicates how many new species are added when a new site is added to the analysis to determine if our study design was robust enough to capture the region's plant diversity (Kindt and Coe 2005).

We used two approaches to assess plant diversity. First, we analyzed the relationships between plot age, depth of organic soil, and depth of the humus F layer and both overall species diversity and richness and functional group richness. Plot age was used as a proxy for development stage (Zhang et al. 2014b). Organic layer thickness was considered an indicator of disturbance severity (Johnstone and Chapin 2006b). Depth of the humus F layer was considered an indicator of productivity (Royer-Tardif and Bradley 2011). The six functional types were trees, shrubs, herbs, graminoids, bryophytes, and lichens. We used the modified

Simpson's diversity index (Simpson 1949) and Margalef's richness index (Margalef 1958) as metrics for plant diversity and richness. The modified Simpson's index quantifies the diversity of the species by taking into account the abundance of each species present in a plot (Simpson 1949; Magurran 1988), whereas Margalef's richness index is a measure of richness based on the presence and absence, not dominance (Chadwick and Canton 1984). We used general additive modeling (GAM) to determine if a quadratic relationship exists between stand age and plant diversity and richness using the package mgcv in R (Wood 2004, 2011). We constrained the regression smoother (k) in the model function to a maximum of two to prevent the fitting of more complex functions.

Stepwise linear mixed models (LMM) were then used to investigate the relationship between environmental factors and plant diversity and richness. LMM were selected to account for the nested structure of our study design as richness values between plots within each location were likely to be more related than values from plots between locations (Zuur et al. 2009). All independent variables were tested for normality and transformed where necessary and then standardized. A bivariate correlation analysis was conducted to identify highly correlated variables using a bivariate correlation threshold of 0.70 (Tabachnick and Fidell 2007). Weakly or non-correlated variables were included in the LMM to test for their significance and their interaction with stand age. Location and disturbance type were included as a random effects as plots within each location had experienced fire, bark beetle, harvesting, or a combination of these disturbances over the last 200 years. We then followed the methods outlined by Zuur et al. (2009) to conduct stepwise LMM in R 3.2.1 (R Core Team 2015) using the packages nlme (Pinheiro et al. 2015) and mgcv (Wood 2004, 2011). The final models were then compared against the null models using ML approaches and ANOVA F tests using the nlme (Pinheiro et al. 2015), lme4 (Bates et al. 2015), and AICcmodavg (Mazerolle 2015) packages. The marginal and conditional coefficients of variation were calculated using the package MuMIn (Barton 2015), and the change in variance was calculated following Nakagawa and Schielzeth (2013). Effects and interaction plots were created using the effects (Fox 2003) and sjPlot (Lüdtke 2015) packages, respectively.

Results

Species richness and abundance

The total number of species recorded (i.e., species richness) across the sample plots was 70, with 4 tree,

15 shrub, 27 herb, 9 bryophyte, 8 lichen, and 6 graminoid species (Table 1). The average richness in each plot was 14 species, with maximum and minimum richness values of 21 and 4, respectively. Similarly, the average cover in the subplots was 115 %, with maximum and minimum abundance of

Table 1 Taxa recorded in the study area

Scientific name	Functional type	Scientific name	Functional type
<i>Achillea millefolium</i> L.s.l. ^a	H	<i>Mertensia paniculata</i> (Aiton) G.Don	H
<i>Aconitum delphinifolium</i> DC. ^a	H	<i>Mimulus guttatus</i> DC.	H
<i>Alnus incana</i> (L.) Moench ^a	S	<i>Orthilia secunda</i> (L.) House	H
<i>Aquilegia formosa</i> Fisch. Ex DC. ^a	H	<i>Oxytropis campestris</i> (L.) DC.	H
<i>Arctostaphylos rubra</i> (Rehd. & Wils.) Fern. ^a	S	<i>Peltigera aphthosa</i> (L.) Willd.	L
<i>Arctostaphylos uva-ursi</i> (L.) Spreng. s.l.	S	<i>Peltigera canina</i> (L.) Willd.	L
<i>Arnica cordifolia</i> Hook. ^a	H	<i>Petasites frigidus</i> (L.) Fries ^a	H
<i>Aster alpinus</i> L.	H	<i>Picea glauca</i> (Moench) Voss ^a	T
<i>Aulacomnium palustre</i> (Hedw.) Schwagr.	B	<i>Pleurozium schreberi</i> (Brid.) Mitt.	B
<i>Betula glandulosa</i> Michx.	S	<i>Polytrichum commune</i> (Hedw.)	B
<i>Carex</i> spp.	G	<i>Populus balsamifera</i> L. ^a	T
<i>Castilleja</i> spp.	H	<i>Populus tremuloides</i> Michx. ^a	T
<i>Cetraria pinastri</i> (Scop.) A. Gray	L	<i>Potentilla anserina</i> L.s.l.	H
<i>Cladina mitis</i> (Sandst.) Hustich	L	<i>Potentilla nana</i> (D.F.K.) Hultén ^a	H
<i>Cladonia</i> spp.	L	<i>Pyrola picta</i> Sm.	H
<i>Cornus canadensis</i> L.	H	<i>Pyrola asarifolia</i> Michx. ^a	H
<i>Dichodontium pellucidum</i> (Hedw.) Schimp.	B	<i>Rhytidiopsis robusta</i> (Hook.) Broth.	B
<i>Dicranum polysetum</i> Sw.	B	<i>Ribes triste</i> Pall.	S
<i>Dicranum scoparium</i> Hedw.	B	<i>Rosa acicularis</i> Lindl. s.l.	S
<i>Elymus glaucus</i> Buckl.	G	<i>Rubus arcticus</i> L. ^a	S
<i>Elymus innovatus</i> (Beal) Pilg.	G	<i>Salix</i> spp.	T
<i>Empetrum nigrum</i> L.	S	<i>Sanicula marilandica</i> L.	H
<i>Chamerion angustifolium</i> L.s.l. ^a	H	<i>Saxifraga tricuspidata</i> Rottb.	H
<i>Equisetum arvense</i> L.	G	<i>Sedum lanceolatum</i> Torr.	H
<i>Erigeron peregrinus</i> (Pursh)	H	<i>Shepherdia canadensis</i> (L.) Nutt. ^a	S
<i>Festuca</i> spp.	G	<i>Solidago multiradiata</i> Ait.	H
<i>Flavocetraria cucullata</i> (Bellardi) Karnefelt & A. Thell	L	<i>Sphagnum papillosum</i> Lindb.	B
<i>Geocaulon lividum</i> (Richards.)	H	<i>Taraxacum officinale</i> F.H. wigg	H
<i>Hedysarum mackenzii</i> (Richards)	H	<i>Tortula ruralis</i> (Hedw.) G. Gaertn.	B
<i>Hookeria lucens</i> (Hedw.) Sm.	B	<i>Usnea hirta</i> (L.) F.H. Wigg.	L
<i>Hordeum brachyantherum</i> Nevski ^a	G	<i>Vaccinium caespitosum</i> Michx.	S
<i>Hypogymnia physodes</i> (L.) Nyl.	L	<i>Vaccinium vitis-idaea</i> L. ^a	S
<i>Juniperus communis</i> L.s.l. ^a	S	<i>Viburnum edule</i> (Michx.) Raf.	S
<i>Ledum groenlandicum</i> Oeder ^a	S	<i>Viola adunca</i> J.E. Smith	H
<i>Linnaea borealis</i> L.	S		
<i>Lupinus arcticus</i> Wats.	H		

T Tree, H herb, S shrub, L lichen, B bryophyte, G graminoid

^a Species identified by the Champagne Aishihik Nation as being culturally important

269 and 18 %, respectively. Richness and abundance data were weakly correlated ($r = 0.25$; $P \leq 0.01$). The species accumulation curve analysis (Figure S1) indicated that 90 % of the total species were captured in the first 60 plots and 10 % in the remaining 30 plots.

Diversity–disturbance relationships

No significant models, linear or non-linear, were found for the relationship between Simpson's index of diversity or overall species richness for age, organic layer, and F layer depths (Table 2, Figure S2a–b, S3a–b, S4a–b). For plant richness, the GAM analysis indicated that a non-linear relationship with age was stronger than a linear one. The relationship with organic layer and F layer was linear. Diversity, age and organic layer had linear relationships, whereas F layer had an asymptotic relationship with diversity declining with increasing depth. For plant functional types, significant models ($P \leq 0.10$) were found for age and organic layer, but not for F layer, although these were all poor models of fit explaining between 5 and 17 % of the variability (Table 2; age: Figure S2c–h; organic layer: Figure S3c–h; F layer: Figure S4c–h). For trees and lichens, significant linear relationships were exhibited for both age and organic layer with tree diversity declining and lichen diversity increasing with age. Both responded negatively with increasing organic layer, whereas the non-linear model for F layer suggests a negative effect on tree richness (Table 2). Graminoids exhibited linear or near linear relationships, which suggests that richness declines

with increasing age and organic layer but not with changes in F layer depth. For shrubs, a significant linear relationship was found with organic layer (Table 2) and a non-significant trend with F layer. Shrub richness tended to increase monotonically with organic layer but decrease with F layer. For age, a non-linear trend was detected, which suggests richness may increase in stands up to ca. 150 years but then decline. Weak but significant non-linear responses were found for herb richness against age and organic layer (Table 2), and a non-significant non-linear trend was found for F layer. Herbs are the only functional type to exhibit non-linear relationships to all three variables; however, the relationships were characteristic of an asymptotic relationship with herb richness declining after 100 years as organic and F layers increase. Bryophyte richness exhibited a significant non-linear response to age but a linear response to organic layer and no response to F layer (Table 2). Bryophyte richness tended to increase monotonically with increasing depth of the organic layer; however, with age, it declined slightly in the first 50 years post disturbance before increasing after 100 years.

Species diversity and richness from linear mixed modeling

For all models, the assessment of random effects identified that the variable location significantly improved model performance compared to the variable disturbance type ($\Delta\text{AIC} > 2$; $P < 0.001$) and that there was no significant improvement in models when both

Table 2 Relationships between plant diversity and plot age, organic layer depth, and F layer depth

	Plot age			Depth of organic layer			Depth of F layer		
	edf	R^2	P	edf	R^2	P	edf	R^2	P
Total diversity	1.00	−0.01	0.90	1.00	−0.01	0.97	1.60	0.03	0.15
Total richness	1.65	0.01	0.39	1.00	−0.01	0.66	1.17	−0.01	0.88
Tree richness	1.00	0.07	0.006	1.00	0.17	<0.001	1.39	0.00	0.71
Shrub richness	1.69	0.02	0.24	1.00	0.08	0.004	1.00	0.00	0.34
Herb richness	1.69	0.06	0.044	1.71	0.05	0.074	1.72	0.02	0.22
Graminoid richness	1.35	0.05	0.045	1.00	0.01	0.14	1.00	−0.01	0.94
Bryophyte richness	1.75	0.06	0.053	1.00	0.06	0.015	1.14	0.00	0.55
Lichen richness	1.00	0.13	<0.001	1.00	−0.01	0.59	1.00	−0.11	0.91

Strength of relationships represented by P values (P) and coefficient of variation (R^2). Significant relationships ($P \leq 0.10$) are bolded. Shape of the relationship represented by the effective degrees of freedom (edf) for the regression smoother fitted by the GAMM model ($k = 2$); an edf of 1 = linear and 2 = quadratic

Table 3 Linear mixed-effects models of environmental variables on overall species diversity and richness

	Simpson's diversity index				Species richness			
	Null	Full			Null	Full		
	Est. (se)	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	Est. (se)	<i>t</i>	<i>P</i>
<i>Fixed effects</i>								
Intercept	1.62 (0.12)	1.61 (0.06)	29.3	<0.001	2.98 (0.19)	2.99 (0.08)	37.1	<0.001
Aridity		−0.237 (0.051)	−4.61	<0.001		−0.36 (0.08)	−4.48	<0.001
Conifer density		0.062 (0.041)	1.54	0.128				
F layer depth		−0.116 (0.039)	−2.97	0.004				
<i>Random effects</i>	VC	VC			VC	VC		
Location	0.094 (0.30)	0.009 (0.10)			0.18 (0.43)	0.00 (0.00)		
Residuals	0.13 (0.35)	0.12 (0.36)			0.60 (0.77)	0.58 (0.76)		
<i>Goodness of fit</i>								
PCV (location)		−90.4 %				−100 %		
PCV (residuals)		−7.6 %				−3.3 %		
$R^2_{\text{GLMM(m)}}$		30.7 %				18.5 %		
$R^2_{\text{GLMM(c)}}$		35.5 %				18.5 %		
AIC	89.8	79.2			223.8	212.9		
BIC	97.3	94.2			231.3	223.0		
ANOVA: null versus full				<0.001	<0.001			

Est. (se) estimate (standard error), *Conifer* density: all conifer species in plot, *F layer depth* fermented layer depth, *Aridity* (based on annual heat moisture index), *Location* locations of transects ($L = 6$), *PCV* proportion of change in variance, $R^2_{\text{GLMM(m)}}$ marginal variability explained by fixed effects, $R^2_{\text{GLMM(c)}}$ conditional variability explained by full model, *AIC* Akaike information criterion, *BIC* Bayesian information criterion, *VC* variance components, *P* significance value, *t t* value statistic from linear mixed-effects model fitted by REML

random effects were considered ($\Delta\text{AIC} < 2$; $P > 0.10$). Disturbance type was therefore removed and the variable location considered as the sole random effect. Models that had both random intercepts and slopes were found not to yield significant improvements ($\Delta\text{AIC} < 2$; $P < 0.001$); therefore, the more parsimonious models with random intercepts only were selected (Zuur et al. 2009). For the overall diversity and richness models, aridity was found to influence both metrics [cf. Table 3; Figure S5b (diversity) and Figure S5d (richness)]. For the Simpson's diversity model, F layer and conifer density along with aridity were included. No interactions between age and environmental variables were detected for these metrics. Overall, aridity had a negative effect on both diversity and richness. For diversity, fine woody debris (FWD) had a negative effect, whereas increasing conifer density had a positive effect (Table 3; Figure S5a, c).

Different response variables were found for the respective plant types from the linear mixed modeling (Table 4, goodness of fit in Table S1, effect plots

illustrated in Figure S5e-s, and interaction plots in Figure S6). For trees, shrubs, herbs, bryophytes, and lichens location had no effect on richness suggesting a common effect across the region, whereas for graminoids, location had a moderate influence suggesting that an inconsistent signal in the effect of environmental variables on richness is present (Table S1).

Climatic variables had divergent effects on richness patterns (Table 4). Temperature was found to exert negative effects on tree, herb, and graminoid richness but have a positive effect on shrub richness. Aridity had a negative effect on shrub richness but a positive effect on herb richness. For bryophytes, aridity was the only significant direct effect detected, and its relationship to richness was non-linear. Following the GAMM analysis of the full model, a quadratic term (Table 4) for aridity was included in the model which significantly improved the model ($\Delta\text{AIC} > 2$). The non-linear response suggests bryophyte richness increases from cold-wet sites to cool-moist sites but then

Table 4 Linear mixed-effects models of environmental variables on species richness and plant functional types

Variables	Trees			Shrubs			Herbs		
	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>
Intercept	2.84 (0.07)	43.5	<0.001	4.08 (0.13)	30.0	<0.001	3.77 (0.18)	21.5	<0.001
FWD (m ³ /ha)	−0.07 (0.09)	−0.72	0.47				0.48 (0.21)	2.33	0.022
OrgD (cm)	−0.19 (0.07)	−2.71	0.008	0.33 (0.15)	2.19	0.018			
MAT (°C)	−0.16 (0.07)	−2.21	0.03	0.72 (0.23)	3.14	0.002	−4.85 (1.50)	−3.23	0.002
MAP (mm)	−0.01 (0.09)	−0.01	0.93				4.52 (1.78)	2.53	0.013
AHMI				−0.92 (0.21)	−4.31	<0.001	6.71 (2.64)	2.54	0.013
AHMI ²									
TSD (stems/ha)									
Conifer (stems/ha)				0.37 (0.17)	2.17	0.033			
Decid (stems/ha)	0.04 (0.07)	0.57	0.57						
Slope (%)				0.55 (0.14)	3.84	<0.001			
TPI									
RootD (cm)									
Clay (%)				−0.35 (0.14)	−2.42	0.018			
Age (years)	−0.14 (0.08)	−1.86	0.07	−0.12 (0.17)	−0.67	0.50			
Age × Decid	0.25 (0.10)	2.54	0.013						
Age × FWD	−0.16 (0.07)	−2.21	0.03						
Age × MAP	0.45 (0.11)	3.98	<0.001						
Age × OrgD				−0.38 (0.13)	−2.89	0.005			
Age × RootD									
Age × TPI									
Age × TSD									
<i>R</i> ² _{GLMM(m)}	45.3 %	AIC	174.7	48.3 %	AIC	299.5	36.2 %	AIC	355.4
<i>R</i> ² _{GLMM(c)}	45.3 %	BIC	204.7	48.3 %	BIC	327.0	36.2 %	BIC	372.9
Variables	Graminoids			Bryophytes			Lichens		
	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>
Intercept	1.98 (0.17)	11.4	<0.001	2.28 (0.12)	18.9	<0.001	2.28 (0.11)	21.4	<0.001
FWD (m ³ /ha)	−0.17 (0.09)	−1.83	0.071						
OrgD (cm)							−0.29 (0.12)	−2.49	0.015
MAT (°C)	−0.49 (0.16)	−2.95	0.004						
MAP (mm)									
AHMI				−0.21 (0.08)	−2.56	0.013			
AHMI ²				−0.32 (0.09)	−3.66	<0.001			
TSD (stems/ha)				0.17 (0.10)	1.81	0.074			
Conifer (stems/ha)							0.27 (0.14)	1.91	0.060
Decid (stems/ha)									
Slope (%)									
TPI				0.16 (0.08)	2.13	0.036			
RootD (cm)				−0.14 (0.08)	−1.76	0.082			
Clay (%)									
Age (years)				0.10 (0.08)	1.17	0.24	0.37 (0.14)	2.61	0.011
Age × Decid									

Table 4 continued

Variables	Graminoids			Bryophytes			Lichens		
	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>	Est. (se)	<i>t</i>	<i>P</i>
Age × FWD									
Age × MAP									
Age × OrgD									
Age × RootD				0.21 (0.08)	2.54	0.013			
Age × TPI				−0.19 (0.08)	−2.46	0.016			
Age × TSD				0.27 (0.07)	3.63	<0.001			
$R^2_{\text{GLMM(m)}}$	23.4 %	AIC	218.4	43.9 %	AIC	184.4	21.8 %	AIC	265.8
$R^2_{\text{GLMM(c)}}$	38.8 %	BIC	230.9	43.9 %	BIC	214.4	21.8 %	BIC	280.8

Est. (se) estimate (standard error), FWD fine woody debris, OrgD organic soil depth, MAT mean annual temperature, MAP mean annual precipitation, AHMI annual heat moisture index, TSD total stem density, Conifer density of conifer species, Decid density of deciduous species, Slope slope of plot, Age age of oldest tree in plot, TPI topographic position index, RootD rooting zone depth (cm), Clay % of soil, Location locations of transects ($L = 6$), PCV proportion of change in variance, $R^2_{\text{GLMM(m)}}$ marginal variability explained by fixed effects; $R^2_{\text{GLMM(c)}}$ conditional variability explained by full model; AIC Akaike Information Criterion, BIC Bayesian Information Criterion, VC Variance Components, *P* significance value, *t* *t* value statistic from linear mixed-effects model fitted by REML

declines as sites become warmer and drier (Figure S5). Herb richness was positively affected by precipitation, whereas for trees, a significant interaction between age and precipitation was detected. The interaction suggests that younger stands typically have less richness than older stands as precipitation increases. The strong climatic signal detected for herbs suggests the wet, cold sites or hot and dry sites have higher herb richness than warm and wet sites.

Edaphic variables had consistent effects on richness patterns (Table 4). Organic layer depth was found to have negative effects on both tree and lichen richness whereas for shrubs, a significant interaction between age and organic layer was detected. The interaction effect suggests that shrub richness increases with increasing organic layer depth in young stands but declines in older stands. Shrubs also exhibited a negative effect with increasing clay content but a positive response with increasing slope, which suggests that shrub richness is promoted on well-drained sites. An interaction between rooting zone depth and age was also detected for bryophytes, which indicates that richness increases in older stands with deeper rooting depths but decreases in younger stands. Rooting zone depth is a measure of edaphic variation, with sites with shallow rooting depths tending to be wet and underlain with permafrost. These sites tended to

be dominated by *Sphagnum* sp. in older stands, which may explain why they have lower richness than older stands on deeper, well-drained soils. The significant interaction between age and topographic position detected for bryophyte richness also suggests that young stands in depressions or lower slopes have lower richness than older stands; however, younger stands on mid to upper slopes are likely to have higher richness than older stands.

Structural variables had varying effects on richness patterns (Table 4). Increasing density of conifer species in plots had a positive effect on both shrub and lichen richness. A significant interaction between age and density of deciduous trees was detected for tree richness, which suggests that young stands with high deciduous density will have lower richness, whereas older stands with high deciduous density should have higher richness. Bryophytes also exhibited a significant interaction between age and total tree density, which suggests that young stands with lower density have higher richness, but older stands with lower density have lower richness. Increased richness in bryophytes is therefore expected in older sites with high tree density. Increasing fine woody debris (FWD) had a positive effect on herb richness but a negative effect on graminoid richness. Tree richness exhibited a significant interaction between age and FWD suggesting that younger sites tend to

increase in tree richness with increasing FWD, whereas older stands decline.

Discussion

According to the IDH, local diversity should be highest when disturbances are neither too frequent nor too rare (Connell 1978) or at moderate levels of environmental stress such as an increase in diversity at the midpoint of a productivity gradient (Grime 1973). In this study, no strong quadratic relationships between time since fire, productivity, and disturbance severity for overall plant diversity and richness were found. In addition, disturbance history was found not to have a significant effect on diversity or richness. Overall, a lack of congruency with the IDH exists in the study region.

Across functional groups, only two significant non-linear relationships were detected (herb richness vs. age and organic layer depth) in this study. While the results for herbs are consistent with the findings of Zhang et al. (2014a) for the boreal forests of Alberta, Canada, and the results for both herbs and bryophytes align with patterns of response across Canada (Zhang et al. 2014b), the lack of significant quadratic relationships between richness and stand age is inconsistent with the findings of Mayor et al. (2012). They found that patterns of richness across multiple functional types in the boreal forests of Alberta generally aligned with the IDH. Our results for tree richness are also inconsistent with tree richness patterns for Canada, which was found to peak at intermediate stand ages (Zhang et al. 2014b). Our findings highlight that multiple factors likely influence the patterns of plant richness and diversity across the region. Classic disturbance–diversity relationships are therefore not sufficient to explain plant richness and diversity patterns in the southwest Yukon.

Climatic and edaphic factors were the primary drivers influencing patterns of overall diversity and richness in the region. Overall diversity and richness exhibited a significant negative association with aridity suggesting that plant diversity declines along an aridity gradient with wetter sites having more diversity than drier sites, which is consistent with patterns in overall plant richness found across Canada (Zhang et al. 2014b). Zhang et al. (2014b) reported the importance of local site conditions, in particular, site

drainage class, on plant diversity. No significant relationships were found between topographic position and overall plant diversity and richness in this study, suggesting that topographic position is not a strong driver of overall patterns. Diversity, however, was found to decrease significantly with increasing F layer depth. This suggests that plant diversity may be responding to a productivity gradient. Soils with thick F layers have simple plant-litter-fungal trophic networks associated with slow and direct nutrient cycling that reduces productivity (Ponge 2013) and can lower plant diversity (Ponge 2003). Aridity itself affects productivity in the boreal forest, with dry sites having lower decomposition rates than moist sites (Holden et al. 2015). This combination of variables indicates that productivity is likely a key factor in explaining overall plant diversity and richness in the study region. The effects of aridity and F layer depth were linear, however, which further strengthens our argument that richness and diversity patterns in the region do not conform to the IDH (Grime 1973).

The influence of environmental factors on richness was not homogenous across plant functional groups, highlighting that different factors have divergent influences. The interactions between stand age and environmental factors were detected when functional group richness was examined points to complex richness patterns that are influenced not only by climate and topography but also by feedbacks between changing structural and edaphic variables as forests age. This finding supports the argument by Bartels and Chen (2010) that plant diversity in the boreal forest varies with resource heterogeneity and quantity in interaction with successional stage.

Our results suggest that tree richness is responding to a climatic and edaphic gradient in interaction with development stage. Our results for temperature contradict Zhang et al.'s (2014b) Canada-wide study. Zhang et al. (2014b) found that tree richness generally increased with temperature, while our model suggests a decline. The interaction between precipitation and age suggests that resource availability (i.e., moisture) is exerting a time-dependent effect on tree richness, whereas temperature has a time-independent effect, which strengthens the Bartels and Chen (2010) hypothesis. Tree richness was strongly influenced by edaphic variables. A consistent decrease in tree richness was found with increasing organic layer depth. The increase in organic layer depth creates

edaphic conditions unsuitable for the region's deciduous species. Lafleur et al. (2015) found that increasing soil organic layer thickness hinders the regeneration and growth of *Populus tremuloides* while Viereck et al. (1993) found that *P. balsamifera* becomes absent from stands as they develop a thick organic soil layer. FWD is an important source of both macro and micronutrients to forest soils (Klockow et al. 2014) as they decay more rapidly than coarse woody debris (Miller 1983; Müller-Using and Bartsch 2009). The relatively high nutrient concentrations and decomposition rates of FWD facilitate nutrient cycling and productivity within forest floors and soils (Klockow et al. 2014). The interaction between age and FWD suggests development stage influences the effect of productivity inputs on richness. The increase in tree richness with increasing FWD in young stands may therefore reflect a productivity gradient that favors recruitment and growth of both coniferous and deciduous species (Johnstone et al. 2010), whereas the decline in richness in older stands may reflect the development of the soil organic layer that reduces productivity over time (van Cleve et al. 1981; Bonan and Shugart 1989; Laamrani et al. 2014).

The interaction between stand age and deciduous species density reflects the common stand dynamics of the region's forests. Young stands dominated by deciduous species tend to lack coniferous species but as stands develop coniferous species recruit and increase richness. The maintenance of a higher deciduous component in mixed stands likely facilitates their persistence in mature stands through the feedbacks that broadleaf species have on edaphic conditions. On older conifer dominated sites the persistence and recruitment of broadleaf species is restricted by the feedbacks conifers species have on edaphic conditions over time (Johnstone et al. 2010).

Our findings highlight that shrub richness in the region is influenced by resource quantity in interaction with development stage. Temperature and aridity were common influences on shrub richness patterns, which is consistent with findings from other studies (Gracia et al. 2007; Zhang et al. 2014b). Our findings diverge from the Canada-wide study of Zhang et al. (2014b) who found that poorly drained sites supported higher richness. The increase in richness with increasing slope suggests that better drained soils promote richness in the region; this has also been found in the subalpine forests of Colorado, USA (Coop et al. 2010).

The decline in richness with increasing clay content and increasing organic soil depth (in older stands) also suggests that these sites do not promote increased shrub richness in the region. This is supported by observations of Viereck et al. (1993) who found that changes in edaphic conditions over time in boreal floodplain forests of Alaska facilitated shifts in shrub communities. The increased richness with increasing organic soil depth in younger stands suggests that these stands may have been burnt less severely in the past (Johnstone and Chapin 2006b), which may have facilitated an increase in richness through increased resource heterogeneity (Boudreault et al. 2002; Bartels and Chen 2010).

Our results also suggest that many of the shrub species present in the region may be shade tolerant. Both Gracia et al. (2007) and Zellweger et al. (2015) attributed relationships between crown cover and richness in Spain and Switzerland, respectively, to shade tolerance. The relationship between increasing slope and richness could also be causing a feedback in stands with high conifer density by promoting light transmission into the understorey (Coop et al. 2010), thereby facilitating the presence of less shade tolerant species and thus promoting increased richness.

Climate was a key driver for herb richness, which aligns with the global understanding of drivers of plant richness (Hawkins et al. 2003). Although richness was primarily influenced by climatic variables, a positive effect of increasing FWD on richness was also detected, suggesting that herb richness increases on sites with higher potential productivity (Klockow et al. 2014). Turkington et al. (1998, 2014) found that herb abundance and cover increased in the study region following a fertilization trial in *P. glauca* dominated stands, which supports the theory that increases in nutrient availability can facilitate increases in herb richness. This is also supported at broader scales by Zhang et al. (2014b) who found that net primary productivity positively influenced herb diversity across Canada's forests. The influence of climate on herb richness aligns with the findings of Chytrý et al. (2012), Zhang et al. (2014b) and Zellweger et al. (2015), all of whom found that warmer sites had lower herb richness or diversity. Zhang et al. (2014b) found that herb richness correlated positively with increasing aridity, whereas Chytrý et al. (2012) found that increased precipitation increased vascular plant richness in the hemi-boreal forests of the Altai region of

Siberia. Our findings therefore appear to be consistent with the pan-boreal understanding that climate and productivity are key drivers of herb richness.

We found that cooler sites had higher graminoid diversity than warmer sites, which is consistent with Coop et al. (2010) who found that graminoid richness in Alberta increased with increasing elevation (i.e., decreasing temperatures). The impact of increasing FWD on graminoid richness could suggest that sites with lower productivity have higher richness, which is opposite to the relationship we found for herbs. As graminoids have been found to respond positively to increasing nutrient supply in the region (Turkington et al. 1998), it is doubtful that the decline in graminoid richness is caused by an increase in site productivity. It is more likely that graminoid richness declines on sites with higher productivity due to competitive interactions with other vascular and non-vascular plants (Schoor et al. 2007). This hypothesis is supported by Turkington et al. (2014) who found that after 20 years of fertilization, stands in the study region became increasingly dominated by herbaceous communities at the expense of shrubs, graminoids, bryophytes, and lichens.

Overall, bryophyte richness patterns in the region are driven by interactions between climate, stand structure, edaphic conditions, and development stage. These interactions result in changes in resource heterogeneity and quantity over time, which drives shifts in bryophyte richness and composition (Boudreault et al. 2002; Stehn et al. 2010). The quadratic relationship between aridity and richness shows that bryophyte richness increases toward the midpoint of the measured aridity gradient. Aridity affects productivity (Holden et al. 2015) and acts as an ecosystem stressor (Mitchell et al. 2015). This suggests that patterns of bryophytes richness in the region may be responding to productivity and stress in a manner consistent with the IDH.

The interactions with age however suggest that richness is also influenced by resource quantity in interaction with development stage (Boudreault et al. 2002; Bartels and Chen 2010). The interactions between conifer density and age suggests that bryophyte dynamics in our region align with those observed by Boudreault et al. (2002) in the eastern boreal forests of Canada. Mature stands (80–120 years old) located on well-drained sites with a high basal area of conifers favor the development of diverse moss

dominated communities including increased liverwort richness, which is sensitive to desiccation in more open forests (Boudreault et al. 2002). Stehn et al. (2010) also found that bryophyte richness and composition in the Appalachian Mountains were sensitive to changes in conifer density. Interestingly, changes in the quantity of fine and coarse woody debris had no significant effect on richness, which is consistent with the findings of Boudreault et al. (2002) but in contrast to the findings of Crites and Dale (1998) and Kruys and Jonsson (1999). The latter authors found that fine and coarse woody debris were important drivers of bryophyte diversity in the boreal forests of Alberta and Sweden, respectively.

The interaction between topographic position and age and rooting zone and age illustrates the Sphagnum versus moss richness dynamic that Boudreault et al. (2002) found in eastern Canada. The increased bryophyte richness with increased rooting zone depth in older stands points to the persistence of well-drained conditions as older sites with shallow rooting have typically been paludified, which leads to changes in bryophyte communities (Boudreault et al. 2002). Paludification occurs where organic material builds over time and eventually reduces soil productivity by lowering soil temperatures and increasing soil moisture (Boudreault et al. 2002). Sphagnum richness increases in older stands that are paludified, typical of depressions and lower slopes, whereas mesic conditions, typical of mid to upper slopes, favor moss species such as *Pleurozium schreberi*, *Polytrichum commune*, and *Dicranum polysetum*. The latter two species were commonly found in our study on mesic sites within young stands (<30 years old), whereas *P. schreberi* was found to decline in older stands (>200 years old). These responses explain why richness increases along the topographic gradient in young stands but declines in older stands.

Lichen richness and diversity are typically influenced by climate and/or structural variables (Werth et al. 2005; Moning et al. 2009). The overall patterns in lichen richness detected in this study highlight that structural and edaphic variables associated with the development stage are the key factors influencing resource quantity, which, in turn, promotes or reduces lichen richness over time. The increase in lichen richness with increasing stand age is consistent with the findings from across the world's boreal forests (Boudreault et al. 2000, 2002; Johansson 2008; Mack

et al. 2008; Asplund et al. 2014; Svensson et al. 2014). The general consensus is that lichen richness and abundance increases in response to either stand age or tree age. Given that our estimates of stand age are from sample trees, the results are congruent with both concepts and indicate that older stands or older trees (coniferous or deciduous) are critical for maintaining lichen richness in boreal landscapes.

We found that increasing organic matter depth had a negative effect on lichen diversity. A decline in lichen abundance, not in richness, on paludified sites in the boreal forests of Quebec has been reported (Boudreault et al. 2002; Zouaoui et al. 2014). The significant effect of conifer tree density on lichen richness suggests that forest structure is playing an influential role on lichen richness patterns in the region. Increases in conifer density can create favorable microclimatic conditions (light and humidity) (Moning et al. 2009; Asplund et al. 2014) and substrates, through the increase in dead branches for lichen colonization (Svensson et al. 2014). An interesting finding in this study is the lack of effect that fine or coarse woody debris had on lichen diversity. In the boreal forests of Sweden (Kruys and Jonsson 1999) and Germany (Moning et al. 2009), lichen diversity tends to increase with increasing volume of woody debris. This suggests that woody debris in the region may be monopolized by bryophytes (Boudreault et al. 2002) or occupied by generalist lichen species (Asplund et al. 2014).

Conclusion

The lack of congruency with the IDH in this region may be due to lower productivity resulting from the cold and dry climate or due to dynamic changes in site productivity over time in response to the presence or absence of fire (Viereck et al. 1993; Johnstone et al. 2010). These dynamics are influenced by complex interactions between topographic and edaphic variables that favor the development and stability of alternative vegetation communities that in turn influence stand composition and productivity post fire (Johnstone et al. 2010). Although we cannot disentangle these processes, our findings that diversity and richness tend to follow linear trends in response to disturbance and productivity gradients, nevertheless, lend support to the arguments of Bartels and Chen

(2010), Hall et al. (2012), and Fox (2013) that a unifying theory of plant diversity dynamics is unlikely even in the boreal forest where it is regarded with broad applicability (Kershaw and Mallik 2013). Our results not only highlight the potential role that forest managers, disturbance, and climate change may have in influencing plant diversity in the region but also articulate that relationships are complex. The ‘one management approach fits all’ concept will not balance the needs for conserving plant diversity in the region, which places the onus on forest managers to consider the implications of harvesting on forest structure and soil properties while continually monitoring the region’s plant diversity in response to the recent bark beetle epidemic and climate change.

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