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Changes in the understory plant community and ecosystem properties along a shrub density gradient

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Abstract: Climate warming is projected to alter the vegetation community composition of arctic and alpine ecosystems including an increase in the relative abundance and cover of deciduous shrubs. This change in plant functional group dominance will likely alter tundra ecosystem structure and function. We conducted an observational study to quantify how the understory vegetation community and ecosystem properties varied along a shrub density and altitudinal gradient in a tundra alpine ecosystem in south-west Yukon. Although there was weak association between shrub density and species richness of understory community, there were large differences in functional group abundance between the different shrub densities; forb cover increased at lower elevations with higher shrub density at the expense of cryptogam and dwarf shrub cover. Litter mass, light interception, and soil carbon:nitrogen ratios all increased with shrub density. Sites with shrubs had higher summer soil temperatures, lower summer soil moisture, and lower percent soil nitrogen than the shrub-free site, although there was no difference in available nutrients among sites. This study presents findings from a nonmanipulated, model system where shrubification has been documented and suggests that direct and indirect effects of increasing shrub dominance are likely to affect the surrounding vegetation and abiotic environment controls.

Key words: deciduous shrubs, alpine tundra, ecosystem properties, plant functional group abundance.

Résumé : Le réchauffement climatique devrait modifier la composition de la communauté végétale des écosystèmes arctique et alpin, notamment par une augmentation à la fois de l'abondance relative et du couvert des arbustes à feuilles caduques. Ce changement dans la dominance de groupe fonctionnel de plantes risque d'altérer la structure et la fonction de l'écosystème toundra. Nous avons mené une étude observationnelle pour quantifier les variations de la communauté végétale en sous-étage ainsi que des propriétés écosystémiques le long d'un gradient de la densité arbustive et d'un gradient altitudinal dans un écosystème alpin de toundra au sud-ouest du Yukon. Même s'il y avait une corrélation faible entre la densité arbustive et la richesse spécifique de la communauté végétale en sous-étage, il existait des écarts considérables au niveau de l'abondance de groupe fonctionnel entre les différentes densités arbustives; le couvert d'herbes non graminéennes s'intensifiait à des altitudes plus basses avec une densité arbustive plus élevée, au détriment du couvert de cryptogames et d'arbustes nains. Quant à la masse de la litière, l'interception de la lumière et le carbone dans le sol: les taux de nitrogène ont tous augmenté avec la densité arbustive. Les aires comportant des arbustes avaient des

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températures du sol plus élevées en été, une humidité du sol réduite en été et un taux d'azote dans le sol plus faible que les aires dépourvues d'arbustes, même s'il n'existait aucune différence entre les sites au niveau de la disponibilité des nutriments. La présente étude expose les résultats provenant d'un système modèle non manipulé où l'expansion arbustive a été documentée et suggère que les effets directs et indirects de la dominance arbustive croissante influeront probablement sur la végétation environnante et les mesures de contrôle du milieu abiotique. [Traduit par la Rédaction]

Mots-clés : arbustes à feuilles caduques, toundra alpine, propriétés écosystémiques, abondance de groupe fonctionnel végétal.

Introduction

Environmental changes are occurring at a global scale; particular attention has been placed on high northern latitudes where climate warming will be disproportionately felt, with the Arctic region warming at a rate above the global mean (IPCC 2014). Paleorecords indicate this region is highly sensitive to climate change, evidenced by large shifts in vegetation community composition between historic warm and cool periods (Bigelow et al. 2003). Currently, climate warming is projected to alter plant composition of arctic and alpine ecosystems through an increase in relative abundance and cover of deciduous shrub species, a process colloquially known as *shrubification* (Myers-Smith et al. 2011).

While nonclimatic factors such as herbivores can modify or constrain climate driven changes in species distribution (i.e., Pajunen et al. 2012; Plante et al. 2014), several lines of evidence suggest that the climate-induced shrubification is occurring across alpine and arctic regions. Ground-based observations have found shrubline advance beyond historical ranges in alpine systems in Alaska, the western Canadian subArctic, and Europe (Anthelme et al. 2007; Cannone et al. 2007; Myers-Smith 2011; Dial et al. 2016). Increases in shrub cover through lateral growth, increased canopy height and recruitment, as well as shrubline advances beyond historical range limits have been observed across the circumboreal north (reviewed in Myers-Smith et al. 2011). In addition, satellite-collected normalized difference vegetation index (NDVI) values, indicative of vegetation productivity, have increased over recent years resulting in the greening of tundra ecosystems (Jia et al. 2009). While NDVI measures are sensitive to a variety of changes to ground-cover, recent work indicates that shrubs are at least partially responsible for these greening trends (Tape et al. 2006; Blok et al. 2011*a*). Lastly, paleoecological records indicate that deciduous shrubs including alder, birch, and willow were once more widespread across circumpolar tundra ecosystems during previous warmer and wetter periods suggesting that shrub species ranges have previously undergone climate-induced shifts during previous periods of favourable climatic conditions (Myers-Smith et al. 2011; Naito and Cairns 2011).

With the increasing dominance of shrubs and the resultant changes to vegetation dominance hierarchies, environmental change is indirectly affecting the abundance and diversity of tundra plant communities. Tundra habitats are regarded as relatively species rich communities where plant–plant interactions are weak and richness is limited by harsh environmental conditions (e.g., low temperatures, high herbivory levels, and nutrient poor soils) (Grime 1979; Anthelme et al. 2007). Shrubs may ameliorate environmental conditions in tundra ecosystems, increasing nutrient and water availability or providing protection from wind and grazing, but at the same time shrub canopies decrease the solar radiation that reaches understory vegetation, increasing competition among understory species (Brooker and Callaghan 1998). Warming (Walker et al. 2006) and fertilization (Gough et al. 2012) experiments across the Arctic have found that species richness

has declined with increasing shrub dominance. The competitive exclusion of shade-intolerant species, in particular lichens and mosses, growing under shrub canopies has been suggested as a mechanism of the observed biodiversity loss (Walker et al. 2006; Pajunen et al. 2011). In contrast, shrubs have also been suggested to facilitate some plant species (Brooker and Callaghan 1998). Despite the ongoing debate over the utility of plant functional groups (Funk et al. 2017), functional groups facilitate the comparison of community composition responses across unique ecosystems and provide generalized predictions on species composition responses to shrubification. Ultimately, future ecosystem composition will depend on the individualistic nature of plant–plant interactions at a species level.

This increase in shrub abundance may alter ecosystem structure and function, as different plant species have varying effects on ecosystem properties (McLaren and Turkington 2010), e.g., albedo (Lantz et al. 2013), soil temperature (Blok et al. 2010; Myers-Smith and Hik 2013), soil moisture (Bueno et al. 2016), and soil nitrogen (Buckeridge and Grogan 2010). Increases in shrub cover have likely already begun to alter ecosystem energy and carbon budgets, potentially compounding or mitigating climate warming effects in the region (Tape et al. 2006; Myers-Smith et al. 2011). Several hypotheses propose that shrubification will alter tundra ecosystem function directly and (or) indirectly by altering both biotic and abiotic controls (as reviewed in Myers-Smith et al. 2011). For example, changes in decomposition rates may be affected by both changes in environmental conditions under shrubs, but also because of changes in litter species composition. Bryophytes exert strong control over tundra soil microclimate, mediating the exchange of water and energy between soil and atmosphere (Blok et al. 2011*b*; Stoy et al. 2012; Soudzilovskaia et al. 2013). Shrub–bryophyte interactions modify these controls, where declines in bryophyte cover under dense shrub canopies have been found to increase ground heat flux partitioning, despite increases in soil evaporation, resulting in warmer summer soil temperatures (Blok et al. 2011*b*), which would increase litter decomposition. In contrast, it has been suggested that shading by shrub canopies may decrease summer soil temperatures (Marsh et al. 2010), which in turn may decrease decomposition rates. Moreover, changes in soil moisture regimes will affect decomposition with predicted increased evapotranspiration rates under shrubs drying soils (Chapin et al. 2000) and potentially leading to microbial moisture limitations. Further, it has been proposed that the increase in shrub abundance will negatively impact decomposition rates due to the recalcitrant nature of deciduous shrub litter (Cornelissen et al. 2007; Myers-Smith et al. 2011, although see McLaren et al. 2017).

To achieve a global perspective on the impacts of shrubification on alpine tundra ecosystem structure and function, multiple, independent observational studies are needed to examine the geographical domain and generality of previously described patterns and processes (Underwood et al. 2000). This study seeks to complement research on the effects of tall, deciduous shrub cover on understory vegetation community, and abiotic ecosystem properties. We worked along a tall, deciduous shrub density and altitudinal gradient in a model alpine tundra system in the Yukon Territory, Canada, where increases in the elevational range limit of deciduous shrub species has been observed over the past few decades (Myers-Smith 2011). We expected plots with higher deciduous shrub cover to have

1. Lower understory vegetation species richness and diversity, in particular loss of cryptogams
2. Greater proportion of incoming light intercepted, accompanied by colder, wetter soils
3. Increased litter accumulation, soil carbon:nitrogen, and soil nutrient availability.

Materials and methods

Site description

The study took place on a north facing alpine plateau in the Kluane Lake region of the south-western Yukon. In the rain shadow of the St. Elias Mountain range, this relatively dry area receives 230 mm of mean annual precipitation, of which around half falls as rain in the summer and the remainder falls as snow, with a mean annual snowfall of 100 cm (Turkington et al. 2002; Myers-Smith 2011). With increasing elevation, the plateau's vegetation transitions from a spruce forest dominated by *Picea glauca*, to shrub tundra with the dominant erect, deciduous shrubs *Salix glauca, Salix pulchra*, and *Salix richardsonii* with an understory dominated by *Mertensia paniculata, Anemone parviflora, Lupinus arcticus*, and the dwarf, prostrate shrub *Salix reticulata*, to an alpine tundra community dominated by the dwarf, prostrate shrub *Salix rotundifolia, Equisetum arvense*, and a number of *Carex* species. We classified the area above treeline into three different shrub habitats: dense shrub tundra (N°60,58.962, W°138,24.680), patchy shrub tundra (N°60,58.699, W°138,34.595), and open alpine tundra (N°60,57.985, W°138,24.919). Patchy shrub tundra is composed of isolated patches of tall shrubs interspersed among alpine tundra habitat. The dense shrub tundra extended upslope approximately 615 m above treeline before transitioning to patchy shrub tundra, which extended approximately 1100 m upslope then transitioned into open tundra.

The observed shrub density gradient is confounded with an elevational gradient. There was a 368 m difference in elevation between the lowest and highest transect, with the average elevation of the dense, patchy, and open habitats being 1342, 1424, and 1666 m, respectively. Using a lapse rate calculated using average summer air temperature data collected from the base of mountain plateau (792 m) and at a nearby site in the plateau's alpine (1734 m) in the 2015 growing season (24th June to 13 August 2015), the estimated air temperature difference between these habitats is 1.3 °C (H. Thomas and I. Myers-Smith, unpublished data; Fig. S1[1]). Soil temperatures along with this elevational gradient, however, do not consistently decrease with an increase in the altitude, and include additional variation in site-specific characteristics which result in variation in soil temperatures (Fig. S1[1]). Aside from shrub density, elevation, and likely air temperature differences, all habitats contained similar environmental characteristics. Both shrubland habitats were composed of the same tall deciduous, erect shrubs species, and the open tundra habitat are effectively void of all tall shrubs. All three habitat types shared roughly the same aspect, slope, and weather conditions.

We designated plots in each of the three shrub habitats, by systematically laying two parallel 50 m transects, avoiding habitat transition zones. Transects were separated by at least 15 m. Five quadrats (1 m × 1 m each) were established along each transect, spaced 10 m apart. Because quadrats were separated by a minimum of 10 m, and there were no significant differences in soil temperature or moisture between the two transects, each quadrat was treated as an independent observation ($n = 10$ quadrats).

Vegetation cover and shrub complexity

The percent cover of all vascular plant species, bryophytes, lichens, and litter was visually estimated in each 1 m² quadrat. Species with low cover (<2% cover) were all assigned a cover of 1%. We calculated aerial cover, allowing species to overlap each other, and thus

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[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2017-0026.

the sum of percent cover could be greater than 100% per quadrat. We determined percent deciduous canopy cover as foliage cover of all tall deciduous shrub species (*Salix* spp. and *Betula glandulosa-nana* complex, referred to *Betula* hereafter). We use "tall shrubs" to refer to erect, multistemmed species (0.4–4.0 m), as defined by Myers-Smith et al. (2011).

Structural complexity of tall shrubs (*Salix* spp. and *Betula*) was estimated along the north edge of each 1 m^2 quadrat using a method adapted from Boelman et al. (2011). We placed a meter stick vertically every 25 cm along the quadrat and counted the number of branches touching the stick within each of the height increments: 0–10, 10–50, 50–100, and >100 cm. Our shrub complexity index is the mean number of woody branch touches per quadrat (the average of the five vertical meter stick insertions).

Ecosystem properties

To determine litter biomass, litter was collected by hand from the soil surface from a 10 cm × 10 cm subquadrat in the south-east corner of each 1 m^2 quadrat. Litter was sorted into woody and nonwoody components, dried at 45 °C for two days, and weighed.

Soil moisture (%) in the top 10 cm of the soil was measured, at two random locations per quadrat, using a water content sensor (Hydrosense Water Content Measurement System; Campbell Scientific, Thuringowa Central, Queensland, Australia). Soil temperature was measured with a soil thermometer at a depth of 5 cm twice within each quadrat. We measured soil moisture and soil temperature within a 3 h time frame (0900–1200 on 16 July 2014) to minimalize variation between sites caused by temporal variation in weather.

We measured surface light intensity within each quadrat at ground level, under the vegetation canopy, using a quantum meter with six evenly spaced sensors on a 50 cm wand (Apogee Instruments Inc., Logan, UT, USA). Surface light intensity was measured in each plot with three measurements taken at 3 s intervals and then averaged. For each transect, light intensity was also measured in an open area adjacent to the transect, 1 m above the vegetation. Measurements were taken within a 2 h time frame approximately centered on solar noon (1330–1530) on 16 July 2014. Light interception index was calculated as the difference between the average open light intensity and the average surface light intensity divided by the average open light intensity.

Within each quadrat, we collected soil cores to the depth of the soil organic layer in three random locations using a 2.5 cm diameter corer. We measured the depth of the organic soil layer, with the exception of a few samples in the open alpine tundra site where frozen soil prevented us from coring the entire organic layer. Soil was homogenized and large roots (>1 mm diameter) removed before further processing. For soil pH, 15 g soil was combined with 30 mL of distilled water, stirred, and allowed to stand for 30 min before measuring. The remainder of the soil was frozen at −20 °C and shipped to the University of Texas at El Paso for further analysis.

Samples to be analyzed for nutrient availability were thawed and extracted with 0.5 M K_2SO_4 by shaking vigorously for 1 min, allowed to settle overnight, and then filtered through glass filter paper. Available ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^-) were analyzed using colorimetric microplate assays (BioTEK Synergy HT microplate reader). The protocol for NH_4^+ followed the Berlethot reaction (Rhine et al. 1998), while the NO_3^- was a modified Griess reaction (Doane and Horwáth 2003) that reduces of nitrate to nitrite and colorimetrically measures nitrite. Phosphate was analyzed using the malachite green assay, (D'Angelo et al. 2001), and then read colorimetrically. A second subsample of soil was dried at 60 °C, ground, and processed for total C and N content using a dry combustion C and N analyzer (Thermo Scientific 2000 Elemental Analyzer).

Table 1. Summary of one-way analysis of variances (ANOVAs) on plant community biodiversity, as well as percent cover of each functional group in an observational study on the effect of shrub density in the Kluane region of the Yukon Territory.

	df	$F(\chi^2)$	P
Richness	2, 27	2.91	0.072
Shannon–Weiner diversity	2, 27	2.70	0.085
Shannon–Weiner evenness	2, 27	3.98	**0.031**
Shrubs (tall + dwarf)	2, 27	4.06	**0.029**
Tall shrub cover	1, 18	4.30	0.054
Dwarf shrub cover	2, 27	$\chi^2 = 5.23$	0.073
Forb cover	2, 27	52.02	**<0.001**
Cryptogam cover	2, 27	14.10	**<0.001**
Graminoid cover	2, 27	2.20	0.142

Note: Cover of forbs and graminoids had unequal variances and were analyzed using Welch's ANOVA. Cover of dwarf shrubs did not conform to assumptions for ANOVA, and the χ^2 (Kruskal–Wallis) is reported instead of F value. Bold values are significant at $P < 0.05$.

Data analysis

Vegetation community data was summarized by the following metrics: species richness, Shannon–Weiner diversity index, and Shannon–Weiner evenness index. When multiple measurements of ecosystem properties were taken per quadrat, the average was used in analysis. Significant differences were assessed across habitat types using a one-way analysis of variance (ANOVA) on each response variable, except the percent cover of forbs, graminoids, and dwarf shrubs; soil moisture; soil pH; and light interception, all of which failed to meet the ANOVA assumptions. Means of these responses were compared across all sites using nonparametric tests: Welch's ANOVA was used for all variables except dwarf shrub percent cover. Dwarf shrubs were not present in all dense and patchy habitats, and transformation did not improve normality; consequently, analysis for this variable was conducted with a Kruskal–Wallis test. For all other variables, ANOVA was performed on log transformed data when data did not meet the assumption of normality (percent cover of cryptogams and shrubs, and litter mass). When there was a significant effect of shrub habitat type, shrub habitats were compared using the posthoc Tukey's comparison of all means.

Results

Vegetation cover and shrub complexity

We observed 43 species including vascular plants, lichens, and bryophytes across all three sites. Species richness and Shannon–Weiner Diversity Index differences across the three shrub habitats were marginally significant (Table 1; Figs. 1*a*, 1*b*). The patchy site was the richest and most diverse, containing 19% more species than the dense site and 12% more diverse than the open site. The sites varied in evenness, with the dense site being most even and the open site being the least even (Table 1; Fig. 1*c*).

Total shrub cover was four times greater at the dense site compared to the open site (Table 1; Fig. 2*d*). The cover of tall shrubs was marginally higher at the dense site than the patchy site (Table 1; Fig. 2*e*) and these two sites varied in shrub complexity, with the dense site being almost two times more complex than the patchy site ($F_{1,18} = 4.770$; $P = 0.0435$). The open site had very few tall shrubs and none were observed along the transects. Dwarf shrub cover varied marginally, with the patchy site tending to have higher cover of dwarf shrub (Table 1; Fig. 2*f*).

Fig. 1. Plant community biodiversity variables (mean ± SE) including (*a*) richness, (*b*) Shannon–Weiner diversity, and (*c*) evenness, across sites varying in shrub density in the Kluane region of the Yukon Territory. Different letters indicate significant differences between vegetation sites (Tukey's comparison of all means).
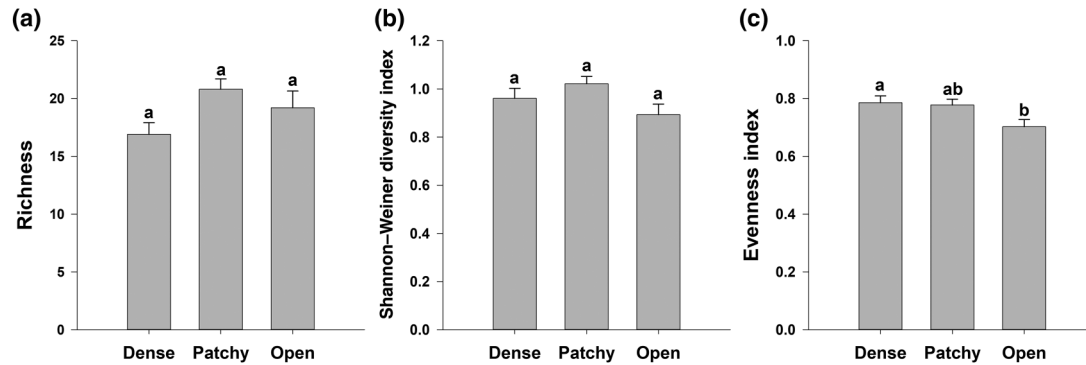

Fig. 2. Mean percent cover (mean ± SE) of different plant functional groups across sites varying in shrub density in the Kluane region of the Yukon Territory. Different letters indicate significant differences between vegetation sites (Tukey's comparison of all means). Analysis of variance performed on log-transformed data for (*c*) cryptogams, (*d*) shrubs, and (*f*) dwarf shrubs.
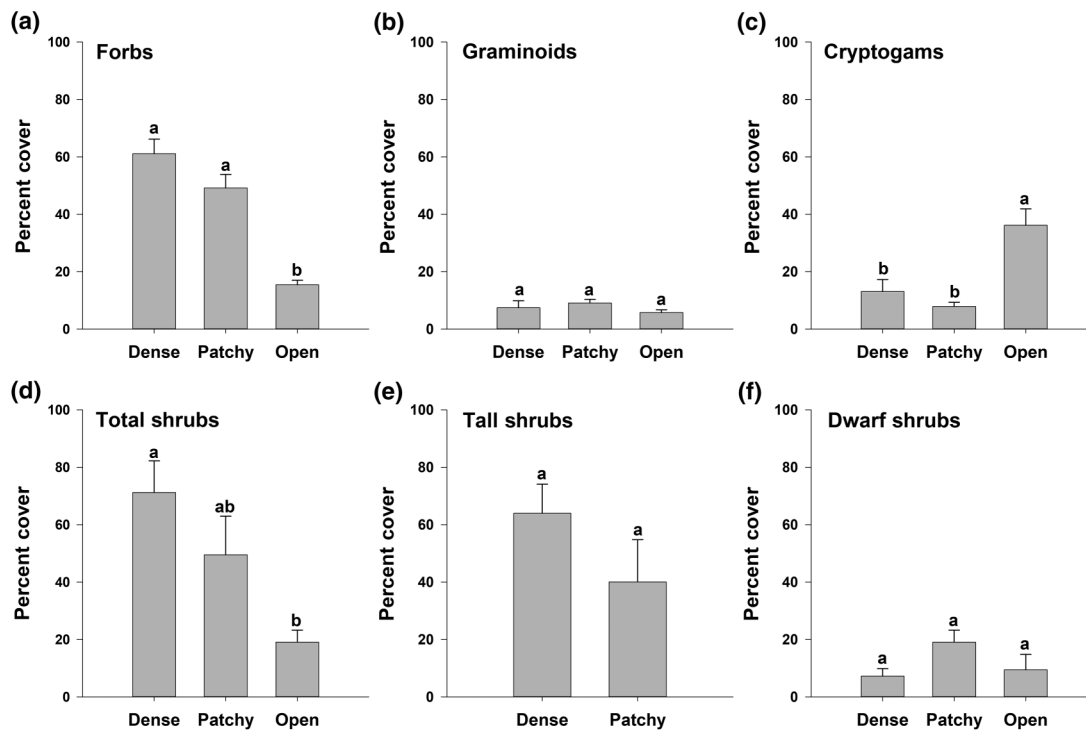
The open site had significantly lower forb cover than the dense and patchy site (Table 1; Fig. 2*a*) but higher cryptogam cover (4.5 times denser than the patchy site) (Table 1; Fig. 2*c*). The three sites did not vary significantly in graminoid percent vegetation cover (Table 1; Fig. 2*b*).

Table 2. Summary of one-way analysis of variances (ANOVAs) on ecosystem properties between sites varying in shrub density in the Kluane region of the Yukon Territory.

Ecosystem property	df	F	P
Organic soil depth	2, 27	1.56	0.228
Soil pH	2, 27	52.36	**<0.001**
Soil temperature	2, 27	7.83	**0.002**
Soil moisture	2, 27	16.20	**<0.001**
Litter weight	2, 27	8.02	**0.002**
Woody litter weight	1, 18	2.14	0.161
Non-woody litter weight	2, 27	5.82	**0.008**
Light interception	2, 27	80.77	**<0.001**
Extractable soil ammonium	2, 27	1.76	0.192
Extractable soil phosphate	2, 27	0.64	0.534
Soil percent nitrogen	2, 27	9.45	**0.008**
Soil carbon:nitrogen	2, 27	5.19	**0.012**

Note: Soil pH, soil moisture, and light interception failed to meet the assumption of equal variances and were analyzed using Welch's ANOVA. Bold values are significant at $P < 0.05$.

Ecosystem properties

Litter mass, percent light interception, and soil carbon-to-nitrogen ratio all increased with shrub cover, with the dense site containing more litter, intercepting more light, and having a higher carbon-to-nitrogen ratio than open site (Table 2; Figs. 3d–3f).

Soil pH did not differ between dense and open sites, although the patchy site had significantly lower pH (Table 2; Fig. 3a). Soil temperature was lower but soil moisture and nitrogen higher in the open site (Table 2; Figs. 3b, 3c, 3g). There was no significant difference between sites in organic soil depth, available ammonium, or available potassium among the three sites (Table 2; Figs. 3h, 3i). Available soil nitrate was below the minimum detectable levels at all sites.

Discussion

Vegetation cover and shrub complexity

Previous studies have found shrub abundance to negatively affect understory species richness (Walker et al. 2006; Anthelme et al. 2007; Myers-Smith 2011; Pajunen et al. 2011; Gough et al. 2012). While we also observed a negative effect on understory species richness with increasing shrub cover, our findings suggest that at low densities shrubs are associated with increased understory species richness. Understory species richness in this study is lowest at low elevations under dense shrub cover, is highest at intermediate elevations under patchy shrub cover, and drops to an intermediate level at high elevations in open alpine tundra. Effects on species richness are likely due to effects of both altitude and shrub density. This species richness pattern is commonly observed in altitudinal species richness studies, where the highest species richness is observed at intermediate elevations that often correspond to transition zones between two distinct habitats (Rahbek 1995; Lomolino 2001; Grytnes 2003). Transitional sites often are associated with a peak in species richness driven by the biotic interchange of species from both bordering habitats (Lomolino 2001). The establishment of a species outside the conditions where a self-propagating population exists [known as the mass effect (Shmida and Wilson 1985)] is often associated with the creation and maintenance of species rich communities along transition zones (Lomolino 2001). The patchy shrub site contained distinct patches of tall shrubs interspersed among alpine tundra meadow, representing an intermediate transition zone from shrubland to open

Fig. 3. Ecosystem properties (mean ± SE) across sites varying in shrub density in the Kluane region of the Yukon Territory. Different letters indicate significant differences between vegetation sites (Tukey's comparison of all means). Analysis of variance performed on log-transformed data for (*d*) litter Weight.
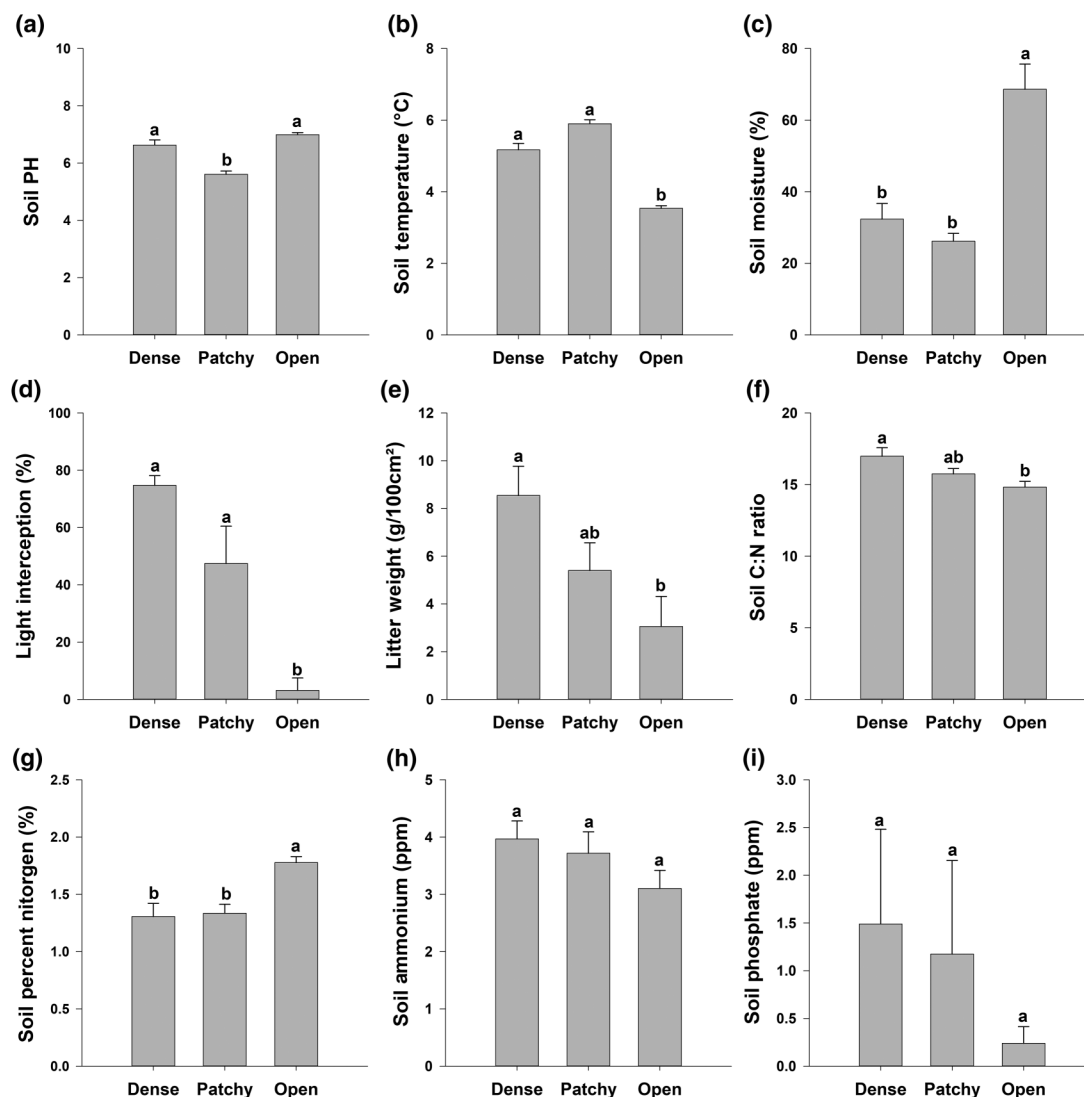
tundra and the observed peak in species richness is driven by the biotic exchange between both habitat types. However, the marginal differences in understory species richness among the three habitat types suggest that biotic interchange is modest in this region.

Although shrub density had marginal effects on understory community richness, there were large shifts in functional group abundance in the understory between shrub habitat types; forb cover increased while cryptogram cover decreased under shrub canopies. Similarly, willow shrub canopies along an alpine gradient in Norway had no effects on richness, but strong effects on community composition (Totland et al. 2004). We found higher forb cover in both shrub habitats than in open tundra, similar to a study by Pajunen et al. (2011) who argue that increases in forb cover result from their higher competitive ability for light, effective utilization of water, or shrubs providing shelter from herbivory and the

elements. Although forbs vary greatly in leaf area and stature, previous studies' suggest that relatively tall species with larger leaf areas drive the competitive advantage under dense shrub canopies and have found positive associations between forb species that contain these traits and shrub cover (Anthelme et al. 2007; Pajunen et al. 2011). In general, the dominant understory species we observed in the shrubland habitats (*M. paniculata, A. parviflora*, and *L. arcticus*), which were all forbs, have larger leaves and taller stature relative to the dominant understory species in the open tundra, which were all nonforbs, (*S. rotundifolia*, *E. arvense*, and *Carex* spp.). In contrast with the forb cover findings, cryptogam cover was lower in shrub habitats than open alpine tundra, also paralleling results reported by Pajunen et al. (2011). Lichen decline with increasing shrub cover is most likely due to shading by shrub canopies, as photosynthetic tissues only comprise a small part of the thallus, although increased litter under shrub canopies has also been linked to lichen decline (Chapin et al. 1995; Cornelissen et al. 2001; Pajunen et al. 2011). While some specific bryophyte species have been found to increase under shrub cover (Pajunen et al. 2011); at the functional group level, bryophyte decline has also been attributed to high levels of leaf litter and competition for light by vascular plants (van der Wal et al. 2005; Walker et al. 2006). We found dwarf shrub cover was marginally higher in the patchy shrubland than the other two habitat types, suggesting at low densities tall shrubs may facilitate dwarf shrubs, as found by Jonasson (1992) in a removal experiment. However, this positive effect was lost under high shrub densities, which also agrees with several previous studies where dwarf shrubs suffer under shading by shrub canopies (Totland et al. 2004; Pajunen et al. 2011; Elmendorf et al. 2012). These changes in understory functional group abundance may hold repercussions for tundra food webs and ecosystem functioning; for example, lichens are an important food source for caribou and reindeer and shrubification and the decline of lichen cover may hold negative implications for these species (Cornelissen et al. 2001).

Evenness of the understory community increased with increasing shrub density, with the forb-dominated understory community of the dense shrub habitat being most even. A study conducted in the French Alps found environmental heterogeneity decreased with increasing shrub cover, resulting in a convergence in understory community driven by the exclusion of specialist-adapted species (Anthelme et al. 2007). Here, we speculate that the interaction between shrub canopies and snow cover may be one mechanism in which shrubs lead to increased understory community evenness. Shrubs alter the transportation of snow by wind, through trapping and holding snow, resulting in greater snow depths (Sturm et al. 2001; Myers-Smith and Hik 2013). Alterations to snow accumulation by shrubs may result in the loss of snowbeds (topographical indentations characterized by increased snow accumulation, later spring thaw, and colder, wetter summer soils) and their associated unique vegetative community (Schöb et al. 2009). The loss of specialist species, which occur at low abundances across the habitat type, would result in increased understory community evenness. We found soil moisture in the open tundra habitat, the least even habitat type, to be the most variable (largest standard error) with certain plots having particularly high soil moisture content, characteristic of alpine snowbeds.

Ecosystem properties

We are unable to separate the effects of shrub density and elevation; the observed soil temperature increase and soil moisture decrease in the shrub habitats is likely, at minimum partially, driven by the lower elevations these habitats occupy. For example, the warmer air temperatures experienced in the lower elevation habitats may result in increased ground heat flux and greater evaporation rates, warming and drying the soils. Elevational air temperature effects on soil temperature are likely to have been

compounded through shrub–bryophyte interactions. Bryophytes are effective soil insulators, often directly affecting soil thermal and hydrological regimes (Gornall et al. 2007; Blok et al. 2011*b*; Bueno et al. 2016) and the reduction in cryptogam cover in the shrubland habitats we examined may promote increased summer soil temperatures. Increases in summer soil temperatures may be partially compensated by shading by shrub canopies (Blok et al. 2010; Myers-Smith 2011; Lantz et al. 2013). We also observed lower soil moisture in the shrubland habitats than the open tundra habitat. Shrubification may dry soils through increased evapotranspiration rates associated with increases in leaf area index compared to tundra vegetation (Chapin et al. 2000). However, shading by shrubs may also limit the amount of evaporation compared to shrub-free sites. Do to the nature of this observational study, we are unable to isolate the affects canopy shading and changes in cryptogam cover have on soil temperature and moisture. We encourage manipulative field experiments to gain insight on the mechanisms driving differences in summer soil microclimate resulting from changes in shrub cover.

Increases in shrub abundance may influence tundra nutrient cycling through altering the quantity and quality of litter and soil organic matter available for microbial decomposition. The soil at the dense shrubland had a higher C:N ratio and lower percent nitrogen than the other two sites, suggesting that the high litter quantity observed here did not result in greater nutrient inputs into the soil. Shrub litter has been suggested to be "low quality" litter, with characteristics such as a high lignin:N ratios (Hobbie 1996), and has been found to decompose more slowly than forb, grass, and sedge litter (Hobbie 1996; Cornelissen et al. 2007). Other studies, in contrast, have shown faster decomposition of shrub litter in the early stages of decomposition (Hobbie and Gough 2004; McLaren et al. 2017) which would result in increased nutrient inputs into soil, although later stage decomposition rates (after 5 years) were similar across tundra species (DeMarco et al. 2014). Finally, changes in abiotic conditions described above may also affect decomposition rates under shrub canopies, regardless of changes in litter quality, as litter decomposition is sensitive to both moisture (Makkonen et al. 2012) and temperature (Hobbie 1996).

Despite changes in both soil organic matter and soil microclimate, we did not find an effect of shrub density along the altitudinal gradient on available soil nutrients. Nutrient availability may be highest in the tundra immediately following spring thaw (McLaren et al. 2018) and this nutrient pulse has been found to differ between shrub and nonshrub communities with differences attributed to variation in snow accumulation, soil moisture, and soil temperature (Buckeridge and Grogan 2010). Our measurements were taken during peak growing season, when the majority of nutrients in the system are likely immobilized by microbes and vegetation is readily absorbing nutrients as they become available.

The potential effects of shrubs on soil properties are complex, and teasing apart the mechanisms driving these differences in ecosystem properties between the different shrub habitats will be difficult, especially given the conflicting results of studies done on different time frames [e.g., short-term vs. long-term decomposition (Hobbie and Gough 2004; DeMarco et al. 2014)], or in different seasons [e.g., postthaw effects vs. summer effects (Buckeridge and Grogan 2010; McLaren et al. 2018)]. Due to the observational nature of this study, it is important to note that our findings are limited in the cause-and-effect paradigm as observed differences may be driven by unquantified variables that covary along the shrub density gradient. We use the contrasting ecosystem properties between sites varying in shrub density to encourage more manipulative studies examining mechanisms that drive shrub effects on ecosystem properties, particularly those which sample at multiple times throughout the year, in order to predict effects of future shrub encroachment on ecosystem structure and function.

Conclusions

Here we conclude that shrub density has marginal effects on understory species richness but large effects on functional group abundance. While not significantly different than the dense or open habitat types, we found the highest understory species richness at intermediate shrub density, suggesting that the patchy habitat is a zonal transition and that the rich vegetative community is driven by biotic exchange of species from the distinct shrubland and open tundra habitats. With increasing shrub density we found a shift to forb-dominant understory community at the expense of cryptogams and dwarf shrubs. These forb-dominant communities are more even, suggesting that tundra species adapted to specific microenvironments, such as those characteristic of snowbed microclimates, may be at risk. The future state of understory communities will be dependent on the extent that shrubs are able to colonize and form dense canopies at range limits. We found differences in both summer soil microclimate and the composition of soil organic matter between communities with different shrub densities, but no relationship with soil available nutrients. Our results suggest that the shift to shrub dominance in tundra ecosystems may have no effect on decomposition rates, or that effects on decomposition rates do not translate to long-term differences in available soil nutrients. This study provides insight, adding to the global perspective, of how changes in shrub density may alter alpine tundra ecosystem structure and function from a nonmanipulated, model alpine system where shrubification has been documented.

Acknowledgements

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