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# Herbaceous Community Structure and Function in the Kluane Region

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**ABSTRACT.** Our research on the herbaceous understory vegetation in the Kluane region, Yukon, has focused on the structure and function of natural forest understory and grassland communities. The research has involved two long-term projects. The first investigated fertilizer addition and mammalian herbivore exclosure in understory vegetation over a 20-year period and showed that nutrient availability, and not herbivory, controlled herbaceous biomass. Fertilization increased the amount and nutrient content of vegetation, but 13 species were lost, whereas natural levels of mammalian herbivory rarely affected this vegetation or its diversity. The second study investigated how removing plant functional groups from a grassland influences its functioning. Over a seven-year period, we determined that the identity of the functional group was important in determining ecosystem properties and that graminoids were more influential than expected from their proportional biomass. In both of these studies, short-term responses were transient and not indicative of longer-term responses of these communities. This finding reinforces the need for long-term experiments, especially in northern ecosystems. The long-term plots from both projects will continue to be valuable, and they may detect shifts in the plant community due to climate change or unique events in the area.

**Key words:** boreal forest, bottom-up, ecosystem function, functional group, grassland, nutrient addition, species diversity, removal experiment, top-down

**RÉSUMÉ.** Notre recherche sur la végétation herbacée de sous-bois dans la région de Kluane, au Yukon, a porté plus précisément sur la structure et la fonction des communautés de forêt naturelle de sous-bois et d'herbages. Cette recherche était composée de deux projets à long terme. Le premier projet consistait à étudier l'ajout de fertilisant et l'exclus de mammifères herbivores dans la végétation de sous-bois sur une période de 20 ans, ce qui a permis de montrer que la disponibilité de nutriments, et non pas l'herbivorisme, contrôlait la biomasse herbacée. La fertilisation a ainsi eu pour effet d'accroître la quantité de végétation ainsi que sa teneur en nutriments, mais 13 espèces ont été perdues, tandis que les taux naturels d'herbivorisme chez les mammifères ont eu peu d'incidences sur cette végétation ou sa diversité. Le deuxième projet consistait à étudier comment le retrait de groupes végétaux fonctionnels dans les herbages influence leur fonctionnement. Pendant une période de sept ans, nous avons déterminé que l'identité du groupe fonctionnel jouait un rôle important dans la détermination des propriétés de l'écosystème et que les graminoides exerçaient une plus grande influence que prévu à partir de leur biomasse proportionnelle. Pour ces deux projets, les réactions à court terme étaient transitoires et non indicatives des réactions à plus long terme au sein de ces communautés. Cette constatation renforce la nécessité de faire des expériences de longue échéance, surtout dans les écosystèmes nordiques. Les résultats à long terme de ces deux projets continueront de revêtir de l'importance et pourraient permettre de déceler des variations sur le plan de la communauté végétale, variations attribuables à des changements climatiques ou à des événements uniques susceptibles de se produire dans la région.

**Mots clés :** forêt boréale, ascendant, fonction de l'écosystème, groupe fonctionnel, herbages, ajout de nutriments, diversité des espèces, expérience de retrait, descendant

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## INTRODUCTION

We have studied the boreal forest understory and grassland vegetation at Kluane, Yukon, since 1990, examining questions about how natural communities are structured

and how they function. We have worked specifically on the grasses and herbs, which are moderately abundant in the understory and nearby grasslands, and which provide a source of relatively high quality food to herbivores, especially in summer. However, the productivity

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of this vegetation is often limited by soil nutrients, especially nitrogen. Plants differ in their abilities to respond to increased nutrient levels, and the community composition response to fertilization is that competitive species become more dominant. Nutrient availability may also influence the ability of species to produce chemicals that deter herbivores and to regrow after herbivory. In addition, herbivory directly affects vegetation quantity and quality.

## UNDERSTORY PLANT COMMUNITY STRUCTURE

To understand some of the linkages between trophic levels in the boreal forest ecosystem, three hypotheses regarding the vegetation were tested (Sinclair et al., 2000; Turkington et al., 2002). The first, the “bottom-up” or resource-control hypothesis, suggests that vegetation is regulated only by nutrient flow from the soil and that the higher trophic levels (herbivores) have no regulating effect on plant productivity or biomass. The second, the “top-down” or consumer-control hypothesis, assumes that top predators are self-regulating and that each level regulates the level below; thus, the plants are limited by herbivores, rather than by nutrients. The third hypothesis is that the vegetation is controlled by both nutrients and herbivores. There are many other models that involve variations and combinations of the top-down and bottom-up hypotheses (e.g., Oksanen et al., 1981; Carpenter et al., 1985; Fretwell, 1987; Oksanen, 1990; Turkington, 2009). Testing these hypotheses involved three experimental treatments: fertilization (reducing limitation by nutrients), herbivore exclusion (removing limitation by herbivory), and fertilization plus herbivore exclusion. These treatments allowed specific predictions about changes in the plant biomass or standing crop under the three hypotheses (Table 1). In some cases, however, response was also assessed using changes in rates of plant turnover, plant nutrient content, or secondary compounds. Between 1990 and 2010, most of these hypotheses were tested directly in the field. Here we present some of the major findings.

### Study Area and Experimental Design

The vegetation in our area is mainly boreal forest dominated by white spruce (*Picea glauca* (Moench) Voss), with an understory dominated by grey willow (*Salix glauca* (L.)) and dwarf birches (*Betula nana* L. and *B. glandulosa* Michx.). The forest herb layer includes *Lupinus arcticus* S. Wats., *Festuca altaica* Torr., *Mertensia paniculata* (Aiton) G. Don, *Anemone parviflora* Michx., *Achillea millefolium* L. ssp. *borealis* (Bong.) Breitung, *Linnaea borealis* L. ssp. *americana*, *Arctostaphylos uva-ursi* (L.) Spreng., *Epilobium angustifolium* L. s.l., and *Solidago multiradiata* Ait., as well as some dwarf shrubs. Most of the studies described were done at two sites with moderately open forest and a well-developed herbaceous understory, and they focused primarily on the understory, without monitoring large

shrubs (> 1 m tall) or trees. Both sites were probably last burned in 1872 (Francis, 1996; Dale et al., 2001). Details of the sites and design are provided by John and Turkington (1995, 1997) and Turkington et al. (1998, 2001, 2002). In 1990, sixteen 5 × 5 m plots were selected in small meadows at each site. At each site, the plots were randomly divided among four treatments: control (no treatment), fence only, fertilizer only, and fence with fertilizer. Fences 1 m high, made of galvanized chicken wire with 2.5 cm mesh, were designed to exclude snowshoe hares, the major herbivore in this ecosystem. Fertilizer (N:P:K 35:10:5) was applied in granular form each year after snowmelt (between mid May and early June) at a rate of 17.5 g N/m<sup>2</sup>/yr, 5 g P/m<sup>2</sup>/yr and 2.5 g K/m<sup>2</sup>/yr. This application rate was used to be consistent with other studies being done in our area (Boutin et al., 2001). Because the project was designed for the long term, we could not use destructive sampling procedures, so percent cover was used as a measure of abundance. The major plant study began in 1990 and continues to date; in 20 years, the study has spanned two complete snowshoe hare cycles and three peaks in hare population density (Boonstra et al., 2014).

*Hypothesis 1: Vegetation is controlled by nutrient availability alone.*

Fertilization resulted in an increase in the amount of herbaceous vegetation, but responses were variable among species, and species richness declined from 29 to 16, a loss of 56%, over 20 years (Fig. 1). Ten of the 11 most abundant species showed a significant fertilizer effect, four increasing in response to fertilizer (*Mertensia*, *Festuca*, *Achillea*, and *Epilobium*) and most others declining (Fig. 2), especially the prostrate shrubs *Linnaea* and *Arctostaphylos*, along with *Anemone*, *Lupinus*, mosses, and *Peltigera* (an N-fixing lichen). Immediate, or transient, responses were not indicative of longer-term responses. Some species showed an initial positive or neutral response to fertilizer, which later reversed (e.g., *Festuca*, *Linnaea*); others, such as *Epilobium*, did not show a significant increase until the fifth year. Plant species were measured as percent cover, and changes in abundance may be due to either increases in the size of individuals, increases in the abundance of individuals, or a combination of the two. Arii and Turkington (2002) showed that the addition of any amount of fertilizer is detrimental to individuals of *Anemone*. Fertilizer effects on herbs in the boreal forest are clearly highly individualistic. However, it is evident that long-term fertilization causes a decline from a community with a moderate number of plant species to a community of low richness dominated by *Epilobium* and *Mertensia*. In general, the untreated community is rather static, but even in the control plots, species such as *Anemone* and *Lupinus* fluctuate from year to year (John and Turkington, 1995; Turkington et al., 1998, 2001, 2002).

A bottom-up hypothesis predicts that the exclusion of mammalian herbivores imposed by fencing would result

TABLE 1. Predicted and observed overall change in plant biomass or nutrient content from each of the three experimental treatments in relation to the three hypotheses. The plus sign (+) indicates biomass increase, and zero (0) indicates no change. Since the response to treatments varied from species to species, this table summarizes the overall direction of change.

Hypothesis:	Fertilizer added		Herbivores excluded		Fertilizer added and herbivores excluded	
	Predicted	Observed	Predicted	Observed	Predicted	Observed
Bottom-up, donor control	+	Supported	0	Supported	+	Not supported
Top-down control	0	Not supported	+	Not supported	+	Not supported
Interactive control	+	Partial support	+	Not supported	+	Not supported

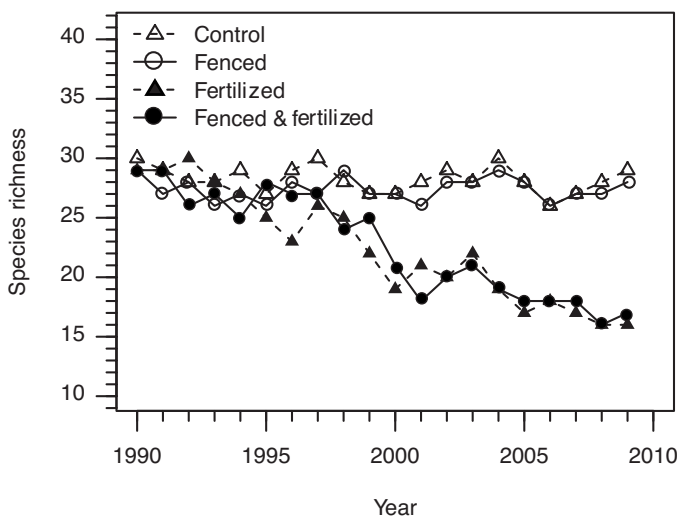


FIG. 1. Species richness (number of species) in plots subjected to fertilization and enclosure treatments from 1990 to 2009. Solid symbols are fertilized plots, and open symbols, unfertilized plots. Triangles with dashed lines are unfenced plots, and circles with solid lines are fenced plots. Based on Turkington et al. (2002).

in no change in the vegetation. After 20 years of herbivore exclusion, this prediction seems verified (Turkington et al., 2002; deKoning, 2011). Likewise, that hypothesis predicts that vegetation removal should increase soil nutrient levels, and Secombe-Hett (1999) has verified that nitrate nitrogen levels were significantly higher ( $p < 0.1$ ) in those plots from which the vegetation was removed.

#### Hypothesis 2: Vegetation is controlled by herbivory alone.

We tested the predictions of this hypothesis that the vegetation standing crop would not increase with fertilizer, but would increase in hare enclosures. Both predictions were rejected for herbivore densities in the normal range, but a herbivore effect could be “forced” when snowshoe hare densities were increased to artificially high values (John and Turkington, 1995; Dlott and Turkington, 2000). Nevertheless, the understory vegetation does produce anti-herbivore compounds. Sharam and Turkington (2005, 2009) showed that *Lupinus* had a daily cycle of sparteine production, and spruce (*Picea glauca*) had an annual cycle of camphor production, both reaching their highest levels during the periods of highest grazing pressure: “nighttime” for *Lupinus* and winter (October to April) for spruce (Fig. 3).

#### Hypothesis 3: Vegetation is controlled by both nutrient availability and herbivory.

For this hypothesis, we must discriminate between plant standing crop or biomass (amount of vegetation present at a particular time) and plant productivity (the rate at which vegetation is produced). Productivity can be increased by fertilization, but the standing crop remains unchanged if the additional biomass is consumed by herbivores. This complication means that detailed and frequent monitoring of individual species populations was needed to test the hypothesis, and it makes a whole community test almost impossible. In one study (John and Turkington, 1997), we monitored 700 individuals of *Anemone* and 854 individuals of *Mertensia*, and in another, Graham and Turkington (2000) monitored 320 clumps of *Lupinus*. These are common herbaceous species in the community that are eaten by snowshoe hares (Secombe-Hett and Turkington, 2008). In the John and Turkington (1997) study, both species responded more strongly to fertilizer addition than to herbivore exclusion, but a significant interaction effect of fertilizer and enclosure was detected. In fertilized plants, there is evidence of higher leaf turnover: production of more buds in spring and a more rapid decline in the number of leaves at the end of the growing season. The prediction that plant productivity would increase in fertilizer plots but biomass would remain unchanged was verified for *Mertensia*, but rejected for *Anemone* and *Lupinus* (Hicks and Turkington, 2000).

#### Summary of Evidence

Most of our findings support the bottom-up hypothesis, in that herbaceous standing crop is controlled by nutrients. After 20 years of fertilization, there was an overall increase in the amount and nutrient content of herbaceous vegetation (deKoning, 2011). Some herbs (*Mertensia*, *Epilobium*) increased mostly at the expense of low-growing, woody ground cover species such as *Linnaea* and *Arctostaphylos*, but also of other species, such as *Lupinus*, and the grass *Festuca* increased for the first three to four years, but then went into a long decline (Figs. 2, 3). We recorded a loss of 13 species from the fertilized plots (Fig. 1), and the evenness of the fertilized plots declined markedly, indicating that some species decrease in abundance even when they are still present. The repeated application of fertilizer reduces the abundance of many species and may ultimately

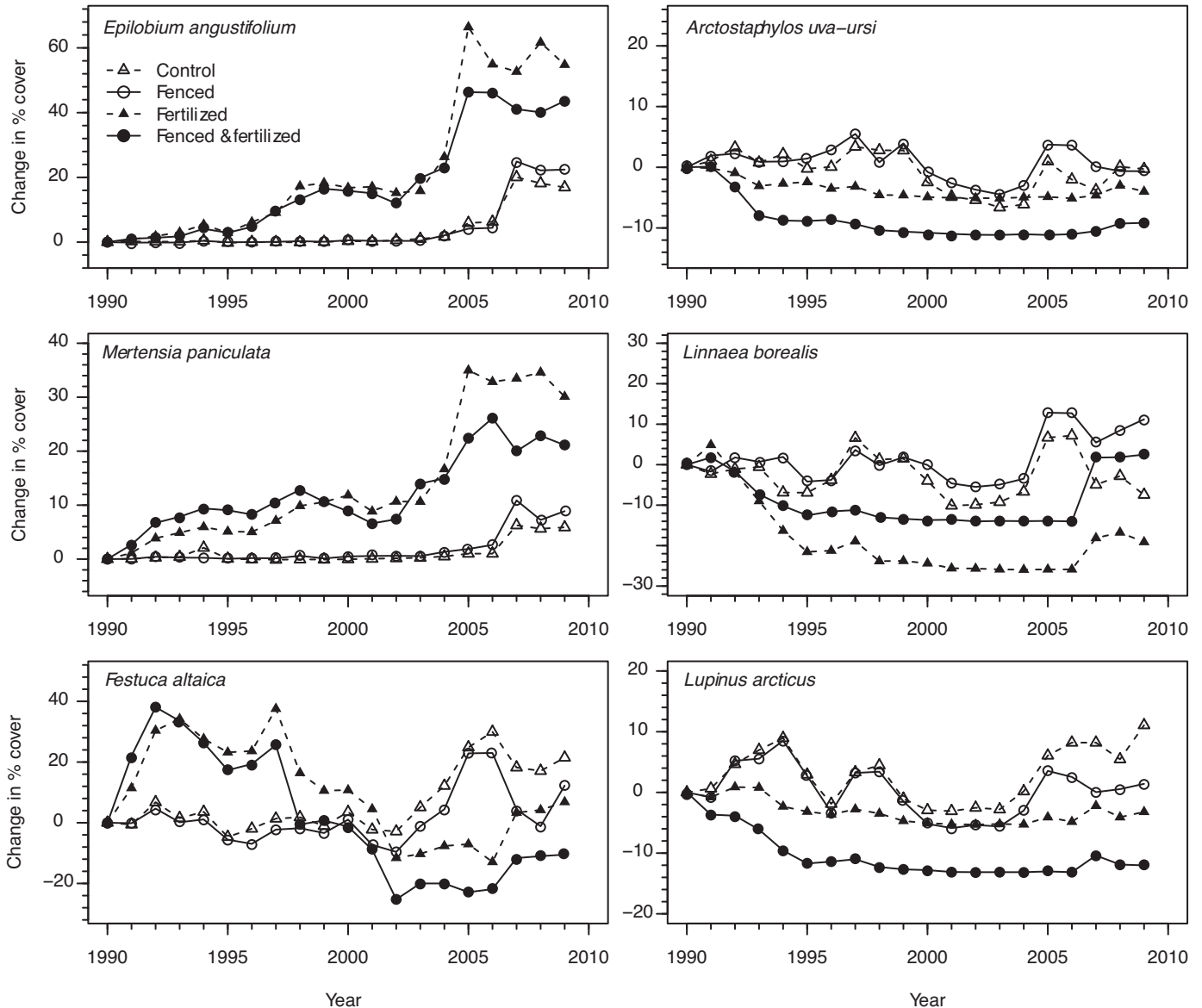


FIG. 2. Change in percent cover of six species, (left) three that initially increased and (right) three that initially decreased, in response to fertilization treatments from 1990 to 2009. Plots were treated from 1990 to 2009. Solid symbols are fertilized plots, and open symbols, unfertilized plots. Triangles with dashed lines are unfenced plots, and circles with solid lines are fenced plots. Error bars have been omitted for clarity. Based on Turkington et al. (2002).

exclude some from the plots as more aggressive species become dominant. However, effects of fertilization are not apparent in other areas. For example, germination rates of seeds collected from fertilized *Epilobium* are not different from those of seeds collected from control plants (Grainger and Turkington, 2012). There were also few effects on phenology; after 16 years of fertilization, only in *Epilobium* did phenological stages occur earlier than in control sites (Fremlin et al., 2011).

There is little evidence that natural levels of mammalian herbivory limit herbaceous vegetation in the Kluane region or affect community diversity, except perhaps during some snowshoe hare peak years. Other studies have shown that herbivory nevertheless has an impact on the shrubs and trees in this region, particularly during the winter when they are the only vegetation available for browsing because of snow

cover. Moderate browsing by snowshoe hares stimulates growth in *Salix* and *Betula*, but during peak years, herbivore pressure on shrubs is intense and results in large negative effects on growth (Dale et al., 2001; Krebs et al., 2001).

Few interactions between exclosure and fertilization were noted; additional growth due to fertilization was not generally removed by herbivores, vegetation abundance rarely increased inside exclosures, and plots that were both fenced and fertilized did not have the lowest species diversity.

In early 2000, after 10 years of treatment, the set of plots described above was divided in two; treatments were continued on half of the plots and discontinued on the other half. The objectives of this modification were to determine the long-term influences of fertilization and herbivory on the plants and the soil microbial community and to monitor



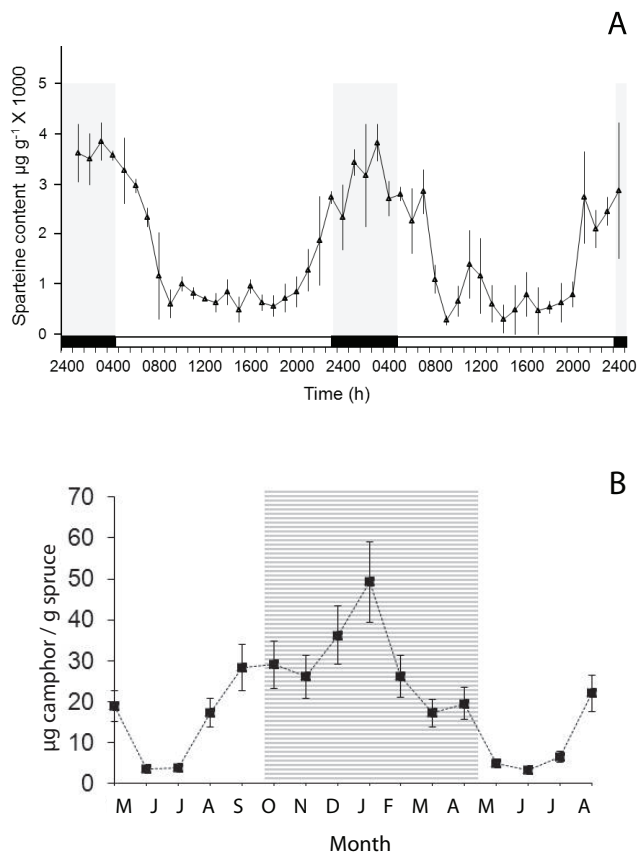


FIG. 3. Fluctuations in anti-herbivore compounds in Arctic lupine (*Lupinus arcticus*) and white spruce (*Picea glauca*). (A) Mean ( $\pm$  SD) sparteine concentrations of dried Arctic lupine samples over a 48-hour period (24–25 June 1995) (modified from Sharam and Turkington, 2005). (B) Camphor concentration ( $\pm$  SE) of 20 white spruce trees, each 6 to 10 m tall, sampled monthly for 16 months in 1995–96. Shading indicates winter months (late September to early April) (modified from Sharam and Turkington, 2009).

the trajectories of these communities after treatments were discontinued. In 2009, deKoning (2011) surveyed plant community composition and analyzed measures of plant tissue chemistry. In addition, he measured the composition and activity of the soil microbial community and the pH and nutrient availability of the soil. Fertilization caused significant changes in the plant community, as described above, and significant alteration of the chemical composition of plant tissue. A decade after treatments ceased, fertilizer plots were showing signs of recovery towards control values in plant community composition and plant tissue quality, but the signs were small. The recovery of the system followed a “cascade of recovery,” beginning with soil chemistry, followed by foliar tissue chemistry, the plant community, and finally the soil microbial community. The detailed results of this study will appear elsewhere.

#### Additional Structuring Factors

In a separate study, conducted in the same general study area, we approached the question of controls over herbaceous plant community structure using a novel experimental approach (Treberg, 2007; Treberg and Turkington, 2010a).

Most studies of density-dependent regulation in plants consider the density of only a single target species, but Treberg and Turkington tested whether regulation can also occur at the level of the entire community. In 1999, on a set of 63 one-meter square plots, we created a series of initial community densities above ( $2\times$ ) and below ( $1/16\times$ ,  $1/8\times$ ,  $1/4\times$ ,  $1/2\times$ ) the average natural field density ( $1\times$ ) by manipulating the abundance of the nine most common species (transplanting or removing them) so that the relative proportions of these nine species were consistent for all densities. At the community level, negative density dependence of mean plant size (i.e., bigger plants at lower densities) was observed for each of the four years of the study, and both the intensity and the importance of competition increased each year. Similarly, at the species level, the mean plant mass of most species was negatively density-dependent. Treberg’s (2007) results demonstrated that density-dependence (actually biomass-dependence) operates at the entire community level and regardless of initial densities; after four years, plots converged to a constant biomass equal to the natural ( $1\times$ ) density (Fig. 4). Facilitation was also an important factor in determining community structure, as shown in a related study (Treberg and Turkington, 2010b).

Although there was convergence of biomass in these plots, species composition remained different for each of the different density treatments. This study area was most recently burned about 80 years ago, and the initial post-fire colonization would have depended on the time of year, the location and abundance of species able to disperse into the site, and the composition of the seed bank. This plant community is primarily made up of perennial plants, and after its establishment, clonal growth would have influenced community composition more than seed dispersal and seedling establishment; it was quite likely still highly influenced by the founder populations after 10 or 20 years. Similarly, after treatment perturbations, subsequent colonization may have been strongly influenced by the same uncontrolled factors. Although competition is clearly an important factor, stochastic effects and “ecological memory” (Hendry and McGlade, 1995) probably also play a large role in the structure of this boreal forest understory community.

Gilbert et al. (2009) extended these studies by investigating how established species in this system may influence colonization by new species. Studies have shown that some communities inhibit new establishment by competition, while others may facilitate colonization (Smith et al., 2004). Furthermore, it is not clear which attributes of community composition are most important in determining such community effects on species establishment: diversity, individual dominant species, and neutral interactions have all been suggested as the most important. Gilbert et al. (2009) developed six different hypotheses based on competition theory, facilitation theory, community diversity, and dominant species. These six hypotheses were difficult to distinguish experimentally, because manipulations of either diversity or dominance change other community properties, such as biomass, as well.

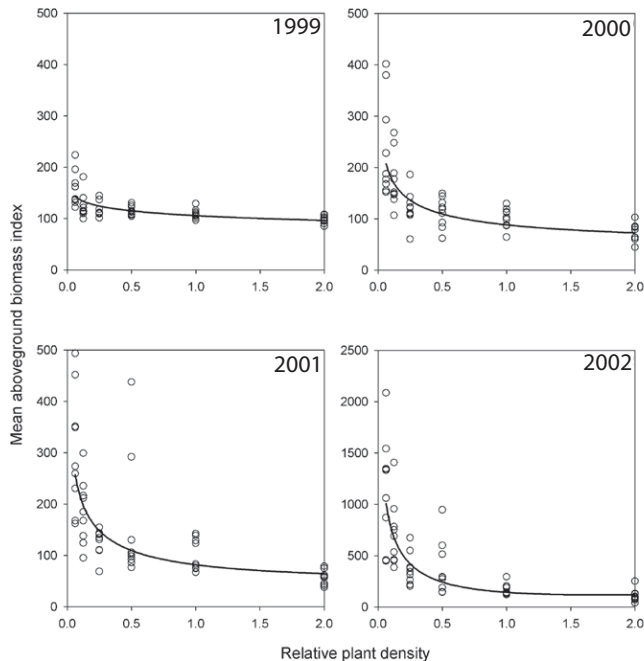


FIG. 4. The effect of initial community density on the mean aboveground plant biomass index (aboveground biomass (g) per plot divided by the community density) for 1999 to 2002. Best-fit lines shown are statistically significant ( $p < 0.001$ ). No significant slope would be expected in the absence of interactions, and a negative slope suggests negative density dependence or competition. Note that the scale for the Y-axis in 2002 is different than for other years. In all years, competition began to reduce mean plant size at  $1/8\times$  the natural community density ( $1\times$ ). In 2001 and 2002, two and three years, respectively, after treatments were initiated, the community reached carrying capacity at approximately the natural density (M.A. Treberg and R. Turkington, unpubl. data).

Gilbert et al. (2009) disentangled the relative contributions of these mechanisms by removing plant biomass (0%, 7%, 100%) from similar boreal forest understory communities. The community studied had two consistently abundant species and several (7–12) rarer species per experimental plot. Removals were conducted in 2004 within each category and were restricted either to the numerically dominant species (species with the highest density), the second most dominant species, or the many low abundance species, thereby separating the effects of species composition from those of biomass. They tested the effects of removal treatments on seedling establishment and survival over the following three growing seasons. The transplanted seedlings included both exotic and native herbs and grasses that were functionally similar to the low-abundance species already present. Competitive effects were driven by one of the abundant species, but were inconsistent with three commonly evoked models of the competition (resource complementarity, competition-colonization trade-off, and neutral models). Removal of many rare species (i.e., reducing species richness) had no effect. Facilitative effects were apparent only following removal of all vegetation, of which the most abundant species comprised more than 80%. These results indicate that abundant species in a community can influence the establishment of new species more than species diversity per se, but the interaction can shift from

facilitative to competitive as the density of the abundant species increases.

#### PLANT COMMUNITY FUNCTION: INFLUENCE OF BIODIVERSITY

Loss of biodiversity has led to concerns that species-impooverished systems will perform less well or less efficiently than their counterparts with a full complement of species. In addition to changes in species number, the composition of communities is also changing; species are being lost, but are also moving into novel environments (e.g., plant invasions, movement of tree lines resulting from global change). These changes in the richness and composition of plant communities are likely to have strong effects on the structure and function of ecosystems. To investigate these questions, we used a removal experiment called a “functional group knock-out.” This was achieved by removing plant functional groups (graminoids, leguminous forbs, and non-leguminous forbs) individually and observing subsequent changes in community dynamics and ecosystem function.

#### Study Area and Experimental Design

This study was done in a dry, open grassland about 15 km north of the previously described sites, on the eastern side of Kluane Lake. The grassland is dominated by *Poa glauca* Vahl and *Carex stenophylla* Wahlenb. subsp. *eleocharis* (Bailey) Hultén, and also contains many non-leguminous forbs (*Erigeron caespitosus* Nutt., *Artemisia frigida* Willd., *Penstemon gormanii* Greene, and *Pulsatilla ludoviciana* (Nutt.) A. Heller), and legumes (dominated by *Oxytropis campestris* (L.) DC.)

The objective was to examine the roles of different plant functional groups in determining ecosystem properties. Species loss is currently happening globally in concert with environmental change, but also as a result of it (e.g., species loss with nitrogen deposition, Hooper et al., 2005). It is important to examine whether the role of the functional groups will be different in different environments (i.e., whether the role of functional group identity is context-dependent). We removed functional groups from the community singly, and we used the difference between the ecosystem properties of a community with a functional group and without it as a measure of that group’s influence. Individual plants were initially removed from 80 plots (each  $1\text{ m}^2$ ) in 2004, using Roundup™ glyphosate non-selective herbicide applied precisely so as not to affect adjacent plants, and removal treatments have been maintained by hand annually to date. Functional groups made up different proportions of the initial biomass, with forbs having the highest abundance, followed by grasses and then legumes. We examined the effects of removals across different environments created by using a fertilization treatment (detailed in McLaren and Turkington, 2010a). The measures of

ecosystem function were the following: above-ground biomass; above and below-ground litter decomposition; nutrient supply rates measured by ion exchange membranes; soil moisture; available soil nutrients; microbial biomass nitrogen and phosphorus; and soil microbial community composition, using both MicroResp™ plates and phospholipids fatty acid (PLFA) analysis.

Remaining functional groups did compensate for the loss of biomass from removal treatments, but the degree of compensation depended on the groups removed and those remaining (McLaren and Turkington, 2010a). In the first four years after removals, biomass had not fully recovered in any of the removal treatments, with biomass recovery in the forb removal plots being particularly slow (McLaren and Turkington, 2010a) because of slow recolonization by the graminoids. Plant composition continued to change, however, and after seven years, there was full biomass compensation in all removal plots except where the forbs, originally the most dominant functional group, had been removed (McLaren and Turkington, 2011a).

In addition to biomass recovery, functional group identity influenced other ecosystem properties within the first four years after removals. Graminoids had a greater impact on ecosystem properties than was expected from their proportional above-ground biomass in the community. Soil moisture, light interception, and soil nutrients (including N, P, K) were all influenced by functional group identity (Fig. 5). The results of this study contrasted with those of many other biodiversity studies, in that legumes had very little effect on the ecosystem properties measured (McLaren and Turkington, 2010a). It has been suggested that the strong effects of legumes in other studies may have resulted from the use of artificial communities, with legumes at higher-than-natural abundances (Diaz et al., 2003). Graminoids also had the strongest impact of any functional group on decomposition, with effects through a variety of mechanisms. We found significant positive effects on leaf decomposition through changes in the decomposition environment for both forbs and graminoids (McLaren and Turkington, 2010b, 2011b). We also found positive effects of graminoids on leaf decomposition through their influence on litter species composition: graminoids both decomposed faster than forbs in monoculture and showed positive, non-additive effects of mixing with litter from other functional groups (McLaren and Turkington, 2011b). Finally, for most ecosystem properties measured, functional group effects were not context-dependent, and functional groups had the same effect on ecosystem properties regardless of fertilization treatments (McLaren and Turkington, 2010a, 2011b).

The soil community is often ignored as part of biodiversity and ecosystem functioning despite its influences on important ecosystem functions, including decomposition and nutrient cycling. Although functional group removals had numerous effects on abiotic ecosystem properties, they had little effect on the structure and diversity of the soil microbial community after five years (Marshall et al., 2011), as measured by substrate-induced respiration (a measure of

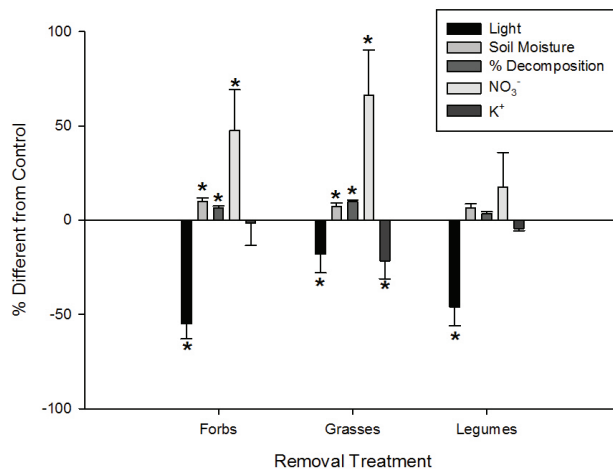


FIG. 5. Difference (%) in five ecosystem properties between plots from which a single functional group (forbs, grasses, or legumes) has been removed and control plots (no removals). Light interception and soil moisture measurements are presented only for data collected in late July in the fourth year after removals. Percent decomposition, nitrate, and potassium values are cumulative growing-season measurements averaged across the first four years of the removal experiment. An asterisk (\*) directly above or below a bar indicates a value significantly different from zero.

metabolic diversity) and phospholipid fatty acid analysis (a measure of microbial community composition). Marshall et al. (2011) suggest that the soil community in this northern Canadian grassland is relatively insensitive to changes in plant community composition, and they hypothesize that in northern ecosystems, where slow decomposition rates mean plant material is only slowly incorporated into the soil, five growing seasons may not provide adequate time to detect the impact of a changing plant community on soil microbes.

## IMPLICATIONS

### *Global Warming and Biodiversity*

It has been suggested that the application of nutrients to northern communities may simulate some of the same effects in the plant community that might be produced by global environmental change (Aerts and Berendse, 1988; Berendse and Jonasson, 1992; Berendse, 1994). Global changes such as increasing CO<sub>2</sub> concentrations, increasing deposition of nitrogen and sulphur pollutants, and rising temperatures will have crucial impacts on nutrient cycles, leading to changes in primary production and species composition. Berendse and Jonasson (1992) argue that climate change will increase the supply of nutrients in northern ecosystems by stimulating decomposition processes, although this response is likely to interact strongly with potential changes in soil moisture (Nadelhoffer et al., 1992). These changes will be modified by the interactions between plants and their environment.

There are limitations, however, to attempting to extrapolate results from experiments that increase nutrient availability with fertilizer to predicting the effects of global



change. Fertilization experiments, including the ones described here, often apply nitrogen and other nutrients at higher levels than might be expected with the above-described changes, in order to induce a response within a shorter environmental time frame. In addition, increased nutrient availability is not likely to be the sole change to ecosystem properties; global change includes potential changes in temperature, precipitation, CO<sub>2</sub> concentration, and other factors. These factors are likely to interact with each other to produce effects on ecosystems not easily predicted from current experimental manipulations (Shaver et al., 2000).

Information about the potential effects of increased nutrient availability, especially in northern ecosystems, may nonetheless be informative of potential community change. In the Kluane region, we might expect that increased nutrient availability will result in the suppression (or elimination) of bryophytes, lichens, prostrate growth forms, and species with low nutrient requirements by faster-growing, more upright clonal species, such as graminoids and the tall forbs *Epilobium*, *Mertensia*, and *Achillea*. Species and vegetation types with low nutrient demands will be the most sensitive to the predicted changes. Increases in shrubs such as *Salix* and *Betula* have also been documented at numerous circumpolar sites (Myers-Smith et al., 2011), and we can only speculate about the consequences of this potential additional food supply on the snowshoe hare cycle.

### *The Value of Long-Term Experiments*

Among the ongoing long-term experiments in northern ecosystems are the LTER experiments at Toolik Lake, Alaska (Shaver et al., 2001), the International Tundra Experiment (ITEX) at a number of circumpolar sites (Arft et al., 1999), and long-term experiments at Abisko, Sweden (e.g., Shaver and Jonasson, 1999). To our knowledge, our experiments are the longest running experiments of their kind in the boreal forest understory. A common conclusion from many of these experiments is that short-term responses are not necessarily indicative of the longer-term responses in these systems (e.g., Toolik Lake: Shaver et al., 2001; ITEX: Elmendorf et al., 2011). In our experiments, initial responses to fertilizer, fencing, and removal treatments are both species-specific and transient. The short-term responses measured over the first few years were poor indicators of longer-term changes in community composition, and perhaps the current 20 years (seven years for the functional group knock-out experiment) will be a poor indicator of longer-term trends. Conclusions might differ had the data been collected after one year (beginning of the hare decline), five years (during a hare low), or 10 years (during a hare peak), but the general trends identified are important. It is likely that ecosystems such as the boreal forest understory, where the herbaceous community is characterized by slow-growing, long-lived plants, never attain equilibrium because the density of hares fluctuates, forests burn, and climate is slowly but constantly changing. This means that

transient responses may be the only ones we have to work with, because permanent shifts in vegetation composition may not be evident until many years later, or a steady state may never be attained.

Another particular value of long-term studies is their potential to provide insight into rare events or episodic phenomena. In 1995, we observed the first major signs of an outbreak of spruce bark beetle. As mature trees die and the canopy becomes more open, light penetration will undoubtedly influence processes at ground level. *Achillea* and *Epilobium* were both minor components of the understory vegetation of our plots until that time, but in 2006, both of these species showed dramatic increases in the fertilized plots. Both species are more typically associated with open areas, and the opening of the canopy, in combination with increased soil fertility, probably stimulated their increase.

Many ecological processes occur slowly, especially in the boreal forest, and therefore initial measurements are unlikely to reflect more sustained long-term responses. This fact will be especially critical in boreal or other high-latitude communities, where the rate of response to ecological processes is slowed by low temperatures and short growing seasons. Such long-term experiments and long-term monitoring studies are particularly critical in systems where the species are long-lived, slow-growing, and have limited rates of dispersal and establishment.

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### REFERENCES

- Aerts, R., and Berendse, F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio* 76:63–69.
- Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., et al. 1999. Responses of tundra plants to experimental warming: A meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69(4):491–511.  
<http://dx.doi.org/10.2307/2657227>
- Arii, K., and Turkington, R. 2002. Do nutrient availability and competition limit plant growth of herbaceous species in the boreal forest understory? *Arctic, Antarctic, and Alpine Research* 34(3):251–261.  
<http://dx.doi.org/10.2307/1552482>



- Berendse, F. 1994. Competition between plant populations at low and high nutrient supplies. *Oikos* 71(2):253–260.  
<http://dx.doi.org/10.2307/3546273>
- Berendse, F., and Jonasson, S. 1992. Nutrient use and nutrient cycling in northern ecosystems. In: Chapin, F.S., III, Jefferies, R.L., Reynolds, J.F., Shaver, G.R., and Svoboda, J., eds. *Arctic ecosystems in a changing climate: An ecophysiological perspective*. San Diego: Academic Press. 337–356.  
<http://dx.doi.org/10.1016/B978-0-12-168250-7.50022-5>
- Boutin, S., Krebs, C.J., Nams, V.O., Sinclair, A.R.E., Boonstra, R., O'Donoghue, M., and Doyle, C. 2001. Experimental design and practical problems of implementation. In: Krebs, C.J., Boutin, S., and Boonstra, R., eds. *Ecosystem dynamics of the boreal forest: The Kluane project*. New York: Oxford University Press. 49–66.
- Boonstra, R., Dantzer, B., Delehanty, B., Fletcher, Q.E., and Sheriff, M.J. 2014. Equipped for life in the boreal forest: The role of the stress axis in mammals. *Arctic* (KLRS 50th Anniversary Issue).  
<http://dx.doi.org/10.14430/arctic4357>
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35(10):634–639.  
<http://dx.doi.org/10.2307/1309989>
- Dale, M.R.T., Francis, S., Krebs, C.J., and Nams, V.O. 2001. Trees. In: Krebs, C.J., Boutin, S., and Boonstra, R., eds. *Ecosystem dynamics of the boreal forest: The Kluane project*. New York: Oxford University Press. 116–137.
- deKoning, P.K. 2011. Consequences and recovery after nutrient enrichment and herbivore reduction in the boreal forest understory. MSc thesis, University of British Columbia, Vancouver.
- Díaz, S., Sysmstad, A.J., Chapin, F.S., III, Wardle, D.A., and Huenneke, L.F. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* 18(3):140–146.  
[http://dx.doi.org/10.1016/S0169-5347\(03\)00007-7](http://dx.doi.org/10.1016/S0169-5347(03)00007-7)
- Dlott, F., and Turkington, R. 2000. Regulation of boreal forest understory vegetation: The roles of resources and herbivores. *Plant Ecology* 151:239–251.  
<http://dx.doi.org/10.1023/A:1026510727987>
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., et al. 2011. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15(2):164–175.  
<http://dx.doi.org/10.1111/j.1461-0248.2011.01716.x>
- Francis, S.R. 1996. Linking landscape pattern and forest disturbance: Fire history of the Shakwak Trench, southwest Yukon Territory. MSc thesis, University of Alberta, Edmonton.
- Fremelin, K.M., McLaren, J.R., DeSandoli, L., and Turkington, R. 2011. The effects of fertilization and herbivory on the phenology of the understory vegetation of the boreal forest in northwestern Canada. *Arctic, Antarctic, and Alpine Research* 43(3):389–396.  
<http://dx.doi.org/10.1657/1938-4246-43.3.389>
- Fretwell, S.D. 1987. Food chain dynamics: The central theory of ecology? *Oikos* 50(3):291–301.  
<http://dx.doi.org/10.2307/3565489>
- Gilbert, B., Turkington, R., and Srivastava, D.S. 2009. Dominant species and diversity: Linking relative abundance to controls of species establishment. *American Naturalist* 174(6):850–862.  
<http://dx.doi.org/10.1086/647903>
- Graham, S.A., and Turkington, R. 2000. Population dynamics response of *Lupinus arcticus* to fertilization, clipping, and neighbour removal in the understory of the boreal forest. *Canadian Journal of Botany* 78:753–758.  
<http://dx.doi.org/10.1139/b00-039>
- Grainger, T.N., and Turkington, R. 2012. Germinability of *Epilobium angustifolium* seeds from plants treated annually with fertilizer for twenty-two years. *Davidsonia* 22(1):2–8.
- Hendry, R.J., and McGlade, J.M. 1995. The role of memory in ecological systems. *Proceedings of the Royal Society London: Biological Sciences* 259(1355):153–159.  
<http://dx.doi.org/10.1098/rspb.1995.0023>
- Hicks, S., and Turkington, R. 2000. Compensatory growth of three herbaceous perennial species: The effects of clipping and nutrient availability. *Canadian Journal of Botany* 78(6):759–767.  
<http://dx.doi.org/10.1139/b00-051>
- Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75(1):3–35.  
<http://dx.doi.org/10.1890/04-0922>
- John, E., and Turkington, R. 1995. Herbaceous vegetation in the understorey of the boreal forest: Does nutrient supply or snowshoe hare herbivory regulate species composition and abundance? *Journal of Ecology* 83(4):581–590.  
<http://dx.doi.org/10.2307/2261626>
- . 1997. A 5-year study of the effects of nutrient availability and herbivory on two boreal forest herbs. *Journal of Ecology* 85(4):419–430.  
<http://dx.doi.org/10.2307/2960566>
- Krebs, C.J., Dale, M.R.T., Nams, V.O., Sinclair, A.R.E., and O'Donoghue, M. 2001. Shrubs. In: Krebs, C.J., Boutin, S., and Boonstra, R., eds. *Ecosystem dynamics of the boreal forest: The Kluane project*. New York: Oxford University Press. 92–115.
- Marshall, C.B., McLaren, J.R., and Turkington, R. 2011. Soil microbial communities resistant to changes in plant functional group composition. *Soil Biology and Biochemistry* 43(1):78–85.  
<http://dx.doi.org/10.1016/j.soilbio.2010.09.016>
- McLaren, J.R., and Turkington, R. 2010a. Ecosystem properties determined by plant functional group identity. *Journal of Ecology* 98(2):459–469.  
<http://dx.doi.org/10.1111/j.1365-2745.2009.01630.x>
- . 2010b. Plant functional group identity differentially affects leaf and root decomposition. *Global Change Biology* 16(11):3075–3084.  
<http://dx.doi.org/10.1111/j.1365-2486.2009.02151.x>
- . 2011a. Biomass compensation and plant responses to 7 years of plant functional group removals. *Journal of Vegetation Science* 22(3):503–515.  
<http://dx.doi.org/10.1111/j.1654-1103.2011.01263.x>

- . 2011b. Plant identity influences decomposition through more than one mechanism. *PLoS One* 6(8): e23702.  
<http://dx.doi.org/10.1371/journal.pone.0023702>
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., et al. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6(4), 045509.  
<http://dx.doi.org/10.1088/1748-9326/6/4/045509>
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., and Linkins, A.E. 1992. Microbial processes and plant nutrient availability in Arctic soils. In: Chapin, F.S., III, Jefferies, R.L., Reynolds, J.F., Shaver, G.R., and Svoboda, J., eds. *Arctic ecosystems in a changing climate: An ecophysiological perspective*. San Diego: Academic Press. 281–300.  
<http://dx.doi.org/10.1016/B978-0-12-168250-7.50019-5>
- Oksanen, L. 1990. Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace, J.B., and Tilman, D., eds. *Perspectives on plant competition*. New York: Academic Press. 445–474.
- Oksanen, L., Fretwell, S.D., Arruda, J., and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118(2):240–261.  
<http://dx.doi.org/10.1086/283817>
- Secombe-Hett, P.E. 1999. Summer diet selection by snowshoe hares. MSc thesis, University of British Columbia, Vancouver.
- Secombe-Hett, P., and Turkington, R. 2008. Summer diet selection of snowshoe hares: A test of nutritional hypotheses. *Oikos* 117(12):1874–1884.  
<http://dx.doi.org/10.1111/j.1600-0706.2008.16773.x>
- Sharam, G.J., and Turkington, R. 2005. Diurnal cycle of sparteine production in *Lupinus arcticus*. *Canadian Journal of Botany* 83(10):1345–1348.  
<http://dx.doi.org/10.1139/b05-104>
- . 2009. Growth, camphor concentration, and nitrogen responses of white spruce (*Picea glauca*) leaves to browsing and fertilization. *Ecoscience* 16(2):258–264.  
<http://dx.doi.org/10.2980/16-2-3256>
- Shaver, G.R., and Jonasson, S. 1999. Response of Arctic ecosystems to climate change: Results of long-term field experiments in Sweden and Alaska. *Polar Research* 18(2):245–252.  
<http://dx.doi.org/10.3402/polar.v18i2.6581>
- Shaver, G.R., Canadell, J., Chapin, F.S., III, Gurevitch, J., Harte, J., Henry, G., Ineson, P., et al. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* 50(10):871–882.  
[http://dx.doi.org/10.1641/0006-3568\(2000\)050\[0871:GWATEA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2000)050[0871:GWATEA]2.0.CO;2)
- Shaver, G.R., Bret-Harte, M.S., Jones, M.H., Johnstone, J., Gough, L., Laundre, J., and Chapin, F.S., III. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82(11):3163–3181.  
[http://dx.doi.org/10.1890/0012-9658\(2001\)082\[3163:SCIWFT\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2)
- Sinclair, A.R.E., Krebs, C.J., Fryxell, J.M., Turkington, R., Boutin, S., Boonstra, R., Secombe-Hett, P., Lundberg, P., and Oksanen, L. 2000. Testing hypotheses of trophic level interactions: A boreal forest ecosystem. *Oikos* 89(2):313–328.  
<http://dx.doi.org/10.1034/j.1600-0706.2000.890213.x>
- Smith, M.D., Wilcox, J.C., Kelly, T., and Knapp, A.K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106(2):253–262.  
<http://dx.doi.org/10.1111/j.0030-1299.2004.13057.x>
- Treberg, M.A. 2007. Community- and species-level consequences of competition in an unproductive environment: An experimental approach using boreal forest understory vegetation. PhD thesis, University of British Columbia, Vancouver.
- Treberg, M.A., and Turkington, R. 2010a. Density dependence in an experimental boreal forest understory community. *Botany* 88(8):753–764.  
<http://dx.doi.org/10.1139/B10-048>
- . 2010b. Facilitation in an unproductive boreal forest understory community. *Journal of Vegetation Science* 21(4):761–771.  
<http://dx.doi.org/10.1111/j.1654-1103.2010.01182.x>
- Turkington, R. 2009. Top-down and bottom-up forces in mammalian herbivore–vegetation systems: An essay review. *Botany* 87(8):723–739.  
<http://dx.doi.org/10.1139/B09-035>
- Turkington, R., John, E., Krebs, C.J., Dale, M.R.T., Nams, V.O., Boonstra, R., Boutin, S., Martin, K., Sinclair, A.R.E., and Smith, J.N.M. 1998. The effects of NPK fertilization for nine years on the vegetation of the boreal forest in northwestern Canada. *Journal of Vegetation Science* 9(3):333–346.  
<http://dx.doi.org/10.2307/3237098>
- Turkington, R., John, E., and Dale, M.R.T. 2001. Herbs and grasses. In: Krebs, C.J., Boutin, S., and Boonstra, R., eds. *Ecosystem dynamics of the boreal forest: The Kluane project*. New York: Oxford University Press. 69–91.
- Turkington, R., John, E., Watson, S., and Secombe-Hett, P. 2002. The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: A ten-year study. *Journal of Ecology* 90(2):325–337.  
<http://dx.doi.org/10.1046/j.1365-2745.2001.00666.x>