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# Vegetation structure modulates ecosystem and community responses to spatial subsidies

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## Abstract

Ecosystem responses to external inputs of nutrients and organisms are highly variable. Theory predicts that ecosystem traits will determine the responses to spatial subsidies, but evidence for how vegetation structure can modulate those effects is lacking. We investigated how vegetation structure (i.e., leaf area index [LAI] and vegetation height) influenced the ecosystem and community responses to insect spatial subsidies in a subarctic grassland. Our experiment consisted of a 2 x 2 manipulation where in one treatment we either blocked flying insects over a 2-year period in 1-m<sup>2</sup> plots near the shore of Lake Mývatn, Iceland where deposition of aquatic adult midges (Diptera: Chironomidae) to land is high, or we left control plots accessible to flying midges. In the second treatment, grassland vegetation was cut (Tall vs. Short) at the start of each season and then allowed to regrow. Within each plot (n = 6 replicates x 4 treatments), we measured litter decomposition and arthropod composition and density. Midge-exclusion cages reduced midge deposition by 81% relative to the open plots. Vegetation cutting initially reduced LAI and vegetation height by 3x and 1.5x, respectively, but these were not different by the end of the second growing season. We found that vegetation structure modulated the effects of midge subsidies on litter decomposition, with taller canopies intercepting more insect subsidies than shorter ones, leading to 18% faster litter decomposition. In contrast, the short-vegetation plots intercepted fewer subsidies, had higher temperatures and sunlight, and thus resulted in no effects of midges on decomposition. However, by the end of the experiment when all vegetation structure characteristics had converged across all plots, we found no differences in decomposition between treatments. The effects of midge subsidies on arthropod composition depended on vegetation structure in the last year, suggesting that arthropod predators might also be responding to vegetation structure effects on insect subsidies. Our findings indicate that vegetation structure can modify the quantity of subsidies entering a recipient ecosystem as aerial insects, resulting in ecosystem- and community-level responses. Thus, changing vegetation structure via habitat disturbances will likely have important implications for ecosystem functions that depend on spatial subsidies.

## INTRODUCTION

Fluxes of nutrients, energy, and organisms across ecosystem boundaries are ubiquitous (Polis et al. 1997). These spatial subsidies can alter recipient systems (Subalusky and Post 2019), with implications for ecosystem structure and function. For instance, aquatic insects can subsidize terrestrial predators such as spiders, reptiles, and birds (Nakano and Murakami 2001, Barrett et al. 2005, Marczak and Richardson 2007), increasing top-down pressure on herbivores and indirectly enhancing plant biomass. Spatial subsidies can also induce bottom-up effects in nutrient-poor ecosystems by releasing limiting nutrients, thereby shifting plant composition and biomass (Gratton et al. 2017). The strength of responses to spatial subsidies is variable across ecosystems (Marczak et al. 2007). Thus, considerable efforts have examined which ecosystem traits help explain the variation of responses, including investigations on recipient ecosystem elevation (Leroux and Loreau 2008), boundary permeability (Cadenasso and Pickett 2001), and perimeter-area ratios (Polis and Hurd 1996). Despite advances in our understanding of how ecosystem traits can affect subsidy impacts on recipient systems (Richardson et al. 2010, Leroux and Loreau 2012, Schindler and Smits 2017), knowledge of how those traits modulate community- and ecosystem-level responses to spatial subsidies is lacking.

One ecosystem trait that has not been investigated, but might strongly influence how spatial subsidies affect recipient systems, is vegetation structure. Vegetation structure—which is comprised by NPP, leaf area, plant composition, and plant height (Van der Maarel and Franklin 2012)—can affect the rate, amount, and distribution of subsidies entering a recipient ecosystem. Furthermore, changes to vegetation structures will likely affect abiotic factors such as soil temperature and light, which may also indirectly influence recipient ecosystem responses to spatial subsidies. Here we use emergent aquatic insects to illustrate how vegetation structure might affect the impacts of spatial subsidies on community and ecosystem outcomes. We present two contrasting hypotheses (Fig. 1). First, tall or dense vegetation may intercept more aerial insects, thereby subsidizing prey availability for canopy-dwelling predators (e.g., web-building spiders) and reducing the input of nutrients into the soil (Fig. 1, “a1”). Short vegetation, in contrast, would allow for insect subsidies to more easily come into contact with the soil and rapidly enter the detrital-resource pool, inducing bottom-up effects in the recipient environment (Fig. 1, “a2”). Alternatively, tall vegetation will ensure that subsidy nutrients are retained in the recipient environment via interception, thus increasing the rate of resource capture (Fig. 1, “b1”), while short vegetation should collect fewer insects on less surface area with most organisms escaping the system and reducing allochthonous nutrients (Fig. 1, “b2”). Differences in subsidy inputs proposed by these two competing hypotheses have implications for community and ecosystem responses to spatial subsidies in the recipient habitat. However, no studies have tested these hypotheses empirically, limiting our ability to generalize the impacts of spatial subsidies across ecosystems with different vegetation structures.

Lake Mývatn (“lake of midges”) in northeastern Iceland is the system in which we test how different vegetation structures can influence ecosystem-level impacts of spatial subsidies. Mývatn is surrounded by a mosaic of short-statured heathlands and tall-statured grasslands (Hoekman et al. 2019), with insect subsidies potentially affecting these plant communities disproportionately. Mývatn is naturally eutrophic and sustains large populations of midges (Diptera: Chironomidae) (Einarsson et al. 2002), which emerge as adults for several weeks each year and form mating swarms over the surrounding landscape (Gardarsson et al. 2004). When not swarming, the adult midges settle in the vegetation where they can become an abundant food resource for predatory arthropods (Hoekman et al. 2019). When the midges die uneaten, their carcasses enter the detrital food web and subsidize the soil biota and increase soil nutrient inputs (Hoekman et al. 2011, Gratton et al. 2017).

We examined how vegetation structure modulated ecosystem-level effects of insect subsidies in a subarctic grassland. We addressed two questions: 1) how does vegetation structure influence the effects of spatial subsidies on litter decomposition? and 2) what effects do vegetation structure and midge reduction have on arthropod composition and densities of trophic guilds (i.e., detritivores, herbivores, and predators)? To address these questions, we altered grassland vegetation structure via cutting and suppressing subsidy inputs. We then monitored litter decomposition and arthropod composition and density over two years. We predicted that short vegetation would allow aerial insects to enter the detrital-resource pool directly, thereby increasing litter decomposition through the release of limiting nutrients (i.e., the Subsidy Consumption Hypothesis, Fig. 1a). We further predicted that detritivore, herbivore, and predator densities would be higher in tall versus short vegetation, but that arthropod composition and densities would decline where insect subsidies were reduced.

## METHODS

### Study site

This study was performed at several locations on the eastern shore of the Kálfaströnd peninsula of Mývatn. Each location receives midge deposition that in high-midge years can be as high as 110 kg ha<sup>-1</sup> in the near-shore (50 m) environment (Dreyer et al. 2015). Mývatn’s midge community is dominated primarily by two species, *Tanytarsus gracilentus* and *Chironomus islandicus*, which together comprise ~90% of the total midge abundance (Lindegaard and Jónasson 1979). The grassland vegetation consisted mainly of forbs (*Ranunculus acris*, *Geum rivale*, and *Potentilla palustris*), grasses (*Deschampsia*, *Poa*, and *Agrostis* spp.), and sedges (*Carex* spp.).

## **Vegetation structure effects on litter decomposition and arthropod communities**

We conducted a 2 x 2 factorial experiment that was spread across 6 replicate blocks. Within each block, four 1 x 1-m plots were established to assess the effects of midge deposition (a full-exclusion cage vs. open plot) and vegetation structure (Tall vs. Short) on litter decomposition and arthropod composition and density (n = 24 total plots). Experimental midge-exclusion cages (n = 12) were 1-m high and constructed from white PVC tubing attached to rebar posts on each plot corner (Supplementary Materials Appendix S1 [Plate A1]). Midge-exclusion cages were covered with white polyester netting (mesh size = 2 mm; Barre Army Navy Store, Barre VT, USA) to block flying insects from entering the plot. The mesh netting also had a ~10-cm gap at ground level to allow ground-active arthropods to enter and exit the cages freely. This cage design has limited effects on other environmental factors, such as sunlight and temperature (Hoekman et al. 2019). Experimental cages were permanently installed in the field in June 2017 and were maintained until August 2018 (i.e., two full plant growing seasons), which corresponded to three periods of midge emergences from the lake: ~1 to 14 August 2017, ~2 to 16 June 2018, and ~26 July to 10 August 2018. The midge-access plots (n = 12) were fully open to allow access to all arthropod groups including midges.

Vegetation structure was manipulated once at the start of each year by cutting the vegetation with garden shears (hereafter referred to the “Short” treatment, n = 12), with the Short plots being cut to ~15 cm residual stubble height in June 2017 and then cut again in May 2018. Short plots had the same grassland community and soil characteristics as the uncut plots (hereafter referred to the “Tall” treatment, n = 12); only the structure was different. All cut plant biomass was removed from the plots and vegetation was allowed to regrow after each cutting.

### *Midge deposition measurements*

We measured midge deposition in all plots to evaluate the efficacy of midge-exclusion cages deployed during the summer. Midge abundance was measured using passive aerial “infall” traps; these traps are indicators of activity-density for flying insects and served as a proxy for midge deposition rates (Hoekman et al. 2019). Each infall trap consisted of a 500-mL clear plastic cup affixed to a 0.5-m post placed in a random corner of a plot. Infall cups were filled with 250 mL of a 1:1 propylene glycol:water solution and a small amount of unscented detergent to capture and kill flying insects. We emptied infall traps every two to three weeks and then identified and counted the contents of each trap.

### *Vegetation structure measurements*

We quantified vegetation structure with two measurements: leaf area index (LAI) and vegetation height. We estimated LAI with an AccuPAR 80 ceptometer (Decagon Accupar, Decagon Devices, Pullman, WA, USA), which measures canopy photosynthetically active radiation (PAR) interception by quantifying PAR above and below the vegetation canopy. We took six PAR measurements (three above and three below the plant canopy) per plot and then averaged them to calculate a composite value for each replicate plot.

Vegetation height was estimated as the average of five measurements of the tallest plant halfway between the center and the edge of each plot along a north-south axis plus the center (i.e., North, South, East, West, and Center). LAI and vegetation height measurements were made on the same four days in this experiment (28 Jul 2017, 31 May 2018, 17 Jul 2018, and 17 August 2018).

To examine how vegetation cutting may influence abiotic variables, such as temperature and sunlight, we installed a temperature/light logger (HOBO Penchant Logger; Onset Computer Corp., Bourne, MA, USA) in one randomly selected Tall and Short plot for 10 d in early August 2018. The loggers were placed on top of the soil surface but underneath the plant canopy; observations were recorded every 15 min. HOBO loggers measure light wavelengths from 150 to 1,200 nm, which are reported in lux units (range = 0 - 320,000 lux).

### *Response variables*

Litter decomposition

We installed litter decomposition bags constructed of 2-mm polyester mesh (Barre Army Navy Store, Barre VT, USA) designed to allow access to litter by microbes and small invertebrates. Plant litter within each bag consisted of a mix of local Icelandic grasses (*Deschampsia*, *Poa*, and *Agrostis*) collected fresh from a nearby grassland. Grass tillers were first dried at 60 °C for 48 h, weighed in 2-g aliquots, and placed into a litter bag. Litter bags were 5 x 5 cm and pinned down horizontally to the soil surface. Two litter bags were installed in each plot at the beginning of the experiment (July 2017). One bag was removed on 24 June 2018 and the other on 17 August 2018 at the end of the experiment. Following collection, remaining grass tillers in each bag were separated from foreign material (ingrown roots, moss, etc.), dried at 60°C for 48 h, and weighed.

#### Arthropod density

Vacuum sampling was used to measure arthropod density in each plot during peak activity each summer (i.e., 16 or 24 July 2017 and 15 or 20 July 2018). Arthropod samples were collected by vacuuming the litter and vegetation using a modified SH 85 Shredder Vac/Blower (Stihl Incorporated, Virginia Beach, Virginia, USA) retrofitted to accept a thin vacuum bag over the sucking end. The vacuum sampler head (0.01 m<sup>2</sup>, fitted with a mesh sampling bag) was pressed firmly against the ground for 10 seconds (i.e., 30 seconds per plot) in three random locations in the plot to remove arthropods from the vegetation and leaf litter. The contents of each bag were placed in a portable Berlese funnel (Bioquip Products Inc., Rancho Dominguez CA, USA) equipped with a 40W bulb and allowed to extract arthropods for 48 h into 70% ethanol. We sorted and identified arthropods to the lowest taxonomic level possible (usually family). Densities were calculated as the number of arthropods per 0.03 m<sup>2</sup>. Refer to Appendix S1 Table S1 for details on the arthropods sampled and their mean annual densities.

#### Data analyses

##### Efficacy of experimental manipulations

We used linear mixed-effects models (LMMs) to examine how our manipulations affected midge deposition (infall trap abundance) and vegetation structure (LAI and vegetation height). The LMMs had three factors and their interactions: (1) midge exclusion [caged vs. uncaged], (2) vegetation structure [Tall vs. Short], and (3) collection date. Random effects in the mixed model included plot nested in block, to account for the repeated sampling of plots across time, and a block effect to account for variability across sites. Midge infall trap abundance was log-transformed prior to analysis, while LAI and vegetation height were square-root transformed. LMMs were fit using the “lme4” package in R version 3.5.2 (Bates et al. 2015, R Development Core Team 2018). Kenward-Roger approximations for degrees of freedom were used to calculate *P* -values (Type III SS) using the “lmerTest” R package (Kuznetsova et al. 2017). Tukey’s HSD post-hoc comparisons were also used to examine treatment effects for individual sample dates using the “emmeans” R package (Lenth et al. 2018).

##### Litter decomposition

To evaluate the effects of midge exclusion and vegetation structure on litter decomposition, we first calculated the proportion of initial litter mass remaining by dividing the mass at each harvest date by initial plant mass in the litter bags. We then performed an LMM on proportion litter decomposed with two fixed factors: (1) midge exclusion [caged vs. uncaged] and (2) vegetation structure [Tall vs. Short]. The random effects included a block term to account for potential variability across sites. We performed separate LMMs for each harvest date (24 June 2018 and 17 August 2018); decomposed litter mass proportions were arcsine-transformed to minimize heteroscedasticity among treatments. We removed extreme values ([?] 3 SD of the mean, 2 removed out of 48 samples) prior to analysis, although the results were similar if they were included (Appendix S1: Table S2). As above, LMMs were fit using the “lme4” package in R version 3.5.2 with Kenward-Roger approximations for degrees of freedom (Type III SS) (Kuznetsova et al. 2017).

##### Arthropod composition and density

We examined arthropod community responses to vegetation structure and midge exclusion using permu-

tational analysis of variance (PERMANOVA: 10,000 permutations; Type III SS) (Anderson et al. 2008). Midge exclusion and vegetation structure were treated as fixed factors, with block as the random effect (Anderson et al. 2008). We performed separate PERMANOVA tests for July 2017 and 2018 dates of the experiment. Prior to analysis, we scaled the data by centering the abundance of each arthropod taxon to a mean of zero and dividing by the standard deviation; taxonomic singletons were removed. A Euclidean dissimilarity distance matrix was calculated between plots using the z-score transformed data. To visualize differences in arthropod composition in two-dimensional space, we conducted either a Canonical Analysis of Principal Coordinates (CAP) ordination constrained by midge exclusion and vegetation structure if there was a strong treatment effect, or a Principal Coordinate Analysis (PCO) for non-significant tests (Anderson et al. 2008). Vector overlays were used to show which arthropod functional guild (i.e., herbivores, predators, or detritivores) was associated with each treatment; a vector reflects partial correlation coefficients for a guild against the two axes.

In addition to the arthropod community analyses, we performed LMMs to test how midge exclusion and vegetation structure affected arthropod functional guild density (herbivores, detritivores, and herbivores) at the end of the experiment (i.e., 2018). We investigated these functional groups because they represent components of arthropod communities (Coleman and Crossley Jr. 2003) that might be directly or indirectly affected by spatial subsidies. The LMM had two fixed factors: (1) midge exclusion [caged vs. uncaged] and (2) vegetation structure [Tall vs. Short]. The block term accounted for variability across the experimental sites. LMMs were fit with the “lme4” package in R version 3.5.2 using Kenward-Roger approximations for degrees of freedom (Type III SS) (Kuznetsova et al. 2017).

### **Vegetation structure effects on midge deposition**

At a site near the study described above (< 20 m away), we performed a separate field experiment to test how vegetation structure can influence midge deposition rates. Here, we manipulated the grassland vegetation to represent tall and short vegetation structures. Half the plots (0.25 m<sup>2</sup>) were manipulated by cutting the vegetation down to ~15 cm using garden shears (“Short” treatment, n = 4); the other plots (“Tall” treatment, n = 4) were left uncut. The experimental treatments were assigned at random. At the end of the experiment (16 August 2018), we measured LAI and vegetation height as described in the experiment above (see the section on *Vegetation structure measurements*).

Within each plot, we installed a pair of infall and pitfall traps to measure canopy interception of midges. We placed the infall traps above the vegetation canopy using a 500-mL clear plastic cup attached to a 1-m post placed in the center of the plot. The pitfall traps were installed in the ground directly beneath the infall trap, with each trap consisting of the same dimensions as the infall traps (i.e., 500 ml, ~ 9 cm in diameter and depth) and being placed flush with the soil surface. Although pitfall traps are generally used to measure ground arthropod activity-density (Coleman and Crossley Jr. 2003), here we repurposed them to estimate canopy interception by counting how many midges reach the soil surface. We calculated canopy interception using the following equation:

$$\text{Canopy Interception}_{\text{CI}} = \frac{i_1 - p_1}{i_1 + p_1},$$

where  $i_1$  and  $p_1$  are the total midges collected for a given infall and pitfall trap, respectively. Because the infall traps were placed above the canopy (representing the maximum amount of midge deposition in the absence of vegetation), and the pitfall traps were placed below the canopy, this equation represents the proportion of midges that were intercepted by the canopy within a given plot. Both infall and pitfall traps contained ~250 mL of a 1:1 mix of propylene glycol and water with a drop of non-scented detergent to serve as a killing agent and preservative (Hall 1991). Altogether there were eight infalls and eight pitfalls (i.e., four pairs); the infall and pitfall traps were left open for 21 d and collected and processed for midges every 7 to 8 d.

### *Data analyses*

We performed Welch’s t-test to evaluate differences in LAI and vegetation height at the end of the 3-week experiment using R version 3.5.2 (R Development Team 2018). We performed LMMs to examine how vegetation structure affected canopy interception of midges as well as midge deposition into pitfall and infall traps. The LMMs had two factors and their interaction: (1) vegetation structure [Tall vs. Short] and (2) collection date. Random effects included plot to account for the repeated sampling of plots across time. To limit heteroscedasticity, we performed arcsine transformations on the proportion of midges intercepted by the plant canopy, whereas infall and pitfall deposition data were log-transformed. We fit the LMMs using the “lme4” package in R (Bates et al. 2015); Kenward-Roger approximations for degrees of freedom were used to calculate  $P$ -values (Type III SS) using the “lmerTest” R package (Kuznetsova et al. 2017).

## RESULTS

### Vegetation structure effects on litter decomposition and arthropod communities

#### *Midge deposition rates*

The midge-exclusion cages reduced midge deposition into experimental plots by over 81%: open plots had daily midge inputs of  $78 \text{ midges} \pm 16 \text{ d}^{-1}$  (mean  $\pm$  SE), whereas midge-exclusion cages received only  $15 \text{ midges} \pm 3 \text{ d}^{-1}$ . The differences between midge deposition in the exclusion and open plots were consistent across both years (Fig. 2), although the magnitude of treatment differences differed depending on the sampling date (LMM,  $F_{5, 100} = 7.13$ ,  $P_{[\text{Midges} \times \text{Date}]} < 0.001$ ).

#### *Vegetation structure measurements and abiotic conditions*

Cutting of the vegetation reduced LAI on average by 50% throughout the experiment (Tall =  $3.49 \pm 0.20$  [mean  $\pm$  SE]; Short =  $1.98 \pm 0.21$ ). However, the effects were most pronounced immediately following cutting events in each season (30 June 2017 and 20 May 2018) and then gradually dissipated by the experiment’s end (LMM,  $F_{3, 60} = 16.34$ ,  $P_{[\text{LAI} \times \text{Date}]} < 0.001$ , Fig. 3a). For the first cut in June 2017, LAI was 3x higher in the Tall than the Short treatment (Tukey’s HSD,  $t = -7.31$ ,  $P_{[\text{LAI}]} < 0.001$ , Fig. 3a). By the end of the experiment, there was no statistical difference between LAI in any of the experimental treatments ( $t = -0.75$ ,  $P_{[\text{LAI}]} = 0.99$ ).

Vegetation height followed the same pattern as LAI, although the magnitude of differences was less apparent. Overall mean height for the plants in the Tall treatment was  $65 \pm 4 \text{ cm}$  (mean  $\pm$  SE) and  $55 \pm 5$  in the Short treatment, but the magnitude of height differences between the treatments depended on collection date (LMM,  $F_{3, 60} = 23.64$ ,  $P_{[\text{Height} \times \text{Date}]} < 0.001$ , Fig. 3b). Vegetation height was ~40% shorter in the Short treatment after the first cut, with a pronounced statistical difference (Tukey’s HSD,  $t = -6.02$ ,  $P_{[\text{Height}]} < 0.001$ ). There was no difference in vegetation height according to cutting by the end of the experiment ( $t = 0.18$ ,  $P_{[\text{Height}]} = 0.99$ , Fig. 3b).

During a 10-day period in the middle of the summer, sensor measurements ( $n = 1,017$  per treatment) showed that vegetation cutting affected the temperature and light of an experimental plot, with the Short plot being a ~0.5 °C warmer ( $10.42 \text{ °C}$  [95% CI = 10.1-10.7]) and receiving ~3x more light (Short = 8,373 lux [95% CI = 7,728-9,017]) on average than the Tall plot ( $9.94 \text{ degC}$  [95% CI = 9.7-10.2]; 2,844 lux [95% CI = 2,611-3,076]).

#### *Litter decomposition*

Litter decomposition for the first set of harvested litter bags (i.e., the start of the second growing season, June 2018) indicated an interaction between vegetation structure and midge exclusion (LMM,  $F_{1, 13} = 13.78$ ,  $P_{[\text{Structure} \times \text{Midges}]} = 0.003$ ). In the Short treatment, the proportion of litter decomposed was unchanged between the midge-exclusion and open plots (Fig. 4a). In the Tall treatment, however, the midge-exclusion plots had 18% less litter decomposition compared to the open plots (Fig. 4a), indicating an interaction between vegetation structure and midge exclusion. The highest litter decomposition rates occurred in the Tall open plots. The last set of litter bags collected at the end of the second growing season (August 2018)

showed no interaction or treatment differences in the amount of litter decomposed ( $P > 0.05$  for all tests, Fig. 4b).

#### *Arthropod composition and density response*

In the first year of the experiment (July 2017), arthropod composition remained unchanged according to vegetation structure or midge exclusion (PERMANOVA;  $P > 0.5$ , Fig. 5a, Appendix S1: Table S3). In 2018, arthropod composition shifted with the effects of midge exclusion depending on vegetation structure ( $Pseudo-F_{1, 4}$  [Structure  $\times$  Midge] = 1.74,  $P = 0.04$ , Appendix S1 Table S3). Arthropod communities in plots with tall vegetation were clustered in the top left quadrant of the CAP ordination, which included both the open and midge-exclusion plots. In contrast, arthropod communities in plots with short vegetation had dissimilar communities based on being an open or a midge-exclusion plot (Fig. 5b). For example, open plots with shorter vegetation structure were clustered in the bottom left quadrant of the ordination, whereas the midge-exclusion plots were separated and grouped on the right side of CAP axis 1 (Fig. 5b). Predators, decomposers, and herbivores were generally correlated with arthropod communities of the Tall plots.

In the final year of the experiment, detritivore density was not affected by vegetation structure (LMM,  $F_{1, 14}$  [Structure] = 2.84,  $P = 0.11$ , Fig. 6a). However, herbivores and predators were both sensitive to plant height, with herbivores 2.86x ( $F_{1, 14}$  [Structure] = 4.87,  $P = 0.04$ ) and predators 1.6x ( $F_{1, 14}$  [Structure] = 6.10,  $P = 0.03$ ) more abundant in the Tall than the Short plots, respectively (Figs. 6b and c, Appendix S1 Table S4).

### **Vegetation structure effects on midge deposition**

#### *Vegetation structure measurements*

At the end of the separate 3-week experiment in 2018, the average LAI for Tall and Short plots was  $2.2 \pm 0.1$  (mean  $\pm$  SE) and  $0.6 \pm 0.1$  (Welch's t-test;  $t = -8.3$ ,  $P < 0.001$ ), respectively. Vegetation height was also much higher in the Tall than Short plots ( $t = -4.60$ ,  $P = 0.02$ ), with average heights of 60 cm  $\pm$  11 and 20 cm  $\pm$  1 for Tall and Short treatments, respectively.

#### *Vegetation canopy interception*

Tall vegetation intercepted 11% more midges when compared to the vegetation in the Short plots (LMM,  $F_{1, 6}$  [Structure] = 8.51,  $P = 0.03$ , Appendix S1 Fig. S1). This pattern was consistent throughout the experiment, as there was no interaction between canopy interception and collection date ( $F_{2, 12}$  [Structure  $\times$  Date] = 0.51,  $P = 0.61$ ). On average, vegetation in the Tall treatment intercepted 95%  $\pm$  0.01 (mean  $\pm$  SE) of midge deposition into the pitfall traps, whereas the vegetation in the Short plots intercepted 85%  $\pm$  0.03 of midge deposition.

#### *Deposition of midges into pitfall and infall traps*

Although there was a statistical difference in the number of midges that reached the pitfall traps (at the soil surface) in the Tall vs. Short plots (LMM,  $F_{1, 6}$  [Structure] = 23.8,  $P = 0.003$ ), both treatments received few midges compared to their respective infall traps located 1 m above the soil surface (Short = 15 midges  $\pm$  3 d<sup>-1</sup> pitfall trap<sup>-1</sup> [mean  $\pm$  SE]; Tall = 4 midges  $\pm$  1 d<sup>-1</sup> pitfall trap<sup>-1</sup>). These estimates were comparable to the infall deposition rates of the midge-exclusion plots (with cages) in the first experiment (i.e., 15 midges  $\pm$  3 d<sup>-1</sup> infall trap<sup>-1</sup>) indicating that few intact midge carcasses actually reach the soil directly whether vegetation is tall or short.

Infall traps in the Short plots received more daily midge inputs than the Tall plots (LMM,  $F_{1, 6}$  [Structure] = 6.81,  $P = 0.04$ ), with the Short plots receiving 196 midges  $\pm$  19 d<sup>-1</sup> infall trap<sup>-1</sup> [mean  $\pm$  SE] and Tall plots receiving 144 midges  $\pm$  20.

## **DISCUSSION**

We found that vegetation structure can influence the effects of spatial subsidies on litter decomposition and arthropod composition. This is further supported by the disappearance of the decomposition effect at the end of the experiment when all vegetation-structure characteristics between plots were similar. We also



found that arthropods in the second year showed an interactive effect of subsidies and vegetation structure, suggesting that arthropods might also be responding to the vegetation structure effects on spatial subsidies. These results support a body of literature showing the impacts of resource subsidies on recipient ecosystems (Polis and Hurd 1995, Nakano et al. 1999, Kato et al. 2003, Piovia-Scott et al. 2019), but this is the first study to demonstrate that vegetation structure can influence those effects.

We predicted that shorter vegetation would allow midges to directly enter the detrital-resource pool, increasing litter decomposition relative to plots with tall vegetation (i.e., the Subsidy Consumption Hypothesis). But, we found that even though midges had easier access to the soil surface in short vegetation, the number of midges reaching the soil was low and insufficient to affect decomposition. Instead, we found that taller vegetation intercepted and retained more midges in the canopy than the shorter vegetation, indicating that midge nutrients had a greater likelihood of entering the soil—a finding more consistent with the Subsidy Percolation Hypothesis (Fig. 1b). This suggests that although canopy-dwelling predators can consume insect subsidies (Hoekman et al. 2019), they do not capture enough insects to reduce subsidy inputs into the detrital pool of the recipient grassland. Our findings also indicate that systems with higher plant biomass (such as our Tall-statured plots) could result in higher capture rates of insect subsidies through a physical interception and retention of the subsidy. This may create a positive feedback between insect allochthony and plant biomass in the recipient ecosystem. However, because we imposed a short-term manipulation to the grassland plant community, this interpretation should be investigated further.

Short-canopy plots had less surface area to intercept midges, resulting in less overall deposition of midges and their nutrients into the soil. Because midges do not immediately perish when they settle in the short vegetation, more midges were presumably lost from the short vegetation plots. It is worth noting that even though we did not directly measure soil nutrient inputs from the midges in this study, we have documented elsewhere that midge deposition can significantly increase soil nitrate and ammonium concentrations (Gratton et al. 2017).

In addition to tall vegetation intercepting more midges, these canopies also foster an environment that is more ideal for soil biota, such as decomposer microbes and arthropods (Liu et al. 2010, Tiemann and Billings 2011, De Smedt et al. 2018). Unlike short vegetation plots that could be more prone to desiccation via increased sunlight and temperature, tall vegetation likely created more stable, moist environments for soil microbial and arthropod communities. For example, we found that entomobryid springtails—an abundant detritivore in this subarctic system—were more than 2x more abundant in the tall than short vegetation (Appendix S1: Table S1). In this subarctic ecosystem (Arnalds and Kimble 2001), dry soil conditions can limit the midge effects on plant biomass and arthropod composition (Webert 2016). Moreover, the soil microbial community was likely responsible for higher rates of litter disappearance in the tall open plots. As mostly carbon-limited organisms (Demoling et al. 2007), the pool of labile carbon via midge inputs (i.e., low C: N ratios [ $\sim 5:1$ ]) likely stimulated microbial activity and increased their biomass (Kolb et al. 2009) when midges were intercepted by the vegetation.

We found that the arthropod communities were affected by both vegetation structure and midge inputs, but only in the last year of the experiment. Higher abundances of decomposers, herbivores, and predators were associated with tall vegetation, with overall lower densities in short vegetation. This was expected because arthropod densities are known to be positively correlated with plant biomass and structure; higher aboveground biomass and structure usually provide more habitat and food resources for terrestrial arthropods (Siemann 1998, Schaffers et al. 2008). We also found disparate communities of arthropods in short vegetation depending on the presence/absence of midges. The large, mobile predators appear to be driving this pattern, which were more associated with the short plots with access to midges. Other studies have documented this aggregative effect of predators when utilizing allochthonous prey subsidies (Henschel et al. 2001, Schmidt and Ostfeld 2008, Yang et al. 2010, Dreyer et al. 2012, Hoekman et al. 2019).

## Conclusions

While other studies have demonstrated the impacts of resource subsidies on recipient ecosystems (Nakano

and Murakami 2001, Sabo and Power 2002, Fukui et al. 2006), we illustrate that vegetation structure could modulate those effects. Plant height altered the impact of spatial subsidies on litter decomposition, with arthropods also responding to the structural effects, and potentially the abiotic conditions, on allochthonous nutrients. Thus, vegetation structure can help predict the ecosystem and community responses to spatial subsidies, because taller plants can intercept more aerial insects, ensuring the capture of critical nutrients within the recipient ecosystem. Because spatial subsidies are ubiquitous across terrestrial ecosystems (Polis et al. 1997), changing vegetation structure via habitat disturbances (e.g., grazing, climate change, or plant invasions) could have implications for ecosystem functions that depend on allochthonous resources. Future research should investigate how environmental and management alterations to vegetation structure can influence recipient ecosystem function.

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## FIGURE LEGENDS

**Figure 1.** Conceptual diagram of the two competing hypotheses by which vegetation structure can influence ecosystem effects of insect subsidies. (a) Subsidy Consumption Hypotheses: (a1) Tall vegetation structure creates more habitat for arthropod predators such as web-building spiders, which in turn consume most of the incoming insect allochthony (flying chironomid midges in this case) that are intercepted by the grassland vegetation and limits midge nutrients from entering the detrital pool. (a2) Shows that in Short vegetation, midges can more easily enter the detrital pool because of less structure, thereby having a more direct effect on soil communities and processes such as decomposition. (b) Subsidy Percolation Hypothesis: (b1) Tall, complex vegetation intercepts most midge nutrients without enough predators to capture them, which then percolate down into the detrital pool. (b2) Because of reduced vegetation structure, midges fly by short vegetation areas until they encounter tall vegetation. This pattern will ultimately lead to reduced midge nutrients in Short vegetation plots.

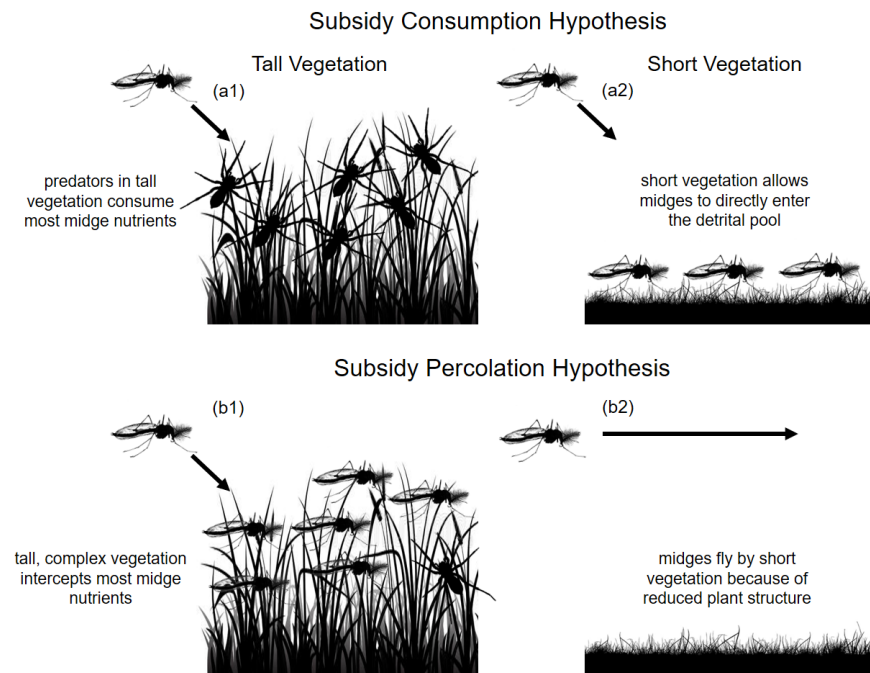
**Figure 2.** Line plots showing midge deposition (mean  $\pm$  SE, points jittered to facilitate visualization) over the course of the 2-year experiment. Midge infall was successfully manipulated by the exclusion cages, which reduced midge density on average by 81% in the 1 x 1-m plots across the experiments. We used follow-up Tukey’s HSD post-hoc tests to examine treatment effects on each collection date. Data are means and standard errors. (\*\*\*)  $P < 0.001$ ; (\*\*)  $P < 0.01$ ; (\*)  $P < 0.05$ .

**Figure 3.** Line plots showing (a) leaf area index [LAI] and (b) vegetation height over the course of the experiment. Gray panels indicate the days in which the vegetation was cut (i.e., 2017-06-30 and 2018-05-20). Follow-up Tukey’s HSD post-hoc tests were conducted to examine treatment effects on each collection date. Data are means and standard errors. (\*\*\*)  $P < 0.001$ ; (\*\*)  $P < 0.01$ ; (\*)  $P < 0.05$ .

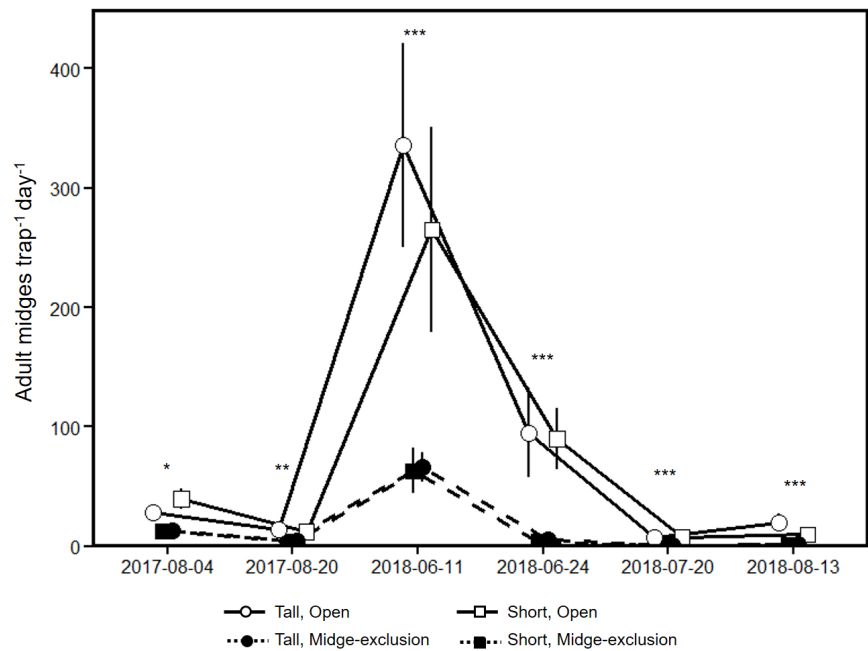
**Figure 4.** Bar plots showing the impact of vegetation structure and midge exclusion on litter decomposition for litter bags harvested on (a) 24 June 2018 and (b) 17 August 2018. Data are means and standard errors; different letters denote  $P < 0.05$  using post-hoc Tukey’s HSD comparisons.

**Figure 5.** The impact of vegetation structure and midge exclusion on arthropod composition in (a) 2017 and (b) 2018. Ordination bi-plots show arthropod data that are based on a Euclidean dissimilarity matrix. Each symbol on the ordination plot represents communities for one of the 24 experimental plots in that year of the experiment. The direction and length of vector overlays indicate the strength of the association (multiple partial correlation coefficient) between the ordination axes and the associated labeled taxon.

**Figure 6.** Bar plots showing the effect of vegetation structure and midge exclusion on arthropod functional densities in 2018 for (a) detritivores, (b) herbivores, and (c) predators. Data are means and standard errors.



**Figure 1.**



**Figure 2.**

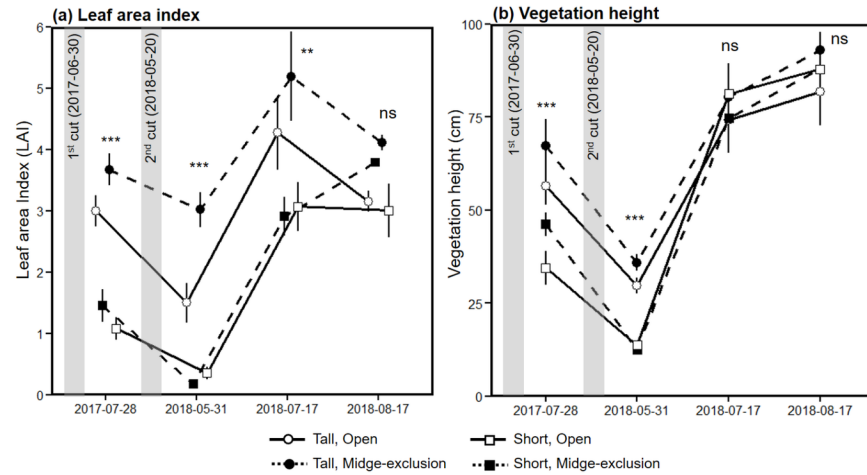


Figure 3.

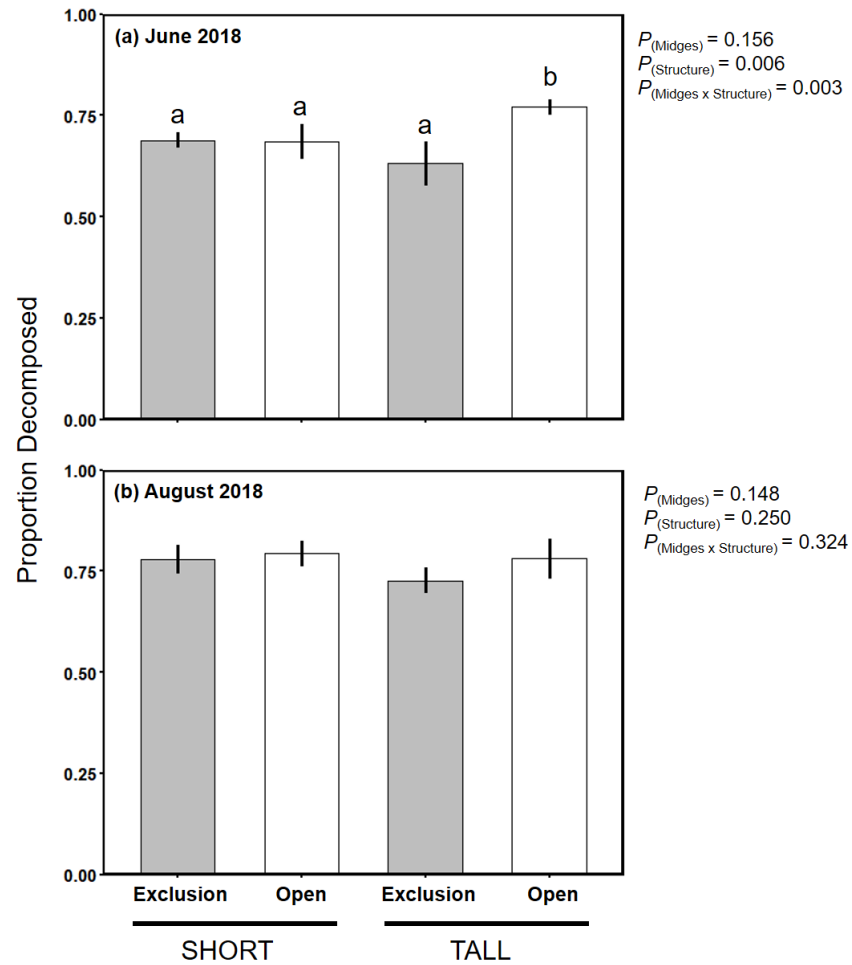
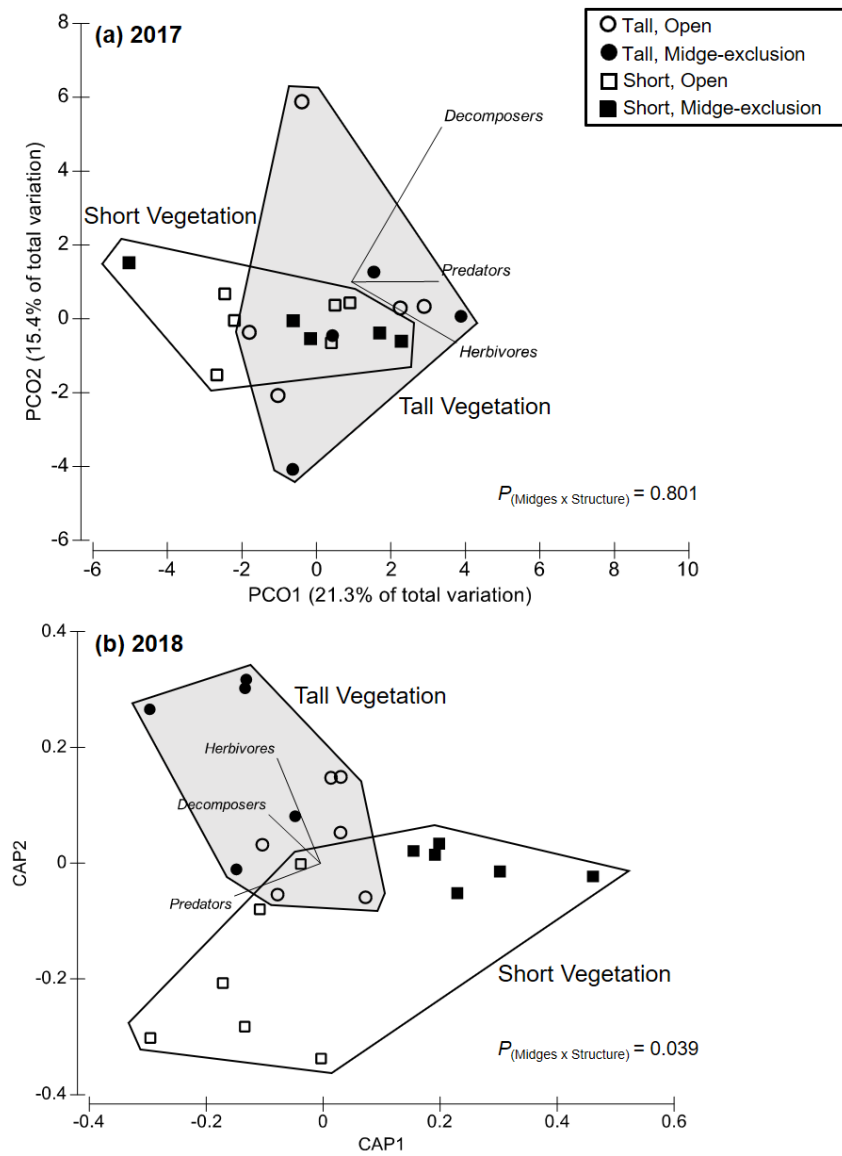


Figure 4.



**Figure 5.**

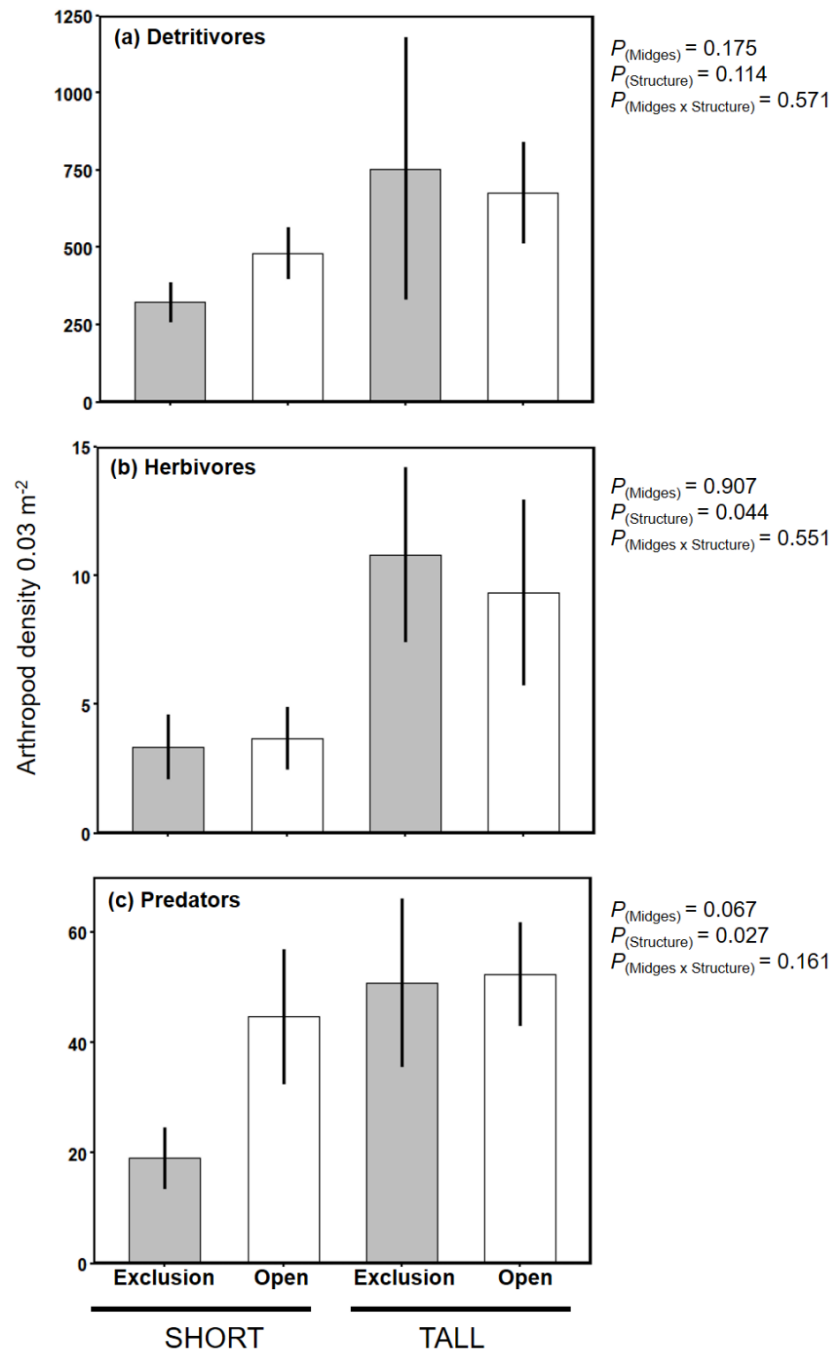


Figure 6.

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