

Vegetation structure modulates ecosystem and community responses to spatial subsidies

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Citation: McCary, M. A., R. D. Jackson, and C. Gratton. 2021. Vegetation structure modulates ecosystem and community responses to spatial subsidies. *Ecosphere* 12(4):e03483. 10.1002/ecs2.3483

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 × 2 manipulation where in one treatment we either blocked flying insects over a 2-yr period in 1-m² plots near the shore of Lake Mývatn, Iceland, where deposition of aquatic adult midges (Diptera: Chironomidae) to land is high, or 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. We then measured litter decomposition and arthropod composition and density within each plot ($n = 6$ replicates × 4 treatments). Midge-exclusion cages reduced midge deposition by 81% relative to the open plots. Vegetation cutting initially reduced LAI and vegetation height by 3× and 1.5×, 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 and had higher temperatures and sunlight, resulting 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 the vegetation structure, suggesting that arthropods might also be responding to the structural effects on spatial subsidies. Our findings indicate that vegetation structure can modify the abiotic environment and 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 rely on spatial subsidies.

Key words: allochthonous resources; arthropods; decomposition; ecosystem processes; spatial subsidies; vegetation structure.

Received 1 December 2020; accepted 10 December 2020; final version received 28 January 2021. Corresponding Editor: Debra P. C. Peters.

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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 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 is comprised of net primary productivity, leaf area, plant composition, and plant height (Van der Maarel and Franklin 2012). Hence, vegetation structure likely mediates how spatial subsidies enter a given ecosystem, such as insects moving from aquatic to terrestrial systems. Different vegetation structures can influence abiotic conditions such as soil temperature and light (Fliervoet and Werger 1984), with canopies providing less shade leading to warmer and drier microhabitats. Such changes to the abiotic environment are likely to influence the soil biota and processing of spatial subsidies. Furthermore, tall-vegetation structures may intercept more aerial insects, subsidizing prey availability for canopy-dwelling predators (e.g., web-building spiders) and reducing allochthonous inputs, while shorter structures may allow for subsidies to more easily come into contact with the soil and enter the detrital-resource pool. The alternative is also possible: Tall vegetation could ensure that subsidy nutrients are retained in the recipient environment via interception, thereby increasing the rate of

resource capture, whereas short vegetation might collect fewer insects on less surface area and reducing allochthonous nutrients. As such, vegetation structure likely affects the rate, amount, and distribution of subsidies entering a recipient ecosystem, with potential community and ecosystem effects. However, no studies have tested how the effects of spatial subsidies are influenced by vegetation structure, limiting our ability to predict their impacts across ecosystems.

Lake Mývatn (lake of midges) in northeastern Iceland is the system in which we test how different vegetation structures can influence community- and 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 contains large populations of midges (Diptera: Chironomidae; Einarsson et al. 2002) that emerge as adults each year and form dense mating swarms over the adjacent landscape (Gardarsson et al. 2004). When not swarming, midges settle in the plant canopy where they can become abundant prey for arthropod predators (Hoekman et al. 2019). When they die uneaten, their carcasses enter the detrital-resource pool where they subsidize the soil biota and increase soil nutrients (Hoekman et al. 2011, Gratton et al. 2017).

We examined how vegetation structure modulated the effects of insect subsidies in a subarctic grassland ecosystem. 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. We further predicted that detritivore, herbivore, and predator densities would be higher in tall vs. short

vegetation, but that arthropod composition and densities would decline where insect subsidies were reduced.

MATERIALS AND 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 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 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 × 2 factorial experiment that was spread across six replicate blocks. Within each block, four 1 × 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 (Appendix S1: Plate S1). Midge-exclusion cages were covered with white polyester netting (mesh size = 2 mm; Barre Army Navy Store, Barre, Vermont, 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 freely enter and exit the cages. 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: ~1–14 August 2017, ~2–16 June 2018, and ~26 July–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 as 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 as 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, Washington, 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). Leaf area index and vegetation height measurements were made on the same four days in this experiment

(28 July 2017, 31 May 2018, 17 July 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, Bourne, Massachusetts, 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 1200 nm, which are reported in lux units (range = 0–320,000 lux).

Litter decomposition.—We installed litter decomposition bags constructed of 2-mm polyester mesh (Barre Army Navy Store, Barre, Vermont, USA) designed to allow access to litter by microbes and small invertebrates. Each bag's plant litter 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 × 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, Virginia Beach, Virginia, USA) retrofitted to accept a thin vacuum bag over the sucking end. The vacuum sampler head (0.01 m², fitted with a mesh sampling bag) was pressed firmly against the ground for 10 s (i.e., 30 s 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, Rancho Dominguez, California, USA) equipped with a 40 W 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 m². Refer to Appendix S1: Table S1 for details on the arthropods sampled and their mean annual densities.

Data analyses.—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. Linear mixed-effects models 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).

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, two removed out of 48 samples) prior to analysis, although the results were similar if they were included (Appendix S1: Table S2). Linear mixed-effects models 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).

We examined arthropod community responses to vegetation structure and midge exclusion using permutational 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 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 important 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. Linear mixed-effects models 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 m²) 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 *Vegetation structure measurements*).

We installed a pair of infall and pitfall traps within each plot 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 plot's center. 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 (CI) using the following equation:

$$CI = \frac{i_1 - p_1}{i_1 + p_1}$$

where i_1 and p_1 are the total midges collected for a given infall and pitfall trap, respectively. The infall traps were placed above the canopy (i.e., no interference by the vegetation), while the pitfall traps were installed directly beneath the canopy. Because the infall and pitfall traps are expected to receive roughly the same number of midges in the absence of vegetation, this equation represents the proportion of midges intercepted by the plant 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 7–8 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 Core 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. We performed arcsine transformations on the proportion of midges intercepted by the plant canopy to limit heteroscedasticity, 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 standard error [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. 1), although the magnitude of treatment differences differed depending on the sampling date (LMM, $F_{5, 100} = 7.13$, midges \times date $P < 0.001$).

Vegetation structure measurements and abiotic conditions.—Cutting of the vegetation reduced LAI on average by 50% throughout the experiment (tall = 3.49 ± 0.20 [mean \pm SE]; short = 1.98 ± 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, $F_{3,60} = 16.34$, LAI \times date $P < 0.001$; Fig. 2a). For the first cut in June 2017, LAI was 3 \times higher in the tall than the short treatment (Tukey's HSD, $t = -7.31$, LAI $P < 0.001$; Fig. 2a). By the end of the experiment, there was no statistical difference between LAI in any experimental treatments ($t = -0.75$, LAI $P = 0.99$).

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 ± 4 cm (mean \pm SE) and 55 ± 5 in the short treatment, but the magnitude of height differences between the treatments depended on collection date (LMM, $F_{3,60} = 23.64$, height \times date $P < 0.001$; Fig. 2b). Vegetation height was $\sim 40\%$ shorter in the short treatment after the first cut, with a pronounced statistical difference (Tukey's HSD, $t = -6.02$, height $P < 0.001$). There was no difference in vegetation height according to cutting by the end of the experiment ($t = 0.18$, height $P = 0.99$; Fig. 2b).

During a 10-d period in the middle of the summer, sensor measurements ($n = 1017$ per treatment) showed that vegetation cutting affected the temperature and light of an experimental plot, with the short plot being a $\sim 0.5^\circ\text{C}$ warmer (10.42°C ; 95% CI = 10.1–10.7) and receiving $\sim 3\times$ more light (short = 8373 lux; 95% CI = 7728–9017) on average than the tall plot (9.94°C ; 95% CI = 9.7–10.2; 2844 lux; 95% CI = 2611–3076).

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, $F_{1,13} = 13.78$, structure \times midges $P = 0.003$). In the short treatment, the proportion of litter decomposed was unchanged between the midge-exclusion and open plots (Fig. 3a). In the tall treatment, however, the midge-exclusion plots had 18% less litter decomposition than the open plots (Fig. 3a), 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

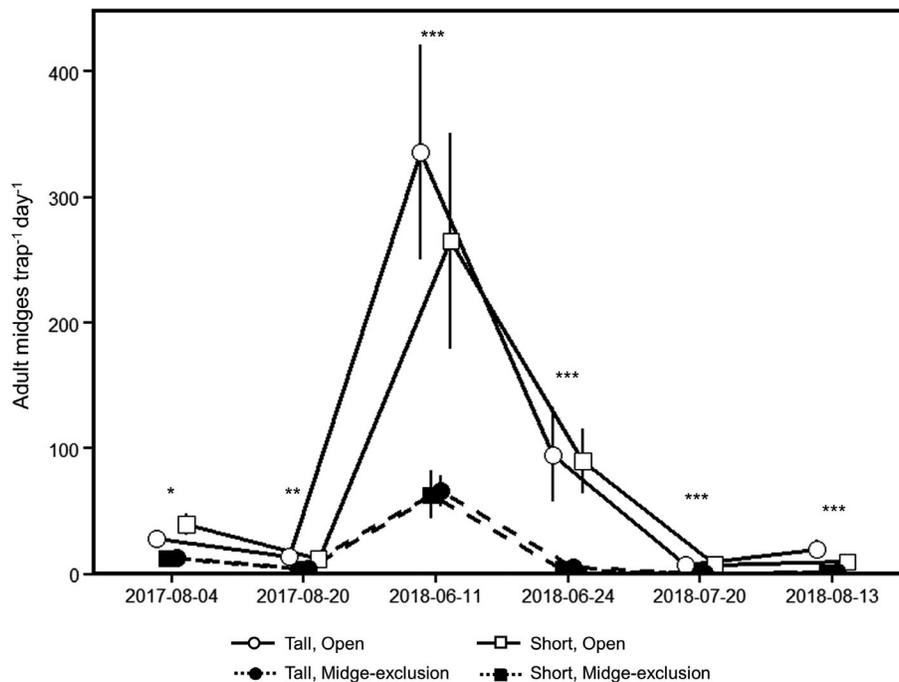


Fig. 1. Line plots showing midge deposition (mean \pm standard error [SE], points jittered to facilitate visualization) over the course of the 2-yr experiment. Midge infall was successfully manipulated by the exclusion cages, which reduced midge density on average by 81% in the 1×1 -m plots across the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

in the amount of litter decomposed ($P > 0.05$ for all tests; Fig. 3b).

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. 4a, Appendix S1: Table S3). In 2018, arthropod composition shifted with the effects of midge exclusion depending on vegetation structure (structure \times midges pseudo- $F_{1,4} = 1.74$, $P = 0.04$; Appendix S1: Table S3). Arthropod communities in plots with tall vegetation were clustered in the top left quadrant of the CAP ordination, including 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. 4b). For example, open plots with shorter vegetation structures 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. 4b). 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, structure $F_{1,14} = 2.84$, $P = 0.11$; Fig. 5a). However, herbivores and predators were both sensitive to plant height, with herbivores $2.86\times$ (structure $F_{1,14} = 4.87$, $P = 0.04$) and predators $1.6\times$ (structure $F_{1,14} = 6.10$, $P = 0.03$) more abundant in the tall than the short plots, respectively (Fig. 5b, 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 ± 0.1 (mean \pm SE) and 0.6 ± 0.1 (Welch's t test; $t = -8.3$, $P < 0.001$), respectively. Vegetation height was also much higher in the tall than the short plots ($t = -4.60$, $P = 0.02$), with average

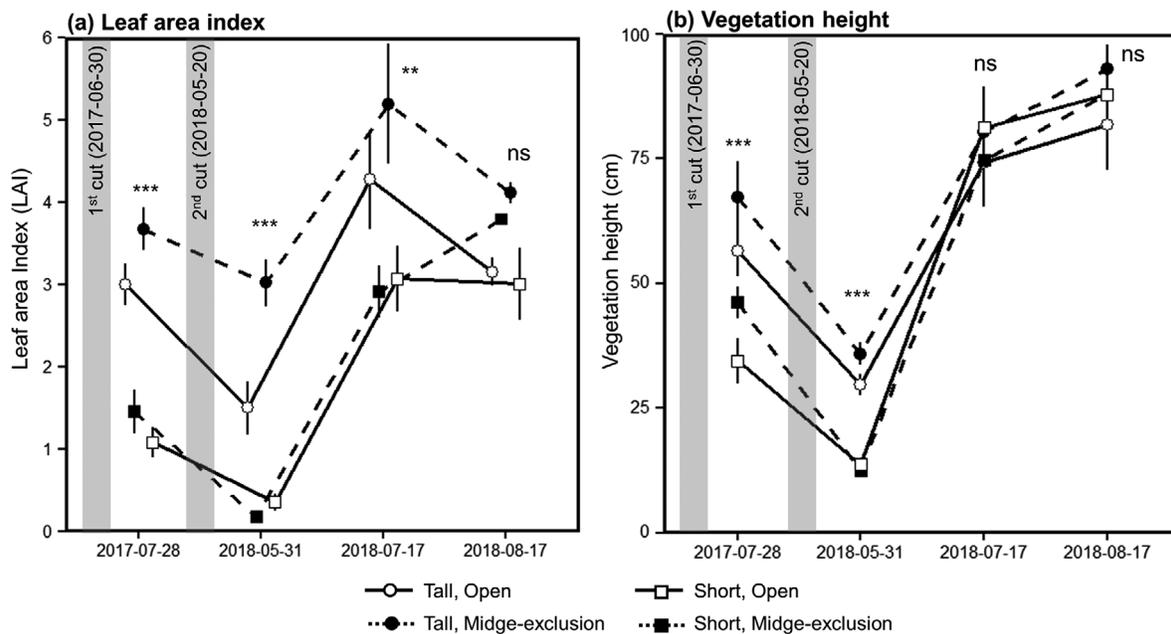


Fig. 2. Line plots showing (a) leaf area index (LAI) and (b) vegetation height over the course of the experiment. Gray panels indicate the days in which the vegetation was cut (i.e., 30 June 2017 and 20 May 2018). Follow-up Tukey's HSD post hoc tests were conducted to examine treatment effects on each collection date. Data are means and standard errors. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

heights of $60 \text{ cm} \pm 11$ and $20 \text{ cm} \pm 1$ 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, structure $F_{1,6} = 8.51$, $P = 0.03$; Appendix S1: Fig. S1). This pattern was consistent throughout the experiment, as there was no interaction between canopy interception and collection date (structure \times date $F_{2,12} = 0.51$, $P = 0.61$). 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, structure $F_{1,6} = 23.8$, $P = 0.003$), both treatments received few midges compared with their respective infall traps located 1 m above the soil surface (short = $15 \pm 3 \text{ midges} \cdot \text{d}^{-1} \cdot \text{pitfall trap}^{-1}$ [mean \pm SE]; tall = $4 \pm 1 \text{ midges} \cdot \text{d}^{-1}$.

pitfall trap^{-1}). These estimates were comparable to the infall deposition rates of the midge-exclusion plots (with cages) in the first experiment (i.e., $15 \pm 3 \text{ midges} \cdot \text{d}^{-1} \cdot \text{infall trap}^{-1}$), 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, structure $F_{1,6} = 6.81$, $P = 0.04$), with the short plots receiving $196 \pm 19 \text{ midges} \cdot \text{d}^{-1} \cdot \text{infall trap}^{-1}$ (mean \pm SE) and tall plots receiving $144 \text{ midges} \pm 20$.

DISCUSSION

Spatial subsidies can have profound effects on ecosystem functioning and structure (Polis et al. 1997, Hoekman et al. 2011, Gratton et al. 2017), although the response magnitude and direction to allochthonous inputs are highly variable across ecosystems (Marczak et al. 2007). Vegetation structure is one ecosystem trait that has the potential to affect community and ecosystem responses to spatial subsidies, given that the

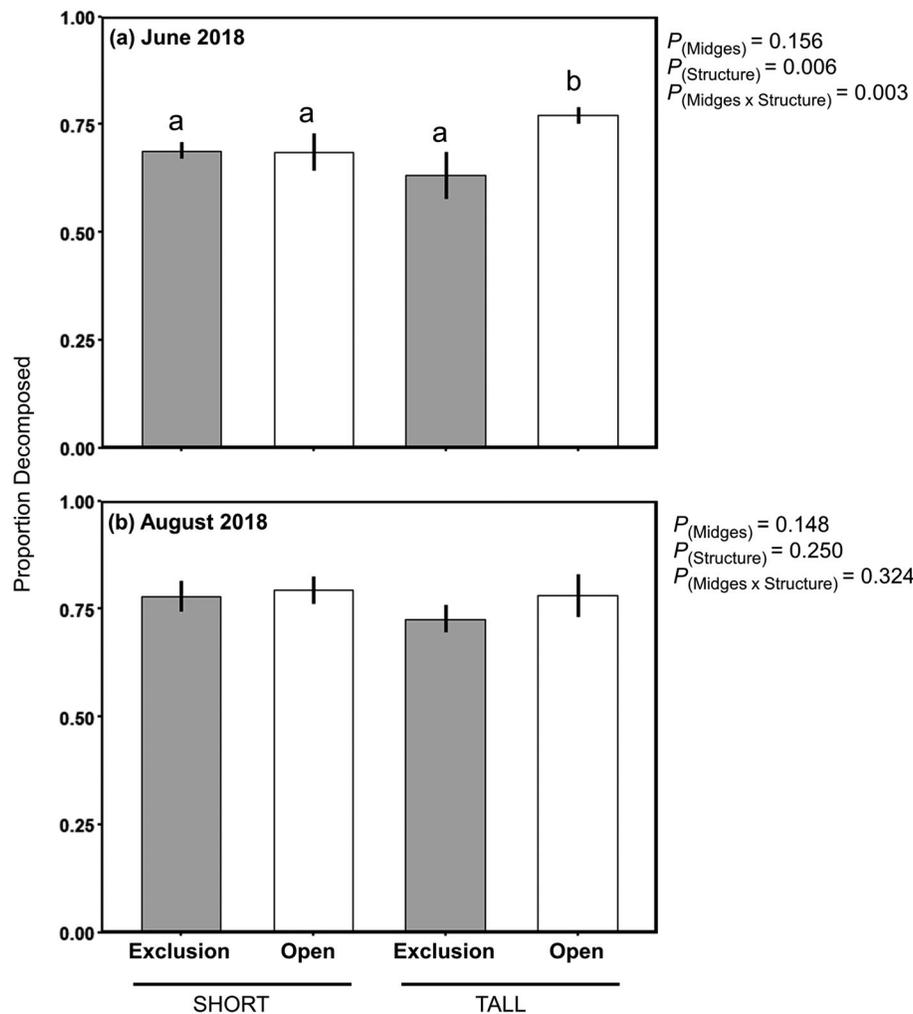


Fig. 3. Bar plots showing the impact of vegetation structure and midge exclusion on litter decomposition for litter bags harvested on (a) 24 June 2018 and (b) 17 August 2018. Data are means and standard errors; different letters denote $P < 0.05$ using post hoc Tukey's HSD comparisons.

canopy structure can influence the rate, amount, and distribution of subsidies entering a recipient ecosystem. We found that vegetation structure can modulate the effects of spatial subsidies on litter decomposition in a subarctic grassland. This is further supported by the disappearance of the decomposition effect at the end of the experiment when all vegetation structure characteristics between plots had converged. 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 structural 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.

Vegetation structure modulates decomposition responses to spatial subsidies

We predicted that shorter vegetation would allow midges to directly enter the detrital-resource pool, increasing litter decomposition relative to tall-vegetation plots. But we found that even though midges had easier access to the soil

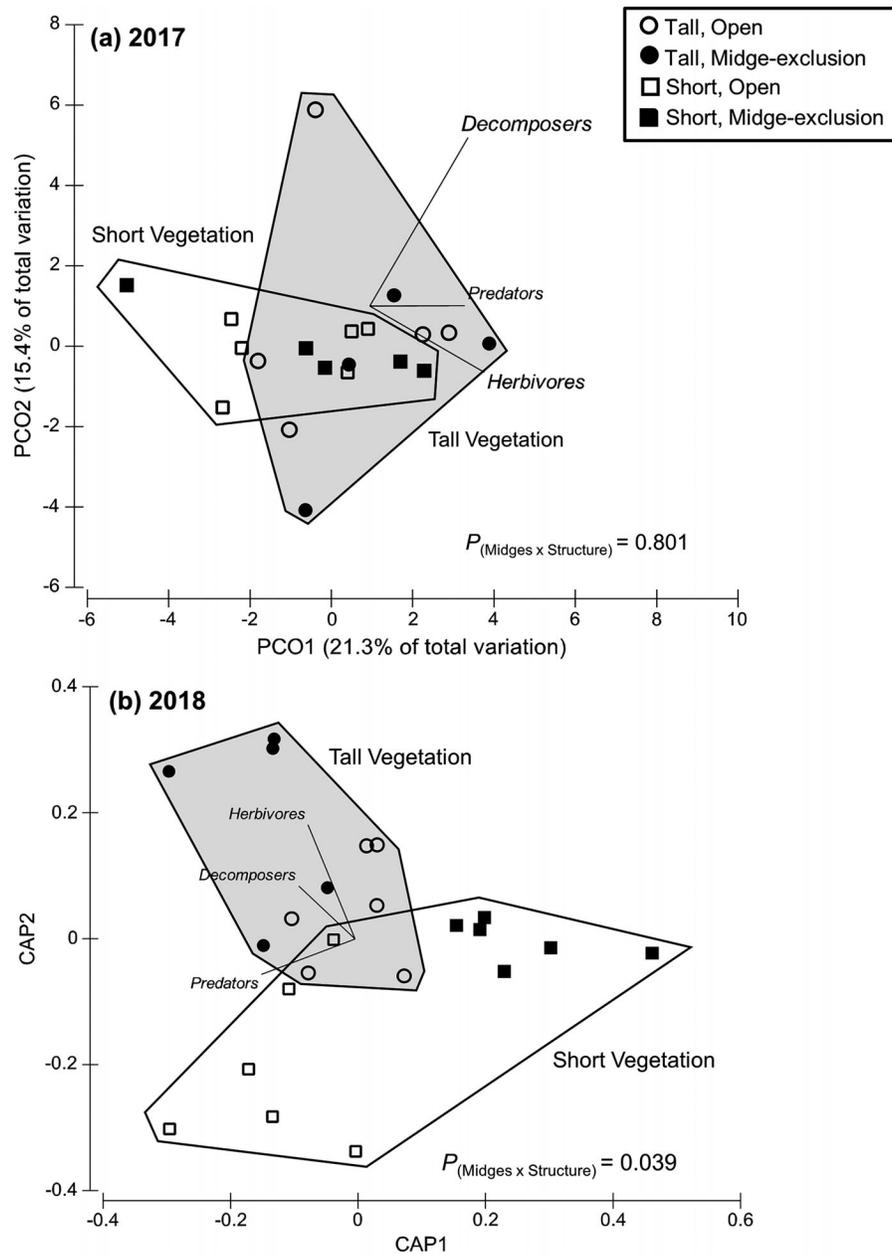


Fig. 4. The impact of vegetation structure and midge exclusion on arthropod composition in (a) 2017 and (b) 2018. Ordination bi-plots show arthropod data that are based on a Euclidean dissimilarity matrix. Each symbol on the ordination plot represents communities for one of the 24 experimental plots 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.

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. This suggests that although canopy-dwelling predators

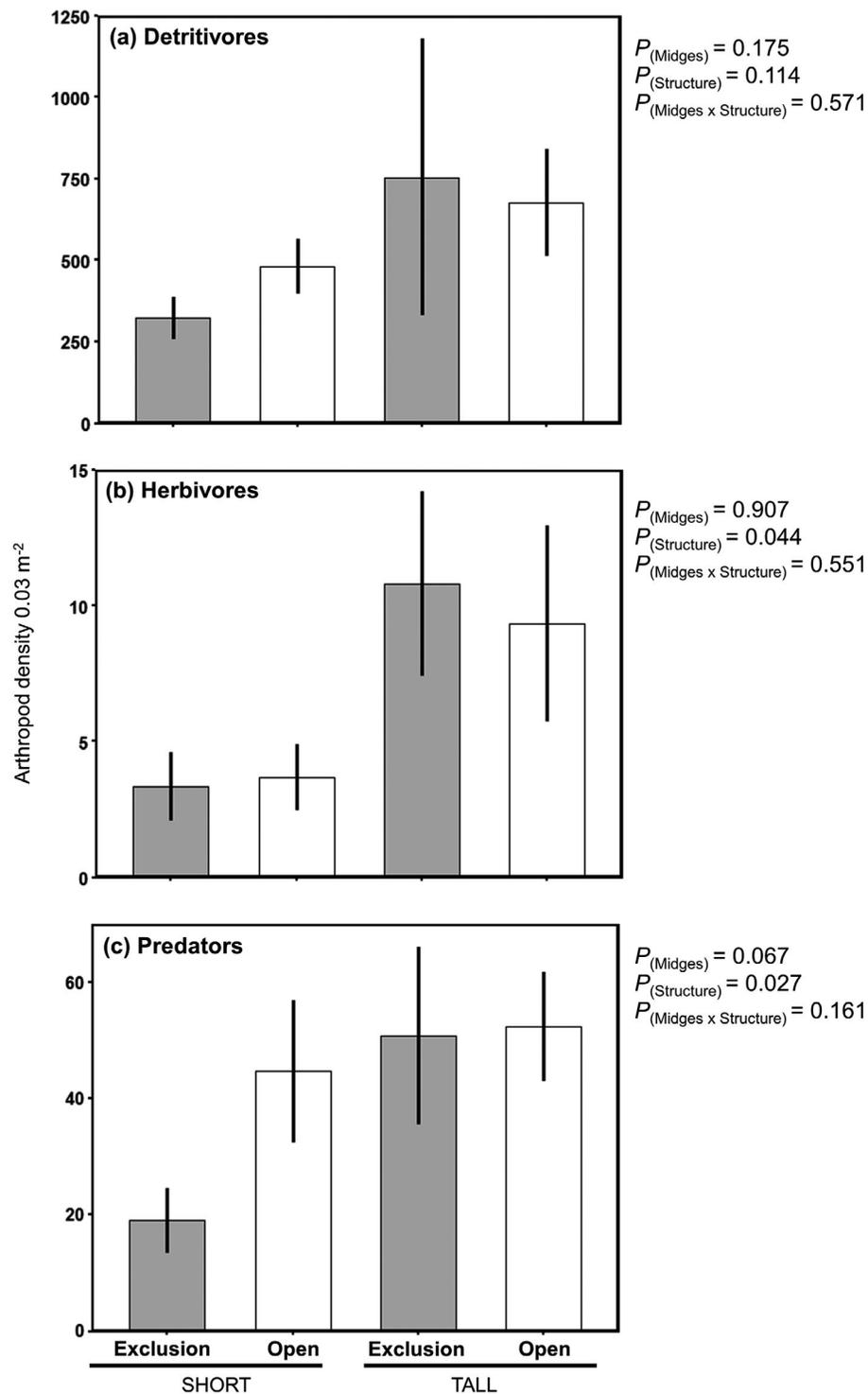


Fig. 5. Bar plots showing the effect of vegetation structure and midge exclusion on arthropod functional densities in 2018 for (a) detritivores, (b) herbivores, and (c) predators. Data are means and standard errors.

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 on 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 2× more abundant in the tall than the 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 litter disappearance rates 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 [~5:1]) likely stimulated microbial activity and increased their

biomass (Kolb et al. 2009) when the vegetation intercepted midges.

It is worth noting that the impacts of vegetation structure and spatial subsidies likely had a time-lag effect on the recipient grassland ecosystem. For example, we found strong structural effects on spatial subsidies in June 2018, which ensued after a full season (i.e., 2017) of plant manipulation. Thus, the litter decomposition results in June 2018 are likely a reflection of the previous year's manipulations. However, after early cutting in 2018 and then allowing the plants to regrow uninterrupted, there were no differences in decomposition by the end of the study. This finding suggests that the vegetation structure effects on decomposition are relatively short-lived if the plants are allowed to regrow in this subarctic system.

Arthropod responses to vegetation structure and spatial subsidies

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 positively correlated with plant biomass and structure; higher above-ground 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 was 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).

Other factors potentially affecting the ecosystem and community responses

Although we revealed apparent effects of spatial subsidies relating to tall vs. short vegetation, our cutting manipulation could have induced unintended collateral effects that influenced our findings. Our initial motivation for cutting the

vegetation was to imitate the two ecosystem types near Mývatn, that is, the heathlands and grasslands. Heathland vegetation in subarctic Iceland is characterized by short-statured woody plants, whereas tall, dense herbaceous plants dominate the grassland ecosystem. While cutting the grassland vegetation was intended to mimic the heathland ecosystem, the experimental manipulation could have stimulated root exudates, stoichiometric changes in plant tissue, or compensatory plant growth—variables we were unable to measure. As such, our results might not perfectly reflect how spatial subsidies can impact ecosystems with natural short vs. tall vegetation.

Vegetation cutting could have also changed the abiotic environment, thereby indirectly affecting the decomposition and arthropod responses to spatial subsidies. For example, we found that the short plots were warmer and received more sunlight than the tall plots. Although vegetation structure likely covaries with temperature and sunlight due to shading effects, our observed results may reflect responses to changes in the abiotic environment caused by vegetation cutting and are not directly due to vegetation structure. Further research should disentangle the structure from the abiotic effects relating to subsidy impacts on recipient ecosystems.

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 possibly the abiotic conditions, on allochthonous nutrients. Thus, vegetation structure might 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) 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 functions that rely on allochthonous inputs.

ACKNOWLEDGMENTS

This research was funded by National Science Foundation grants DEB-LTREB-1556208 and DEB-1611638. We thank Árni Einarsson and the Mývatn Research Station for facilitating this research. We also thank the following people who assisted with the data collection: A. McCormick, J. Phillips, J. Botsch, A. Ward, K. Book, A. Lewis, K. Chen, J. Harris, and K. Jorgenson.

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DATA AVAILABILITY

All data and accompanying analysis scripts are available on GitHub: https://github.com/mmccar26/KAL_Iceland_2021_Manuscript

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3483/full>