

Reducing allochthonous resources in a subarctic grassland alters arthropod food webs via predator diet and density

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Abstract. Emergent aquatic insects can be major conduits of resources moving from freshwater to adjacent terrestrial ecosystems. These allochthonous resources can influence the structure and function of adjacent ecosystems, yet their effect on arthropod consumer populations remains largely unknown. In this study, we investigated how flying adult midges influence terrestrial arthropod food webs in subarctic grasslands by blocking midge inputs over four years in 2 × 2-m plots near the shore of Lake Mývatn, Iceland, where midge abundances are naturally high. We examined responses of terrestrial arthropods by measuring their densities, community composition, and stable isotopes ($\delta^{13}\text{C}$) in midge-exclusion and open (control) plots. Cage treatments significantly reduced midge deposition into exclusion plots (99% reduction) relative to control plots but were designed to allow ground-active arthropods to move freely among plots. Predator densities (e.g., spiders and harvestmen) were on average 30% lower in exclusion plots relative to control plots, while no other trophic guild (detritivores, omnivores, or herbivores) showed a response to midge exclusion. As a result, blocking midges shifted arthropod communities toward a composition dominated by springtails, mites, and aphids relative to large predators such as wolf spiders and harvestmen. All trophic guilds (detritivores, omnivores, and predators), except for herbivores, were more depleted in $\delta^{13}\text{C}$ in midge-exclusion plots, indicating an increased reliance on terrestrial (i.e., plant-based) resources when midge inputs were blocked. Arthropod predators were the only guild that had both a depleted $\delta^{13}\text{C}$ and a negative density response to midge exclusion. Apart from predators, these results indicate a weak association between resource type (aquatic vs. terrestrial) and density responses across most arthropod guilds in this grassland system. Overall, our findings suggest that aquatic insect subsidies have significant effects on terrestrial arthropod communities, but predators appear most responsive to insect allochthony in subarctic grasslands.

Key words: allochthony; arthropod community; experimental manipulation; food webs; Iceland; isotopes; lake-land linkages; midges; spatial subsidies.

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INTRODUCTION

Allochthony, defined as the flow of energy, material, and organisms across ecosystems (Polis et al. 1997), is a widespread phenomenon (Loreau and Holt 2004, Polis et al. 2004). Such

resource movement can have profound effects on recipient ecosystems by altering the quality and quantity of the local resource pool. For example, N-rich emergent aquatic insects can be important prey for many terrestrial consumers (Sabo and Power 2002, Paetzold et al. 2005), leading to

increased predator abundance (Rose and Polis 1998, Murakami and Nakano 2002). Allochthonous inputs can also increase detrital resource pools through leaf litter entering adjacent streams or riparian ecosystems (Sánchez-Piñero and Polis 2000). As such, allochthony is now considered an important ecological flow that can significantly influence local food webs (Marczak et al. 2007), communities (Paetzold et al. 2006), and ecosystems (Richardson and Sato 2015).

Where allochthonous resources enter recipient food webs, the subsequent ecosystem responses will depend on the subsidy. For example, nitrogen runoff into a stream from a nearby riparian forest would enter an aquatic food web differently when compared to leaf litter. In the latter case, leaf litter will enter the detritus pool (Hall et al. 2000), whereas nitrogen runoff will likely enter the food web as primary production via stimulation of algal and plant growth (Bisson et al. 1992). Moreover, the impact of an allochthonous resource will be linked to the form in which it enters. Emergent aquatic insects, for example, can either enter local food webs as live prey or as dead carcasses, each with a different consequence for the ecosystem. Live insect resources may increase apparent competition among local prey if the subsidy has a positive influence on arthropod predator populations (Henschel et al. 2001). On the other hand, dead insect carcasses that are added to detritus will subsidize arthropod detritivores, potentially indirectly affecting predators (Hoekman et al. 2011). Thus, predicting the impact of allochthonous resources requires knowledge of the resource type and where it will enter the recipient food web.

Resource availability in the recipient ecosystem is also important for determining the potential outcomes of allochthony (Marczak et al. 2007). For example, in arid coastal ecosystems with naturally low resource availability, marine detrital subsidies can significantly increase densities of terrestrial detritivorous and predaceous arthropods when compared to adjacent areas without detrital inputs (Polis and Hurd 1996). In contrast, systems with abundant resources may be less sensitive to allochthony because resource levels are already high (Paetzold et al. 2008). For instance, Recalde et al. (2016) showed that the exclusion of aquatic insects from a highly

productive tropical stream only affected riparian predator densities, whereas all other arthropod groups (e.g., omnivores, detritivores, and herbivores) did not respond to the removal of allochthonous resources. The impact of allochthonous resources is therefore context-dependent: The type of resource, where it enters food webs, and the characteristics of the local habitat will dictate the effects of allochthony.

One system where context dependency is likely important is Lake Mývatn, Iceland. At Mývatn (“lake of midges”), substantial numbers of midges (Diptera: Chironomidae) emerge in the summer and move to adjacent terrestrial ecosystems where they create dense mating swarms. Mated females return to the lake to lay eggs, but the males stay behind and die on the terrestrial landscape, subsidizing the local food web. Mývatn is surrounded by a mosaic of resource-low heathlands and resource-abundant grasslands, and the two ecosystems may have different responses to midge subsidies. Previous research in heathlands surrounding Mývatn shows that repeated additions of midge carcasses increased detritivore and predator densities, a likely consequence of bottom-up nutrient effects and/or the direct consumption of midges (Hoekman et al. 2011). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios also indicated that midges were readily incorporated in terrestrial food webs, particularly for detritivores and predators (Hoekman et al. 2012). Thus, in resource-low heathlands surrounding Mývatn, the addition of midge carcasses appears to have strong bottom-up effects on consumer populations (Hoekman et al. 2011, 2012, Gratton et al. 2017).

Despite our understanding of how Icelandic heathlands respond to midge allochthony, it is unknown how midges will influence consumer populations in subarctic grasslands. To address this knowledge gap, we examined the effects of emergent adult midges on grassland arthropod food webs by blocking midge inputs over four years on the shores of Lake Mývatn where midge abundances are naturally high. We evaluated three questions: (1) What influence does midge blocking have on the densities of terrestrial arthropod trophic guilds (i.e., detritivores, herbivores, omnivores, and predators)? (2) What are the respective changes in arthropod community composition once midges are excluded? and (3)

How does midge exclusion affect terrestrial arthropod diets? We predicted that blocking insect subsidies will decrease the densities of predators, detritivores, and omnivores because they regularly consume midges or their carcasses, while herbivores would be unaffected due to their reliance on plants. As population densities change as a consequence of midge blocking, we predicted communities with proportionally fewer predators, omnivores, and detritivores but relatively more herbivores. Lastly, we predicted that arthropods with decreased densities in the midge-exclusion manipulation would exhibit isotopic ratios consistent with greater consumption of plant-based resources given the absence of the abundant midge allochthony (Gratton et al. 2008).

MATERIALS AND METHODS

Experimental design

We conducted a four-year (2008–2011) experiment on the shores of Lake Mývatn in Northeastern Iceland (65° N, 17° W). Our study site (80 × 50 m), on the Kálfaströnd peninsula on the eastern shore of Mývatn, receives high-midge inputs that can range from 110 kg·ha⁻¹·yr⁻¹ of midge deposition in the first 50 m from Mývatn in a high year (e.g., 2008) to as low as 5 kg·ha⁻¹·yr⁻¹ in a low year (Dreyer et al. 2015). The midge (Diptera: Chironomidae) assemblage at Mývatn is dominated by two species, *Tanytarsus gracilentus* and *Chironomus islandicus*, which together comprises 90% of the total midge abundance (Lindegaard and Jónasson 1979). The study area is dominated by grasses (*Deschampsia*, *Poa*, and *Agrostis* spp.), sedges (*Carex* spp.), and forbs (*Ranunculus acris*, *Geum rivale*, and *Potentilla palustris*). The arthropods of this grassland ecosystem are numerically dominated by omnivorous mites (Acari) and detritivorous springtails (Collembola). Common arthropod predators include wolf spiders (Lycosidae), harvestmen (Opiliones), sheet-web spiders (Linyphiidae), and rove beetles (Staphylinidae). The herbivore community consists mainly of aphids (Aphididae).

We established 2 × 2-m permanent plots in six blocks spread across the grassland site. Each block included two treatment levels: an open control plot and a full-exclusion cage to prevent midge deposition into established plots. Control

plots ($n = 6$) were open to allow complete access to all arthropods. Experimental midge-exclusion cages ($n = 6$) were 1 m high and constructed from white PVC tubing affixed to rebar posts on each corner of the plot (Appendix S1: Plate S1). Exclusion cages were entirely covered with white polyester netting (mesh size = 1 mm; Barre Army Navy Store, Barre, Vermont, USA) to prevent flying insects (primarily midges) from entering the plot. However, the mesh netting was left with a 10–20 cm gap at ground level to allow non-flying (ground crawling) arthropods to enter and exit the cages freely. The cages had minor effects on other environmental conditions as they experienced similar temperature (mean ± standard error [SE]: caged = 8.7°C ± 1.23; uncaged = 7.4°C ± 0.41; $P = 0.31$ [t -test]) and light (caged = 971.06 ± 180.3 lumens/ft²; uncaged = 785.3 ± 142.8, $P = 0.42$) gradients. The experimental cages were set up in the field (in the same locations as in prior years) from the middle/end of May to mid-August in each year, corresponding to the period of midge emergence (Einarsson et al. 2002).

In the summer months during which midge-exclusion cages were up, midge activity was measured in all plots to evaluate the efficacy of the cages. Midge abundance was measured using passive aerial infall traps. Infall traps are indicators of activity density for flying insects and serve as a proxy for midge deposition rates per m². Each infall trap consisted of a 1-L clear plastic cup attached to a 0.5-m post placed in the middle of a plot; cups were filled with 250 mL of a 1:1 ethylene glycol: water solution and a small amount of unscented detergent to capture and kill insects. Infall traps were emptied approximately every ten days; the contents of each trap were then counted and identified to midge morphospecies (small midges, likely *T. gracilentus*; large midges, likely *C. islandicus*). Midge infall mass was calculated by multiplying the number of midges of each morphospecies collected by their average dry mass (reported in g·m⁻²·d⁻¹). Here, midge species of *T. gracilentus* and *C. islandicus* accounted for 97% and 2% of the collected flying insects, respectively. Cages decreased midge infall into experimental plots by over 99%: Control plots had high daily midge inputs (2.35 ± 0.40 g·m⁻²·d⁻¹ [mean ± SE]), while exclusion cages received almost no midges

($0.01 \pm 0.01 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). The differences between midge deposition in the control and exclusion plots were consistent across all years of the experiment (Appendix S1).

Arthropod sampling

Vacuum sampling was used to measure arthropod density in each plot during the summer months of each year in the experiment (2008–2011). 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. An open-bottomed plastic box ($50 \times 36 \text{ cm}$, 0.176 m^2) was quickly and haphazardly placed on the ground within each plot. The vacuum was pressed firmly on the vegetation within the plastic box repeatedly to cover the entirety of the enclosed area twice. The same area within a plot was not vacuumed again within the same year. 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 using a dissecting microscope (20–40 \times); arthropods were identified to the lowest taxonomic level possible, usually family, and assigned to a trophic guild (e.g., detritivores, herbivores, omnivores, and predators). Densities were calculated as the number of arthropods per 0.176 m^2 . Refer to Appendix S2 for full details on the arthropods sampled, trophic classification, and mean annual densities.

Isotope sample collection and preparation

To estimate the reliance of terrestrial arthropods on aquatic vs. terrestrial resources, we collected arthropods from the control and exclusion plots for analysis of naturally occurring stable isotope ratios of ^{13}C to ^{12}C . In 2009 and 2010, we collected arthropod taxa throughout the summer but increased our sampling effort in early August during peak plant biomass and arthropod abundance. Arthropods for isotope analysis were either collected by hand or with vacuum samplers (see *Arthropod sampling* section). In the latter case, the contents of each vacuum bag were quickly emptied into white plastic trays in the

field and arthropods were collected live using aspirators or forceps. After collection, arthropod samples were immediately frozen for storage and eventually sorted into taxonomic groups with enough biomass for isotope assays. Samples were dried (50°C for $>48 \text{ h}$) and weighed (≈ 0.5 – 1.5 mg dry mass depending on C concentration) into tin capsules (Costech Analytical Technologies, Valencia, California, USA) for isotope analysis. Most arthropods were placed directly into the capsules (singly or bulked to achieve a minimum mass for analysis), though large spiders ($>1.5 \text{ mg}$ each dry mass) were ground to powder to homogenize their tissues before being weighed. To collect enough tissue mass to run isotope analyses, arthropods for each group were aggregated across several plots of the same treatment. Midges and terrestrial plants were also collected for isotope analyses to help elucidate the isotope values of potential aquatic and terrestrial basal resources. Samples were analyzed for stable isotopes of C at the University of California–Davis Stable Isotope Facility (Davis, California, USA) in 2009 and the Colorado Plateau Stable Isotope Facility (Flagstaff, Arizona, USA) in 2010. Ratios of $^{13}\text{C}/^{12}\text{C}$ are expressed relative to known standards (Vienna PeeDee Belemnite [VPDB]) in per mil (‰) notation. Measurement errors (standard deviation [SD]) of our duplicate samples for $\delta^{13}\text{C}$ were 0.26 in 2009 ($n = 22$) and 0.10 in 2010 ($n = 52$). Analytical measurement error (SD) for $\delta^{13}\text{C}$ was 0.08 ($n = 205$).

Statistical analyses

Arthropod abundance.—Arthropod density from vacuum samples was analyzed using linear mixed-effects model (LMMs; Zuur et al. 2009) with three fixed factors: (1) cage treatment (control vs. exclusion), (2) month (June–August), and (3) year (2008–2011). We also included a treatment \times month and a treatment \times year interaction to evaluate how midge exclusion changed arthropod densities throughout the experiment. Because we were mostly interested in the treatment effects across years (i.e., constraining seasonality), we did not include a year \times month interaction in our models. Furthermore, because we had limited years ($n = 4$), we decided it was a reasonable simplification to ignore temporal autocorrelation in our models. Linear mixed-effects models were performed separately for the

four main arthropod trophic guilds: detritivores, herbivores, omnivores, and predators (Appendix S2). These groups were evaluated because they are abundant and represent critical components of terrestrial arthropod food webs (Coleman et al. 1999, Bardgett 2005). The random effects included plot nested in block, to account for the repeated sampling of plots across time, and a block effect to account for potential variability across the site. Arthropod density data were either log or 4th-root-transformed to ensure homoscedasticity of variance. Linear mixed-effects models were fit using the lme4 package in R (Bates et al. 2015, R Development Core Team 2016). For alternative model fits, such as the inclusion of seasonality and temporal autocorrelation, see Appendix S3.

Because appropriate calculation of degrees of freedom is debated in mixed models due to maximum-likelihood estimation (Luke 2017), we used Kenward–Roger approximations to calculate *P*-values (Type III summed squares of factors) for degrees of freedom using the lmerTest R package (Kuznetsova et al. 2017). This method estimates the denominator degrees of freedom from the data by matching the first two moments of the Wald *F* statistics and the approximating *F* distribution (Kenward and Roger 1997). The Kenward–Roger approximation also adjusts the covariance matrix for the fixed effects parameters by accounting for unexplained variation, thereby minimizing Type I error (Luke 2017). Kenward–Roger methods are ideal for randomized block, split-plot, and repeated measures designs (Kenward and Roger 1997).

Arthropod community composition.—Arthropod community responses to treatment were examined using permutational analysis of variance (PERMANOVA: 10,000 permutations; Type III SS; Anderson et al. 2008). We first investigated whether midge blocking affected community composition through time; this was done by treating treatment and year as fixed factors and nesting treatment within block as the random effects (Anderson et al. 2008). Because we used annually averaged data and therefore had only four years of data for community analyses, we did not account for temporal autocorrelation. An initial PERMANOVA revealed a weak treatment × year interaction (*P* = 0.094; Appendix S3), so we performed PERMANOVA tests for

each year (2008, 2009, 2010, and 2011) separately. For these analyses, we calculated a Bray–Curtis dissimilarity distance matrix between experimental plots (using each lowest-level taxonomic group, 4th-root-transformed). To visualize differences in arthropod composition in two-dimensional space, we performed a principal coordinate analysis (PCoA). Vector overlays were used to visualize which taxa were associated with each treatment; a vector reflects Spearman’s correlation coefficient of an arthropod taxon with the two axes (vectors of the most important groups for each trophic guild are reported). PERMANOVAs and PCoAs were performed using PRIMER-E/PERMANOVA+ software (Anderson et al. 2008).

Variation in $\delta^{13}\text{C}$ across midge-exclusion treatments.—Because two different stable isotope facilities were used to analyze arthropod $\delta^{13}\text{C}$ ratios in 2009 and 2010, we did not combine years in our analyses. Furthermore, to collect enough arthropod tissue to run stable isotopes, arthropod samples were aggregated across multiple plots of the same treatment. Thus, variations in arthropod $\delta^{13}\text{C}$ values in 2009 and 2010 were analyzed using *t*-tests (control vs. midge-exclusion treatment). Analyses were first done by combining all the taxa according to trophic guild (detritivores, herbivores, omnivores, and predators), and the second analyses were performed separately for each taxon. All *t*-tests were performed using R version 3.3.0 (R Development Core Team 2016); Bonferroni corrections were conducted using the *p.adjust* function in R.

RESULTS

Terrestrial arthropod density response to midge exclusion

Over four years, 195,878 arthropods were collected by vacuum sampling, representing 12 orders and 41 families (Appendix S2). Omnivorous mites (Acari) and detritivorous springtails (Collembola) were the most abundant arthropods, representing 76% and 19% of all sampled arthropods, respectively. Herbivores such as aphids (Aphididae) comprised of 3% of the entire collection. Predators, which were mostly represented by spiders (Araneae), harvestmen (Opiliones), and rove beetles (Staphylinidae), collectively accounted for 2% of collected arthropods.

The density of arthropods was variable (both within a year and among years) throughout the experiment across all trophic guilds (Appendix S2). However, for almost all trophic feeding guilds, there was no evidence that midge exclusion had any effect on terrestrial arthropod density. This pattern was true for detritivores (Fig. 1a, $P = 0.33$, Table 1a), herbivores (Fig. 1b, $P = 0.85$, Table 1b), and omnivores (Fig. 1c, $P = 0.48$, Table 1c), though all three guilds had

slightly higher mean densities in the exclusion plots relative to the controls. The only trophic guild that was significantly affected by midge exclusion was predators (Fig. 1d, $P = 0.032$, Table 1d). Predator densities were lowest in exclusion plots, which were on average 30% lower in density compared to the controls over the four-year experiment when densities are back-transformed. No trophic guild showed a treatment \times month or treatment \times year interaction

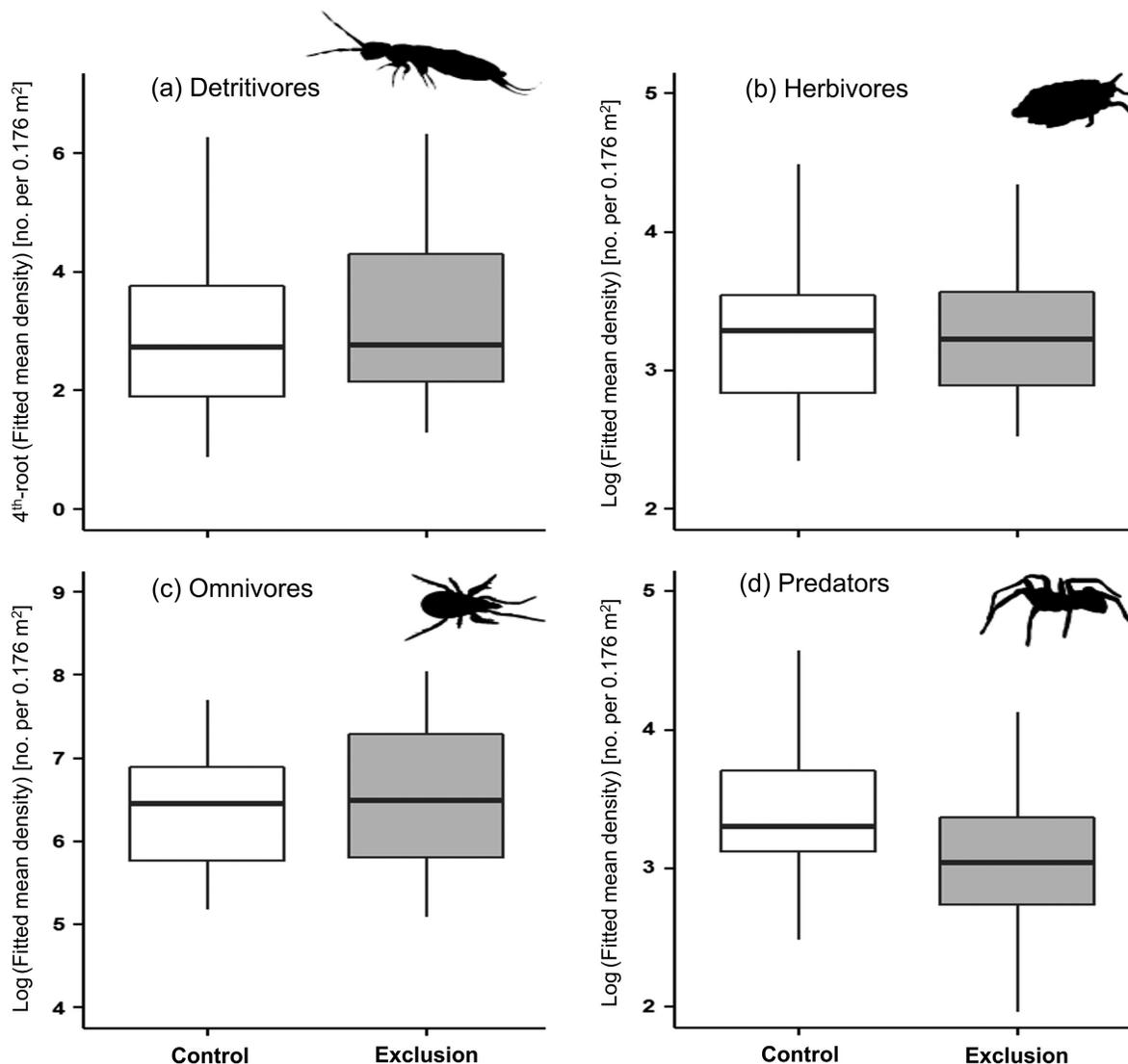


Fig. 1. The effects of midge exclusion on mean (a) detritivore, (b) herbivore, (c) omnivore, and (d) predator density. Values are fitted means calculated from the linear mixed-effect models. Error bars represent the range of the data.

Table 1. Results from the linear mixed-effects models testing for the main and interactive effects of treatment, month, and year on detritivore, herbivore, omnivore, and predator density.

Factor	Numerator df	Residual df	F value	P
Detritivores				
Treatment	1	8	1.09	0.329
Month	3	120	55.61	<0.001
Year	3	120	2.22	0.090
Treatment × Month	3	120	0.28	0.837
Treatment × Year	3	120	0.66	0.581
Herbivores				
Treatment	1	8	0.04	0.845
Month	3	120	6.04	0.007
Year	3	120	2.27	0.050
Treatment × Month	3	120	0.00	0.999
Treatment × Year	3	120	0.55	0.650
Omnivores				
Treatment	1	7	0.55	0.481
Month	3	120	6.09	<0.001
Year	3	120	68.76	<0.001
Treatment × Month	3	120	0.22	0.884
Treatment × Year	3	120	0.55	0.646
Predators				
Treatment	1	14	4.90	0.032
Month	3	120	6.22	<0.001
Year	3	120	21.65	<0.001
Treatment × Month	3	120	0.35	0.686
Treatment × Year	3	120	2.10	0.103

Note: Bold values indicate $P < 0.05$.

($P > 0.1$; Table 1), suggesting that treatment effects were consistent both within a season and across years.

Arthropod community composition

Arthropod community composition did not differ in midge-exclusion plots and controls in the first three years of the experiment (PERMANOVA; Table 2), although the P -values for all three years were relatively low ($0.1 < P < 0.26$). However, by the end of the four-year experiment (2011), arthropod community composition indicated a divergence between treatments ($P = 0.04$; Table 2d). The difference in community composition between midge exclusion at the end of the

Table 2. Two-factor permutational analysis of variance (PERMANOVA) results for arthropod composition for 2008–2011.

Source	df	SS	MS	Pseudo-F	P
2008					
Treatment	1	291.53	291.53	1.63	0.113
Block	5	1165.30	233.07	1.31	0.162
Residuals	5	892.42	178.48		
Total	11	2349.30			
2009					
Treatment	1	434.94	434.94	1.26	0.263
Block	5	1644.70	328.95	0.95	0.576
Residuals	5	1724.90	344.99		
Total	11	3804.60			
2010					
Treatment	1	411.95	411.95	1.43	0.165
Block	5	2453.10	490.61	1.71	0.014
Residuals	5	1438.40	287.68		
Total	11	4303.40			
2011					
Treatment	1	446.22	446.22	2.08	0.040
Block	5	1769.00	353.80	1.65	0.029
Residuals	5	1071.10	214.22		
Total	11	3286.30			

Notes: PERMANOVAs were performed with 10,000 permutations using the Type III SS and calculated on a Bray-Curtis dissimilarity matrix. Values indicated in bold are P -values < 0.05 .

experiment is evident in the PCoA ordination with the position of the control plots separate (lower left) from the exclusion plots (upper right, Fig. 2d). Springtail (Collembola) and mite (Acari) densities were positively correlated with midge-exclusion plots and negatively correlated with the open control plots (Fig. 2d), consistent with the trends seen in the decrease in overall density of these groups in the mixed-model analysis (Fig. 1a, c). In contrast, harvestmen and wolf spiders were negatively correlated with the exclusion plots and positively correlated with control plots (Fig. 2d), also consistent with the overall density effects (Fig. 1d).

Arthropod $\delta^{13}\text{C}$ response to midge exclusion

For this experiment, the average $\delta^{13}\text{C}$ values for midges and terrestrial plants at Lake Mývatn were -12.6‰ (SEM = ± 0.45) and -27.9‰ (± 0.08), respectively. Therefore, for our analyses, more enriched $\delta^{13}\text{C}$ values suggest an isotopic ratio that is more associated with aquatic-based midges, whereas more negative (i.e., depleted)

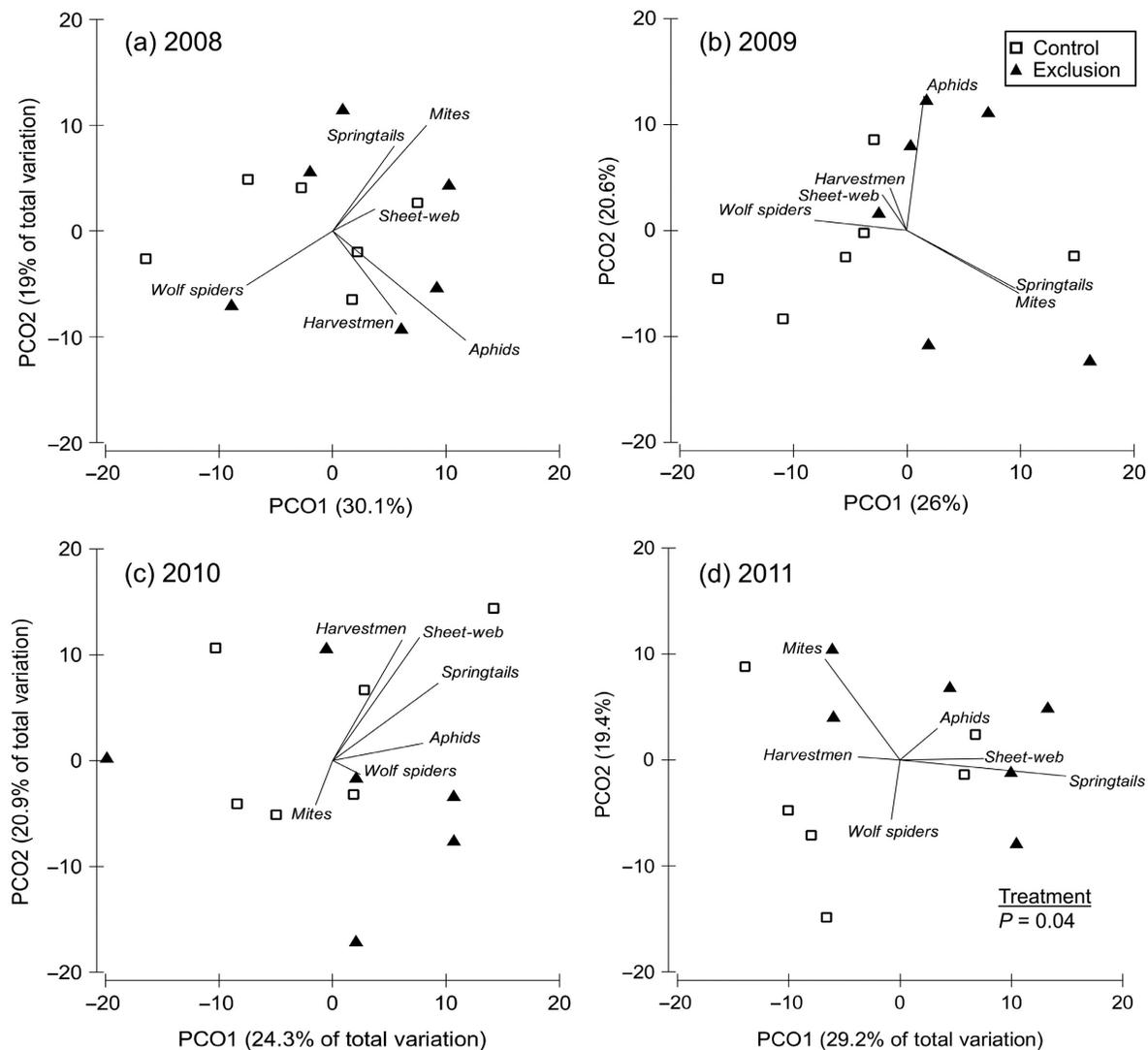


Fig. 2. Principal coordinate analysis (PCoA) plots illustrating the changes in arthropod community composition as a function of midge exclusion in (a) 2008, (b) 2009, (c) 2010, and (d) 2011. Principal coordinates analysis (PCoA) bi-plots of arthropod data are based on a Bray-Curtis dissimilarity matrix (fourth-root-transformed data). Each symbol on an ordination plot represents averages for one of the 12 experimental plots in that year of the experiment. The length and direction of vector overlays indicate the strength of the association (Spearman's correlation coefficient) between the ordination axes and the associated labeled taxon, showing the most common taxa for each trophic level. Aphids = herbivore; Harvestmen = predator; Mites = omnivores; Sheet-web spiders = predators; Springtails = detritivore; Wolf spiders = predators.

values indicate a more terrestrial plant-based diet.

Trophic guild responses.—On average, carbon isotopic ($\delta^{13}\text{C}$) values of omnivores, detritivores, and predators were more depleted in midge-exclusion plots compared the control plots (Fig. 3a, b). The direction and magnitude of

change in $\delta^{13}\text{C}$ between treatments were consistent in 2009 and 2010 (Table 3), with detritivores on average showing depletion by 18%, omnivores by 20%, and predators with 13% lower $\delta^{13}\text{C}$ values in the midge-exclusion treatment (Fig. 3a, b). Herbivores did not exhibit a difference in $\delta^{13}\text{C}$ values between the midge-exclusion

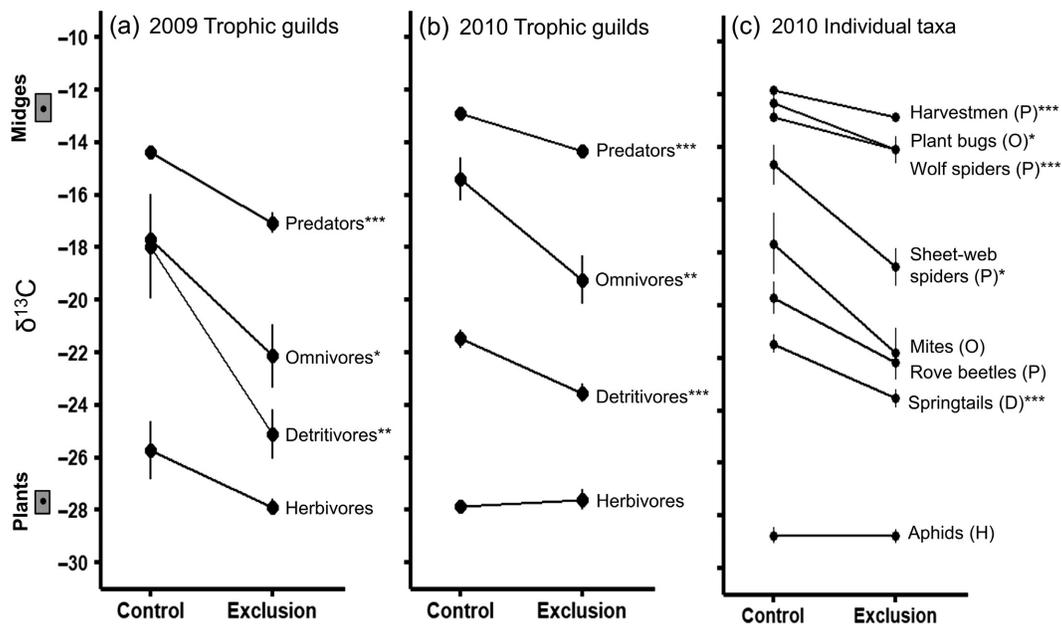


Fig. 3. Mean $\delta^{13}\text{C}$ (‰) values (\pm SEM) for control and exclusion plots for (a) 2009 trophic guilds, (b) 2010 trophic guilds, and (c) 2010 individual arthropod taxa. Higher $\delta^{13}\text{C}$ values indicate a greater proportion of C in an organism is from aquatic sources (midge-based), while lower values indicate terrestrial C (plant-based) sources. Average $\delta^{13}\text{C}$ values of midges and terrestrial plants at Mývatn (Mean \pm SEM indicated on Y-axis in gray rectangles) were -12.6 and -27.9 , respectively. Increased sampling intensity in 2010 for isotopic analyses allowed for a finer taxonomic resolution for individual arthropods. Asterisks indicate differences between groups significant at *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; individual taxa represent Bonferroni corrections. Values of standard errors were sometimes too small (range = 0.09 – 1.3) and may be obscured by the mean symbols. Abbreviations are D, detritivore; H, herbivore; O, omnivore; and P, predator.

and open plots in either year (t -test, $P \geq 0.1$, Table 3).

Responses of individual taxa.—In 2010, increased sampling intensity for isotope analyses enabled us to refine the taxonomic resolution for the majority of the arthropod groups (Table 3). Arthropod predators, such as harvestmen, wolf spiders, and sheet-web spiders, showed markedly depleted $\delta^{13}\text{C}$ values in exclusion plots, which on average were depleted by 8%, 9%, and 21%, respectively (Fig. 3c). Omnivorous mites and plant bugs (Miridae) were also affected by midge exclusions, showing $\delta^{13}\text{C}$ depleted by 19% and 12% in exclusion plots relative to controls (Fig. 3c). Similarly, detritivorous springtails (Collembola) exhibited depleted $\delta^{13}\text{C}$ values in exclusion plots, which were 9% lower than the control plots. The values of $\delta^{13}\text{C}$ isotope values for aphids, which were the most abundant

herbivore taxon collected in this study, did not respond to midge exclusion (Fig. 3c).

DISCUSSION

Although allochthonous resources can alter ecosystem processes and food web structure in recipient systems (Richardson et al. 2010), the context in which they occur will likely dictate the effects of allochthony (Subalusky and Post 2018). We evaluated the effects of emergent aquatic insects in a subarctic grassland by blocking midge inputs from entering half of the experimental plots. We found that blocking midges shifted the diets of all trophic guilds (except herbivores) from aquatic (midge-based) to terrestrial (plant-based) C resources. However, this shift in resource consumption did not affect the densities of most trophic groups (i.e., detritivores,

Table 3. Summary statistics (means and SEM) of $\delta^{13}\text{C}$ (‰) for the main arthropod trophic guilds and taxa collected at Lake Mývatn for isotopic analysis in years 2009 and 2010.

Taxon, by trophic group	2009					2010				
	Control		Exclusion		P-value	Control		Exclusion		P-value
	n	$\delta^{13}\text{C}$ (SEM)	n	$\delta^{13}\text{C}$ (SEM)		n	$\delta^{13}\text{C}$ (SEM)	n	$\delta^{13}\text{C}$ (SEM)	
<i>Detritivores</i>										
Collembola†, ‡	9	-17.97 (1.99)	7	-25.12 (0.95)	0.008	9	-21.47 (0.35)	10	-23.55 (0.35)	<0.001
<i>Herbivores</i>	21	-25.73 (1.1)	17	-27.88 (0.32)	0.074	43	-27.88 (0.24)	45	-27.6 (0.39)	0.547
Aphididae†	-	-	-	-	-	6	-28.74 (0.3)	6	-28.77 (0.26)	0.168
Cicadellidae	-	-	-	-	-	10	-26.16 (0.19)	10	-26.88 (0.29)	0.626
Curculionidae	-	-	-	-	-	12	-28.4 (0.24)	17	-28.36 (0.14)	1
Lepidoptera	-	-	-	-	-	13	-28.09 (0.55)	11	-27.7 (0.76)	1
<i>Omnivores</i>	18	-17.67 (1.34)	14	-22.13 (1.2)	0.019	33	-15.4 (0.82)	31	-19.23 (0.93)	0.003
Acari†	10	-21.56 (1.53)	9	-22.66 (1.53)	1	19	-17.66 (1.17)	20	-21.8 (0.93)	0.108
Miridae†	8	-12.82 (0.24)	5	-21.17 (2.19)	0.093	14	-12.33 (0.41)	11	-14.08 (0.51)	0.011
<i>Predators</i>	121	-14.39 (0.24)	89	-17.06 (0.37)	<0.001	190	-12.89 (0.15)	218	-14.33 (0.19)	<0.001
Lycosidae†	42	-13.96 (0.26)	32	-15.99 (0.47)	0.002	80	-12.85 (0.13)	87	-14.06 (0.19)	<0.001
Opiliones†	37	-13.75 (0.21)	35	-15.13 (0.22)	<0.001	79	-11.85 (0.09)	93	-12.86 (0.12)	<0.001
Linyphiidae†	20	-18.47 (0.69)	20	-22.17 (0.58)	0.001	12	-14.67 (0.76)	24	-18.56 (0.71)	0.011
Staphylinidae†	-	-	-	-	-	9	-19.72 (0.61)	8	-22.18 (0.64)	0.167
Saldidae	-	-	-	-	-	8	-12.64 (0.6)	4	-12.18 (0.45)	1

Notes: P-values represent outputs from a Welch two-sample *t*-test; Bonferroni corrections were applied only to individual taxa. - indicates no data were taken.

† Individual taxon is illustrated in Fig. 3.

‡ Collembola were the only detritivore group collected for isotopic analyses.

herbivores, and omnivores) except for predators. Midge blocking therefore shifted arthropod community composition by the end of the four-year experiment, resulting in relatively increased detritivore, herbivore, and omnivore densities, and fewer predators compared to control plots. These findings suggest that while aquatic insect subsidies can enter recipient terrestrial food webs through multiple trophic levels, the removal of allochthonous resources in subarctic grasslands has limited effects on arthropod communities, with only the predators showing a detectable response after the four-year experiment.

The findings of this study stand in contrast to previous experiments that took place in a heathland ecosystem near Lake Mývatn (Hoekman et al. 2011, 2012). Rather than removing live midges using cages (since there are few midges in Lake Helluvaðstjörn), dead midges collected from Mývatn were added as dried carcasses to simulate allochthonous inputs. These experiments demonstrated that adding allochthonous midges to heathlands led to significant bottom-up effects such that most arthropod groups increased in abundance by the end of the study (Hoekman et al. 2011). In the present grassland

study, only predators responded to manipulations of allochthonous resources, showing a shift to a terrestrial-based diet and a decrease in abundance where midges were excluded. Because the arthropod predators in this system are more responsive to live prey (Dreyer et al. 2016), it is not surprising that they declined in abundance where fewer living midges were available. The abundance of live midges in the open plots likely influenced large mobile predators to move away from the caged plots.

Our expectation for relatively immobile arthropods (i.e., springtails and mites) would be that in the absence of midges, the utilization of the relatively lower quality in situ plant-based resources would result in lower densities. However, for detritivores and omnivores, we found no differences in density when midges were removed. This finding begs the question: Why did omnivores or detritivores not respond to midge exclusion despite the isotopic data indicating shifts in diets to more terrestrial-based resources? We propose two hypotheses for the observed patterns of this study. First, the lack of density responses by detritivores and omnivores might be attributed to the relatively large ambient

detrital and plant resource pool that is characteristic at Lake Mývatn (Gratton et al. 2008), relative to heathland vegetation. Accumulated living and dead plant biomass at Mývatn—presumably aided by annual midge fertilization at this location (Gratton et al. 2017)—represent a resource pool that could sustain detritus-consuming arthropods even in the absence of midge inputs over the four years of this study. Available above-ground plant biomass was measured at our site in 2009, and an average of 9203 g/m² dw was harvested (R. Jackson, M. Raudenbush, and C. Gratton, *unpublished manuscript*). This contrasts with the midge-addition experiment at the heathland site (Lake Helluvaðstjörn) where estimates of standing biomass were on average 6167 g/m² (R. Jackson, M. Raudenbush, and C. Gratton, *unpublished manuscript*). The relatively large quantity of plant biomass and the local detrital resource pool at Mývatn may explain why detritivore and omnivore densities were not sensitive to allochthony as the heathland study.

An alternative explanation for the lack of detritivore and omnivore response to the midge exclusions may be related to arthropod mobility and/or top-down effects. Because most of the arthropod predators in this system are large and mobile (e.g., wolf spiders, ground beetles, and harvestmen), it is possible that predators simply aggregated to the open plots where midges were abundant, vacating the midge-exclusion plots. Detritivores and omnivores were likely unable to disperse to high-midge plots to the same extent because of their limited mobility. Thus, the reduction in arthropod predators in the midge-exclusion plots, coupled with the inability of detritivores and omnivores to move to plots where midges were abundant, may have favored springtail and mite densities via reduced predation rates (as also suggested by the trend in higher densities in the midge-exclusion plots). In contrast, in the control plots, increased predation intensity on detritivores as a result of higher predator densities could have decreased decomposer levels even in the face of higher resource (i.e., midge) availability. This interaction could explain the arthropod composition shift at the end of the experiment, which was more dominated by large arthropod predators in the control plots and more represented by detritivores, omnivores, and herbivores in the midge-exclusion plots. This type

of apparent competition—between midges and local detritivore prey—can occur when allochthonous inputs alter predator densities (Henschel et al. 2001).

Because of our experimental design and low statistical power, we cannot definitively rule out arthropod mobility and/or top-down effects as being the main drivers of the consumer responses. Nevertheless, previous research in this system suggests these factors are likely unimportant in determining detritivore and omnivore responses, which may be explained by predator behavior. Dreyer et al. (2016), for example, showed that arthropod predation rates on local prey (e.g., herbivores, detritivores, and omnivores) tended to decrease when midges were present, even in cases of elevated predator densities. Even though Dreyer et al. (2016) was a short-term study, their findings suggest that midges distract arthropod predators from local prey rather than increasing predation pressure. This predator behavior when midges are present may also explain their higher densities in the open control plots of this study; other studies have reported similar predator responses to aquatic insects flying into adjacent terrestrial habitats (Marczak and Richardson 2007, Recalde et al. 2016).

CONCLUSION

The results from our grassland study in subarctic Iceland show how allochthonous resources (i.e., midges) can have different influences on consumer populations. We found that detritivore and omnivore abundance did not change despite clear evidence showing consumption of nutrient-rich subsidies when midges were available in grasslands near Lake Mývatn. In contrast, our previous heathland research (Hoekman et al. 2011) revealed that these same groups (e.g., springtails and mites) had dramatic increases when dead-midge carcasses from Mývatn were added. Taken together, our results show that even in subarctic ecosystems, the effects of insect allochthony appear context-dependent. Thus, understanding the characteristics of the local habitat and the composition of the consumer community is crucial for predicting the outcomes of insect allochthony on recipient ecosystems.

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