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Long-term nutrient addition alters arthropod community composition but does not increase total biomass or abundance

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A simple bottom–up hypothesis predicts that plant responses to nutrient addition should determine the response of consumers: more productive and less diverse plant communities, the usual result of long-term nutrient addition, should support greater consumer abundances and biomass and less consumer diversity. We tested this hypothesis for the response of an aboveground arthropod community to an uncommonly long-term (24-year) nutrient addition experiment in moist acidic tundra in arctic Alaska. This experiment altered plant community composition, decreased plant diversity and increased plant production and biomass as a deciduous shrub, *Betula nana,* became dominant. Consistent with strong effects on the plant community, nutrient addition altered arthropod community composition, primarily through changes to herbivore taxa in the canopy-dwelling arthropod assemblage and detritivore taxa in the ground assemblage. Surprisingly, however, the loss of more than half of plant species was accompanied by negligible changes to diversity (rarefied richness) of arthropod taxa (which were primarily identified to family). Similarly, although long-term nutrient addition in this system roughly doubles plant production and biomass, arthropod abundance was either unchanged or decreased by nutrient addition, and total arthropod biomass was unaffected. Our findings differ markedly from the handful of terrestrial studies that have found bottom-up diversity cascades and productivity responses by consumers to nutrient addition. This is probably because unlike grasslands and salt marshes (where such studies have historically been conducted), this arctic tundra community becomes less palatable, rather than more so, after many years of nutrient addition due to increased dominance of *B. nana*. Additionally, by displacing insulating mosses and increasing the cover of shrubs that cool and shade the canopy microenvironment, fertilization may displace arthropods keenly attuned to microclimate. These results indicate that terrestrial arthropod assemblages may be more constrained by producer traits (i.e. palatability, structure) than they are by total primary production or producer diversity.

Nutrient availability is a major determinant of many ecosystem properties, including primary and secondary production and community structure (Chapin et al. 1986, Gruner et al. 2008). An array of nutrient addition experiments has not only confirmed that plant growth in most natural systems is nutrient-limited (Downing et al. 1999, Elser et al. 2007, Gruner et al. 2008, Fay et al. 2015), but has also shown that there can be complex feedbacks among nutrient availability, primary production, and producer community structure, especially after many years of manipulation (Leibold et al. 1997, Worm and Duffy 2003, Hillebrand et al. 2007). Those few terrestrial nutrient addition studies that have incorporated consumers have generally explored top–down effects of consumers on producers, rather than the other way around (Gruner et al. 2008). They also tend to focus on the roles of mammalian herbivores (Borer et al. 2014), while ignoring other potentially important consumers (e.g. insects).

Theory suggests that as primary productivity increases with nutrient addition, more consumer biomass can be supported (Oksanen 1981, White 1978). Likewise, the secondary effects of nutrient addition on producer community composition and diversity should affect consumer community composition and diversity (Hunter and Price 1992, Hutchinson 1959). A handful of studies – most from grasslands and salt marshes – have demonstrated such bottom–up effects on arthropod communities, which respond at spatial and temporal scales compatible with many nutrient addition experiments. Short-term (<3 years) experiments show that increased nutrient availability increases plant biomass and arthropod abundance (Hurd and Wolf 1974, Kirchner 1977, Siemann 1998, Gruner and Taylor 2006, Wimp et al. 2010). Long-term studies in grasslands (5–14 years) have shown that when nutrient addition homogenizes the plant community, total arthropod abundance is increased (Siemann 1998, Haddad et al. 2000) even if arthropod diversity declines in tandem with plants (Haddad et al. 2000).

Evidence from aquatic systems suggests that outcomes for consumer communities are not always predicted by

producer community responses to nutrient addition. For example, in temperate lakes, if long-term nutrient loading favors well-defended or toxic algal species, consumers do not show a bottom-up productivity response even when the total amount of primary production is greatly increased (Leibold 1989, Leibold et al. 1997). Changes to producer community physical structure can also negate bottom-up nutrient addition effects on some consumers (Gough et al. 2016). For instance, nutrient addition in benthic marine habitats shifts the producer community from eelgrass to dense microalgae; the enhanced structural complexity impedes fish foraging and reduces overall consumer abundance (Deegan et al. 2002). Such findings suggest that producer traits control whether the direct effects of nutrient availability on primary production and diversity are passed along to consumers.

As in most aquatic and terrestrial communities, long-term nutrient addition in moist acidic tussock tundra, a common and well-studied plant community type in northern Alaska, increases primary production and homogenizes the producer community (Gough et al. 2000, Shaver et al. 2014). This occurs because a deciduous shrub, *Betula nana* ssp. *exilis*, becomes dominant while displacing lower-stature and slower-growing species including sedges, mosses, dwarf evergreen shrubs and lichens (Shaver et al. 2014). *Betula*'s woody stem tissue, which is low in N relative to the graminoids and evergreens it replaces, accounts for the majority of producer biomass after six or more years of fertilization. Relative to other deciduous shrubs in this plant community, *Betula nana* ssp. *exilis* is less palatable to vertebrate herbivores (Christie et al. 2015) and is not the preferred forage of local insect larvae (MacLean and Jensen 1985). Furthermore, aerial branching and litter deposition by *Betula* in fertilized plots creates a canopy and ground microenvironment cooler than that of unfertilized tussock tundra (Myers-Smith et al. 2011). Altogether, long-term nutrient addition in moist acidic tundra alters not only primary production, but also plant community traits relevant to consumers (Gough et al. 2012, 2016).

In this study, we examined the response of aboveground arthropod communities – a complex assemblage of herbivores, pollinators, detritivores and predators – to 24 years of experimental nutrient addition in moist acidic tussock tundra. To our knowledge, aboveground arthropod community responses to nutrient addition in moist acidic tundra have not yet been examined. The only relevant example comes from subarctic shrub heath, where nine years of nutrient addition leads to an increase in the abundance of graminoids and graminoid-feeding insects (Richardson et al. 2002). Moreover, comparisons among tundra ecosystems suggest that terrestrial arthropod communities in moist acidic tundra should be sensitive to the effects of nutrient addition. For example, more naturally productive habitats associated with greater shrub abundance harbor greater plant canopy-dwelling insect biomass (Boelman et al. 2015, Sweet et al. 2015) and more diverse ground-dwelling arthropod assemblages (Rich et al. 2013).

Based on general bottom–up theory from terrestrial communities and our knowledge of the plant community response to this treatment (Shaver et al. 2014), we hypothesized that: 1) fertilized tundra communities would support greater abundance and biomass of consumers, consistent with observed increases in primary production and plant biomass, 2) decreased plant diversity in nutrient addition plots would decrease arthropod diversity, and 3) altered plant community composition in nutrient addition plots would yield a distinct arthropod community.

Material and methods

Study system

This study was performed near Toolik Lake, in arctic Alaska (68°38'N, 149°43'W, elevation 719 m). Moist acidic tundra is characterized by mosses, lichens, a tussock-forming graminoid (*Eriophorum vaginatum*), dwarf evergreen shrubs, and low-growing deciduous shrubs including dwarf birch *Betula nana* and dwarf willows *Salix* spp. (Shaver et al. 2014). Annual production is limited not only by nutrient-poor soils, but also by extremely short growing seasons (about 70 days at our study site) (Shaver et al. 2014).

Nutrient addition

Fertilization experiments were established in moist acidic tundra in 1989 by the Arctic Long-Term Ecological Research (LTER) group (Shaver et al. 2014). The LTER maintains four experimental blocks in this plant community, established in an area of homogenous vegetation. Each block was comprised of ten 5 × 20 m plots separated from adjacent plots by 2 m walkways. Within each block, one plot was designated a control (no nutrient addition) and one was designated +NP (nitrogen and phosphorus addition) (other plots were dedicated to other experimental treatments not sampled in this study). The LTER applies N (10 $g \cdot m^{-2} \cdot year^{-1}$ of ammonium nitrate) and P (5 $g \cdot m^{-2} \cdot year^{-1}$ of orthophosphate) to the ground via broadcast fertilization of pellets in early June each year, immediately after snowmelt.

Arthropod sampling and processing

Arthropod sampling was conducted three times during the 2013 growing season: 13–15 June, 11–13 July and 8–10 August. We sampled ground-dwelling arthropods with four pitfall traps placed in a 1 × 1 m grid near the center of each plot to avoid edge effects. Traps consisted of a clear plastic sample cup (approximately 9 cm in diameter, 15 cm deep), placed level with the ground surface and filled 4 cm deep with 75% ethanol. Traps were left out for 48 h, at which point the contents were brought to the laboratory for processing.

We also sampled canopy-dwelling arthropods during each pitfall sampling window (13 June, 12 July and 8 August 2013) with a modified leaf vacuum (Stewart and Wright 1993). We standardized sampling of canopy-dwelling arthropods in each plot by sampling an area of 1 m^2 over the ground and a volume of 0.5 m^3 of the canopy (encompassing the tallest shrubs). Total vacuum sampling time in each plot was 90 s; the pattern and rate of sampling through each habitat type was done by the same person and in a standardized way. The vacuum sampling quadrat was located near the center of each plot, 1 m away from the pitfall traps to minimize disturbance.

Arthropods were identified using published keys (Marshall 2006, Triplehorn and Johnson 2005) to the family level with three exceptions: parasitic Hymenoptera from the vacuum samples were identified to superfamily, while those from pitfall traps were identified only as Parasitica; Collembola were identified to order; and mites were identified as subclass Acari. We estimated the total biomass of each taxon in each sample separately by applying published taxon-specific allometric equations to the average body length of the first five individuals encountered, multiplied by its abundance (detailed methods available in Pérez et al. 2016). Body length was measured to the nearest 0.01 mm using a digital microscope camera. Additionally, a trophic group was assigned to each taxonomic group following conventions used in other studies of tundra arthropods (Gelfgren 2010) (Supplementary material Appendix 1 Table A1).

Plant community response measures

To document the plant community response to long-term fertilization, we estimated plant cover near the peak of the growing season after 24 years of fertilization, in early July 2013, in eight 1 × 1 m quadrats within each plot. We estimated plant cover for each vascular plant species, with additional categories for all mosses and all lichens, which were not identified to species. In each quadrat, we also estimated the mean and maximum height of evergreen and deciduous shrub species to the nearest cm.

Statistical analysis

All statistical analyses were performed in R ver. 3.2.4 (<www.r-project.org>). In all analyses of arthropod data, canopy- and ground-dwelling arthropod assemblages were analyzed separately, owing to the different temporal and spatial scales of the two sampling methods. Because we were interested in the effects of treatment, rather than seasonality, we first summed arthropod abundance or biomass (of each taxon, functional group, or the total assemblage) for each sampling location (pitfall cup – n = 32, four per plot; or vacuum quadrat – n = 8, one per plot) across the three dates, following a similar study (Siemann 1998).

Arthropod abundance and biomass

To determine whether arthropod abundance or biomass varied according to treatment, we used linear mixed effects models (Zuur et al. 2009) in R package 'lme4' (Bates et al. 2014) and 'lmerTest' (Kuznetsova et al. 2014). All models included treatment as a fixed factor and experimental block as a random effect. Models were created first for total assemblage abundance and biomass, and then separately for each functional group. Models of arthropod abundance were fit with a lognormal Poisson distribution (O'hara and Kotze 2010). When model residuals were overdispersed (all models except canopy parasitoid, canopy predator and ground herbivore abundance), we incorporated an additional observation-level random effect (Bolker et al. 2009, Harrison 2014). Models of biomass were fit with a Gaussian distribution where biomass values were first ln-transformed (except ground-dwelling herbivore biomass, which was ln + 1 transformed) (Zuur et al. 2009).

Arthropod diversity

Because arthropod taxonomic richness differences could be attributed to differences in abundance (Hurlbert 1971), we calculated individual-based rarefied richness values and rarefaction curves using the 'rarefy' function in R package vegan (Oksanen et al. 2013). We calculated rarefied richness from arthropod abundances summed across all samples of each treatment. Rarefied richness values for control and fertilized assemblages were considered significantly different if standard errors of rarefaction iterations did not overlap at the lowest number of individuals caught for the two treatments. To determine the extent to which additional sampling might have more fully characterized the community, we calculated abundance-based extrapolated richness values using the bias-corrected Chao index (Chao et al. 2014) with the vegan function 'estimateR' (Oksanen et al. 2013).

Arthropod community composition

To determine whether treatment affected arthropod community composition, we fit multivariate generalized linear models to the canopy- and ground-dwelling abundance data using R package 'mvabund' (functions 'manyglm' and 'anova.manyglm') (Wang et al. 2012). We used this model-based method to analyze arthropod community composition because, unlike distance-based methods (e.g. PRIMER), multivariate generalized linear models can account for the confounding mean–variance relationships that often exist in ecological count data by modeling multivariate abundance data with a negative binomial distribution (Warton et al. 2012). Model terms were tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations; we simultaneously performed tests for univariate (single-taxon) responses to treatment, adjusting these univariate p-values to correct for multiple testing (Wang et al. 2012). To account for repeated measures, we constrained resampling to experimental blocks. For each taxon, we calculated its percentage share of total treatment deviance as a measure of its contribution to community dissimilarity in control and fertilized plots. We used non-metric multidimensional scaling (NMDS) analysis in R package 'vegan' to visualize differences in arthropod community composition for each assemblage (Oksanen et al. 2013).

Arthropod size structure

Just as our analyses of arthropod community composition helped determine which taxa were driving changes to total arthropod abundance, we performed an analysis of arthropod size structure to determine which groups were driving changes to total arthropod biomass independently of changes to arthropod abundance. We used a variance decomposition approach modified from Lepš et al. (2011) to differentiate between nutrient addition's effects on arthropod community size structure resulting from community turnover (abundance of small versus large taxa) versus within-taxon size variation (sizes of individuals within taxa). First, using measures of individual arthropods (a subset of the total), we calculated three community parameters for each assemblage and trophic group: 1) a specific community-weighted mean (CWM) body size calculated from the average size of each taxon in each treatment, 2) a fixed CWM calculated from the body size of each taxon averaged across treatments, and

3) within-taxon variability, the difference between specific and fixed CWMs (Lepš et al. 2011). Both CWMs were weighted by the total abundance of each taxon in each sampling location, summed across sampling dates. We then analyzed linear mixed-effects models for each community parameter. Finally, we extracted treatment sums-of-squares (SS) from each model using 'lmerTest' and calculated the contributions of each aspect of size structure to treatment effects on (specific) CWM body size as:

$$\text{contribution of turnover} = 100 \times (SS_{\textit{fixed}\ \text{CWM}}/SS_{\textit{specific}\ \text{CWM}})$$

$$\text{contribution of within-taxon size variation} = 100 \times (SS_{\textit{within-taxon}}/SS_{\textit{specific}\ \text{CWM}})$$

$$\text{covariation} = 100 \times ([\ SS_{\textit{specific}\ \text{CWM}} - SS_{\textit{fixed}\ \text{CWM}} - SS_{\textit{within-taxon}}]/[\ SS_{\textit{specific}\ \text{CWM}}])$$

Plant community response measures

We evaluated differences in plant species cover at the level of plant cover quadrats (n = 64, eight quadrats per plot, four plots per treatment) with a permutational MANOVA, constraining permutations to blocks (function 'adonis' in R package 'vegan', Oksanen et al. 2013). We used linear mixed effects models to evaluate treatment effects on species density (plant species per m^2), diversity (Shannon's H'), and canopy height within plant cover quadrats (n = 64); these models retained experimental block as a random effect.

Data deposition

Data available from the Arctic Long-Term Ecological Research (LTER) database: doi:10.6073/pasta/69632de5304cd35672c1bf4f8d1e702d (Asmus et al. 2017).

Results

Plant community

The plant community in control plots – a mixture of dwarf deciduous and evergreen shrubs, sedges, mosses, and lichens – differed from that of fertilized plots, which were dominated by *Betula nana* and a forb (cloudberry, *Rubus chamaemorus*) (Fig. 1; $F_{1,63} = 111.2$, $p = 0.001$). Species density in fertilized plots was 5 ± 0 species m^{-2}, a lower density than that of controls (13 ± 0 species m^{-2}, $F_{1,59} = 1199.3$, $p < 0.001$). Diversity in fertilized plots (H' = 1.0 ± 0.1) was also lower than that of controls (H' = 2.1 ± 0.1, $F_{1,59} = 613.1$, $p < 0.001$). In addition, maximum plant canopy height in fertilized plots was 55.8 ± 5.5 cm, more than double the maximum canopy height in controls (23.9 ± 0.5 cm, $F_{1,59} = 106.0$, $p < 0.001$). Increased canopy height corresponded to greater maximum height of *Betula* in fertilized plots relative to controls ($F_{1,62} = 157.5$, $p < 0.001$).

Arthropod abundance and biomass

Canopy assemblage

In the canopy, treatment affected neither total abundance nor the abundance of predators, herbivores, detritivores or biting flies ($p > 0.05$, Table 1, Fig. 2). In addition, treatment had no effect on total canopy-dwelling biomass, nor predator, parasitoid, herbivore nor biting fly biomass (Fig. 2,

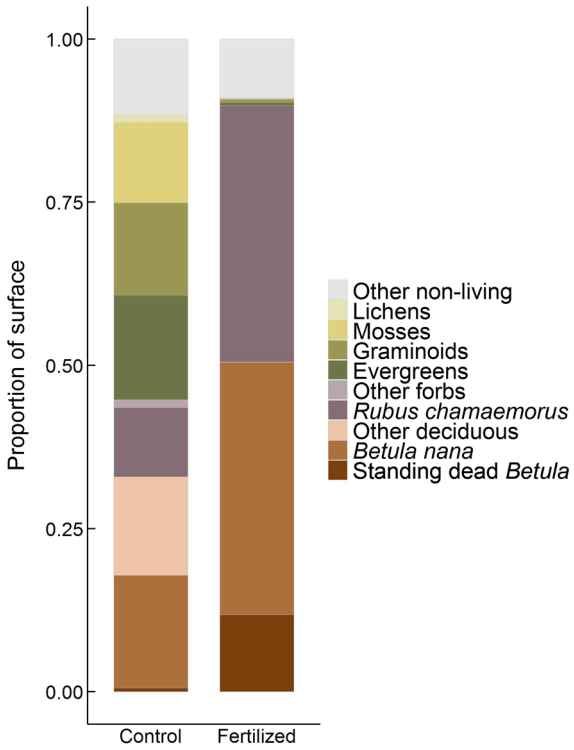

Figure 1. Visually estimated ground cover after 24 years of fertilization. Non-living includes loose litter, bare ground, frost boils (cryoturbation), vole activity (e.g. nests and haying), and standing dead shrubs (*Salix* spp.).

Table 1, $p > 0.05$). The two canopy-dwelling groups for which there were significant treatment effects were parasitoids and detritivores (an assortment of flies that rely upon detrital resources as larvae, Supplementary material Appendix 1 Table A1). Parasitoids were more abundant in fertilized canopies than in controls (Fig. 2, Est = 0.54 ± 0.25, $p = 0.03$), and the total biomass of canopy-dwelling detritivores was five times greater in fertilized plots relative to controls (Fig. 2, Est = 1.53 ± 0.48, $p = 0.019$).

Greater canopy-dwelling detritivore biomass in fertilized canopies was caused partly by a marginally significant difference in abundance ($p = 0.059$, Fig. 2), and by significantly larger canopy detritivore body size in fertilized plots relative to controls (Fig. 3, $F_{1,6} = 19.7$, $p = 0.004$). Greater canopy detritivore body size resulted from a shift towards larger detritivore taxa in fertilized canopies relative to controls (Table 2).

Alongside this effect on canopy detritivore body size, canopy arthropods were on average larger in fertilized canopies relative to controls (Fig. 3, Supplementary material Appendix 1 Table A2, $F_{1,3} = 16.8$, $p = 0.03$). This resulted from larger body size of detritivores, canopy herbivores ($F_{1,6} = 36.4$, $p = 0.001$), and canopy predators (Fig. 3, Supplementary material Appendix 1 Table A2, $F_{1,5} = 4.0$, $p = 0.09$). Larger canopy herbivore body size resulted from a shift in community composition towards greater relative abundance of large-bodied taxa (e.g. Miridae; Supplementary material Appendix 1 Table A1) relative to small-bodied taxa (e.g. Homopterans; Supplementary material Appendix 1 Table A1).

Table 1. Results from linear mixed effects models of arthropod abundance and biomass. Biting flies were not present in ground assemblage wsamples. Values in bold indicate where treatment was significant ($p < 0.05$).

		Abundance			Biomass		
		Est	SE	Pr(>|z|)	Est	SE	Pr(>|t|)
Canopy	Total						
	Intercept	4.58	0.13	<0.001	3.24	0.30	<0.001
	Treatment	0.21	0.18	0.266	0.53	0.34	0.220
	Parasitoids						
	Intercept	**1.77**	**0.28**	**<0.001**	–1.32	0.84	0.168
	Treatment	**0.54**	**0.25**	**0.030**	0.75	1.19	0.548
	Predators						
	Intercept	2.15	0.20	<0.001	0.56	0.48	0.294
	Treatment	–0.15	0.25	0.535	0.78	0.69	0.301
	Herbivores						
	Intercept	3.08	0.19	<0.001	1.44	0.25	0.001
	Treatment	–0.09	0.27	0.742	0.25	0.32	0.480
	Detritivores						
	Intercept	3.22	0.25	<0.001	**1.19**	**0.34**	**0.013**
	Treatment	0.56	0.30	0.059	**1.53**	**0.48**	**0.019**
	Biting Flies						
	Intercept	3.31	0.44	<0.001	2.58	0.58	0.005
	Treatment	–0.17	0.55	0.754	–0.34	0.75	0.684
Ground	Total						
	Intercept	**5.47**	**0.12**	**<0.001**	5.74	0.16	<0.001
	Treatment	**–0.29**	**0.12**	**0.021**	0.06	0.14	0.681
	Parasitoids						
	Intercept	2.15	0.14	<0.001	–1.11	0.39	0.019
	Treatment	0.04	0.17	0.805	–0.14	0.51	0.781
	Predators						
	Intercept	**3.12**	**0.11**	**<0.001**	5.70	0.17	<0.001
	Treatment	**0.34**	**0.10**	**<0.001**	0.07	0.14	0.615
	Herbivores						
	Intercept	0.45	0.20	0.026	0.81	0.27	0.029
	Treatment	–0.33	0.31	0.288	–0.54	0.27	0.053
	Detritivores						
	Intercept	**5.31**	**0.14**	**<0.001**	0.80	0.39	0.077
	Treatment	**–0.47**	**0.18**	**0.009**	0.93	0.46	0.053

Ground assemblage

Unlike in the canopy, total ground-dwelling arthropod abundance was lower in fertilized plots relative to controls (Fig. 2, Table 1, Est = –0.29 ± 0.12, p = 0.021), a result of reduced detritivore abundance (Fig. 2, Table 1, Est = –0.47 ± 0.18, p = 0.009). In contrast with this effect on detritivores, total ground-dwelling predator abundance was greater in fertilized plots relative to controls (Fig. 2, Table 1, Est = 0.34 ± 0.10, $p < 0.001$). The opposing treatment effects on predator and detritivore abundances decreased the predator:prey abundance ratio ('prey' = detritivores plus herbivores) from 1:9 in control plots to 1:3 in fertilized plots (Fig. 2, Est = 0.31 ± 0.15, p = 0.042).

Despite these treatment effects on ground-dwelling predator, detritivore and total arthropod abundances, treatment had no effect on the biomass of the total assemblage nor the biomass of any trophic group (Table 1, $p > 0.05$). Lower detritivore abundances were cancelled out by greater relative abundances of large-bodied detritivore taxa in fertilized plots relative to controls (e.g. Diptera: Tipulidae: Supplementary material Appendix 1 Table A1), as evidenced by a treatment effect on the fixed community-weighted mean body size (Fig. 3, Supplementary material Appendix 1 Table A2, $F_{1,30} = 12.2$, p = 0.002). Meanwhile, greater predator abundances were cancelled out by smaller predator body sizes in fertilized plots relative to controls (Fig. 3, Supplementary material Appendix 1 Table A2, $F_{1,30} = 60.5$, $p < 0.001$). Smaller ground-dwelling predator body size resulted primarily from within-taxon size differences (Table 2), especially for the dominant ground-dwelling predator taxon, wolf spiders (Araneae: Lycosidae; Supplementary material Appendix 1 Table A1). Wolf spiders were more abundant ($F_{1,27} = 12.5$, p = 0.001, Supplementary material Appendix 1 Table A1), but were also smaller in fertilized plots relative to controls ($F_{1,27} = 5.9$, p = 0.022; data not shown), resulting in equivalent total wolf spider biomass in fertilized and control plots ($p > 0.05$; data not shown). Despite reduced predator body size, ground-dwelling arthropods in fertilized plots were on average larger in fertilized plots relative to controls (Fig. 3, $F_{1,27} = 4.7$, p = 0.039, Supplementary material Appendix 1 Table A2), primarily due to differences in community composition (Table 2).

Arthropod diversity

After rarefaction to the lowest arthropod abundance in control and fertilized treatments, fertilized canopies had 3 ± 1 fewer taxa relative to control canopies (Fig. 4). Canopy parasitoid and predator diversity were lower in fertilized plots relative to controls, while canopy herbivore richness

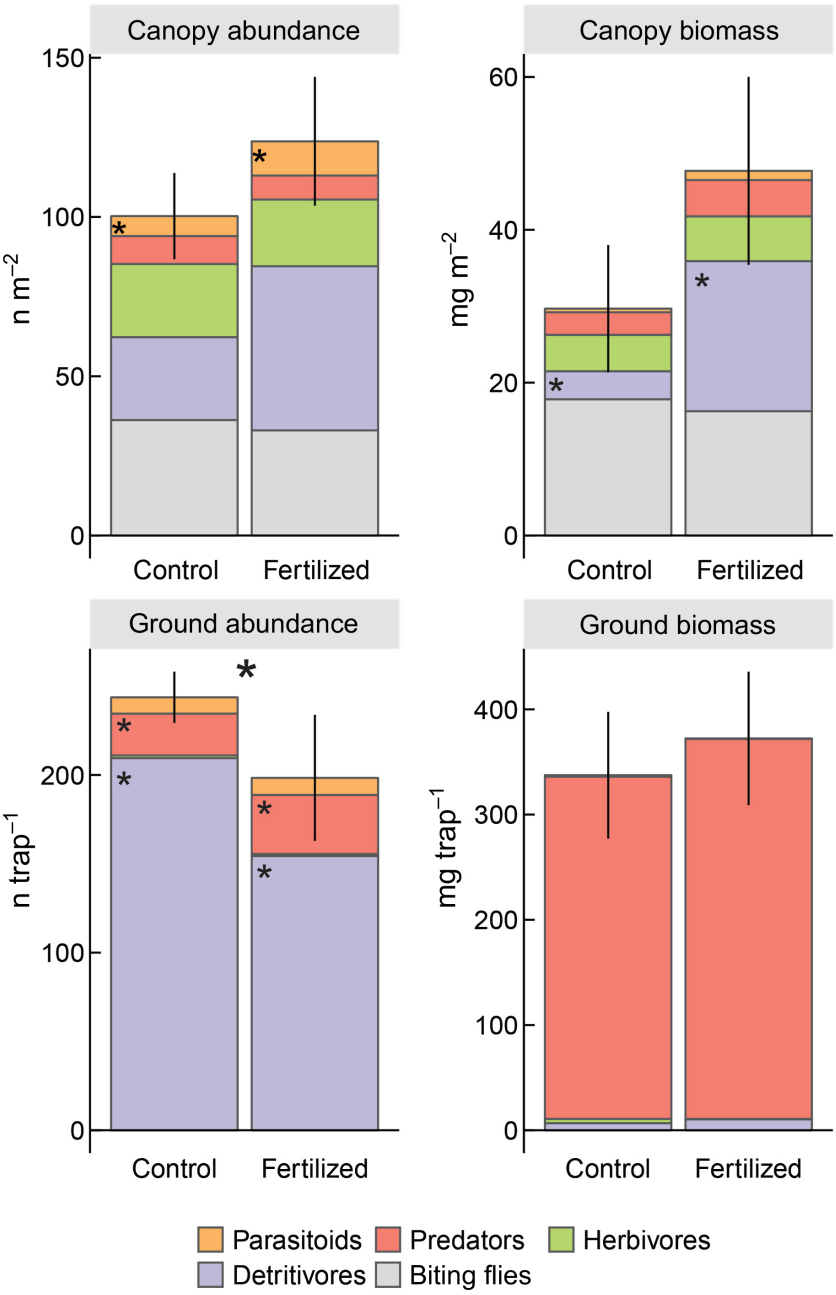

Figure 2. Arthropod abundance (left panels) and biomass (right panels) means in control and fertilized plots in the canopy assemblage (top panels) and on the ground (bottom panels). Asterisks above bars indicate significant treatment differences in total abundance or biomass; asterisks within bars indicate significant treatment differences for the trophic group indicated ($p < 0.05$). Error bars are 1 SE for total biomass or abundance (n = 4 blocks).

was greater in fertilized canopies relative to controls, and canopy detritivore richness did not differ by treatment (Fig. 4).

In contrast, rarefied richness was greater in fertilized ground assemblages relative to controls (5 ± 1 additional taxa, Fig. 4). This was primarily driven by greater rarefied richness of ground-dwelling herbivores and detritivores in fertilized plots. Ground-dwelling predator diversity did not differ according to treatment (Fig. 4).

Visual inspection and extrapolation of the rarefaction curves suggested that, at this level of identification, the ground and canopy assemblages as a whole were well-sampled, although many individual trophic groups would have benefited from additional sampling (Supplementary material Appendix 1 Table A3).

Arthropod community composition

In the canopy, 74% of taxa were common to both treatments, while on the ground 65% of taxa were common to both treatments. The majority of taxa unique to one treatment or another were rare (<2 individuals; Supplementary material Appendix 1 Table A1). Nevertheless, community composition differed in response to fertilization in both the

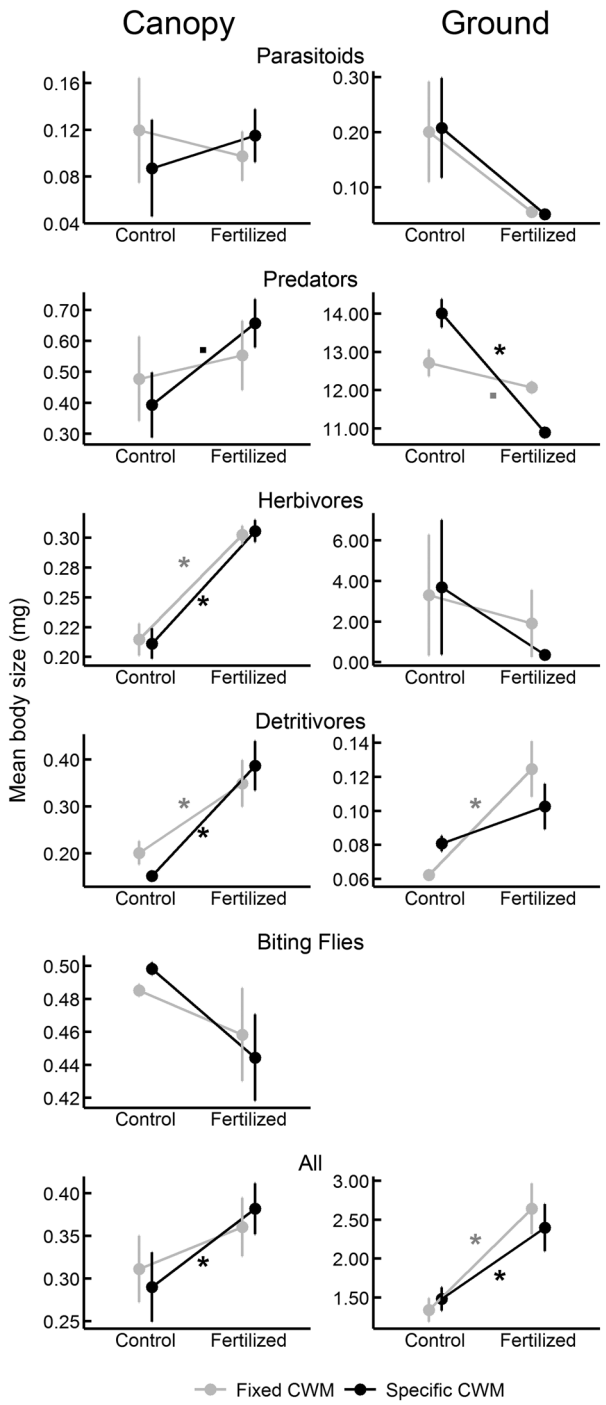

Figure 3. Community-weighted mean (CWM) arthropod body size for each assemblage and trophic group. Gray lines represent 'fixed' CWMs calculated from the average body size of each taxon averaged across treatments (treatment differences result only from turnover, i.e. relative abundances of large versus small taxa); black lines represent a treatment-'specific' CWM calculated from the average body size of each taxon within each treatment (thus, treatment differences result both from turnover and differences in body size within taxa). Significance of treatment differences for CWMs are marked for each type of mean (*, $p < 0.05$;·, $p < 0.10$). Error bars are 1 SE (n = 4 blocks).

canopy (Dev = 97.7, p = 0.039) and the ground assemblage (Dev = 162.5, p = 0.001) (Fig. 5A–D).

Table 2. Percentage contribution of community turnover, within-taxon body size variation and their covariation to treatment variance in community-weighted mean (CWM) body size, by assemblage and trophic group. Positive covariation means that a treatment with typically large taxa had larger-than-average individuals within those taxa (and vice versa); negative covariation means that a treatment with typically large taxa had smaller-than-average individuals within those taxa (and vice versa). Percentages greater than 100 occur wherever treatment differences for fixed CWM body size and/or intra-taxon size variation were greater than treatment differences for the treatment-specific CWM.

Assemblage	Group	Turnover	Within-taxon	Covariation
Canopy	All	28.9	21.4	49.7
	Parasitoids	63.0	321.7	–284.7
	Predators	8.2	51.0	40.9
	Herbivores	86.4	0.5	13.1
	Detritivores	39.7	13.7	46.6
	Biting flies	24.8	25.2	50.0
Ground	All	202.3	17.8	–120.2
	Parasitoids	86.2	0.5	13.3
	Predators	4.2	63.1	32.7
	Herbivores	20.6	28.6	50.8
	Detritivores	815.6	344.4	–1060.1

In the canopy, herbivore taxa had the greatest effect on community dissimilarity in control and fertilized plots, contributing 40% of total treatment deviance (Fig. 5E). The remainder of canopy treatment deviance was spread somewhat evenly among parasitoid, predator and detritivore taxa, which contributed 10, 20 and 30% of treatment deviance, respectively (Fig. 5E). Herbivores from family Delphacidae contributed the most to community dissimilarity and were by themselves affected by treatment (Fig. 5, Dev = 14.5, $p_{adj} = 0.017$). Delphacids comprised on average 10% of the abundance in control canopies, but were completely absent from fertilized canopies (Supplementary material Appendix 1 Table A1). In arctic tundra habitats, this family is known to specialize on graminoids such as *Carex* and *Eriophorum* (Wilson 1997); cover of these plant species has drastically declined in fertilized plots (Fig. 1). Two additional herbivore taxa and two detritivore taxa contributed substantially (>5% deviance) to community dissimilarity, although without univariate treatment effects (Fig. 5, $p > 0.05$). All four of these taxa were more abundant in fertilized plots relative to controls (Supplementary material Appendix 1 Table A1).

In the ground assemblage, detritivore taxa contributed the most to community dissimilarity (63% of deviance), with predator and herbivore taxa contributing the remainder (23% and 13%, respectively; parasitoids contributed <1%; Fig. 5F). In addition to altering ground assemblage composition, treatment affected the abundance of three individual taxa: springtails from order Symphypleona, mites (Acari), and predaceous beetles from family Staphylinidae ($p_{adj} < 0.05$). These three taxa also dominated the overall community response to fertilization (Fig. 5). Relative abundance of Symphypleona was 93% lower in fertilized plots relative to controls (Supplementary material Appendix 1 Table A1), while mites and Staphylinid beetles were respectively 6 and 5 times more abundant in fertilized plots relative to controls (Supplementary material Appendix 1 Table A1).

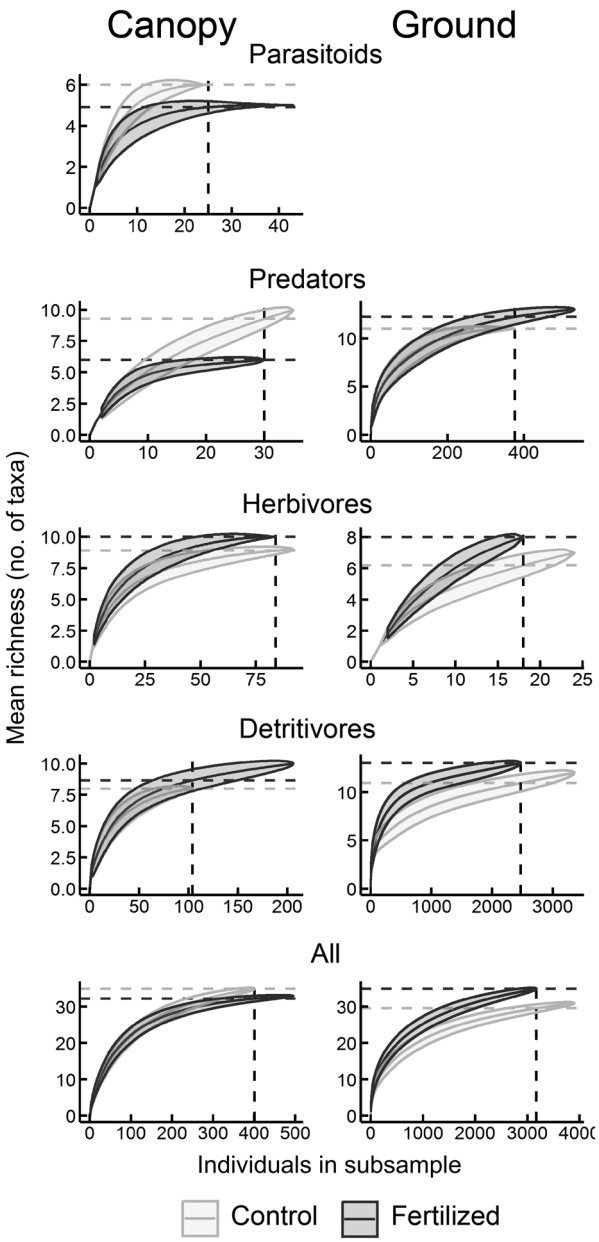

Figure 4. Taxon rarefaction curves of the canopy- and ground-dwelling arthropod assemblages, by trophic group and in total. Rarefied richness values are indicated by horizontal dashed lines; shaded areas represent standard errors of iterations of the assemblage abundance data.

Discussion

Fertilization did not increase total arthropod abundance or biomass

Contrary to our first hypothesis, total canopy assemblage biomass and abundance were unaffected by fertilization. Further, fertilization reduced total arthropod abundance in the ground assemblage but did not affect total biomass of ground-dwelling arthropods. These findings were surprising in comparison with similar studies conducted in grasslands and coastal salt marshes. In those ecosystems, both short- and long-term soil nutrient additions increase total arthropod abundance (Hurd and Wolf 1974, Kirchner 1977, Siemann 1998, Haddad et al. 2000, Gruner and Taylor 2006, Wimp et al. 2010).

Changes to top–down control by predators including songbirds (Aunapuu 2004) and wolf spiders may have mitigated some bottom–up effects of nutrient addition on consumers. For example, in the ground assemblage of fertilized plots, a deeper litter layer may provide wolf spiders with some protection from intra-guild predation (Finke and Denno 2002, Rickers and Scheu 2005). Lower intraguild predation would increase the survivorship of smaller, younger wolf spiders, aligning with our observations of decreased mean wolf spider body size, increased wolf spider abundance and lower detritivore abundance in fertilized plots relative to controls. In turn, a greater abundance of small wolf spiders may have led to the observed increase in detritivore body size, because smaller wolf spiders will presumably take smaller detritivores as prey.

Another explanation for the surprising negative and neutral responses of arthropod abundance and biomass is that long-term nutrient addition in moist acidic tundra reduces plant palatability, which could cancel out the positive effects of increased plant biomass on consumers. Specifically, dominance of *Betula* includes a shift towards relatively unpalatable woody stem tissue and plant species (Shaver et al. 2014). This shift toward a less palatable community in moist acidic tundra may be a unique response among nutrient addition experiments in herbaceous plant communities (Clark et al. 2007). In contrast to tundra, after many years of nutrient addition temperate grasslands become dominated by relatively palatable C_3 grasses and forbs (Isbell et al. 2013), and salt marshes' near-monoculture of *Spartina* grasses increase in N content (Murphy et al. 2012).

In another contrast to nutrient addition in salt marshes, where an accumulation of dead thatch benefits many arthropods (Finke and Denno 2002, Murphy et al. 2012), long-term nutrient addition in moist acidic tundra may create an unfavorable canopy and surface microenvironment for arctic arthropods. In the Arctic, shrubs create a shadier, colder canopy microenvironment (Myers-Smith et al. 2011, Shaver et al. 2014), which could have effects on the growth and movement patterns of the resident arthropods. In particular, the cooling effect of shrubs could be responsible for the observed increase in ground-dwelling detritivore body size (Atkinson and Sibly 1997), while also decreasing the movement (and therefore capture) rates of surface-active predators like wolf spiders. In addition to these temperature effects, nutrient addition leads to the loss of the moss cover that insulates the soil and regulates soil moisture (Blok et al. 2011). These changes likely drove out some arthropod taxa, given the sensitivity of many arctic species to decreased solar radiation and fluctuations in soil moisture (Strathdee and Bale 1998, Danks 2004, Høye and Forchhammer 2008, Hansen et al. 2016).

Fertilization decreases plant diversity, but not arthropod richness

Contrary to our second hypothesis, fertilization did not decrease arthropod diversity (rarefied richness). Instead, we

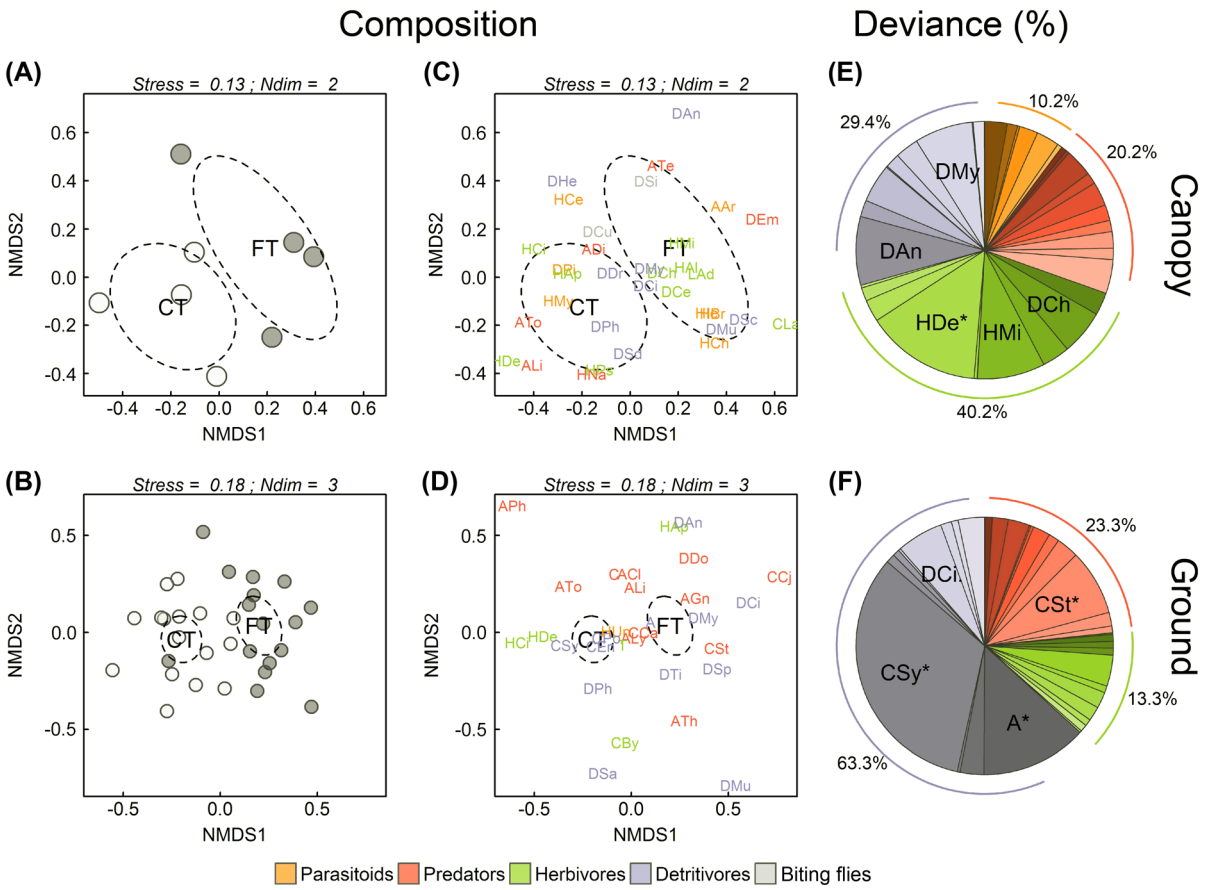

Figure 5. Non-metric multidimensional scaling (NMDS) solutions for canopy (A, C) and ground dwelling (B, D) arthropod community composition. Black text and dashed ellipses indicate centroids and 95% CI for each treatment. (A, B) NMDS coordinates for vacuum and pitfall samples are shown as filled (fertilized) and open (control) circles. (C, D) coordinates for each taxon are labeled with abbreviations and colored by functional group (see Supplementary material Appendix 1 Table A1 for corresponding taxon names). (E, F) percent share of total treatment deviance by taxon from multivariate generalized linear models of canopy (E) and ground (F) assemblage taxonomic composition. Taxa contributing >5% of total deviance are labeled with their abbreviation. Asterisks (*) indicate taxa for which there was a significant univariate effect of treatment ($p_{adj} < 0.05$) and dots (.) indicate marginally significant treatment effects ($p_{adj} < 0.1$). Labeled arcs indicate the subtotal of deviance for each trophic group; biting flies (canopy and ground) and parasitoids (ground only) contributed <1% to deviance.

found that fertilization's effect on arthropod diversity was dependent upon microhabitat, with decreased diversity in fertilized canopies (as expected), but increased diversity in the fertilized ground assemblage. We interpret these results cautiously, because although the differences between control and fertilized richness were significant, they were small (3–5 taxa), and furthermore, the taxa identified in this study are likely each represented by multiple species. Even so, the changes to arthropod diversity were unexpected in comparison with similar studies (Siemann 1998, Haddad et al. 2000, Wimp et al. 2010) and small relative to the loss of >50% of plant species from fertilized plots. This suggests that tundra arthropod diversity is somewhat robust to plant species loss.

On the other hand, some taxa were dramatically affected; fertilization seems to have nearly driven out a moss-associated detritivore (Collembola: Symphypleona) and a graminoid-associated herbivore (Hemiptera: Delphacidae). In the canopy, decreased abundance of these Delphacids may have propagated through the food web, contributing to the absence of taxa known to predate on this family (Hemiptera: Anthocoridae, Nabidae; Diptera: Pipunculidae) relative to control plots (Supplementary material Appendix 1 Table A1).

Fertilization alters both plant and arthropod community composition

Supporting our third hypothesis, arthropod community composition differed in control and fertilized plots. As part of a whole-community response to fertilization, we expected to (and did) see changes to the community composition of first-order consumers most directly tied to the plant community—detritivores and herbivores (Hunter and Price 1992). These compositional changes suggest a functional response from the arthropod community, even though total abundance, total biomass and total diversity were mostly unaffected by nutrient addition.

Treatment effects on community composition also contributed to changes in arthropod body size structure (Table 2), with fertilized plots supporting larger taxa (the exception being ground-dwelling predatory arthropods, which were smaller in fertilized plots relative to controls). A study of arthropod communities in fertilized grasslands

(Lind et al. 2017) similarly found that soil nutrient addition increased mean arthropod body size, indicating this effect may widespread. Relative to taxa with small body size, large taxa have greater per capita nutrient demands (Brown et al. 2004). The larger herbivores and detritivores in fertilized plots may have capitalized on increased N-concentrations in non-woody plant tissues even as total N constrained their total abundance and/or biomass. These changes to arthropod community composition and body size, together with the losses of certain arthropod taxa, point to possible changes in food web and ecosystem processes (e.g. herbivory, predation, nutrient cycling) resulting from nutrient addition.

Conclusion

Overall, our results were surprising and in contrast with similar studies of bottom–up effects on arthropod community structure. We found that nutrient addition altered arthropod community composition, but did not affect total arthropod diversity, abundance or biomass as predicted. Despite the dramatic increase in plant productivity and substantial reduction of plant species diversity, nutrient addition did not increase arthropod abundance and biomass or reduce arthropod diversity. As predicted, plant community changes were associated with shifts in arthropod community composition, and in some cases losses of arthropod taxa, suggesting bottom–up effects from plants to arthropod consumers. In this community, the availability of palatable (non-woody) plant tissues, and not total plant production, likely set the upper limit on arthropod biomass and abundance in fertilized plots. Our findings recall how eutrophication of aquatic systems can increase primary production while detrimentally affecting consumers, and provides a striking contrast to the handful of terrestrial studies that have found parallel plant and arthropod responses to nutrient addition.

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Supplementary material (available online as Appendix oik-04398 at <www.oikosjournal.org/appendix/oik-04398>). Appendix 1.