

1 **Long-term nutrient addition alters ~~consumer~~-arthropod community composition but does**
2 **not increase total biomass or abundance**

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15 **ABSTRACT**

16 A simple bottom-up hypothesis predicts that plant responses to nutrient addition should
17 determine the response of consumers: more productive and less diverse plant communities, the
18 usual result of long-term nutrient addition, should support greater consumer abundances and
19 biomass and less consumer diversity. We tested this hypothesis for the response of an
20 aboveground arthropod community to an uncommonly long-term (24-year) nutrient addition
21 experiment in moist acidic tundra in arctic Alaska. This experiment altered plant community
22 composition, decreased plant diversity and increased plant production and biomass as a
23 deciduous shrub (*Betula nana*) ~~replaced graminoids, cryptogams and dwarf evergreen~~
24 ~~shrubs became dominant~~ Consistent with strong effects on the plant community, nutrient
25 addition altered arthropod community composition, primarily through changes to herbivore taxa
26 in the canopy-dwelling arthropod assemblage and detritivore taxa in the ground assemblage.
27 Surprisingly, however, the loss of more than half of plant species was accompanied by negligible
28 changes to diversity (rarefied richness) of arthropod taxa (which were primarily identified to
29 family). Similarly, although long-term nutrient addition in this system roughly doubles plant
30 production and biomass, arthropod abundance was either unchanged or decreased by nutrient
31 addition, and total arthropod biomass was unaffected. Our findings differ markedly from the
32 handful of terrestrial studies that have found bottom-up diversity cascades and productivity
33 responses by consumers to nutrient addition. This is probably because unlike grasslands and salt
34 marshes (where such studies have historically been conducted), this arctic tundra community
35 becomes less palatable, rather than more so, after many years of nutrient addition due to
36 increased dominance of *B. nana*. Additionally, by displacing insulating mosses and increasing
37 the cover of shrubs that cool and shade the canopy microenvironment, fertilization may displace

38 arthropods keenly attuned to microclimate. These results indicate that terrestrial arthropod
39 assemblages may be more constrained by producer traits (i.e., palatability, structure) than they
40 are by total primary production or producer diversity.

41

42 INTRODUCTION

43 Nutrient availability is a major determinant of many ecosystem properties, including
44 primary and secondary production and community structure (Chapin et al. 1986, Gruner et al.
45 2008). An array of nutrient addition experiments has not only confirmed that plant growth in
46 most natural systems ~~are~~is nutrient-limited (Downing et al. 1999, Elser et al. 2007, Fay et al.
47 2015, Gruner et al. 2008), but has also shown that there can be complex feedbacks among
48 nutrient availability, primary production, and producer community structure, especially after
49 many years of manipulation (Hillebrand et al. 2007, Leibold et al. 1997, Worm and Duffy 2003).
50 Those few terrestrial nutrient addition studies that have incorporated consumers have generally
51 explored top-down effects of consumers on producers, rather than the other way around (Gruner
52 et al. 2008). They also tend to focus on the roles of mammalian herbivores (e.g., Borer et al.
53 2014), while ignoring other potentially important consumers (e.g., insects).

54 Theory suggests that as primary productivity increases with nutrient addition, more
55 consumer biomass can be supported (Oksanen 1981, White 1978). Likewise, the secondary
56 effects of nutrient addition on producer community composition and diversity should affect
57 consumer community composition and diversity (Hunter and Price 1992, Hutchinson 1959). A
58 handful of studies—most from grasslands and salt marshes – have demonstrated such bottom-up
59 effects on arthropod communities, which respond at spatial and temporal scales compatible with
60 many nutrient addition experiments. Short-term (<3 years) experiments show that increased

61 nutrient availability increases plant biomass and arthropod abundance (Gruner and Taylor 2006,
62 Hurd and Wolf 1974, Kirchner 1977, Siemann 1998, Wimp et al. 2010). Long-term studies in
63 grasslands (5-14 years) have shown that when nutrient addition homogenizes the plant
64 community, total arthropod abundance is increased (Haddad et al. 2000, Siemann 1998) even if
65 arthropod diversity declines in tandem with plants (Haddad et al. 2000).

66 Evidence from aquatic systems suggests that outcomes for consumer communities are not
67 always predicted by producer community responses to nutrient addition. For example, in
68 temperate lakes, if long-term nutrient loading ~~tends to favor~~ well-defended or toxic algal
69 species, ~~and in such cases~~ consumers do not show a bottom-up productivity response even when
70 the total amount of primary production is greatly increased (Leibold 1989, Leibold et al. 1997).
71 Changes to producer community physical structure can also negate bottom-up nutrient addition
72 effects on some consumers (Gough et al. 2016). For instance, nutrient addition in benthic marine
73 habitats shifts the producer community from eelgrass to dense microalgae; the enhanced
74 structural complexity impedes fish foraging and reduces overall consumer abundance (Deegan et
75 al. 2002). Such findings suggest that producer traits control whether the direct effects of nutrient
76 availability on primary production and diversity are passed along to consumers.

77 As in most aquatic and terrestrial communities, long-term nutrient addition in moist
78 acidic tussock tundra, a common and well-studied plant community type in northern Alaska,
79 increases primary production and homogenizes the producer community (Gough et al. 2000,
80 Shaver et al. 2014). This occurs because a deciduous shrub, *Betula nana* ssp. *exilis*, becomes
81 dominant while displacing lower-stature and slower-growing species including sedges, mosses,
82 dwarf evergreen shrubs and lichens (Shaver et al. 2014). *Betula*'s woody stem tissue, which is
83 low in N relative to the graminoids and evergreens it replaces, accounts for the majority of

84 producer biomass after six or more years of fertilization. Relative to other deciduous shrubs in
85 this plant community, *Betula nana* ssp. *exilis* is ~~known to be unpalatable~~ less palatable to
86 vertebrate herbivores (Christie et al. 2015) and is not the preferred forage of local insect larvae
87 (MacLean and Jensen 1985). Furthermore, a Aerial branching and litter deposition by *Betula* in
88 fertilized plots creates a canopy and ground microenvironment cooler than that of unfertilized
89 tussock tundra (Myers-Smith et al. 2011). Altogether, long-term nutrient addition in moist acidic
90 tundra alters not only primary production, but also plant community traits relevant to consumers
91 (Gough et al. 2016, Gough et al. 2012).

92 In this study, we examined the response of aboveground arthropod communities —a
93 complex assemblage of herbivores, pollinators, detritivores and predators —to ~~to~~ 24 years of
94 experimental nutrient addition in moist acidic tussock tundra. To our knowledge, aboveground
95 arthropod community responses to nutrient addition in moist acidic tundra have not yet been
96 examined. The only relevant example comes from subarctic shrub heath, where 9 years of
97 nutrient addition leads to an increase in the abundance of graminoids and graminoid-feeding
98 insects (Richardson et al. 2002). Moreover, comparisons among tundra ecosystems suggest that
99 terrestrial arthropod communities in moist acidic tundra should be sensitive to the effects of
100 nutrient addition. For example, more naturally productive habitats associated with greater shrub
101 abundance harbor greater plant canopy-dwelling insect biomass (Boelman et al. 2015, Sweet et
102 al. 2015) and more diverse ground-dwelling arthropod assemblages (Rich et al. 2013).

103 Based on general bottom-up theory from terrestrial communities and our knowledge of
104 the plant community response to this treatment (Shaver et al. 2014), we hypothesized that: 1)
105 fertilized tundra communities would support greater abundance and biomass of consumers,
106 consistent with observed increases in primary production and plant biomass, 2) decreased plant

107 diversity in nutrient addition plots would decrease arthropod diversity, and 3) altered plant
108 community composition in nutrient addition plots would yield a distinct arthropod community.

109

110 **Study system**

111 This study was performed near Toolik Lake, in arctic Alaska (68°38'N, 149°43'W, el.
112 719m). Moist acidic tundra is characterized by mosses, lichens, a tussock-forming graminoid
113 (*Eriophorum vaginatum*), dwarf evergreen shrubs, and low-growing deciduous shrubs including
114 dwarf birch (*Betula nana*) and dwarf willows (*Salix* spp.) (Shaver et al. 2014). Annual
115 production is limited not only by nutrient-poor soils, but also by extremely short growing
116 seasons (about 70 days at our study site) (Shaver et al. 2014).

117

118 **Nutrient addition**

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

128

129 **Arthropod sampling and processing**

130 Arthropod sampling was conducted three times during the 2013 growing season: June 13-
131 15, July 11-13, and August 8-10. We sampled ground-dwelling arthropods with four pitfall traps
132 placed in a 1x1 m grid near the center of each plot to avoid edge effects. Traps consisted of a
133 clear plastic sample cup (approximately 9 cm in diameter, 15 cm deep), placed level with the
134 ground surface and filled 4 cm deep with 75% ethanol. Traps were left out for 48 hours, at which
135 point the contents were brought to the laboratory for processing.

136 We also sampled canopy-dwelling arthropods during each pitfall sampling window (13
137 June, 12 July and 8 August 2013) with a modified leaf vacuum (Wilson et al. 1993). We
138 standardized sampling of canopy-dwelling arthropods in each plot by sampling an area of 1m²
139 over the ground and a volume of 0.5 m³ of the canopy (encompassing the tallest shrubs). Total
140 vacuum sampling time in each plot was 90 seconds; the pattern and rate of sampling through
141 each habitat type was done by the same person and in a standardized way. The vacuum sampling
142 quadrat was located near the center of each plot, 1 m away from the pitfall traps to minimize
143 disturbance.

144 Arthropods were identified using published keys (Marshall 2006, Triplehorn and Johnson
145 2005) to the family level with three exceptions: parasitic Hymenoptera from the vacuum samples
146 were identified to superfamily, while those from pitfall traps were identified only as Parasitica;
147 Collembola were identified to order; and mites were identified as subclass Acari. We estimated
148 the total biomass of each taxon in each sample separately by applying published taxon-specific
149 allometric equations to the average body length of the first five individuals encountered,
150 multiplied by its abundance (detailed methods available in Pérez et al. 2016) . Body length was
151 measured to the nearest 0.01mm using a digital microscope camera. Additionally, a trophic

152 group was assigned to each taxonomic group following conventions used in other studies of
153 tundra arthropods (Gelfgren 2010) (see Table S1).

154

155 **Plant community response measures**

156 To document the plant community response to long-term fertilization, we estimated plant
157 cover near the peak of the growing season after 24 years of fertilization, in early July 2013, in
158 eight 1x1 m quadrats within each plot. We estimated plant cover for each vascular plant species,
159 with additional categories for all mosses and all lichens, which were not identified to species. In
160 each quadrat, we also estimated the mean and maximum height of evergreen and deciduous
161 shrub species to the nearest cm.

162

163 **Statistical Analysis**

164 All statistical analyses were performed in R version 3.2.4 (R Core Team 2015). In all
165 analyses of arthropod data, canopy- and ground-dwelling arthropod assemblages were analyzed
166 separately, owing to the different temporal and spatial scales of the two sampling methods.

167 Because we were interested in the effects of treatment, rather than seasonality, we first summed
168 arthropod abundance or biomass (of each taxon, functional group, or the total assemblage) for
169 each sampling location (pitfall cup—N = 32, 4 per plot; or vacuum quadrat – N = 8, 1 per plot)
170 across the three dates, following a similar study (Siemann 1998).

171 *Arthropod abundance and biomass.* To determine whether arthropod abundance or
172 biomass varied according to treatment, we ~~first summed the biomass and abundance of taxa~~
173 ~~within each sampling location (pitfall cup, vacuum plot) across the three sampling~~
174 ~~dates (Siemann 1998), and then evaluated biomass and abundance responses using used linear~~

175 mixed effects models (Zuur et al. 2009) in R package lme4 (Bates et al. 2014) and lmerTest
176 (Kuznetsova et al. 2014). All models included treatment as a fixed factor and experimental block
177 as a random effect. Models were created first for total assemblage abundance and biomass, and
178 then separately for each functional group. Models of arthropod abundance were fit with a
179 lognormal Poisson distribution (O'hara and Kotze 2010). When model residuals were
180 overdispersed (all models except canopy parasitoid, canopy predator and ground herbivore
181 abundance), we incorporated an additional observation-level random effect (Bolker et al. 2009,
182 Harrison 2014). Models of biomass were fit with a Gaussian distribution where ~~responses~~
183 biomass values were first \ln transformed (except ground-dwelling herbivore ~~abundance and~~
184 biomass, which ~~were was~~ $\ln+1$ transformed) (Zuur et al. 2009).

185 *Arthropod diversity.* Because arthropod taxonomic richness differences could be
186 attributed to differences in abundance (Hurlbert 1971), we calculated individual-based rarefied
187 richness values and rarefaction curves using the *rarefy* function in R package vegan (Oksanen et
188 al. 2013). We calculated rarefied richness from arthropod abundances summed across all samples
189 of each treatment. Rarefied richness values for control and fertilized assemblages were
190 considered significantly different when-if standard errors of rarefaction iterations did not overlap
191 at the lowest number of individuals caught for the two treatments. To determine the extent to
192 which additional sampling might have more fully characterized the community, we calculated
193 abundance-based extrapolated richness values using the bias-corrected Chao index (Chiu et al.
194 2014) with the vegan function *estimateR* (Oksanen et al. 2013).

195 *Arthropod community composition.* To determine whether treatment affected arthropod
196 community composition, we fit multivariate generalized linear models to the canopy- and
197 ground-dwelling abundance data using R package mvabund (functions *manyglm* and

198 *anova.manyglm*) (Wang et al. 2012). We used this model-based method to analyze arthropod
199 community composition because, unlike distance-based methods (e.g., PRIMER), multivariate
200 generalized linear models can account for the confounding mean-variance relationships that
201 often exist in ecological count data by modeling multivariate abundance data with a negative
202 binomial distribution (Warton et al. 2012). ~~Our models assumed a negative binomial distribution~~
203 ~~for arthropod abundances and included treatment as the independent variable.~~ Model terms were
204 tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with
205 999 iterations; we simultaneously performed tests for univariate (single-taxon) responses to
206 treatment, adjusting these univariate *P*-values to correct for multiple testing (Wang et al. 2012).
207 To account for repeated measures, we constrained resampling to experimental blocks. For each
208 taxon, we calculated its percentage share of total treatment deviance as a measure of its
209 contribution to community dissimilarity in control and fertilized plots. We used non-metric
210 multidimensional scaling (NMDS) analysis in R package *vegan* to visualize differences in
211 arthropod community composition for each assemblage (Oksanen et al. 2013).

212 *Arthropod size structure.* Just as our analyses of arthropod community composition
213 helped determine which taxa were driving changes to total arthropod abundance, we performed
214 an analysis of arthropod size structure to determine which groups were driving changes to total
215 arthropod biomass independently of changes to arthropod abundance. We used a variance
216 decomposition approach modified from Lepš et al. (2011) to differentiate between nutrient
217 addition's effects on arthropod community size structure resulting from community turnover
218 (abundance of small vs. large taxa) versus within-taxon size variation (sizes of individuals within
219 taxa). First, using measures of individual arthropods (a subset of the total), we calculated three
220 community parameters for each assemblage and trophic group: (1) a *specific community-*

221 *weighted mean* (CWM) body size calculated from the average size of each taxon in each
 222 treatment, (2) a *fixed CWM* calculated from the body size of each taxon averaged across
 223 treatments, and (3) *within-taxon variability*, the difference between specific and fixed CWMs
 224 (Lepš et al. 2011). Both CWMs were weighted by the total abundance of each taxon in each
 225 sampling location, summed across sampling dates. We then analyzed linear mixed-effects
 226 models for each community parameter. Finally, we extracted treatment sums-of-squares (SS)
 227 from each model using lmerTest and calculated the contributions of each aspect of size structure
 228 to treatment effects on (*specific*) CWM body size as:

$$\text{Contribution of turnover} = 100 * (\text{SS}_{\text{fixed CWM}} / \text{SS}_{\text{specific CWM}})$$

$$\text{Contribution of within-taxon size variation} = 100 * (\text{SS}_{\text{within-taxon}} / \text{SS}_{\text{specific CWM}})$$

$$\text{Covariation} = 100 * ([\text{SS}_{\text{specific CWM}} - \text{SS}_{\text{fixed CWM}} - \text{SS}_{\text{within-taxon}}] / [\text{SS}_{\text{specific CWM}}])$$

232 *Plant community response measures.* We evaluated differences in plant species cover at
 233 the level of plant cover quadrats (N = 64, 8 quadrats per plot, 4 plots per treatment) with a
 234 permutational MANOVA, constraining permutations to blocks (function *adonis* in R package
 235 *vegan*, Oksanen et al. 2013). We used linear mixed effects models to evaluate treatment effects
 236 on species density (plant species per m²), diversity (Shannon's H'), and canopy height within
 237 plant cover quadrats (N = 64); these models retained experimental block as a random effect.-

239 RESULTS

240 Plant community

241 The plant community in control plots –a mixture of dwarf deciduous and evergreen
 242 shrubs, sedges, mosses, and lichens—differed from that of fertilized plots, which were
 243 dominated by *Betula nana* and a forb (cloudberry, *Rubus chamaemorus*) (Fig. 1; F_{1,63} = 111.2, P

244 = 0.001). Species density in fertilized plots was 5 ± 0 species/m², a lower density than that of
 245 controls (13 ± 0 species/m², $F_{1,59} = 1199.3$, $P < 0.001$). Diversity in fertilized plots ($H' = 1.0 \pm 0.1$)
 246 was also lower than that of controls ($H' = 2.1 \pm 0.1$, $F_{1,59} = 613.1$, $P < 0.001$). In addition,
 247 maximum plant canopy height in fertilized plots was 55.8 ± 5.5 cm, more than double the
 248 maximum canopy height in controls (23.9 ± 0.5 cm, $F_{1,59} = 106.0$, $P < 0.001$). Increased canopy
 249 height corresponded to greater maximum height of *Betula* in fertilized plots relative to controls
 250 ($F_{1,62} = 157.5$, $P < 0.001$).

251

252 **Arthropod abundance and biomass**

253 *Canopy assemblage.* In the canopy, treatment affected neither total abundance nor the
 254 abundance of ~~any trophic group predators, herbivores, detritivores or biting flies~~ ($P > 0.05$, Table
 255 1, Fig. 2). In addition, treatment had no effect on total canopy-dwelling biomass, nor predator,
 256 parasitoid, herbivore nor biting fly biomass (Fig. 2; Table 1; $P > 0.05$). The ~~one-two canopy-~~
 257 ~~dwelling groups~~ for which there ~~was were a~~ significant treatment effects ~~was were parasitoids~~
 258 ~~and canopy-dwelling~~ detritivores (an assortment of flies that rely upon detrital resources as
 259 larvae, see Table S1). ~~Parasitoids were more abundant in fertilized canopies in controls (Fig. 2;~~
 260 ~~Est=0.54±0.25, P=0.03), and t~~The total biomass of canopy-dwelling detritivores was 5 times
 261 greater in fertilized plots relative to controls (Fig. 2; ~~F_{1,6}=10.1, P=0.02~~Est=1.53±0.48,
 262 ~~P=0.019~~).

263 Greater canopy-dwelling detritivore biomass in fertilized canopies was caused ~~not by~~
 264 ~~greater detritivore abundance~~ partly by a non-significant difference in abundance ($P=0.059$, Fig.
 265 2), ~~but rather and~~ by larger canopy detritivore body size in fertilized plots relative to controls

266 (Fig. 3; $F_{1,6} = 19.7$, $P = 0.004$). Greater canopy detritivore body size resulted from a shift towards
 267 larger detritivore taxa in fertilized canopies relative to controls (Table 2).

268 Alongside this effect on canopy detritivore body size, canopy arthropods were on average
 269 larger in fertilized canopies relative to controls (Fig. 3; Table S2; $F_{1,3} = 16.8$, $P = 0.03$). This
 270 resulted from larger body size of detritivores, canopy herbivores ($F_{1,6} = 36.4$, $P = 0.001$), and
 271 canopy predators (Fig. 3; Table S2; $F_{1,5} = 4.0$, $P = 0.09$). Larger canopy herbivore body size
 272 resulted from a shift in community composition towards greater relative abundance of large-
 273 bodied taxa ~~taxa~~ (e.g., Miridae; Table S1) relative to small-bodied taxa (e.g., Homoptera;
 274 Table S1).

275 *Ground assemblage.* Unlike in the canopy, total ground-dwelling arthropod abundance
 276 was lower in fertilized plots relative to controls (Fig. 2; Table 1; ~~$F_{1,27} = 5.3$, $P = 0.030$~~ Est=-
 277 0.29 ± 0.12 , $P = 0.021$), a result of reduced detritivore abundance (Fig. 2; Table 1; ~~$F_{1,27} = 6.5$, $P =$~~
 278 ~~0.017~~ Est=- 0.47 ± 0.18 , $P = 0.009$). In contrast with this effect on detritivores, total ground-dwelling
 279 predator abundance was greater in fertilized plots relative to controls (Fig. 2; Table 1; ~~$F_{1,27} =$~~
 280 ~~12.5 , $P = 0.001$~~ Est= 0.34 ± 0.10 , $P < 0.001$). The opposing treatment effects on predator and
 281 detritivore abundances decreased the predator:prey abundance ratio (“prey” = detritivores plus
 282 herbivores) from 1:9 in control plots to 1:3 in fertilized plots (Fig. 2; ~~$F_{1,30} = 4.2$, $P =$~~
 283 ~~0.049~~ Est= 0.31 ± 0.15 , $P = 0.042$).

284 Despite these treatment effects on ground-dwelling predator, detritivore and total
 285 arthropod abundances, treatment had no effect on the biomass of the total assemblage nor the
 286 biomass of any trophic group (Table 1; $P > 0.05$). Lower detritivore abundances were cancelled
 287 out by greater relative abundances of large-bodied detritivore taxa in fertilized plots relative to
 288 controls (e.g., Diptera: Tipulidae; Table S1), as evidenced by a treatment effect on the fixed

289 community-weighted mean body size (Fig. 3; Table S2; $F_{1,30} = 12.2$, $P = 0.002$). Meanwhile,
290 greater predator abundances were cancelled out by smaller predator body sizes in fertilized plots
291 relative to controls (Fig. 3; Table S2; $F_{1,30} = 60.5$, $P < 0.001$). Smaller ground-dwelling predator
292 body size resulted primarily from within-taxon size differences (Table 2), especially for the
293 dominant ground-dwelling predator taxon, wolf spiders (Araneae: Lycosidae; Table S1). Wolf
294 spiders were more abundant ($F_{1,27} = 12.5$, $P = 0.001$, Table S1), but were also smaller in fertilized
295 plots relative to controls ($F_{1,27} = 5.9$, $P = 0.022$; data not shown), resulting in equivalent total
296 wolf spider biomass in fertilized and control plots ($P > 0.05$; data not shown). Despite reduced
297 predator body size, ground-dwelling arthropods in fertilized plots were on average larger in
298 fertilized plots relative to controls (Fig. 3, $F_{1,27} = 4.7$, $P = 0.039$, Table S2), primarily due to
299 differences in community composition (Table 2).

300

301 **Arthropod diversity**

302 After rarefaction to the lowest arthropod abundance in control and fertilized treatments,
303 fertilized canopies had 3 ± 1 fewer taxa relative to control canopies (Fig. 4). Canopy parasitoid
304 and predator diversity were lower in fertilized plots relative to controls, while canopy herbivore
305 richness was greater in fertilized canopies relative to controls, and canopy detritivore richness
306 did not differ by treatment (Fig. 4).

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

311 Visual inspection and extrapolation of the rarefaction curves suggested that, at this level
312 of identification, the ground and canopy assemblages as a whole were well-sampled, although
313 many individual trophic groups would have benefited from additional sampling (Table S3).

314

315 **Arthropod community composition**

316 In the canopy, 74% of taxa were common to both treatments, while on the ground 65% of
317 taxa were common to both treatments. The majority of taxa unique to one treatment or another
318 were rare (<2 individuals; Table S1). Nevertheless, community composition differed in response
319 to fertilization in both the canopy (Dev = 97.7, $P = 0.039$) and the ground assemblage (Dev =
320 162.5, $P = 0.001$) (Fig. 5 A-D).

321 In the canopy, herbivore taxa had the greatest effect on community dissimilarity in
322 control and fertilized plots, contributing 40% of total treatment deviance (Fig. 5E). The
323 remainder of canopy treatment deviance was spread somewhat evenly among parasitoid, predator
324 and detritivore taxa, which contributed 10, 20 and 30% of treatment deviance, respectively (Fig.
325 5E). Herbivores from family Delphacidae contributed the most to community dissimilarity and
326 were by themselves affected by treatment (Fig. 5; Dev = 14.5, $P_{\text{adj}} = 0.017$). Delphacids
327 comprised on average 10% of the abundance in control canopies, but were completely absent
328 from fertilized canopies (Table S1). In arctic tundra habitats, this family is known to specialize
329 on graminoids such as *Carex* and *Eriophorum* (Wilson 1997); cover of these plant species has
330 drastically declined in fertilized plots (Fig. 1). Two additional herbivore taxa and two detritivore
331 taxa contributed substantially (>5% deviance) to community dissimilarity, although without
332 univariate treatment effects (Fig. 5; $P > 0.05$). All four of these taxa were more abundant in
333 fertilized plots relative to controls (Table S1).

334 In the ground assemblage, detritivore taxa contributed the most to community
335 dissimilarity (63% of deviance), with predator and herbivore taxa contributing the remainder
336 (23% and 13%, respectively; parasitoids contributed <1%; Fig. 5F). In addition to altering
337 ground assemblage composition, treatment affected the abundance of three individual taxa:
338 springtails from order Symphypleona, mites (Acari), and predaceous beetles from family
339 Staphylinidae ($P_{adj} < 0.05$). These three taxa also dominated the overall community response to
340 fertilization (Fig. 5). Relative abundance of Symphypleona was 93% lower in fertilized plots
341 relative to controls (Table S1), while mites and Staphylinid beetles were respectively 6 and 5
342 times more abundant in fertilized plots relative to controls (Table S1).

343

344 DISCUSSION

345 Fertilization did not increase total arthropod abundance or biomass

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

353 Changes to top-down ~~(predator) control~~ control by predators including songbirds
354 (Aunapuu 2004) and wolf spiders may have mitigated some bottom-up effects of nutrient
355 addition on consumers. For example, in the ground assemblage of fertilized plots, a deeper litter
356 layer may provide wolf spiders with some protection from intra-guild predation (Finke and

357 Denno 2002, Rickers and Scheu 2005). Lower intraguild predation would increase the
358 survivorship of smaller, younger wolf spiders, aligning with our observations of decreased mean
359 wolf spider body size, increased wolf spider abundance and lower detritivore abundance in
360 fertilized plots relative to controls. In turn, a greater abundance of small wolf spiders may have
361 led to the observed increase in detritivore body size, because smaller wolf spiders will generally
362 take smaller detritivores as prey.

363 Another explanation for the surprising negative and neutral responses of arthropod
364 abundance and biomass is that long-term nutrient addition in moist acidic tundra reduces plant
365 palatability, cancelling out the positive effects of increased plant biomass on consumers. The
366 shift towards relatively unpalatable woody stem tissue and plant species in moist acidic tundra,
367 via the dominance of *Betula*, may be a unique response among nutrient addition experiments in
368 herbaceous plant communities (Clark et al. 2007). In contrast to tundra, after many years of
369 nutrient addition temperate grasslands become dominated by relatively palatable C₃ grasses and
370 forbs (Isbell et al. 2013), and salt marshes' near-monoculture of *Spartina* grasses increase in N
371 content (Murphy et al. 2012).

372 In another contrast to nutrient addition in salt marshes, where an accumulation of dead
373 thatch benefits many arthropods (Finke and Denno 2002, Murphy et al. 2012), long-term nutrient
374 addition in moist acidic tundra may create an unfavorable canopy and surface microenvironment
375 for arctic arthropods. In the Arctic, shrubs create a shadier, colder canopy microenvironment
376 (Myers-Smith et al. 2011, Shaver et al. 2014), which could have effects on the growth and
377 movement patterns of the resident arthropods. In particular, the cooling effect of shrubs could be
378 responsible for the observed increase in ground-dwelling detritivore body size (Atkinson and
379 Sibly 1997), while also decreasing the movement (and therefore capture) rates of surface-active

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380 predators like wolf spiders. In addition to these temperature effects, nutrient addition leads to the
381 loss of the moss cover that insulates the soil and regulates soil moisture (Bløk et al. 2011). These
382 changes likely drove out some arthropod taxa, given the sensitivity of many arctic species to
383 decreased solar radiation and fluctuations in soil moisture (Danks 2004, Høye and Forchhammer
384 2008, Strathdee and Bale 1998).

385

386 **Fertilization decreases plant diversity, but not arthropod richness**

387 Contrary to our second hypothesis, fertilization did not decrease arthropod diversity
388 (rarefied richness). Instead, we found that fertilization's effect on arthropod diversity was
389 dependent upon microhabitat, with decreased diversity in fertilized canopies (as expected), but
390 increased diversity in the fertilized ground assemblage. We interpret these results cautiously,
391 because although the differences between control and fertilized richness were significant, they
392 were small (3-5 taxa), and furthermore, the taxa identified in this study are likely each
393 represented by multiple species. Even so, the changes to arthropod diversity were unexpected in
394 comparison with similar studies (Haddad et al. 2000, Siemann 1998, Wimp et al. 2010) and
395 small relative to the loss of >50% of plant species from fertilized plots. This suggests that tundra
396 arthropod diversity is somewhat robust to plant species loss.

397 On the other hand, some taxa were dramatically affected; fertilization seems to have
398 nearly driven out a moss-associated detritivore (Collembola: Symphypleona) and a graminoid-
399 associated herbivore (Hemiptera: Delphacidae). In the canopy, decreased abundance of these
400 Delphacids may have propagated through the food web, contributing to the absence of taxa
401 known to predate on this family (Hemiptera: Anthocoridae, Nabidae; Diptera: Pipunculidae)
402 relative to control plots (Table S1).

403

404 **Fertilization alters both plant and arthropod community composition**

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

411 Treatment effects on community composition also contributed to changes in arthropod
412 body size structure (Table 2), with fertilized plots supporting larger taxa (the exception being
413 ground-dwelling predatory arthropods, which were smaller in fertilized plots relative to
414 controls). [A study of arthropod communities in fertilized grasslands \(Lind et al. *in press*\)](#)
415 [similarly found that soil nutrient addition increased mean arthropod body size, indicating this](#)
416 [effect may widespread.](#) Relative to taxa with small body size, large taxa have greater per capita
417 nutrient demands (Brown et al. 2004). The larger herbivores and detritivores in fertilized plots
418 may have capitalized on increased N concentrations in non-woody plant tissues even as total N
419 constrained their total abundance and/or biomass. These changes to arthropod community
420 composition and body size, together with the losses of certain arthropod taxa (described above),
421 point to [possible](#) changes in food web and ecosystem processes (e.g., herbivory, predation)
422 resulting from nutrient addition.

423

424 **Conclusion**

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425 Overall, our results were surprising and in contrast with similar studies of bottom-up
426 effects on arthropod community structure. We found that nutrient addition altered arthropod
427 community composition, but did not affect total arthropod diversity, abundance or biomass as
428 predicted. Despite the dramatic increase in plant productivity and substantial reduction of plant
429 species diversity, nutrient addition did not increase arthropod abundance and biomass or reduce
430 arthropod diversity. As predicted, plant community changes were associated with shifts in
431 arthropod community composition, and in some cases losses of arthropod taxa, suggesting
432 bottom-up effects from plants to arthropod consumers. In this community, the availability of
433 palatable (non-woody) plant tissues, and not total plant production, likely set the upper limit on
434 arthropod biomass and abundance in fertilized plots. Our findings recall how eutrophication of
435 aquatic systems can increase primary production while detrimentally affecting consumers, and
436 provides a striking contrast to the handful of terrestrial studies that have found parallel plant and
437 arthropod responses to nutrient addition. Our results indicate that in some cases, producer traits
438 exert stronger bottom-up control on consumer communities than the amount of primary
439 production.

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440

441 **ACKNOWLEDGEMENTS**

442 We thank J. Laundre, L. Van Der Pol, K. Contreras, K. Daly, S. Meierotto, S. Sweet, J. Perez, H.
443 Chmura, J. Krause, J. Stuckey and PolarTREC teacher N. Kemp for assistance in the laboratory
444 and field, and D. Sikes and J. Demuth for providing laboratory space. This manuscript was
445 greatly improved with input from three anonymous reviewers and Kimberly LaPierre. This
446 research was supported by National Science Foundation Grants DEB 102683 to support the
447 Arctic LTER to G. Shaver, OPP 0908502 to L. Gough, and DEB 1210704 to A. Koltz, as well as

448 funding from CREOi and the National Geographic Committee for Research and Exploration to
449 A. Koltz.
450

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573 **Table 1.** Results from linear mixed effects models of arthropod abundance and biomass. Biting
 574 flies were not present in ground assemblage samples.

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

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Measure	Assemblage	Group	Sum-Sq	Mean-Sq	NumDF	DenDF	F-value	Pr(>F)	
Abundance	Canopy	All	0.09	0.09	1	3	0.9	0.403	
		Parasitoids	0.45	0.45	1	3	2.5	0.215	
		Predators	0.04	0.04	1	6	0.1	0.719	
		Herbivores	0.02	0.02	1	6	0.1	0.764	
		Detritivores	0.53	0.53	1	3	2.4	0.221	
		Biting-Flies	0.07	0.07	1	3	0.1	0.791	
		-	-	-	-	-	-	-	-
-	Ground	All	0.69	0.69	1	27	5.3	0.030	*
		Parasitoids	0.02	0.02	1	27	0.1	0.777	
		Predators	0.93	0.93	1	27	12.5	0.001	**
		Herbivores	0.38	0.38	1	30	1.5	0.236	
		Detritivores	1.91	1.91	1	27	6.5	0.017	*
-	-	-	-	-	-	-	-	-	
-	-	-	-	-	-	-	-	-	
Biomass	Canopy	All	0.57	0.57	1	3	2.4	0.220	
		Parasitoids	1.14	1.14	1	6	0.4	0.548	
		Predators	1.20	1.20	1	6	1.3	0.301	
		Herbivores	0.13	0.13	1	3	0.6	0.480	
		Detritivores	4.67	4.67	1	6	10.1	0.019	*
		Biting-Flies	0.23	0.23	1	3	0.2	0.684	
		-	-	-	-	-	-	-	-
-	Ground	All	0.03	0.03	1	27	0.2	0.681	
		Parasitoids	0.39	0.39	1	27	1.3	0.274	
		Predators	0.04	0.04	1	27	0.3	0.615	
		Herbivores	2.36	2.36	1	27	4.1	0.053	
		Detritivores	7.00	7.00	1	27	4.1	0.053	

577

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

<u>Assemblage</u>	<u>Group</u>	<u>Turnover</u>	<u>Within-taxon</u>	<u>Covariation</u>
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

584

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

588

589 **Figure 2.** Arthropod abundance (left panels) and biomass (right panels) means in control and
590 fertilized plots in the canopy assemblage (top panels) and on the ground (bottom panels).

591 Asterisks above bars indicate significant treatment differences in total abundance or biomass;
592 asterisks within bars indicate significant treatment differences for the trophic group indicated
593 ($P < 0.05$). Error bars are 1SE for total biomass or abundance ($n = 4$ blocks).

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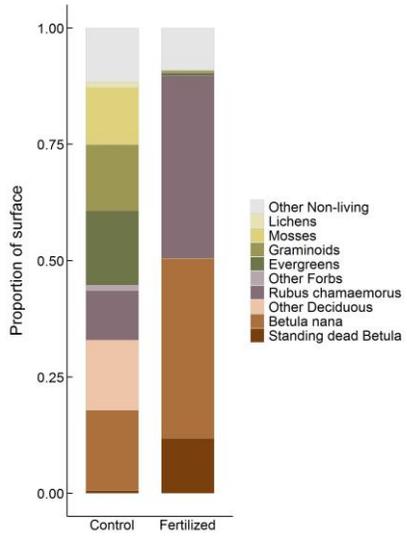
595 **Figure 3.** Community-weighted mean (CWM) arthropod body size for each assemblage and
596 trophic group. Gray lines represent “fixed” CWMs calculated from the average body size of each
597 taxon averaged across treatments (treatment differences result only from turnover, i.e., relative
598 abundances of large vs. small taxa); black lines represent a treatment-“specific” CWM calculated
599 from the average body size of each taxon within each treatment (thus, treatment differences
600 result both from turnover and differences in body size within taxa). Significance of treatment
601 differences for CWMs are marked for each type of mean (*, $P < 0.05$; ·, $P < 0.10$). Error bars are
602 1SE ($n = 4$ blocks).

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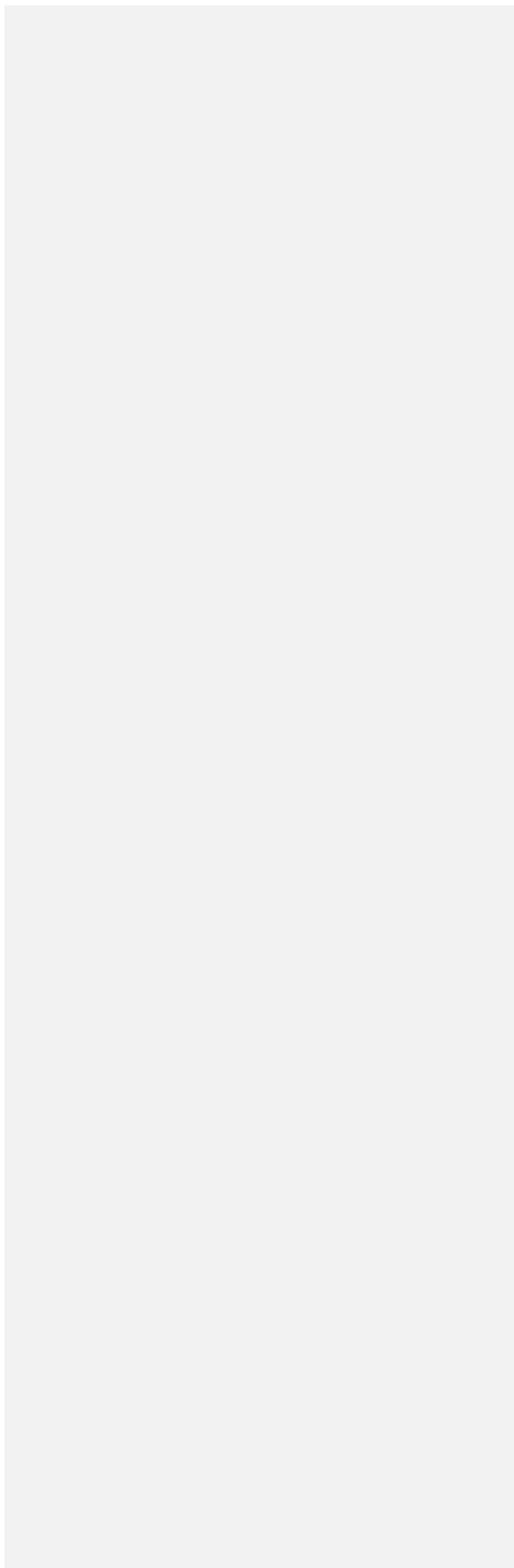
604 **Figure 4.** Taxon rarefaction curves of the canopy- and ground-dwelling arthropod assemblages,
605 by trophic group and in total. Rarefied richness values are indicated by horizontal dashed lines;
606 shaded areas represent standard errors of iterations of the assemblage abundance data.

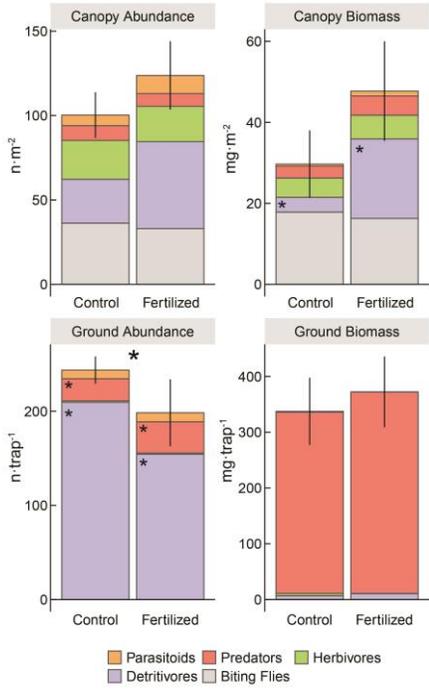
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608 **Figure 5.** Non-metric multidimensional scaling (NMDS) solutions for canopy (A,C) and ground
609 dwelling (B,D) arthropod community composition. Black text and dashed ellipses indicate
610 centroids and 95% CI for each treatment. A, B: NMDS coordinates for vacuum and pitfall
611 samples are shown as filled (fertilized) and open (control) circles. C, D: Coordinates for each
612 taxon are labeled with abbreviations and colored by functional group (see Supp. Table 1 for
613 corresponding taxon names). E, F: percent share of total treatment deviance by taxon from
614 multivariate generalized linear models of canopy (E) and ground (F) assemblage taxonomic
615 composition. Taxa contributing >5% of total deviance are labeled with their abbreviation.
616 Asterisks (*) indicate taxa for which there was a significant univariate effect of treatment (P_{adj}
617 <0.05) and dots (.) indicate marginally significant treatment effects (P_{adj} <0.1). Labeled arcs
618 indicate the subtotal of deviance for each trophic group; biting flies (canopy and ground) and
619 parasitoids (ground only) contributed <1% to deviance.
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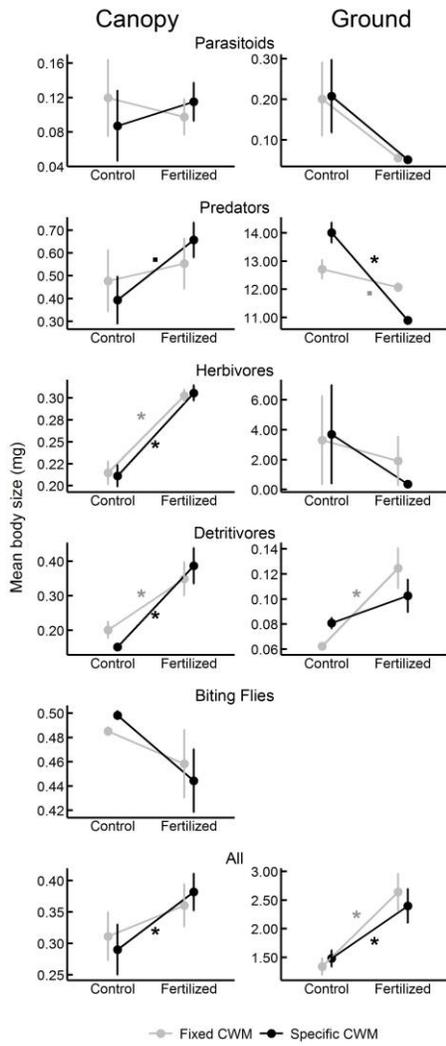


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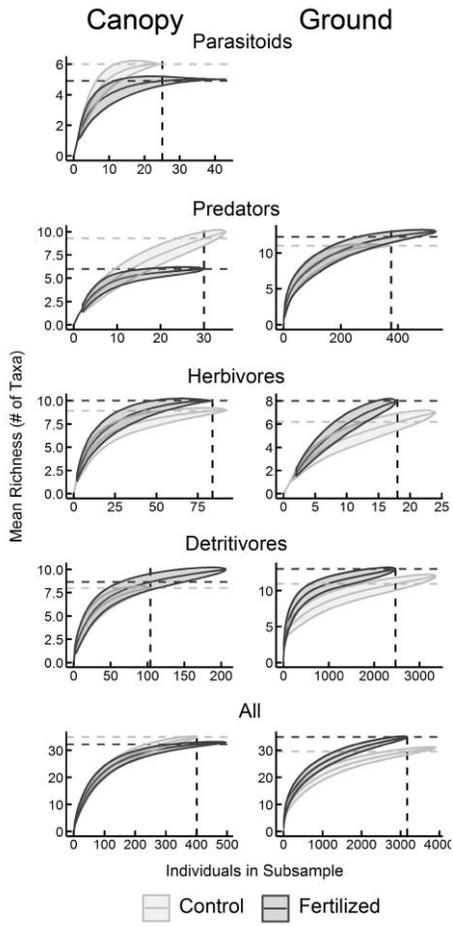




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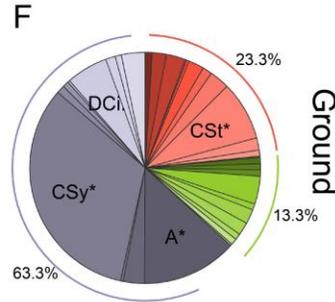
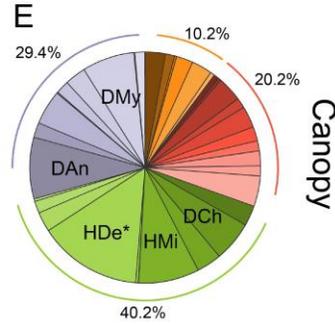
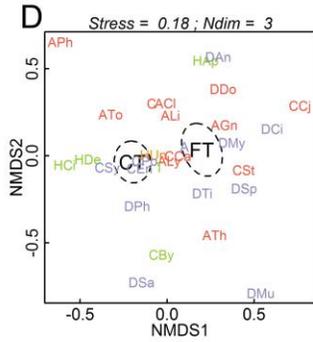
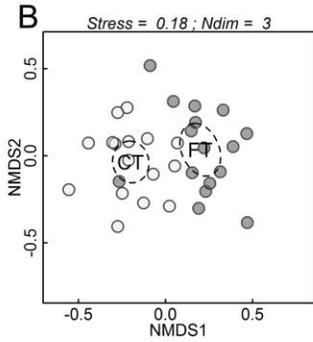
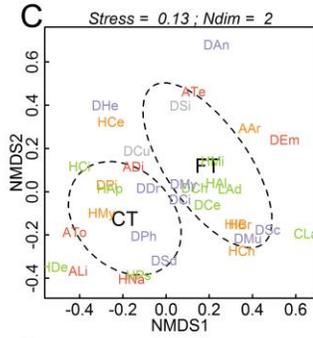
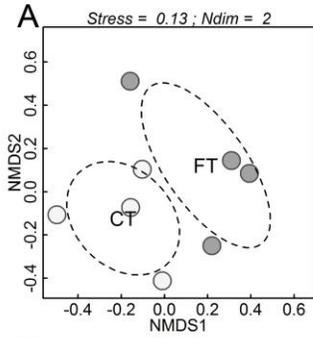
625
626



627
628

Composition

Deviance (%)



Parasitoids Predators Herbivores Detritivores Biting Flies

629
630