

1 Title:

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3 The detritus-based microbial-invertebrate food web contributes disproportionately
4 to carbon and nitrogen cycling in the Arctic

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33

34 **Abstract**

35

36 The Arctic is the world's largest reservoir of soil organic carbon and
37 understanding biogeochemical cycling in this region is critical due to the potential
38 feedbacks on climate. However, our knowledge of carbon (C) and nitrogen (N)
39 cycling in the Arctic is incomplete, as studies have focused on plants, detritus,
40 and microbes but largely ignored their consumers. Here we construct a
41 comprehensive Arctic food web based on functional groups of microbes (e.g.,
42 bacteria and fungi), protozoa, and invertebrates (community hereafter referred to
43 as the invertebrate food web) residing in the soil, on the soil surface and within
44 the plant canopy from an area of moist acidic tundra in northern Alaska. We used
45 an energetic food web modeling framework to estimate C flow through the food
46 web and group-specific rates of C and N cycling. We found that 99.6% of C
47 processed by the invertebrate food web is derived from detrital resources (aka
48 'brown' energy channel), while 0.06% comes from the consumption of live plants
49 (aka 'green' energy channel). This pattern is primarily driven by fungi,
50 fungivorous invertebrates, and their predators within the soil and surface-dwelling
51 communities (aka the fungal energy channel). Similarly, >99% of direct
52 invertebrate contributions to C and N cycling originate from soil- and surface-
53 dwelling microbes and their immediate consumers. Our findings demonstrate that
54 invertebrates from within the fungal energy channel are major drivers of C and N
55 cycling and that changes to their structure and composition are likely to impact
56 nutrient dynamics within tundra ecosystems.

57 **Introduction**

58

59 The Arctic is a major reservoir of global organic carbon (C) and considered an
60 extremely important region in terms of its potential feedbacks to climate change
61 (Crowther et al. 2016; Schuur et al. 2008). Of central concern is that climate
62 warming is accelerating soil microbial respiration more than it is facilitating
63 increased plant uptake of carbon dioxide (CO₂) in this region, thereby
64 transforming the Arctic from a sink to a source of atmospheric C. Plants and
65 microbes are not the only actors in this system, as there is a diverse assemblage
66 of consumers within the "green" (living plant-based) and "brown" (detritus-based)
67 food webs. Interactions within and between these two food webs—predation,
68 herbivory, detritivory – can directly affect the uptake, storage and mineralization
69 of C and N (e.g., Bardgett and Wardle 2010). Arthropods and other invertebrates,
70 including protozoans, comprise a large portion of the animal biomass on the
71 tundra, outweighing their vertebrate counterparts by an order of magnitude by
72 some estimates (Legagneux et al. 2012; Moore and deRuiter 2012). This
73 suggests that as a group they may play an important role in affecting processes
74 such as decomposition, primary production, and nutrient cycling.

75 The importance of invertebrates in regulating energy and nutrient flow
76 through Arctic communities was recognized as early as 1923 by Summerhayes
77 and Elton in their report on Bear Island in the Norwegian Svalbard archipelago
78 (Summerhayes and Elton 1923). Yet almost 100 years later, while there have
79 been numerous studies on the natural history of Arctic vertebrates and to a

80 lesser extent invertebrates, few have addressed their influence on ecosystem
81 structure and functioning in an integrated manner (see Oksanen et al. 1981).
82 Notable exceptions include studies on the effects of vertebrate and soil
83 invertebrate herbivores on plant communities (e.g., Gauthier et al. 2004; Gough
84 et al. 2012; Mosbacher et al. 2016; Sjögersten et al. 2012) and the role of soil
85 invertebrates, whose activity has been linked to C storage and N cycling in the
86 tundra (e.g., Moore and deRuiter 2012; Moore et al. 2003; Sistla et al. 2013). In
87 contrast, surface- and canopy-dwelling arthropods have typically been studied in
88 terms of their role as a food source for birds (Boelman et al. 2015; Bolduc et al.
89 2013; Legagneux et al. 2012) – and not in terms of their impact on lower trophic
90 levels or any particular ecosystem processes per se (but see Lund et al. 2017).
91 This may be due in part to the low abundances of aboveground invertebrate
92 herbivores (Danks 1992; Gelfgren 2010), which suggests that invertebrate
93 consumption of plant biomass and effects on nutrient cycling are low within this
94 system (Haukioja 1981). However, the proportionally higher abundances of
95 detritivores as compared to herbivores suggest that the former may have a
96 greater influence on C and N cycling than the latter (Ryan 1977).

97 Several frameworks have emerged that integrate aboveground and
98 belowground assemblages, green and brown food webs, and the roles of active
99 predators to study their impacts on ecosystem processes (e.g., Bardgett and
100 Wardle 2010; Moore et al. 2003; Schmitz 2008a). For example, Bardgett and
101 Wardle (2010) review how the activities and interactions of belowground
102 communities may influence the productivity, diversity, and composition of plant

103 communities. Moore et al. (2003) and Schmitz (2008a) focused on how
104 belowground and aboveground invertebrate predators can impact
105 biogeochemical cycling and other aspects of ecosystem functioning. These
106 integrative frameworks seem appropriate to study Arctic systems, as several
107 characteristics of Arctic invertebrate communities suggest that there should be
108 strong links between the aboveground and belowground realms and between the
109 green and brown components of the food web that are mediated by mobile
110 arthropods. For example, many Arctic species are broad generalists that feed
111 upon several different resources within their own and other trophic levels (Roslin
112 et al. 2013; Wirta et al. 2015b). In particular, surface-dwelling generalist
113 predators (e.g., wolf spiders and beetles) that serve as important links between
114 the green and brown food webs in other herbaceous plant communities (Bardgett
115 and Wardle 2010; Birkhofer et al. 2008; Scheu 2001; Wardle 2002), are
116 extremely abundant in the Arctic tundra compared to most other groups
117 (Gelfgren 2010; Høye and Forchhammer 2008; Rich et al. 2013; Wyant et al.
118 2011). Applying the integrated approach advocated above toward the study of
119 Arctic invertebrate communities – and in particular to addressing the links
120 between the green and brown food webs -- would help us in identifying the role of
121 these communities in regulating C and N dynamics in the tundra.

122 A comprehensive characterization of the invertebrate community would
123 enable us to estimate the importance of these organisms in influencing ecological
124 processes, and in turn, strengthen predictions about the response of this food
125 web to disturbances such as climate change. To this end, we integrated samples

126 from the soil, surface, and canopy habitats to build a complete microbial-
127 invertebrate food web for the Arctic tundra (hereafter referred to as the
128 invertebrate food web). Using these data, we then took an energetic food web
129 modeling approach to quantify C and N flow through the web and estimate
130 contributions by different functional feeding groups to respiration, N
131 mineralization, and recycling of organic C and N. Based on previously published
132 work in tundra ecosystems (e.g., Ryan 1977), we hypothesized that (a)
133 organisms within the brown food web (i.e., invertebrates derived from detritus)
134 would process the majority of energy and have a larger direct impact on C and N
135 cycling than organisms within the green food web (i.e., those derived from live
136 plant biomass). Given the large abundance of surface-dwelling generalist
137 predators on the Alaskan tundra (Rich et al. 2013; Wyant et al. 2011), we also
138 hypothesized that (b) these predators would serve as a major hub linking the
139 green and brown food webs.

140

141 **Methods**

142

143 Study area

144

145 This study was performed in an area of moist acidic tundra on the North
146 Slope of Alaska (68.952° N, 150.208° W, elev. 414m), 37 km NW of Toolik Field
147 Station and the Arctic Long-Term Ecological Research (LTER) site (Fig. 1). Moist
148 acidic tundra (Bliss and Matveyeva 1992) is the dominant ecosystem type in this

149 part of the Arctic, comprising more than 50% of the land area (Jandt et al. 2012).
150 Mean soil pH at our site is 4.4 ± 0.2 (Bret-Harte et al. 2013) and mean annual
151 temperature is 10°C . Primary and secondary production are limited by the
152 extremely short growing seasons, with mean temperatures above freezing for
153 only three months (June, July, August) of the year (Hobbie et al. 2003). The plant
154 community is characterized by mosses, dwarf evergreen shrubs, low-stature
155 deciduous shrubs and graminoids (Bret-Harte et al. 2013; Shaver and Chapin
156 1991). A comprehensive plant harvest in 2011 showed that total live plant
157 biomass at our site was 1500 g m^{-2} and that aboveground net primary
158 productivity (ANPP) was $200 \text{ g m}^{-2}\text{yr}^{-1}$, with over half of annual production being
159 from graminoids (see Bret-Harte et al. 2013).

160

161 Sampling and processing of surface, canopy, and soil invertebrate communities

162

163 Differences in sizes and life history traits of organisms within the three
164 microhabitats (i.e., soil, soil surface, and plant canopy) necessitated using a
165 variety of sampling methods to characterize the entirety of the invertebrate food
166 web. We established three parallel 50-meter transects, adjacent to those used by
167 Bret-Harte et al. (2013), separated by 5-meters each for sampling the soil,
168 surface, and canopy communities. Our samples were collected in July during
169 peak plant biomass (July 18-25, 2013).

170 The canopy and surface arthropod communities were sampled every five
171 meters along two of the three transects (total of ten samples each of canopy and

172 surface). We sampled surface-dwelling organisms using pitfall traps comprised of
173 clear cups (9 cm in diameter, 15 cm deep), filled $\frac{1}{4}$ full with a 75% ethanol
174 solution. Traps were left out for one week (July 18-25), after which their contents
175 were transferred to vials until further processing. Canopy-dwelling organisms
176 were sampled on July 18, 2013 with a modified leaf vacuum in a 1-m² area for 90
177 seconds at each location. Collected arthropods were placed in muslin bags and
178 stored at -20°C until sorted and then stored in 75% ethanol until identification.
179 Canopy and surface-dwelling arthropods were identified to the family level using
180 published keys (Marshall 2006; Triplehorn and Johnson 2005), with the exception
181 of Collembola and Acari, which were identified only to subclass and any captured
182 larvae, which were identified to order. We estimate that at this level of taxonomic
183 resolution, our sampling methods detected roughly 82.5% of aboveground
184 arthropod taxa (Online Resource 1).

185 For soil-dwelling organisms, we took soil samples every ten meters along
186 the first transect (total of five samples) on July 18, 2013. Half of each soil sample
187 was divided into 5-10 g subsamples to estimate the densities of bacteria, fungi,
188 Protozoa, rotifers, tardigrades, enchytraeids, nematodes, and insects (larvae and
189 adults). The other half of the sample was kept intact to estimate densities of soil
190 dwelling microarthropods and soil bulk density (see Gough et al. 2012 and Sistla
191 et al. 2013). Samples were taken without regard to the plants present at each
192 location along the sampling transect in order to capture the variability in vascular
193 plant composition and associated roots present at our study site.

194 Fungal and bacterial densities were estimated from 5-g subsamples of soil
195 using epifluorescent microscopy techniques (Bloem 1995). Fungi samples were
196 stained with a calcofluor fluorescent brightener (see Frey et al. 1999) and read at
197 334-365 nm wavelength. Bacteria samples were stained with 5-(4,6
198 dichlorotriazin-2-yl) aminofluorescein (DTAF) and read at 490 nm wavelength.
199 Active fungal biomass was estimated as 10% of total fungal biomass (see
200 Ingham and Klein 1984).

201 Protozoan (i.e., ciliates, flagellates, and amoeba) densities were
202 estimated via the most probable number technique (Darbyshire et al. 1974),
203 using a 10-g subsample of soil serially diluted with tenfold dilutions to 10^{-6} ml,
204 and incubated at 14°C with *E. coli* as a food source for 5 days. Population
205 densities were estimated from distribution of presence and absence data across
206 dilutions using the Most Probable Number Estimate Program (EPA 2013), the
207 most common current approach for estimating soil protozoa biomass (Coleman
208 et al. 2004; Crotty et al. 2012). Nematodes were extracted from 5 g of soil using
209 the Baermann wet funnel technique (Baermann 1917). Isolated specimens were
210 preserved using 10% formalin solution, counted and sorted into functional groups
211 using compound microscopy. Enchytraeids, rotifers, tardigrades, and insect
212 larvae were counted using a dissecting microscope from 5-g subsamples of soil
213 immersed in deionized water.

214 The densities of soil dwelling arthropods were estimated from the
215 remaining half of the soil sample by 5-day heat-extraction into a solution of 90%
216 ethanol and 10% glycerin using Tullgren funnels (Moore et al. 2000).

217

218 Microbial and invertebrate biomass estimates

219

220 Biomass estimates were obtained by multiplying the field estimates of
221 population densities by taxon-specific estimates of the biomass of individuals.
222 For surface and canopy insects, these estimates were based on allometric
223 equations (Gruner 2003; Hódar 1997; Sabo et al. 2002; Sample et al. 1993)
224 parameterized to the average body lengths (to 0.01 mm) of the first five
225 individuals of a group encountered in each sample and the size of the sample
226 area (see Pérez et al. 2016). The area sampled was explicit for canopy insects,
227 set at 1 m². For surface-dwelling arthropods caught by pitfall traps, we used the
228 equation $\lambda = Nt / (2 \cdot R \cdot L)$ of Stoyan and Kushka (2001), where Nt is the average
229 number of animals caught trap-day⁻¹, R is the radius of the trap (0.0254 m), and L
230 is the distance (m) a given animal group can walk in a day (personal
231 observations and published movement estimates). Biomass values (mg C m⁻²)
232 for soil-dwelling microbial and invertebrate functional groups (i.e., bacteria, fungi,
233 collembola, enchytraeids, mites, nematodes, protozoa, rotifers, and tardigrades)
234 were estimated from our density estimates and published information on mean
235 individual dry weights (Hunt et al. 1987), corrected for soil bulk density.

236

237 Functional group assignment and food web structure

238

239 The food web was based on the biomass estimates and trophic interactions
240 among functional groups of organisms and basal resources. Functional groups
241 were based on primary food sources, feeding mode, habitat, and life history traits
242 (Moore et al. 1988), which were determined from field and laboratory
243 observations and published accounts (Online Resources 2, 3). All groups with
244 the exception of biting flies were assumed to receive their energy from terrestrial
245 sources. Based upon the known natural history of biting flies (and to a lesser
246 extent non-biting midges), we assumed that this group relies substantially on
247 aquatic resources acquired during the larval stage (i.e., diatoms and aquatic
248 detritus) and to a lesser degree on blood meals (for reproduction) and nectar (to
249 sustain flight activity) as adults (Danks 1992; Lundgren and Olesen 2005).
250 Connectance (sensu May 1972) was estimated from the number of functional
251 groups and basal resources (S) and trophic links (L) as $C=2L/(S*(S-1))$.
252 Additionally, in order to compare the trophic structure of each sub-web, we
253 grouped functional groups into broader trophic groups (e.g., herbivore, predator,
254 etc.) following conventions that have been used in previous tundra arthropod
255 studies (e.g., Gelfgren 2010 and references therein; see Online Resource 2).

256

257 Energy fluxes and nutrient cycling

258

259 We simulated C fluxes between functional groups and rates of organic and
260 inorganic C and N cycling for all functional groups using methods previously
261 described for soil food webs (de Ruiter et al. 1994; Hunt et al. 1987; Moore and

262 deRuiter 2012). Based upon the biomass estimates, this approach accounts for
263 known death rates, feeding preferences, assimilation efficiencies, production
264 efficiencies, and C:N ratios when deriving C and N cycling rates ($\text{mg C m}^{-2} \text{yr}^{-1}$;
265 $\text{mg N m}^{-2} \text{yr}^{-1}$) for each functional group and the entire food web (see de Ruiter et
266 al. 1994; Hunt et al. 1987). To do this, the model assumes that the system is at a
267 steady state and that biomass production is equal to biomass loss from predation
268 and natural death over a given unit of time. For any given trophic interaction,
269 feeding rates, egestion rates, and mineralization rates of C and N are calculated
270 as described by Moore and deRuiter (2012) and Andrés et al. (2016). We
271 assumed that 50% of the estimated dry weight biomass of each group was C
272 (Doles 2000; Hunt et al. 1987). Based on death rates and the assimilation
273 efficiencies of each group, we calculated the total amount of organic C and N that
274 would be recycled back to the system from the unassimilated biomass of prey
275 (egestion — leavings, orts and feces) and the corpses of organisms that died
276 non-predatory deaths (Zou et al. 2016). Estimates of inorganic C and N
277 mineralization are based on the production efficiencies, assimilated consumption,
278 and the C:N ratios of each functional feeding group.

279 The model accounts for both consumers with a single prey source and
280 consumers with multiple prey sources by allowing feeding rates to depend upon
281 the biomass of available prey. We assumed that soil-dwelling organisms primarily
282 feed within the soil portion of the food web (Moore et al. 1988) but that there are
283 some cross-feeding relationships between the soil and surface sub-webs and the
284 surface and canopy sub-webs (e.g., generalist predators, biting flies; see Online

285 Resource 3). Feeding preferences for a particular prey item within the same
286 habitat were assigned a value of 1. For those surface and canopy-dwelling
287 organisms with cross-feeding relationships, consumption of potential prey in
288 other habitats or of prey that move between habitats (i.e., flies) were assumed to
289 happen less frequently and were thus assigned preference values of either 0.1 or
290 0.9. For basal resources, we assumed that detritus, diatoms, lichen, moss, live
291 plant biomass (roots, aboveground vascular plant tissue, pollen), and blood were
292 not limiting resources. We assigned theoretical values of 2,500,000 mg C m⁻² to
293 detritus, 300,000 mg C m⁻² to diatoms, and 300 mg C m⁻² to all others. Under the
294 steady state assumption, this does not affect the overall flux estimates but does
295 allow us to estimate the fluxes from basal resources to consumers.

296 We ran 1000 simulations of the model to get an estimate of the variability
297 across model runs. Each simulation had the same connectance and feeding
298 preference matrices as input but different biomass estimates for each functional
299 group. Specifically, due to the large variances and high coefficients of variations
300 associated with the measured field estimates of biomass and the skewed nature
301 of the distributions of these biomass estimates (i.e., often to the right), biomass
302 estimates for each particular simulation were obtained by randomly sampling the
303 gamma distribution of the biomass of each functional feeding group. The shape
304 and scale of these gamma distributions were defined by the means and standard
305 deviations of the biomass estimates from our field samples. Sampling from the
306 gamma distribution obviates the problem of unrealistic negative values for
307 biomass that would result from using a normal distribution and the need to create

308 an arbitrary or ad hoc solution if a normal distribution were used (Bolker 2008).
309 Thus, our simulations accounted for uncertainty in the absolute biomass
310 contributions of the various groups to the entire community.

311

312 Sensitivity analysis

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314 We tested the robustness of our model results by comparing them to
315 those of other model runs that were based upon incomplete food webs and an
316 additional food web without any specified feeding preferences (i.e., any potential
317 prey was assigned a 1, whereas non-prey items were assigned 0s). For the
318 incomplete food webs, we removed each functional feeding group from the
319 network, one at a time, while holding the rest of the food web constant. We reran
320 the model 1000 times for each of these modified food webs (each time
321 manipulating the biomass values of the remaining groups, as described above)
322 and collected information on the total recycled organic C and N from egestion
323 (i.e., leavings, orts, and feces) and corpses (due to natural deaths), total
324 inorganic mineralized C and N, and total C consumed by the entire community (in
325 mg C or N m⁻² year⁻¹).

326 Additionally, we explored the importance of including any given functional
327 feeding group for the overall stability based on the diagonal strength (*aka s-min*)
328 of the Jacobian matrix of the food web developed by de Ruiter et al. (1995) and
329 Neutel et al. (2002). To calculate *s-min* the diagonal elements are based on the
330 mass-specific natural (i.e., non-predatory) death multiplied by a constant 's'.

331 Stability was estimated by determining the value of 's' needed to ensure that the
332 real parts of all the eigenvalues of the matrix are negative (e.g., de Ruiter et al.
333 1995; Moore and deRuiter 2012; Moore and William Hunt 1988; Rooney et al.
334 2006). An *s-min* value of one indicates that the diagonal strength ensuring
335 stability of the food web is dependent solely on the specific death rates of the
336 functional groups. Hence low *s-min* values ($s-min \leq 1$) indicate more stable food
337 webs relative to those with high *s-min* ($s-min \geq 1$).

338

339 **Results**

340

341 Food web structure and biomass

342

343 We identified 33 functional feeding groups across the entire food web,
344 including samples from the soil, surface, and canopy habitats (Online Resource
345 2). Food web connectance was calculated as 0.32.

346 We calculated the dry biomass of the entire invertebrate food web as
347 15,161 mg m⁻² (Table 1). Of this, 99.7% was comprised of microbial biomass
348 (14,244 mg fungi m⁻²; 878 mg bacteria m⁻²). In considering the structure of the
349 rest of the food web (i.e., excluding fungi and bacteria), soil-dwelling organisms
350 made up the majority of biomass (45.1%), while surface and canopy communities
351 comprised 23.8% and 31.1% of the biomass, respectively (Fig. 2). Biomass of
352 soil-dwelling organisms was dominated by fungivores, which accounted for
353 75.6% of the biomass within the soil habitat (Table 1; Fig. 2); those fungivores

354 with the most biomass included cryptostigmatid mites and collembola. Bactivores
355 (amoebae, rotifers, nematodes), predators (ciliates, mites, nematodes,
356 tardigrades), omnivores (nematodes) and other mixed-feeding microbivores
357 contributed progressively decreasing amounts of biomass to the soil food web.
358 Only 0.7% of the soil food web was comprised of belowground herbivores
359 (phytophagous nematodes). Biomass within the community of surface-dwelling
360 organisms was largely dominated by predators (95.7% of surface community),
361 the majority of which was from predaceous beetles and wolf spiders. The canopy
362 was the only habitat in which herbivores, primarily true bugs from families
363 Cicadellidae and Delphacidae, comprised more than 1% of biomass within the
364 local community (4.9% of canopy biomass). Detritivores, predators and
365 parasitoids also each contributed 1.5%, 0.7% and 0.8% respectively to canopy
366 biomass (Table 1). More than 92% of the canopy biomass was comprised of
367 hematophagous biting flies, 99.6% of which was from mosquitos. However, we
368 acknowledge that this estimate of mosquito biomass is possibly inflated due to
369 the collection method (i.e., attraction by mosquitoes to CO₂ emitted by
370 researchers during vacuum sampling).

371

372 Food web energetics

373

374 Model results show that the majority of C flow within this food web is
375 derived from detritus that enters the food web via consumption by fungi, bacteria,
376 or detritivores (99.6% of total C flow; 60,686 mg C m⁻² yr⁻¹), after which it is re-

377 distributed among their respective consumers (Fig. 3; Online Resource 3). At the
378 level of primary consumption, our estimates indicate that 15 times more C enters
379 the detrital food web through the fungal channel (92.6% of total C flow; 56,360
380 mg C m⁻² yr⁻¹) than through the bacterial channel (6.19%; 3,772 mg C m⁻² yr⁻¹).
381 The large amount of C processed by the fungal energy channel in this tundra
382 food web is also evidenced by the disproportionately larger biomass of
383 fungivores when compared to bacterivores in both the soil and surface habitats
384 (biomass of fungivores 19x more than that of bacterivores; Table 1; Fig. 2).

385 Conversely, model results indicate that very little C enters the food web
386 via herbivory (direct consumption of living primary production). Flow estimates of
387 C from both belowground and aboveground herbivory made up only 0.06% of
388 total energy flow (28 mg C m⁻² yr⁻¹). As a consequence, estimated C flow from
389 herbivores to predators is very small (3.04% of total C flow to predators; 1.30 mg
390 C m⁻² yr⁻¹). Rather, the majority of C flow to predators, particularly at the soil
391 surface, originates from the detrital pool (85.05% of total C flow to predators;
392 36.48 mg C m⁻² yr⁻¹). Cannibalism and intraguild predation are a substantial
393 source of C for several of the predators as well (9.76% of total C flow to
394 predators; 4.19 mg C m⁻² yr⁻¹).

395

396 Contributions by invertebrate food web to C and N cycling

397

398 Estimates of C mineralization (i.e., CO₂ respiration), N mineralization,
399 unassimilated organic C and N, and organic C and N from the corpses of

400 organisms that died natural deaths were also derived from the model for each
401 functional feeding group (see Table 1 for means and standard errors across all
402 model runs). Total C mineralization for the entire food web was estimated as
403 42,326 mg CO₂-C m⁻² yr⁻¹; total N mineralization was 4072 mg N m⁻² yr⁻¹. Our
404 estimates for the total organic C and N recycled back to the system by the
405 natural death of individuals (non-predation events) were 18,020 mg C m⁻² yr⁻¹
406 and 1956 mg N m⁻² yr⁻¹.

407 The microbial community was responsible for the majority of this nutrient
408 cycling (e.g., 99.4% and 99.2% of total C and N mineralization, respectively).
409 Estimated rates of C and N cycling were all an order of magnitude higher in fungi
410 than in bacteria (Table 1). Excluding microbes, total C mineralization and N
411 mineralization across the remainder of the food web were estimated as 229 mg C
412 m⁻² yr⁻¹ and 32 mg N m⁻² yr⁻¹. Total organic C and N from egestion were 373 mg
413 C m⁻² yr⁻¹ and 44.5 mg N m⁻² yr⁻¹, while recycled organic C and N from natural
414 deaths were 109 and 15 mg m⁻² yr⁻¹ respectively (Table 1). Soil-dwelling
415 organisms were the largest contributors to all forms of C and N cycling. In
416 particular, total respiration rates of soil-dwelling Collembola and cryptostigmatid
417 mites were much higher than for any other animals. These groups were followed
418 by the omnivorous nematodes and non-cryptostigmatid mites. In terms of N
419 mineralization, omnivorous nematodes, soil-dwelling collembolan,
420 cryptostigmatid mites, and amoebae were among the groups that contributed the
421 most. In addition to non-cryptostigmatid mites, Enchytraeids and biting flies,

422 these same groups were also those that contributed the most organic C and N
423 from egestion and from corpses due to non-predatory natural deaths (Table 1).

424

425 Sensitivity analysis

426

427 The results of our energetic food web model were robust to changes in the
428 structure of the network and to changes in feeding preferences. Specifically, we
429 found that excluding almost any functional feeding group from the network did
430 not qualitatively change our main results that the majority of C entering the
431 invertebrate food web is via the detrital pool and that among the invertebrates
432 (i.e., not including microbes), soil-dwelling organisms are the largest contributors
433 to C and N cycling (Online Resource 4). However, those models that excluded
434 fungi or bacteria resulted in lower estimates of total C consumption, rates of total
435 C and N mineralization, and rates of total C and N contributions from the corpses
436 of non-predatory natural deaths (Online Resource 4, 5). Exclusion of fungi had
437 the most drastic effect on estimates of C and N cycling, cutting the total C flow of
438 the food web from 60,871 mg C m⁻² to 4,676 mg C m⁻² and drastically reducing
439 the amount of organic and inorganic C and N contributed by the community
440 (Online Resource 4, 5). Exclusion of several of the different soil-dwelling groups
441 from the food web (e.g., soil-dwelling Collembola, cryptostigmatid and predatory
442 mites, Enchytraeids) also resulted in lower estimates of total egested organic C
443 and N, while excluding bacteria resulted in a higher estimate of egested organic
444 C (Online Resource 4, 5).

445 The results from these additional models also indicated that the tundra
446 invertebrate food web is highly stable. Exclusion of any functional feeding group
447 or changes to the feeding preferences still resulted in all food webs having stable
448 configurations (mean *min-S* values < 1; Online Resource 4). The food web
449 showed particularly high stability when bacteria or soil-dwelling Collembola were
450 excluded, while stability was lower when surface-dwelling spiders (e.g., wolf
451 spiders and surface web spiders) were not included in the network (Online
452 Resource 4).

453

454 **Discussion**

455

456 We characterized the structure of an Arctic invertebrate community by
457 integrating data from the soil, soil surface, and canopy habitats and modeled C
458 and N flow using an energetics-based food web model (Moore and deRuiter
459 2012). At our site in N. Alaska, we found that the majority of non-microbial
460 biomass contained within the invertebrate food web is comprised of soil-dwelling
461 organisms (45%), while surface and canopy communities contribute 24% and
462 31%, respectively. Consequently, invertebrate contributions to C and N cycling
463 were also primarily derived from soil-dwelling organisms. Higher nutrient flow
464 through the soil community was likely due in part to so much material entering
465 the overall food web from detrital resources (99.6%) as opposed to from live
466 plant biomass (0.06%). This pattern of uneven distribution of nutrient flow
467 between the brown and green webs confirmed our first hypothesis and

468 demonstrates that organisms reliant on detritus have a disproportionately larger
469 impact on C and N cycling in tundra ecosystems than those reliant on live plant
470 biomass.

471

472 Invertebrates within the brown food web process more nutrients than those within
473 the green food web

474

475 Our model results confirmed that organisms within the brown food web –
476 and not the green food web -- process the majority of nutrients within this
477 community. Furthermore, in accordance with findings from previous studies on
478 soil food webs in tundra (e.g., Moore et al. 2004; Moore and William Hunt 1988;
479 Rooney et al. 2006; Sistla et al. 2013), we found that detrital energy enters the
480 brown food web primarily via fungi and their consumers (aka, the fungal energy
481 channel), while the bacterial energy channel appears to play a smaller role in the
482 breakdown of detrital matter. These results were robust to changes in the
483 composition of the food web and to altering the feeding preferences within the
484 network (Online Resources 4, 5). The large disparity in both biomass and C flow
485 between the green and brown food webs suggests that overall, basal consumers
486 within the brown food web, particularly the fungal community, are less
487 constrained than herbivores in their ability to acquire energy from this system.
488 Part of this difference may be due in part to some tundra herbivores having
489 longer life spans and lower turnover rates than many of the soil-dwelling
490 organisms (Søvik et al. 2003; Strathdee and Bale 1998). In addition, a portion of

491 the brown food web is active year-round under the snow (Koltz unpublished,
492 Clein and Schimel 1995; Zettel 2000), whereas arthropod consumers within the
493 green food web, unlike their vertebrate counterparts, appear to only have access
494 to plant resources during a very restricted window of the summer active season
495 (Bolduc et al. 2013; Høye and Forchhammer 2008; Huitu et al. 2003; Laperriere
496 and Lent 1977). A shorter active season among herbivores may be due to
497 differences in overwintering strategies and cold hardiness between herbivores
498 (e.g., MacLean 1983) and detritivores (Hodkinson et al. 1998). Regardless, such
499 a short period of herbivore activity likely limits the amount of invertebrate
500 biomass that can accumulate within the green food web.

501 The disproportionate contribution of the brown food web to C and N
502 cycling suggests that changes to the structure of soil- or surface-dwelling
503 communities will have much larger effects on ecosystem functioning than any
504 changes within the canopy community. Additionally, while all simulated food
505 webs were stable despite functional group exclusions (Online Resource 4), we
506 observed greater changes in stability when soil-dwelling groups were excluded
507 (especially bacteria and Collembola). These results suggest that soil organisms
508 also play a more important role in maintaining food web stability relative to their
509 aboveground counterparts. In particular, fungal-feeding detritivores (e.g.,
510 Collembola, cryptostigmatid and non-cryptostigmatid mites) process a large
511 amount of C in this system (also see Moore and deRuiter 2012; Rooney et al.
512 2006; Sistla et al. 2013) and are known to be sensitive to changes in pH (van
513 Straalen and Verhoef 1997), temperature (Bokhorst 2008; Coulson et al. 1996;

514 Day et al. 2009; Harte et al. 1996) and moisture (Convey et al. 2003; Day et al.
515 2009; Tsiafouli et al. 2005; Verhoef and Selm 1983). These groups and others
516 have shown idiosyncratic responses to warmer temperatures and the associated
517 lower soil moisture brought on by climate change (Hinzman et al. 2005) in the
518 polar regions (e.g., Coulson et al. 1996; Koltz et al. unpublished; Nielsen and
519 Wall 2013 and references therein), which could have consequences for C and N
520 cycling and food web stability. Similarly, changes in plant community composition
521 that affect the quality or quantity of litter inputs can influence the structure and
522 composition of soil and surface-dwelling communities (Bardgett and Wardle
523 2010; Kaspari and Yanoviak 2009; Moore et al. 1988; Wyant et al. 2011). Shrub
524 expansion, which is currently occurring in some areas of the Arctic (Myers-Smith
525 et al. 2011), has been linked to changes in the composition of the surface-
526 dwelling arthropod community (Rich et al. 2013) and a homogenization of soil
527 food web structure (Sistla et al. 2013). The results of our analysis suggest that
528 such community-level changes may have cascading effects; further replication of
529 these methods across a variety of habitats would give us a better understanding
530 of how variation in invertebrate food web structure may influence nutrient cycling
531 and food web stability.

532

533 Consumption of live plant biomass by invertebrate herbivores is very small

534

535 Our model estimates that aboveground and belowground invertebrate
536 herbivores on the tundra only consume 0.0019% of standing plant biomass

537 annually. This is extremely low when compared to temperate and tropical
538 systems where herbivorous arthropods can consume 1-35% of annual primary
539 productivity (Coleman et al. 1976; Curry 1986; Detling 1988; Schmidt and Kucera
540 1973; Suzuki et al. 2013). Specifically, while total live plant biomass is
541 approximately 1500 g m^{-2} at our study site (Bret-Harte et al. 2013), our model
542 estimates show that invertebrate herbivores only consume roughly 0.028 g C m^{-2}
543 of this biomass per year (Online Resource 3). These estimates are even lower
544 than those from Devon Island in the High Arctic by Whitfield (1972), which
545 indicated that invertebrate herbivores take ~1% of primary production. Overall
546 our results suggest that consumptive effects of invertebrate herbivores are very
547 small on the tundra, although model results by Wolf et al. (2008) and Barrio et al.
548 (2017) suggest that these baseline levels may increase in the future with climate
549 change. Rare herbivore outbreaks can also result in huge reductions to plant
550 biomass (e.g., Lund et al. 2017; Pedersen and Post 2008). Such outbreaks are
551 not known to occur in the Alaskan Arctic, but they have been documented in
552 parts of Arctic Greenland (Lund et al. 2017; Pedersen and Post 2008) and are
553 relatively common in the boreal forest (Soja et al. 2007; Volney and Fleming
554 2000) and in some areas of the Subarctic (Jepsen et al. 2008; Kaukonen et al.
555 2013). As treeline shifts northward and temperatures rise, these invertebrate
556 herbivore outbreaks are expected to increase in intensity and frequency (Dale et
557 al. 2001; Soja et al. 2007; Volney and Fleming 2000), with potential
558 consequences for previously unaffected areas of the Arctic (Jepsen et al. 2011).
559

560 Surface-dwelling predators link the brown and green food webs

561

562 Our sampling showed that the majority of biomass at the soil surface
563 consists of generalist predators (95.7% surface invertebrate biomass; Fig. 2).
564 Consistent with our second hypothesis, model results indicated that these
565 predators likely serve as an important link between the green and brown food
566 webs (Fig. 3; Online Resource 3). The role of generalist predators in linking these
567 food webs has been widely acknowledged in temperate ecosystems (e.g., Scheu
568 2001) but has received less attention in the Arctic. Our estimates indicate that
569 among surface-dwelling predators, up to 27% of their energy resources may
570 come from the canopy web while up to 46% may originate from the soil food web.
571 Intraguild predation within and across habitats also appears to play an important
572 role in sustaining predator populations (30% of C flow to surface predators). The
573 generalist feeding behavior and high level of connectivity of surface-dwelling
574 predators in this community may provide another potential explanation for the
575 small amount of herbivore biomass. For example, soil-dwelling or intraguild prey
576 may subsidize larger predator populations that are especially effective at keeping
577 herbivore densities low (see Polis and Holt 1992; Schmitz 2008b). Our
578 understanding of the role of these predators would benefit from further
579 experimental and molecular work (e.g., Wirta et al. 2015a) that could confirm the
580 strength of these feeding interactions, what proportion of prey comes from each
581 sub-web, and how these interactions might vary seasonally and across habitats
582 in the Arctic.

583 Whereas surface predators are the most important interface between
584 green and brown energy pathways, flies with aquatic life cycles (midges,
585 hematophagous flies, and others) serve as a bridge between aquatic and
586 terrestrial systems in this food web (Dreyer et al. 2015). In particular,
587 hematophagous flies (i.e., biting flies, especially mosquitoes) dominated the
588 biomass of the canopy invertebrate assemblage and mobilized the largest fluxes
589 of C and N of any group in the canopy food web (Fig 3; Online Resource 3). Our
590 sampling methodology likely resulted in an overestimate of biting fly density
591 (abundance m^{-2}), the majority of which was comprised of mosquitoes (99.6%).
592 We stress that alongside other standardized methods of quantifying mosquito
593 abundance (see Hoekman et al. 2016), an unbiased estimate of mosquito density
594 would be a valuable tool for ecological accounting in the Arctic, particularly
595 because we know that Arctic mosquitoes respond positively to warming (Culler et
596 al. 2015). On the whole, however, our results are consistent with anecdotal
597 observations of mosquito populations in Arctic regions (Danks 1992) and with
598 previous studies documenting the primacy of flies in Arctic pollinator networks
599 (Tiusanen et al. 2016).

600

601 Food web structure of the tundra invertebrate community

602

603 Our approach of integrating the communities of soil-, surface- and plant
604 canopy-dwelling invertebrates enabled us to characterize this system from the
605 perspective of the aboveground and belowground habitats, as well as the green

606 and brown energy channels. Overall connectance for the invertebrate tundra food
607 web was 32%, which is comparable to those of other published webs given the
608 number of nodes ($S=33$) within our food web (Briand 1983). Seasonal dynamics
609 of different taxonomic groups vary throughout the Arctic summer, meaning that
610 the structure of this invertebrate food web can also be quite variable (e.g., Høye
611 and Forchhammer 2008). While our model simulations did incorporate aspects of
612 community-level variability, more frequent sampling of the entire invertebrate
613 community (e.g., soil, surface, and canopy-dwelling) throughout the active period
614 would provide us with a better understanding of the seasonal variation in the
615 structure and functional role of this food web.

616

617 Conclusions

618

619 Understanding the structure and function of the biological community is
620 the first step in being able to predict how it might respond to disturbance. This
621 study characterized the microbial-invertebrate food web in an Arctic tundra
622 ecosystem, including soil, surface, and canopy-dwelling organisms. Our findings
623 show that soil-dwelling organisms comprise the majority of biomass within this
624 community and process more energy and nutrients than surface- or canopy-
625 dwelling organisms. Our model results also indicate that invertebrate herbivores
626 and their consumers that derive their energy from live plant matter (i.e., biota
627 within the green food web) play a lesser role in processing nutrients and in
628 mineralizing C and N on the tundra in comparison to those organisms derived

629 from detrital resources. Consequently, changes to the structure and composition
630 of the brown food web are likely to have a much greater impact on Arctic
631 ecosystem functioning than any changes to the green food web. Given the
632 sensitivity of many soil- and surface-dwelling organisms to changes in
633 temperature and moisture, shifts in food web structure caused by climate change
634 could have previously unforeseen consequences for C storage and nutrient
635 cycling in the Arctic tundra. Future work will benefit from comparing the structure
636 and energy flow of this food web and its potential role in nutrient cycling across
637 the entire growing season, between different Arctic regions and habitats, and in
638 response to climate change and other forms of disturbance.

639

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651

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945 **Table 1** Functional feeding groups, biomass, and estimated rates of organic and
946 inorganic C and N cycling by organisms sampled from the soil, surface, and
947 canopy habitats in an area of moist acidic tundra in N. Alaska. Biomass is
948 presented as the mean \pm SE (in parentheses) mg C of the collected field samples.
949 Surface and canopy data were combined by functional group for each set of
950 paired plots (see sampling methods). Certain rare taxa that were typically
951 associated with one habitat type that happened to be caught in another were
952 disregarded. These included Acari, spiders from the family Thomisidae, and
953 Coleoptera from the families Staphylinidae and Latridiidae that were caught in
954 canopy samples, and Acari, Diptera, and spiders from the family Araneidae that
955 were caught at the soil surface. Biomass estimates of Acari are from the soil
956 sampling data only. Spiders from the family Linyphiidae use a variety of habitats,
957 so biomass estimates were combined from the canopy and surface samples.
958 Data on spider egg sacs were not included. Rates of C and N cycling for each
959 functional feeding group are the mean \pm SE of 1000 model simulations based on
960 the biomass estimates. These rates include those from nutrients recycled back to
961 the system from corpses of organisms that died non-predatory deaths and from
962 the unassimilated biomass of prey (egestion – leavings, orts and feces), as well
963 as rates of inorganic C and N mineralization. Biomass and rates of C and N
964 cycling are expressed in mg C or N m⁻² yr⁻¹.

965

Functional Feeding Group	Trophic Group	Abbreviation in Fig. 2	Biomass (mg C m ⁻²)	Non-predatory natural deaths		Unassimilated biomass of prey		Mineralized Nutrients	
				(mg C m ⁻² yr ⁻¹)	(mg N m ⁻² yr ⁻¹)	(mg C m ⁻² yr ⁻¹)	(mg N m ⁻² yr ⁻¹)	(mg CO ₂ -C m ⁻² yr ⁻¹)	(mg N m ⁻² yr ⁻¹)
Amoebae	Bactivore	Amoebae	1.004 (1.076)	5.798 (0.195)	0.828 (0.027)	0.794 (0.026)	0.198 (0.006)	9.061 (0.306)	2.912 (0.098)
Bacteria	Bacteria	Bacteria	878.340 (698.041)	1003.807 (25.510)	250.951 (6.377)	0.000 (0.000)	0.000 (0.000)	2640.428 (59.813)	94.301 (2.136)
Beetles (predaceous)	Predator	PredBeetles	0.734 (2.582)	0.228 (0.028)	0.041 (0.005)	0.594 (0.072)	0.096 (0.012)	0.356 (0.043)	0.052 (0.006)
Ciliates	Predator	Ciliates	0.239 (0.169)	1.418 (0.030)	0.202 (0.004)	0.187 (0.004)	0.046 (0.001)	2.134 (0.046)	0.684 (0.014)
Collembola									
Soil-dwelling	Fungivore	SoilColl	6.604 (6.035)	26.469 (0.775)	3.308 (0.096)	95.445 (2.491)	9.544 (0.249)	62.039 (1.619)	5.368 (0.140)
Surface-dwelling	Fungivore	SurfCollem	0.359 (0.251)	1.462 (0.031)	0.182 (0.003)	4.323 (0.094)	0.432 (0.009)	2.809 (0.061)	0.243 (0.005)
Enchytraeids	Microbivore	Enchy	1.735 (1.690)	8.397 (0.254)	1.679 (0.050)	63.743 (1.921)	6.377 (0.192)	12.748 (0.384)	0.426 (0.012)
Flagellates	Bactivore	Flagell	0.037 (0.032)	0.190 (0.005)	0.019 (0.000)	0.370 (0.012)	0.092 (0.003)	0.350 (0.011)	0.118 (0.003)
Flies									
Biting	Hematophage	BitingFlies	5.006 (0.833)	4.946 (0.026)	1.052 (0.005)	18.549 (0.100)	1.940 (0.010)	7.419 (0.040)	0.241 (0.001)
Crane Flies	Detritivore	CraneFlies	0.001 (0.004)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Herbivorous	Herbivore	HerbFlies	0.141 (0.106)	0.146 (0.003)	0.029 (0.000)	0.594 (0.015)	0.059 (0.001)	0.237 (0.006)	0.007 (0.000)
Non-biting Midges	Detritivore	NonbitMidges	0.048 (0.078)	0.068 (0.003)	0.013 (0.000)	0.274 (0.013)	0.028 (0.001)	0.109 (0.005)	0.004 (0.000)
Saprophagous	Detritivore	SapDiptera	0.225 (0.228)	0.343 (0.011)	0.070 (0.002)	1.367 (0.045)	0.136 (0.004)	0.546 (0.018)	0.016 (0.000)
Fungi	Fungi	Fungi	14244.236 (7889.573)	16907.239 (307.676)	1690.723 (30.767)	0.000 (0.000)	0.000 (0.000)	39457.050 (718.028)	3945.705 (71.802)
Lepidoptera	Herbivore	Lepid	0.070 (0.256)	0.014 (0.001)	0.002 (0.000)	0.072 (0.007)	0.007 (0.000)	0.029 (0.002)	0.002 (0.000)
Mites									
Cryptostigmatic	Fungivore	CrypMites	12.698 (16.296)	26.222 (1.031)	3.277 (0.128)	89.197 (3.228)	8.919 (0.322)	57.978 (2.098)	5.017 (0.181)
Nematophagous	Predator	NemMites	0.252 (0.361)	0.466 (0.021)	0.058 (0.002)	1.920 (0.099)	0.192 (0.009)	1.248 (0.064)	0.108 (0.005)
Non-cryptostigmatic	Fungivore	NonCrypMites	2.284 (1.885)	9.021 (0.234)	1.127 (0.029)	30.278 (0.790)	3.027 (0.079)	19.680 (0.513)	1.703 (0.044)
Predatory	Predator	PredMites	1.038 (1.271)	1.866 (0.069)	0.233 (0.008)	4.918 (0.180)	0.594 (0.021)	4.795 (0.176)	0.568 (0.020)
Nematodes									
Bacteriophagous	Bactivore	BacNem	0.160 (0.154)	0.817 (0.025)	0.081 (0.002)	2.447 (0.107)	0.611 (0.026)	2.312 (0.101)	0.781 (0.034)
Fungivorous	Fungivore	FungNem	0.049 (0.068)	0.187 (0.008)	0.018 (0.000)	1.438 (0.076)	0.143 (0.007)	0.555 (0.029)	0.055 (0.002)
Omnivorous	Omnivore	OmnNem	1.735 (1.690)	13.988 (0.431)	1.398 (0.043)	31.992 (0.930)	7.987 (0.232)	30.232 (0.879)	10.205 (0.296)
Phytophagous	Herbivore	PhytoNem	0.203 (0.308)	0.436 (0.020)	0.043 (0.002)	8.906 (0.673)	0.890 (0.067)	1.870 (0.141)	0.187 (0.014)
Predatory	Predator	PredNem	0.127 (0.283)	0.674 (0.048)	0.067 (0.004)	2.611 (0.188)	0.649 (0.046)	1.645 (0.118)	0.553 (0.039)
Rotifers	Bactivore	Rotifers	0.253 (0.348)	1.566 (0.070)	0.156 (0.007)	2.832 (0.127)	0.708 (0.031)	2.677 (0.120)	0.904 (0.040)
Spiders									
Canopy, web-building	Predator	CanWebSpid	0.104 (0.122)	0.110 (0.003)	0.027 (0.000)	0.210 (0.007)	0.043 (0.001)	0.205 (0.007)	0.037 (0.001)
Crab Spiders	Predator	CrabSpid	0.049 (0.174)	0.048 (0.006)	0.012 (0.001)	0.092 (0.011)	0.016 (0.002)	0.090 (0.010)	0.012 (0.001)
Other surface-active	Predator	SurfSpid	0.350 (0.692)	0.075 (0.004)	0.018 (0.001)	0.158 (0.010)	0.027 (0.001)	0.154 (0.010)	0.021 (0.001)
Surface, web-building	Predator	SurfWebSpid	0.093 (0.088)	0.094 (0.002)	0.023 (0.000)	0.203 (0.006)	0.028 (0.000)	0.198 (0.006)	0.016 (0.000)
Wolf Spiders	Predator	WolfSpid	2.163 (0.836)	1.080 (0.013)	0.270 (0.003)	2.304 (0.032)	0.393 (0.006)	2.247 (0.031)	0.287 (0.005)
Tardigrades	Predator	Tardig	0.203 (0.308)	1.530 (0.074)	0.153 (0.007)	3.668 (0.183)	0.913 (0.045)	3.466 (0.173)	1.166 (0.058)
True Bugs	Herbivore	TrueBugs	0.690 (0.381)	0.676 (0.011)	0.107 (0.001)	2.813 (0.049)	0.281 (0.004)	1.125 (0.019)	0.068 (0.001)
Wasps (parasitic)	Parasitoid	Parasitoids	0.190 (0.219)	0.205 (0.007)	0.048 (0.001)	0.812 (0.029)	0.162 (0.005)	0.325 (0.011)	0.056 (0.002)
		Total	15161.422	18019.600	1956.231	373.128	44.554	42326.13	4071.837
		Total Excluding Microbes	38.846	108.554s	14.556	373.128	44.554	228.655	31.831

966 **Figure captions**

967 **Fig. 1** Study site location on the North Slope of Alaska (68.952° N, 150.208°
968 W, elev. 414m), approximately 37 km NW of Toolik Field Station and the Arctic
969 Long-Term Ecological Research (LTER) site. The site is characterized as moist
970 acidic tundra, which is the dominant ecosystem type in this area of the
971 Arctic.

972

973 **Fig. 2** Biomass estimates of the different trophic groups by habitat (canopy, soil
974 surface, and soil) within the invertebrate food web in an area of moist acidic
975 tundra of N. Alaska. The y-axis shows the total dry biomass in mg C m⁻² of all
976 organisms within the invertebrate food web by the contribution from each habitat.
977 The x-axis indicates the proportion of biomass represented by each trophic group
978 within the different habitats. Fungal and bacterial biomass estimates are not
979 included here (see Table 1).

980

981 **Fig. 3** Visualization of the energetic food web model of the invertebrate
982 community in an area of moist acidic tundra in N. Alaska. Node sizes are
983 proportional to the log-transformed average biomass (mg C m⁻²) of that functional
984 feeding group (except for bacteria, fungi, and basal resources (i.e., roots,
985 aboveground plant tissue, pollen, mammal blood, diatoms, detritus), whose node
986 sizes were standardized due to their biomass estimates being too large to display
987 comparatively with the other groups). Edges represent the feeding relationships
988 between groups, and based on model results, edge widths are proportional to the

989 amount of C transfer ($\text{mg C m}^{-2} \text{yr}^{-1}$) between these groups (except from detritus
990 to bacteria and fungi, the quantities of which are much larger than shown here).
991 See Table 1 for actual biomass estimates of the different functional feeding
992 groups; model results of C flow rates between groups are contained in Online
993 Resource 3. Nodes are color-coded by trophic group, which match those in Fig. 2.
994 This figure was generated using the igraph package (Csardi and Nepusz 2006) in
995 R with the LGL algorithm.

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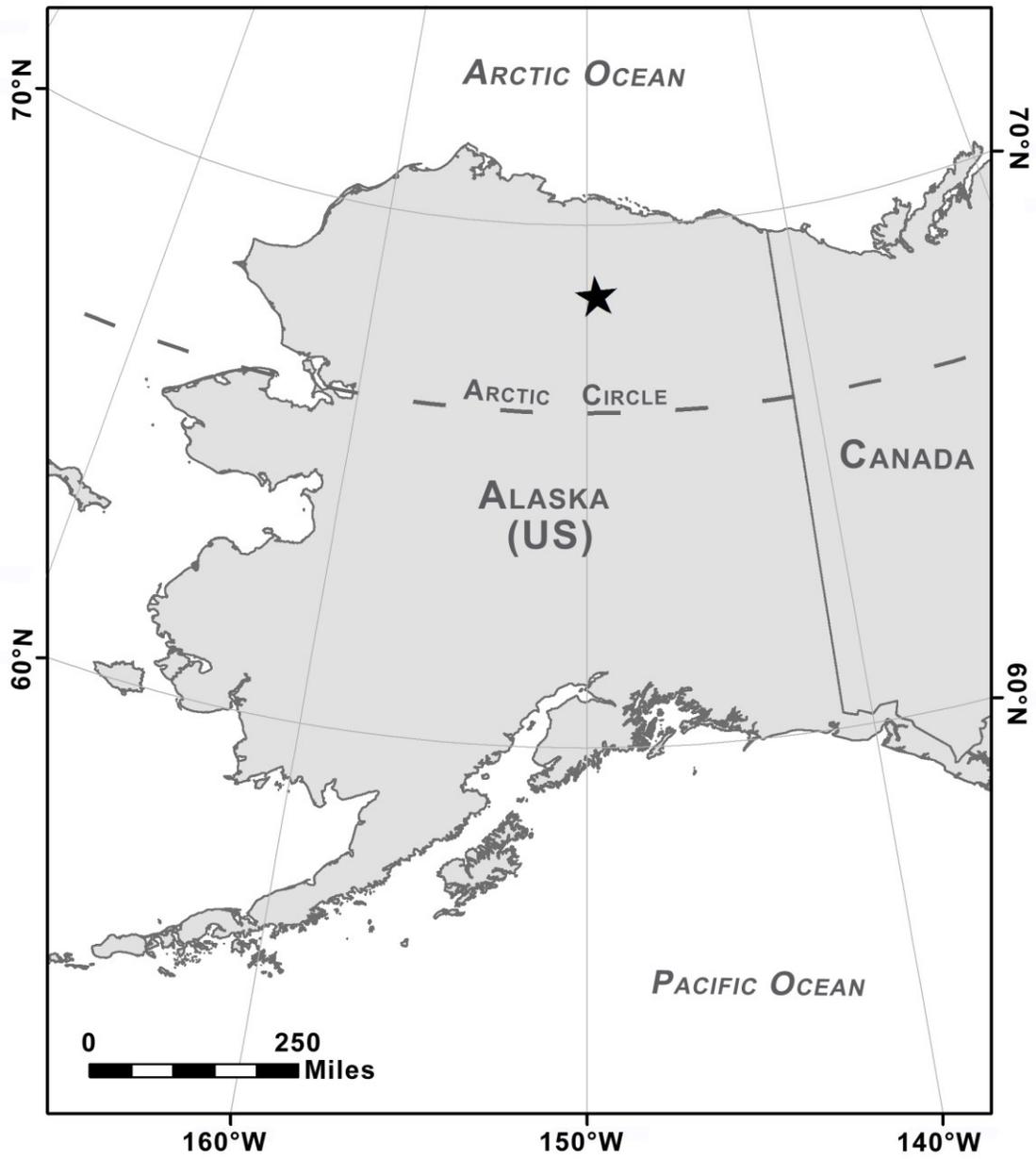
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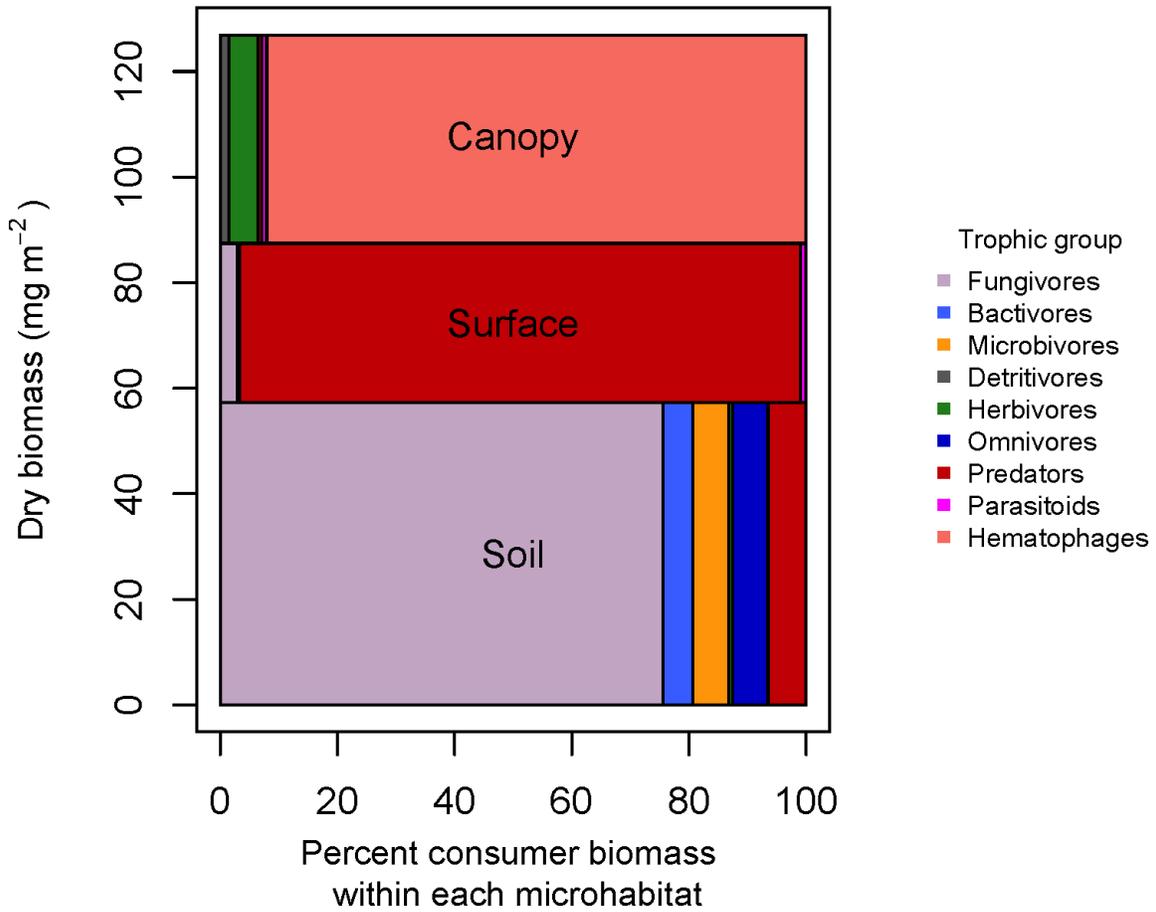
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Fig. 1



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Fig. 2

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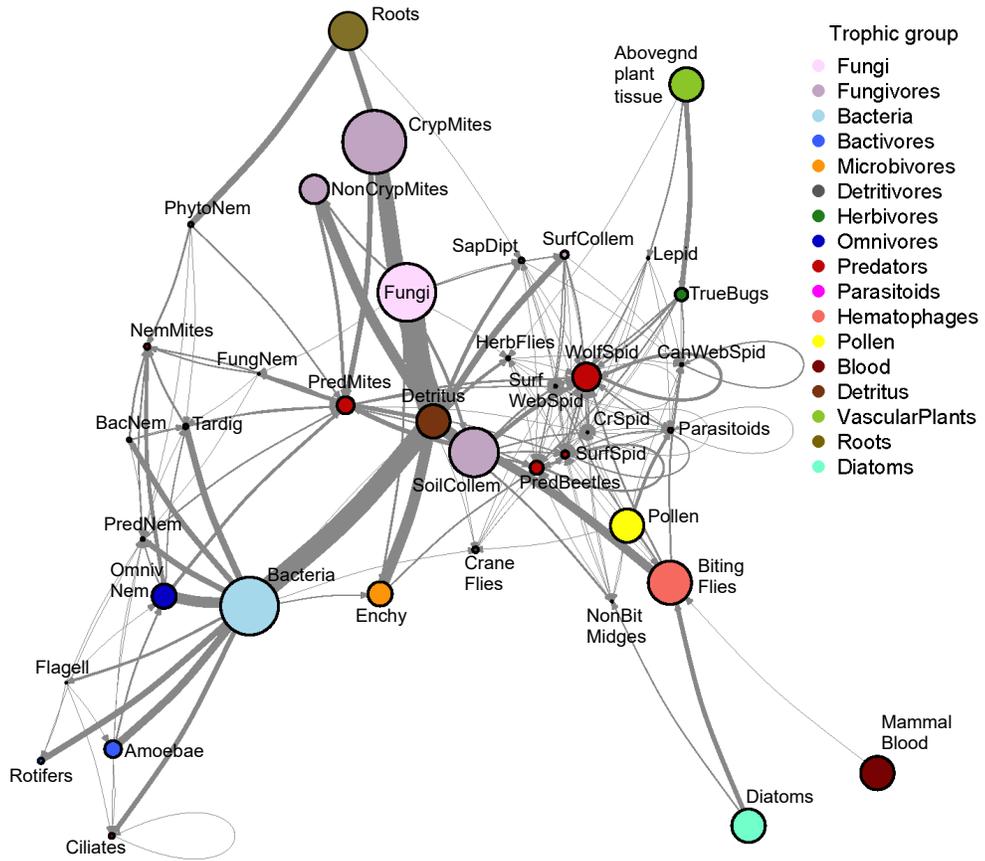
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1029 Fig. 3

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1040 **Captions for Online Resources**

1041 **Online Resource 1** (pdf)

1042 Taxon rarefaction curve for surface and canopy communities sampled in July
1043 2013 near Toolik Lake, Alaska. A total of 33 taxa were sampled; Estimates of
1044 extrapolated species richness suggest that the surface and canopy community
1045 actually contains 40 ± 7.1 taxa, indicating that we were able to capture roughly
1046 82.5% of the aboveground arthropod community with our sampling methods and
1047 at this level of taxonomic resolution.

1048

1049 **Online Resource 2** (pdf)

1050 Designations of functional feeding and trophic groups for all arthropod families
1051 sampled from canopy and surface habitats. Trophic groups were used in
1052 reporting the biomass and trophic structure of each habitat type (see main text;
1053 Fig. 2) and functional feeding groups were used in the energetics-based food
1054 web model (Fig. 3; Online Resource 3).

1055

1056 **Online Resource 3** (excel file)

1057 Parameters used to initialize the energetics-based food web model and the
1058 simulated C flow rates between all consumer functional feeding groups within the
1059 invertebrate tundra food web. Included are estimates of the C:N ratio, death rate
1060 (DR), assimilation efficiency (AE), production efficiency (PE), and biomass (mean
1061 and standard deviation) for each functional feeding group. We assumed that
1062 detritus, diatoms, lichen, moss, live plant biomass (roots, vascular plants, pollen),

1063 and blood were not limiting resources and thus assigned theoretical values of
1064 2,500,000 g C m⁻² to detritus, 300,000 mg C m⁻² to diatoms, and 300 mg C m⁻² to
1065 all others. Estimates of C flow rates (mg C m⁻² yr⁻¹) are from the complete
1066 (sampled) food web with assigned feeding preferences (see methods in main
1067 text). Zeroes denote no consumptive relationship between groups. Cross-habitat
1068 feeding relationships (e.g., between soil- and surface-dwelling organisms or
1069 surface- and canopy-dwelling organisms) are indicated by boldface type.

1070

1071 **Online Resource 4** (excel file)

1072 Summarized model results from the complete, sampled food web and all food
1073 web manipulations. Food web manipulations included not specifying feeding
1074 preferences and removing each sampled functional feeding group from the
1075 network, one at a time, while holding the rest of the food web constant. The
1076 results shown here are the mean and standard errors from 1000 model runs for
1077 each food web configuration. Estimates for total C flow and all rates of organic
1078 and inorganic C and N cycling are for the entire food web and expressed in mg C
1079 or N m⁻² yr⁻¹. *S-min* is a measure of stability, estimated by determining the value
1080 of 's' needed to ensure that the real parts of all the eigenvalues of the matrix are
1081 negative (e.g., de Ruiter et al. 1995; Moore and deRuiter 2012; Moore and
1082 William Hunt 1988; Rooney et al. 2006). An *s-min* value of one indicates that the
1083 diagonal strength ensuring stability of the food web is dependent solely on the
1084 specific death rates of the functional groups. Hence low *s-min* values (*s-min* ≤ 1)
1085 indicate more stable food webs relative to those with high *s-min* (*s-min* ≥ 1).

1086 **Online Resource 5** (pdf)
1087 Differences in the role of the invertebrate community in C consumption and
1088 cycling rates of organic and inorganic C and N between the complete, sampled
1089 food web vs. those without feeding preferences or with individual functional
1090 feeding groups excluded (see methods in main text).