HIGHLIGHTED STUDENT RESEARCH

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Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem

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Abstract

Ecosystem engineers create physical changes in abiotic and biotic material, and through this process control the availability of resources for other species. Predators that abandon large portions of their prey may be ecosystem engineers that create habitat for carrion-dependent invertebrates that utilize carcasses during critical life-history periods. Between 04-May-2016 and 04-Oct-2016, we sampled beetle assemblages at 18 carcasses of prey killed by pumas and matching control sites in the southern Greater Yellowstone Ecosystem, USA, to measure the extent to which beetle families utilized these carcass "habitats". We used generalized linear-mixed models and linear-mixed effect models to examine changes in beetle abundance, species richness, and Simpson's Index of Diversity. We estimated kill rates and carrion production rates for individual pumas to better assess the impact of pumas on invertebrate communities. We collected 24,209 beetles representing 215 species. We identified eight beetle families that had significantly higher abundance at carcasses than control sites. Carcasses had a statistically large to very large effect (determined using Cohen's d) on beetle abundance, richness, and diversity for the initial 8 weeks of sampling. Our research revealed strong effects of an ecosystem engineer on beetle assemblages while highlighting the potential role of apex predators in creating and modifying physical habitats for carrion-dependent species. This suggests that there may be consequences for invertebrate communities where apex predators exist at reduced numbers or have been eradicated. The ecological role of invertebrates is often overlooked, yet they are essential taxa that provide critical ecological services upon which we depend.

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Introduction

Ecosystem engineering is the ecological process by which an organism creates, modifies, or maintains habitat (Jones et al. 1994, 1997), and subsequently increases habitat heterogeneity and species richness (Jones et al. 1997; Wright et al. 2002). Arguably, all species engineer their ecosystems to some extent, and thus research has highlighted those engineers that have significant effects on their ecological systems (Wright and Jones 2006). For example, North American beavers (*Castor canadensis*) (Wright et al. 2002), Arctic foxes (*Vulpes lagopus*) (Gharajehdaghipour et al. 2016), African bush elephants (*Loxodonta africana*) (Pringle 2008), and termites (Infraorder Isoptera) (Jouquet et al. 2011) are among the species that have been identified as significant ecosystem engineers because of their effects on habitat. Many of these animals are also considered keystone species, defined as species that disproportionately affect their communities

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given their biomass (Power et al. 1996; Soulé et al. 2005). Wright and Jones (2006), however, underscore the distinction between an ecosystem engineer and a keystone species; the former emphasizes ecological process, while the latter emphasizes the outcomes of processes and behaviors. Generally, predators are not often considered ecosystem engineers, but many are classified as keystone species because of the strong and wide-spread impact their predation behavior can have on community structure (e.g., trophic cascades; Winnie and Creel 2017) (Paine 1966; McLaren and Peterson 1994). Some predators, however, may be ecosystem engineers as well. In addition to directly and indirectly impacting prey species (e.g., through mortality and behavioral-mediated changes), predation may create habitat for invertebrate scavengers and decomposers that require carrion for critical life-history stages.

Carrion is the decaying flesh of dead animals and an ecological resource exploited by a diverse array of scavengers and decomposers that contributes to ecosystem structure, habitat heterogeneity, and biodiversity (DeVault et al. 2003; Wilson and Wolkovich 2011; Moleón et al. 2014; Moleón and Sánchez-Zapata 2015). Vertebrate scavengers facilitate energy transfer between trophic levels, increase linkages in food webs, and are essential vectors in spreading nutrients and other benefits of carrion across diverse terrestrial and aquatic ecosystems (DeVault et al. 2003; Wilson and Wolkovich 2011; Moleón and Sánchez-Zapata 2015). For numerous beetle species, however, carrion resources are not just food, but also key habitat where they complete crucial life-history events. For example, hide beetles (Family Dermestidae) and burying beetles (Family Silphidae) utilize carcasses as breeding and brooding habitat (Trumbo 1992; Hoermann et al. 2011). Carrion beetles (Family Silphidae) commune, seek mates, and reproduce on carcasses (Anderson and Peck 1985). Furthermore, the larvae of carrion beetles utilize carcasses as both sustenance and refuge until they have achieved their adult form.

Predators, such as gray wolves (*Canis lupus*) and pumas (*Puma concolor*), hunt prey larger than themselves and often abandon portions of their prey, which then become a substantial resource for diverse species (Wilmers et al. 2003; Selva et al. 2005; Elbroch et al. 2017b). Carrion provided by predators may function as important habitat for beetle scavengers and be more valuable than carrion provided by other processes such as disease, starvation, and old age. For example, predators provide carrion to their ecological communities throughout the entire year and across varied habitats, whereas carrion provided by other processes typically occurs in pulses during seasonal migrations as road kill, offal abandoned by human hunters

in fall and early winter, or in late winter when some animals succumb to starvation (Wilmers et al. 2003; Selva and Fortuna 2007). Pulsed carrion produced in late fall through winter are likely less valuable to invertebrate scavengers because mammalian scavengers consume most winter carrion before beetles emerge on the landscape (Elbroch et al. 2017b; O'Malley et al. 2017). Carrion-dependent beetles, in particular, require fresh carcasses when they begin to flourish on the landscape between spring and summer, which is a period when natural deaths (e.g., disease, starvation, old age) are low. Therefore, predators are likely crucial for creating "habitat" for many beetle species, and pumas, which disproportionately provision ecological communities with large carcasses where they are present (Elbroch and Wittmer 2012; Elbroch et al. 2017b), may be top among them.

In this study, we sampled beetle assemblages at carcasses of prey killed by pumas and matching control sites in the southern Greater Yellowstone Ecosystem, USA, to document the array of beetle species that utilized these resources. We hypothesized that beetle abundance and species richness would be higher at carcasses than control sites. We also hypothesized that beetle diversity at carcasses would increase over the lifetime of carcasses, as early-colonizing, dominant species decreased (e.g., northern carrion beetles, *Thanatophilus lapponicus*; Ratcliffe 1996) and late-arriving species began to utilize carcasses. We predicted that carcasses would have a large effect on beetle biodiversity metrics, providing evidence that pumas are ecosystem engineers creating critical habitat for beetles, and perhaps other invertebrate scavengers and decomposers as well.

Methods

Study area

Our study spanned 2000 km^2 of the southern Greater Yellowstone Ecosystem, north of Jackson, *Wyoming* (43.51330, −110.34419). Elevations in the study area ranged from 1800 m to > 3600 m. The area was characterized by short, cool summers and long winters. Plant communities at lower elevations included sagebrush (*Artemisia* spp.) and cottonwood (*Populus angustifolia*). The primary tree species at higher elevations were Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Our study area included a diverse community of large mammals. Carnivores in the study area included wolves (*Canis lupus*), black

bears (*Ursus americanus*), grizzly bears (*U. arctos*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). Ungulates included elk (*Cervus elaphus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and white-tailed deer (*Odocoileus virginianus*).

Puma capture and locating kills

This research was conducted as part of a larger, long-term study on pumas described elsewhere (Elbroch et al. 2017a, b). We captured pumas during winter months in the Bridger-Teton National Forest. We used trailing hounds to tree pumas, and then safely and humanely fit them with a GPS collar (Lotek Globalstar S or Iridium M, Newmarket, Ontario; Vectronics Globalstar GPS Plus, Berlin, Germany). Our capture protocols adhered to the guidelines outlined by the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by two independent Institutional Animal Care and Use Committees (IACUC): the Jackson IACUC (Protocol 027-10EGDBS-060210) and National Park Service IACUC (IMR_GRTE_Elbroch_Cougar_2013-2015). We programed all of our GPS collars to acquire simultaneous location data every 2 h.

Beetle collection and abundances at carcasses and controls

We uploaded GPS data from collared pumas to Globalstar and Iridium satellites 1–6 times daily. We used ArcGIS 10.0 (ESRI, Redlands, CA) to display location data and to identify GPS clusters, which we defined as location with ≥ 2 GPS points within 150 m of each other, and where a puma spent ≥ 4 h (Elbroch et al. 2017b). We transferred puma location data to handheld GPS units, which we then used to guide us in the field to locate GPS clusters. If we located prey remains, we studied the area for signs of struggle, blood patterns, bite marks on the carcass itself, and the body parts consumed to determine whether the puma had killed the animal or was scavenging.

For this research, we conducted field investigations of kill sites as soon as possible after the puma had departed the area, as determined from GPS data, so as not to disturb the animal while it fed. If the prey was an ungulate with edible remains apparent, we initiated weekly beetle sampling. We set up three barrier pitfall traps around each carcass and replicated the set up at control sites established 20 m away within the same habitat type, and with similar vegetation (Hansen and New 2005). Our individual traps consisted of two, 32-ounce plastic cups filled with odorless soapy water

that served as a killing and short-term preserving agent. We fixed a cup flush with the ground to both ends of each smooth, three-foot metal barrier. We positioned traps to surround carcasses, while also maintaining corridors through which some immigrating beetles could avoid traps and access carcasses.

We returned to each site once per week to collect adult beetle specimens, refill trap stations with soapy water, and fix damages caused by mammalian scavengers. We separated the specimens from unwanted material and rinsed them with clean water before we transferred them into dram vials with 90% isopropyl alcohol. We sent specimens to the Marsh Laboratory at Montana State University for species identification, and then counted them to determine relative abundance. We used a Pearson's Chi-squared test with a Bonferroni correction to test which beetle families had significantly more individuals at carcasses than control sites, limiting our tests to beetle families that had estimated counts greater than five. We also calculated effect size (Cohen's *d*) for summed abundance, richness, and diversity to better understand the strengths of the effects of carrion on beetle biodiversity metrics, if any, and ultimately determine whether pumas should be considered ecosystem engineers.

Quantifying and comparing beetle abundance, species richness, and diversity

We assigned each collection of beetles to 7-day time periods. We used generalized linear-mixed models with negative binomial distributions and a log link function to test for significant differences in beetle abundance and species richness between carcasses and their controls using the R package *MASS* (Venables and Ripley 2002). For our models, the fixed effects were group (i.e., carcasses and controls), time, group*time interaction, caching (a binomial variable representing whether the puma covered the carcass in debris or not), and prey species. We also included individual carcasses and controls as random effects. Then we used linear-mixed effect models to test for differences in Simpson's Index of Diversity using the R package *lmerTEST* (Kuznetsova et al. 2017). We calculated diversity using the Simpson's Index of Diversity (1-D) (Simpson 1949), which creates a metric ranging from 0 to 1, in which the larger the number the greater the diversity of the sample. We conducted a logit transformation on our diversity measurements using the 'logit' function in the R package *gtools* (Warnes et al. 2018). We calculated marginal means and Cohen's *d* for two different time periods: (1) our full collection period of 19 weeks, and (2) an 8-week time period, which was the point when biodiversity at carcasses stopped increasing and exhibited an

asymptote, as determined with a piecewise regression analysis in the R package *segmented* (Vito and Muggeo 2003).

Quantifying puma resource provisioning

We replicated the methods of Elbroch and Wittmer (2012) to estimate age-specific prey weights and the amount of prey-resource abandoned per kill, allowing us to compare our provisioning data with their puma research in Patagonia. We used CyberTracker-certified researchers (Elbroch et al. 2011) to conduct site investigations as well as to determine the approximate age of prey. We assumed that 68% of an ungulate's weight (Wilmers et al. 2003) and 95% of a small vertebrate's weight (Ackerman et al. 1986) was edible material for pumas. We used the timestamps associated with the location data collected from the GPS collars to determine how many hours an individual puma spent at a carcass site. Lacking actual consumption rates, we used hourly consumption rates for captive pumas to estimate how much meat individual pumas consumed (Danvir and Lindzey 1981). Once we estimated the prey weight and amount of resource consumed by individual pumas, we calculated how much edible resource was provisioned by each puma at each kill site ($n = 190$) during our field season.

We calculated kill rates (prey animals/week) for individual pumas monitored continuously (i.e., every cluster was investigated in the field) for ≥ 4 weeks during the time period of this study (Elbroch et al. 2014). For pumas in which there was a gap in monitoring due to poor collar performance, and thus two or more sampling periods of continuous monitoring greater than 4 weeks in length, we calculated kill rates for each period separately, and reported their average. Then we used these kill rates and the mean amount of meat abandoned by individual pumas, determined as described above, to estimated weekly carrion production by individual pumas in our study.

Results

Puma carrion production and beetles

From 31-Mar-2016 to 03-Sept-2016, we investigated 501 GPS clusters for six pumas in the field, and found 190 kill sites, 261 bed sites, 21 carcasses scavenged rather than killed by pumas, and 29 sites with no evidence of specific behaviors. We sampled beetle communities at 18 fresh carcasses preyed on by pumas (Table 1), and initiated

Table 1 Eighteen carcasses sampled for beetle assemblages

Carcass number	Species	Sex	Age (subjective)	Estimated kill date	Estimated prey mass (kg)	Puma ID	Carcass utilized (%)	Estimated meat consumed (kg)	Edible resource abandoned (kg)
1	Elk*	F	Adult	31-Mar	236	F109	76–100	19.1	141.4
2	Elk*	U	Calf	03-Apr	148	F61	76–100	15.0	85.6
3	Elk*	F	Yearling	23-Apr	193	F109	76–100	6.8	124.4
4	Elk*	U	Calf	27-Apr	158	F109	76–100	10.9	96.5
5	Deer*	F	Adult	27-Apr	82	F61	51–75	27.3	28.5
6	Elk	F	Yearling	09-May	196	M85	26–50	31.4	101.9
7	Elk*	U	Calf	09-May	158	F109	76–100	10.9	96.5
8	Elk*	F	Yearling	10-May	196	F109	76–100	15.0	118.3
9	Elk*	U	Calf	10-May	158	F109	76–10	10.9	96.5
10	Deer*	F	Adult	02-Jun	82	F49	26–50	23.2	32.6
11	Elk*	F	Adult	07-Jun	236	F61	51–75	15.0	145.5
12	Deer*	U	Yearling	08-Jun	64	F72	76–100	19.1	24.4
13	Elk*	M	Yearling	19-Jun	178	F61	51–75	19.1	101.9
14	Deer	U	Yearling	04-Jul	65	F109	76–100	19.1	25.1
15	Sheep	F	Adult	16-Aug	60	F109	76–100	47.8	9.2
16	Deer	F	Adult	28-Aug	82	F61	76–100	19.1	36.7
17	Elk	F	Yearling	01-Sep	169	F49	26–50	23.2	91.7
18	Deer	M	Adult	03-Sep	90	F72	76–100	10.9	50.3

Carcass utilized (%) is the amount of carcass consumed by the individual puma and other vertebrate scavengers when beetle sampling began

*Carcasses used for mixed effect models

Table 2 Puma kills, and the amount of edible resources abandoned

Puma ID	n	Mean prey mass (kg/SE)	Mean meat consumed (kg/SE)	Mean edible resource abandoned (kg/SE)	Kill rate (animals/wk)	Carrion production (kg/wk)
F47	32	52 (11)	13.2 (2.0)	22.4 (6.2)	1.3	29.1
F49	34	33 (6)	10.5 (1.1)	13.0 (3.3)	1.9	24.7
F61	27	62 (12)	15.1 (1.6)	27.9 (7.3)	1.2	33.5
F72	36	47 (10)	11.3 (1.6)	21.8 (5.9)	1.8	39.2
M85	31	72 (15)	9.9 (1.4)	39.5 (9.2)	1.1	43.5
F109	30	81 (16)	11.0 (1.6)	44.2 (10.2)	1.3	57.5

Here we report the number of kills documented by individual pumas (*n*), mean (± standard error) estimated prey mass, mean meat consumed per kill, and the mean amount of edible resource abandoned per kill. We also report each puma's kill rate in animals/week and the amount of carrion they produced per week, estimated simply by multiplying the kill rate by the mean meat they abandoned per kill

sampling of beetle scavengers on average 15 ± 11 |SD| days after an ungulate was killed. The carcasses were sampled weekly for an average duration of 12 ± 6 weeks. Pumas cached (i.e. covered the carcass in debris) 11 of 18 carcasses sampled for beetles. Individual pumas on average killed 1.4 ± 0.3 animals and produced 37.9 ± 11.7 kg of carrion each week over the course of this study (Table 2).

We collected 24,209 beetles, comprising 215 species and 33 families. Of our collection, 83.07% ($n = 20,111$) of our total specimens were found at carcasses. The northern carrion beetle was the most abundant species, comprising 60.6% of our total specimens; 98.27% ($n = 14,674$) were found at carcasses in comparison to control sites ($n = 254$). Our Chi-squared analysis identified eight beetle families that had significantly more individuals at carcasses in comparison to control sites (Table 3).

Linear-mixed effect analyses

We excluded six fresh carcasses from analyses: five sites were sampled late in the season when cold temperatures drastically reduced beetle presence at carcasses, and the sixth was usurped by coyotes after the second collection. We found that carcasses had a large to very large effect (Cohen's *d*) (Sawilowsky 2009) on abundance, species richness, and diversity of beetle assemblages during the first eight sampling weeks, and a medium effect over the full 19 weeks of sampling (Table 4). Beetle abundance and species richness were significantly higher at carcasses in comparison to control sites (Table 4, Fig. 1).

Our models revealed that "Group" and "Time" had a significant effect on beetle abundance, species richness, and diversity (Table 5). Beetle abundance and species richness did not differ between kills cached by pumas and those not cached (Table 5). Species richness did not differ between

carcass species (elk and mule deer), but beetle abundance decreased significantly faster at deer carcasses than elk carcasses (Table 5).

Discussion

Our research revealed the large to very large effect (Cohen's *d*) of puma predation on the composition of beetle assemblages in the southern GYE, and thus provided strong evidence that pumas function as ecosystem engineers that have a significant effect on species richness and habitat heterogeneity (Wright et al. 2002; Pringle 2008; Jouquet et al. 2011; Gharajehdaghipour et al. 2016). These effects were most pronounced during the first 8 weeks of sampling, emphasizing that carrion is an important but ephemeral ecological resource in space and time (Barton et al. 2013). These effects were also more pronounced at larger carcasses of elk than deer, emphasizing the ecological importance of large carrion over small (Moleón and Sánchez-Zapata 2015). Similar to pumas in other geographic regions (Elbroch et al. 2014), individual pumas in our study killed 1.4 animals and produced 37.9 kg of carrion per week, providing a continuous supply of new carrion for vertebrate and invertebrate scavengers across the landscape and during critical life-history stages for beetles and other species that occur during the spring and summer.

We identified eight beetle families, comprising 113 species, which were disproportionately detected at carcasses as compared to control sites. Many of these families are known to utilize carcasses during their critical life-history stages, including courtship, mating, egg-laying, refugia, and for food for developing young (e.g., Family Dermestidae, Anderson and VanLaerhoven 1996; Family Carabidae, Lövei and Sunderland 1996; Family Cleridae, Majka 2006; Family

Table 3 A summary of the beetle families and number of individuals trapped with Pearson's Chi-squared tests

Family	# of species	# of individual beetles		χ^2	P value
		Carcass	Control		
Silphidae	6	14,861	1114	11,830	<0.001*
Carabidae	35	1480	1308	10.6	<0.001*
Curculionidae	22	680	404	70.3	<0.001*
Tenebrionidae	5	537	525	0.14	0.71
Staphylinidae	15	855	57	698	<0.001*
Histeridae	7	573	78	376	<0.001*
Scarabaeidae	20	352	176	58.7	<0.001*
Elateridae	27	191	229	3.44	0.06
Dermestidae	5	298	22	238	<0.001*
Cleridae	3	71	0	71.0	<0.001*
Chrysomelidae	10	27	29	0.071	0.79
Byrrhidae	6	35	16	7.08	0.01
Lucanidae	1	27	16	2.81	0.09
Cicindelinae	3	16	23	1.26	0.26
Geotrupidae	1	14	20	1.06	0.30
Cerambycidae	10	23	11	4.24	0.04
Trachypachidae	1	27	21	0.75	0.39
Scolytinae	4	5	15	5.00	0.03
Cryptophagidae	4	8	10	0.22	0.64
Nitidulidae	5	6	3		
Hydrophilidae	2	6	1		
Cantharidae	2	4	3		
Coccinellidae	4	4	2		
Leiodidae	3	0	4		
Scydmaenidae	1	1	3		
Trogidae	1	4	0		
Buprestidae	3	2	2		
Melyridae	3	1	2		
Meloidae	2	0	2		
Anthicidae	1	0	2		
Micropeplidae	1	1	0		
Mordellidae	1	1	0		
Oedemeridae	1	1	0		

Eight beetle families were trapped significantly more at carcasses than control sites

*Bonferroni adjustment with significance at P value <0.0026

Scarabaeidae, Midgley et al. 2012; Family Staphylinidae, Wang et al. 2017). We also detected significantly more beetles of the Family Curculionidae at carcasses, which was unexpected because they are primarily plant feeders.

Table 4 Effect size (Cohen's *d*) and mean (SD) beetle abundance, species richness, and Simpson's Index of Diversity at 12 carcasses and control sites for time periods 1–8 and time periods 1–19

	Mean (SD)		
	Carcass	Control	Effect size
Time periods 1–8			
Abundance	211 (304)	25 (20)	1.12 (0.67)
Richness	11.6 (4.9)	8.4 (4.1)	1.02 (1.12)
Diversity	0.55 (0.25)	0.80 (0.12)	− 1.43 (0.71)
Time periods 1–19			
Abundance	99 (216)	21 (23)	0.59 (0.26)
Richness	8.7 (4.8)	6.9 (3.8)	0.49 (0.62)
Diversity	0.68 (0.23)	0.78 (0.14)	− 0.74 (0.22)

Nevertheless, they might have colonized ungulate carcasses because the stomachs of ungulate prey were full of partially digested vegetation. Furthermore, we detected several beetle families known to utilize carrion, but were too rare to be statistically significant at carcasses. For example, we collected four individuals of the small Family Trogidae, all of which are known to utilize carcasses a few months after death (Vaurie 1955). Similarly, we collected three species from the genus *Omosita* (Family: Nitidulidae), which are often found in the later stages of carrion decomposition (DiZinno et al. 2002).

Generally, arthropod assemblages rapidly occupy carcasses, attain maximum abundance and richness quickly, and then decline (i.e., they exhibit a unimodal distribution; Schoenly and Reid 1987). We observed that beetle assemblages at carcasses typically peaked in abundance and richness during our first collection week, which was on average 15 ± 11 |SD| days after the prey was killed. The initial peak in beetle abundance and richness may be due to several factors. First, we commenced sampling only after the puma abandoned the site. Therefore, we likely started sampling during the active decay stage and missed the period of initial mass beetle immigration to the carcass. Additionally, if the first stage (i.e., the fresh stage) does not emit a significant number of volatile compounds that signal the location of the carcass (Kalinová et al. 2009), or those compounds are hindered by caching or other puma behaviors, species richness may have increased slowly during this stage. Further, vertebrate scavengers typically dominated large carcasses in the first week following predation (Elbroch et al. 2017a, b), and their competitive dominance may have impeded access

Fig. 1 Changes (mean ± 95% CI) in beetle (**a**) abundance (**b**) species richness (**c**) and Simpson's Index of Diversity for 12 fresh carcasses (filled circles) and controls (open circle)
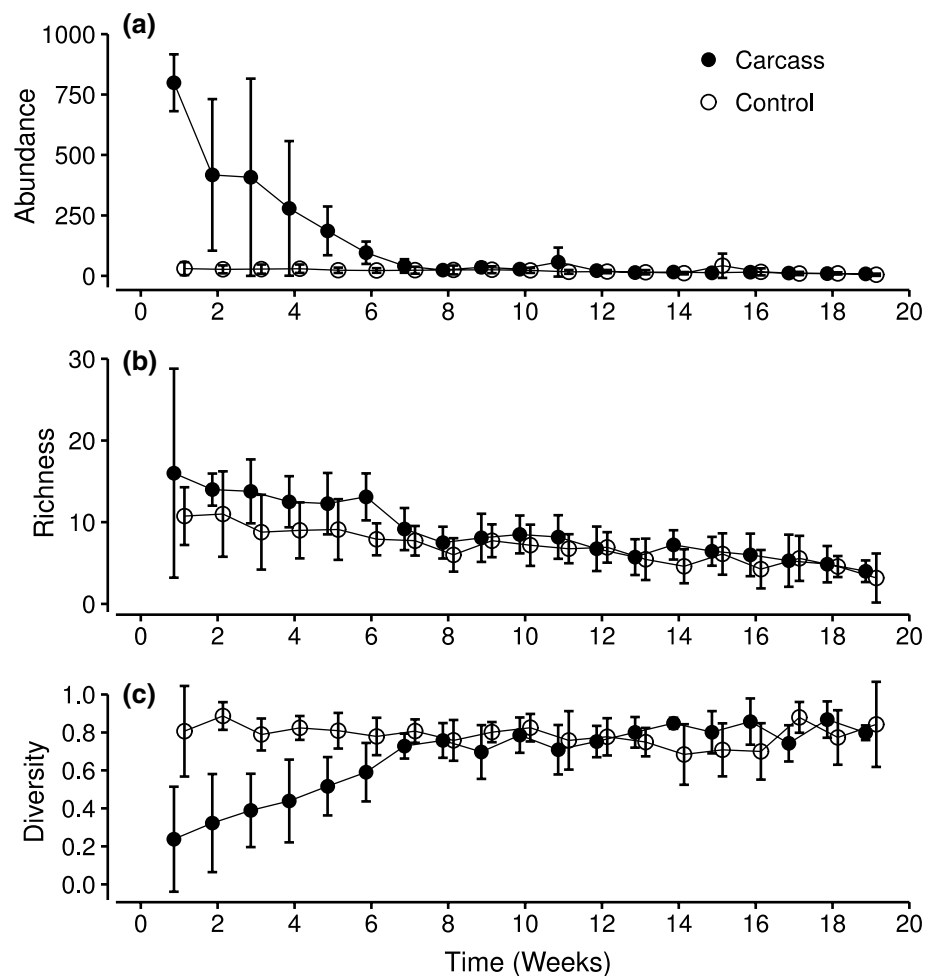
to carrion for beetles, diminishing the typical unimodal pattern of beetle abundance and richness during the first week of decomposition (Pechal et al. 2014).

The northern carrion beetle's quick arrival in large numbers, competitive dominance, and short residency at carcasses impacted numerous biodiversity metrics, including high peaks in beetle abundance and low peaks in diversity in early collections. The large abundance of northern carrion beetles in overall sampling created such an unevenness that beetle diversity skewed as a consequence (evenness assesses inequity in the distribution of species richness; Wilsey and Potvin 2000). Thus, the Simpson's Index of Diversity was typically higher at control sites even though beetle abundance and species richness was higher at carcasses. Adult northern carrion beetles exhibit exceptional sensory abilities that allow them to detect and colonize carcasses early in the fresh stage. They then monopolize space on carcasses, their large bodies providing them greater food reserves and physical dominance over competitors (Ratcliffe 1996; Hocking

and O'Regan 2015). Adult northern carrion beetles are also known to dominate fresh meat in cold-adapted environments (Anderson and Peck 1985; Ratcliffe 1996).

Our findings demonstrate the large effect that an apex carnivore had on beetle assemblages in the southern GYE. Coleopteran species at carrion have been well documented globally (Anderson and Peck 1985; Anderson and VanLaerhoven 1996), but research pertaining to the importance of predator-produced carrion has primarily focused on vertebrate scavengers (e.g., Selva et al. 2005; Allen et al. 2015; Inger et al. 2016; Elbroch et al. 2017b). Invertebrates are an often-overlooked yet essential taxa that provide numerous critical ecological services upon which we depend (e.g., Prather et al. 2012; Barton and Evans 2017). If ecologists can determine how predators create and modify physical and chemical resources essential to the persistence and diversity of the various invertebrate scavengers and decomposers, we may be able to predict their engineering effects on invertebrate distributions at larger scales (Wright and Jones 2004),

Table 5 Estimates of fixed effects for 12 carcasses and controls from time periods 1–19

	Fixed effects	Estimate (SE)	Z value		P value
Abundance	Carcass	6.26 (0.16)	40.12		< 0.01
	Control	− 2.75 (0.22)	− 12.45		< 0.01
	Carcass ~ time	− 0.24 (0.01)	− 16.99		< 0.01
	Control ~ time	0.20 (0.02)	9.70		< 0.01
	Not cached	6.43 (0.22)	29.08		< 0.01
	Cached	− 0.41 (0.33)	− 1.25		0.21
	Not cached ~ time	− 0.25 (0.02)	− 12.12		< 0.01
	Cached ~ time	0.012 (0.03)	0.39		0.70
	Deer	6.47 (0.31)	20.87		< 0.01
	Elk	− 0.15 (0.36)	− 0.41		0.69
	Deer ~ time	− 0.34 (0.04)	− 9.68		< 0.01
	Elk ~ time	0.10 (0.04)	2.65		< 0.01
Richness	Carcass	2.80 (0.07)	37.68		< 0.01
	Control	− 0.39 (0.11)	− 3.58		< 0.01
	Carcass ~ time	− 0.07 (0.01)	− 9.52		< 0.01
	Control ~ time	0.018 (0.01)	1.72		0.09
	Not cached	2.89 (0.09)	32.20		< 0.01
	Cached	− 0.20 (0.14)	− 1.46		0.14
	Not cached ~ time	− 0.07 (0.009)	− 7.42		< 0.01
	Cached ~ time	− 0.005 (0.01)	− 0.38		0.70
	Deer	2.78 (0.14)	20.5		< 0.01
	Elk	0.10 (0.16)	0.67		0.50
	Deer ~ time	− 0.10 (0.02)	− 5.91		< 0.01
	Elk ~ time	0.03 (0.02)	1.64		0.10
	Fixed effects	Estimate (SE)	t value	df	P value
Diversity	Carcass	− 0.80 (0.36)	− 2.19	114	0.03
	Control	2.38 (0.51)	4.62	115	< 0.01
	Carcass ~ time	0.20 (0.03)	6.67	330	< 0.01
	Control ~ time	− 0.18 (0.04)	− 4.15	330	< 0.01

Carcass, Not Cached, and Deer are treated as baseline intercepts and baseline slopes. Estimates for abundance and richness are log transformed, and diversity estimates are logit transformed. Subsequent estimates are differences from baseline. P values < 0.05 are considered significant

as well as gain additional insights into the cascading effects of predator removal on other species (Prugh et al. 2009; Ripple et al. 2014).

Compliance with ethical standards

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