SEASONAL DIVERSITY AND EFFICIENCY OF THE SCAVENGER GUILD AT THE CARY INSTITUTE OF ECOSYSTEM STUDIES

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Abstract. Scavengers provide an important ecosystem service by removing carrion from the environment. Although temperature and season are known to influence scavenging, these impacts are highly region-specific and few studies have explored these trends in the northeastern United States. We used carrion-baited camera traps to examine the diversity and efficiency of scavengers at the Cary Institute of Ecosystem Studies in Millbrook, NY during summer and winter. In addition, we used exclosures to measure carcass removal due to invertebrate scavenging. We found that vertebrate scavenger species richness and carcass removal were significantly greater in summer than in winter. We also found that carcass removal was significantly lower when vertebrates were excluded from the carcass than when they had access to it. These findings will allow us to better understand seasonal trends in vertebrate scavenging while highlighting the importance of accounting for invertebrates in scavenger study design.

INTRODUCTION

Vertebrate scavengers play critical roles in ecosystems throughout the world. By consuming carcasses, scavengers prevent the spread of disease and reduce the need for costly waste-disposal services (O'Bryan et al. 2018). In addition, scavengers disperse the nutrients and energy contained in carcasses throughout the landscape at a larger scale than other decomposers, thereby recycling these nutrients in the upper trophic levels (Beasley et al. 2015).The additional interspecies linkages in food webs provided by scavengers also enhance the stability of ecosystems, which may make them more resilient to disturbance (Beasley et al. 2015). Scientists agree that while likely important, these ecosystem services are not well understood, necessitating more research on the efficiency of carcass removal via vertebrate scavenging (Beasley et al. 2015, Inger et al. 2016). There is also a need for research on the diversity of scavenger guilds, because different animals may have different ecological roles or may provide these services more efficiently. For example, vultures have a unique digestive system that eliminates most pathogens found in carcasses, reducing the spread of disease more effectively than other scavengers (Houston and Cooper 1975). Population declines of vultures in India have led to severe economic losses and disease spread, despite the presence of other scavengers (Markandya et al. 2008). In addition to retaining unique scavenger roles, a diverse guild allows for different routes of nutrient dispersal, increasing spatial heterogeneity of resources within an ecosystem.

There are several factors that may influence both the efficiency and diversity of scavenger guilds. In temperate ecosystems, seasonal variation in temperature and weather may have an impact. As air temperature increases, microbial and invertebrate activity increases, allowing for carcasses to decompose faster (Ray et al. 2014). Therefore, carcasses are available to vertebrate scavengers for a shorter period of time during warm summer months, which has been shown to impact scavenger diversity and efficiency in previous studies (DeVault et al. 2004, Turner et al. 2017). Animals may also be more likely to consume carrion during harsh winter months when there are fewer additional resources available (Ray et al. 2014). However, challenges such as snow and frozen carcasses may impede vertebrate scavenging in the winter.

In addition to seasonal impacts, animal population sizes often fluctuate inter-annually due to complex species interactions and environmental and demographic stochasticity (MacArthur 1955). This fluctuation may cause changes in scavenger diversity and efficiency between years. Spatially, habitat-related factors such as vegetation type, canopy cover, and soil type may impact which locations are favored by scavengers and which provide better access to carcasses. For example, Turner et al. (2017) found that carcasses placed in clearcut habitats were found by scavengers 50% faster than those in other habitat types.

Studies by DeVault et al. (2004) and Turner et al. (2017) tested the impact of both temperature and habitat type on scavenger efficiency and diversity, finding higher species richness and a higher percentage of carcasses consumed in the cooler seasons. In contrast a similar study in Germany found that a greater percentage of carcasses were consumed in the warmer seasons, and that invertebrates played a larger role in carcass removal than vertebrates (Ray et al. 2014). This demonstrates how regional differences in climate and the composition of scavenger communities may impact scavenger efficiency.

Few studies have examined temporal variation in scavenger guild efficiency and diversity in the Northeast United States or accounted for the role of non-vertebrate decomposers in carcass removal in this region. In this study, we explore seasonal trends in scavenger guild diversity and efficiency in New York's Hudson Valley.

The goals of this study are 1) to provide data for an ongoing study at the City University of New York (CUNY) on scavenger guilds and their efficiency in New York; 2) to compare the efficiency of carcass removal when vertebrates have access with when they do not; and 3) to examine the effect of season, year, and site on species richness, scavenger success, carcass removal rate, and time of detection. Our hypotheses are as follows: 1) We expect summer will have higher scavenger species richness and efficiency compared to winter, 2) We expect no difference between scavenger species richness and efficiency across the four sites at Cary, 3) We expect a difference in species richness between 2017 and 2018 due to stochastic community changes, and 4) We expect carcass removal rate to be higher when vertebrate scavengers have access than when they do not.

METHODS

Study Site

Experiments took place at four sites at Cary Institute of Ecosystem Studies in Millbrook, NY: Lovelace Rd, Maintenance, Tire Field, and Greenhouse (Figure 1). The Cary Institute property is a second-growth forest with some herbaceous fields, and each site is near the edge of these two types of habitat.

Field Methods

Fresh, intact chicken carcasses were purchased from a live market in New York City. The average weight of these carcasses was 1.5 kg. One camera was placed at each site attached to a vertical tree, facing a chicken carcass 2 to 4 meters away. The carcass was attached to a tree with galvanized wire to prevent removal from the camera's view. The camera took three burst photos at three second intervals when motion was detected. Experiments were conducted as one week replicates with five replicates in summer 2017 (May - August), four replicates in winter 2017/2018 (December - February), and four replicates in summer 2018 (June - August). The carcass was weighed at the beginning, middle, and end of each replicate to account for biomass loss relative to the starting mass. We fully removed carcasses at the end of each week, and a week was allowed in between replicates to prevent animals from becoming habituated to bait.

During two replicates in summer 2018, an exclosure treatment was run concurrently with the exposed carcass at each site. Exclosures were made from hardware cloth and horse fence sealed into a box shape using hog rings (Figure 2). A hole at the lower face of the exclosure ensured that the chicken has contact with the ground similarly to the exposed carcass. An additional layer of hardware cloth was attached to extend about one foot from the edge of the main cage as an apron, to prevent vertebrates from reaching under the cage (Figure 2). Exclosures were staked into the ground using four earth anchors just outside the cage and garden staples around the outer edge of the hardware cloth apron. We ran a cable through the earth anchors and secured it to keep the cage tightly attached to the ground. Exclosures were placed equidistant to the exposed carcass from the tree on which cameras were mounted. A second camera was mounted on the same tree facing the exclosure, 90 to 180 degrees from the other camera. Exclosure experiments followed a paired sample design to ensure both exposed and exclosure treatments were experiencing the same environmental conditions.

Camera images were viewed and categorized by species, and data on time and temperature were extracted from the images. Images were grouped into observations, where we defined an observation as a period of time in which a scavenger triggers the camera at intervals less than fifteen minutes apart. If an individual of the same species returned after fifteen minutes it was considered a new observation.

Statistical Analysis – Diversity

All statistical analyses were carried out using the R programming environment.

The R package `rich` was used to determine species richness, and an estimated species accumulation curve was produced using bootstrap estimation. We ran a generalized linear model with a Poisson distribution to test for differences in species richness between 4 sites, two seasons, and two years. Exclosure treatments were included in this analysis.

Statistical Analysis – Efficiency

We defined carcass removal rate as the percent of starting carcass biomass that was lost in a given period of time. To determine carcass removal rate, final carcass weights were divided by starting weights to determine percent biomass loss for each replicate. We used a linear model to determine the impact of season, year, and site on percent biomass loss. Exclosure treatments were not included in this analysis.

We defined a scavenging success as any part of the carcass being consumed by a vertebrate within one week. Binary values for success were assigned based on the camera trap images. A generalized linear model with a binomial distribution was used to determine whether scavenging success is impacted by site, season, or year. Exclosure treatments were not included in this analysis.

We defined detection time as the number of hours it took for a scavenger to look at, approach, sniff, or consume the carcass. We used a linear model to determine the impact of site, season, and year on detection time. Replicates in which carcasses were never discovered by a vertebrate were omitted from this analysis. Exclosure treatments were included.

Statistical Analysis - Exclosure Experiments

We used a paired t-test to determine if there was a significant difference in carcass biomass loss between exposed treatments and exclosure treatments. Six paired exclosure samples were included in this analysis.

Statistical Analysis - Testing for Experimental Biases

We used a linear model to determine whether carcass removal rate and detection time varied by replicate number, to determine whether animals learned the location of bait at our sites over time. We also used a linear model to compare detection time and carcass removal between the paired exclosure replicates and the non-exclosure replicates, to determine whether the additional carcass attracted scavengers more quickly.

RESULTS

Diversity

Over the course of 13 replicates at four sites each, there were 499 observations of 12 different vertebrate scavenger species (Table 1). The estimated species accumulation curve approaches an asymptote at about 20 samples (Figure 3). All 12 species were observed in summer, while only 7 were observed in winter (Table 1). In summer, the most commonly observed species was *Procyon lotor* (24.5%), followed by *Cathartes aura* (21.8%) and *Corvus brachyrhynchos* (20.0%, Table 1). In winter, the most commonly observed species was *Procyon lotor* (34.9%), followed by *Canis latrans* (25.4%) and *Vulpes vulpes* (22.2%, Table 1). Mean species richness per sample was significantly greater in summer than in winter ($p = 0.0039$, Figure 4). An average of 2.4 species per sample were observed in summer while an average of 1.1 species per sample were observed in winter. There was no significant difference in mean species richness per sample between sites or between years ($p > 0.1$, $p = 0.946$, Figure 4).

Efficiency

Mean percent carcass biomass loss was significantly greater in summer than in winter on both the fourth day and the seventh day of the experiments ($p = 0.016$, $p = 0.0016$, Figure 5). Carcasses lost 40% more biomass by the fourth day (Figure 5A) and 52% more by the seventh day (Figure 5B) in summer than in winter. There was no significant difference in carcass removal between sites or between years on the fourth day ($p = 0.11$, $p = 0.93$) or the seventh day ($p = 0.75$, $p = 0.95$). Twice as many carcasses were consumed by vertebrates in summer than in winter ($p = 0.001$, Figure 6). Site and year did not affect scavenger success ($p > 0.4$ for all sites, $p = 0.97$). Detection time did not vary significantly between sites, years, or seasons ($p = 0.3, 0.7, 0.1$).

Exclosure Experiments

Six exclosures successfully prevented vertebrate access to the enclosed carrion. Percent carcass biomass loss was significantly greater in exposed treatments than exclosure treatments on both the fourth day ($p = 0.047$) and the seventh day ($p = 0.0062$, Figure 7). Carcasses within exclosures lost an average of 58.6% of their biomass over seven days (Figure 7). There was one outlier in which the carcass in the exclosure gained mass over the seven days (Figure 7). When this outlier is removed from the paired t-test, the difference in carcass biomass loss between exposed and exclosure treatments is significant on the seventh day ($p = 0.008$) but nonsignificant on the fourth day ($p = 0.12$).

Testing for Experimental Biases

There was no significant difference in detection time or carcass removal between paired exclosure experiments and non-exclosure experiments ($p = 0.2, 0.2$). There was also no relationship between replicate number and detection time ($p = 0.6$) or carcass removal ($p = 0.1$).

DISCUSSION

Diversity

Our estimated species accumulation analysis produced a curve that approaches an asymptote at around 15 samples, indicating that our 36 samples in summer and 15 samples in winter are sufficient to represent true species richness of the scavenger guild at our study sites. We found raccoons to be the most common scavenger in both summer and winter, which is consistent with current knowledge that this opportunistic species is a highly abundant mesopredator in the United States (Troyer et al. 2014). There was a greater presence of avian scavengers during summer than in winter, which may be explained by the partial migration patterns of turkey vultures and crows in the Northeast region (Ward and Raim 2011, Dodge et al. 2014). Bobcats and red foxes were more commonly observed in winter than in summer, which may be due to reduced prey availability in the harsher winter season (Ray et al. 2014). Our linear model found a greater species richness in summer than in winter. There are three potential drivers that may have contributed to this result. First, the aforementioned migration of turkey vultures made them absent from the winter experiments. Second, snow cover and freezing in the winter may have prevented certain animals from accessing carcasses. Third, cold temperatures slow the decomposition process, which may prevent carcasses from being detected olfactorily by animals. However, our detection time analysis produced a nonsignificant result, indicating that this is less likely to have been a factor. The nonsignificant result for site-related differences in species richness was likely due to the similarity of the four sites in terms of location and habitat type. Lastly, the lack of difference in species richness between years suggests that any fluctuations in scavenger populations were not significant enough to affect the number of species visiting the study area.

Efficiency

We found that carcass removal was greater in the summer than in the winter. As previously discussed, frozen or snow-covered carcasses are more difficult for some scavengers to access and consume even if discovered, which may explain the decrease in carcass removal in the winter (Huggard 1993, Selva et al. 2005). Invertebrates are also more active in the summer, so the greater observed carcass removal may be partially due to invertebrate scavengers.

Scavenging success was also greater in the summer than in the winter, which indicates that the observed seasonal difference in carcass removal was not only due to invertebrate activity, because this metric was based on camera images of vertebrates feeding on the carcass.

Interestingly, despite the seasonal differences in carcass removal and scavenging success, there was no difference in detection time between summer and winter. This may be explained by two factors. First, many of the winter images showed scavengers looking at or approaching the carcass without actually feeding on it. Animals may discover the carcass and be unable to access it due to freezing or snow, preventing carcass removal or scavenging success. Second, carcasses that were never discovered were not included in this analysis, but they were included in determining carcass removal and scavenging success.

Exclosure experiments

Our paired exclosure experiments resulted in greater carcass removal in exposed treatments than exclosure treatments. This emphasizes that vertebrate scavengers are very important to completing the ecosystem service of carcass removal, even in the summer months when invertebrate activity is high. Carcasses in exclosures lost an average of 58.6% of their biomass in one week, due entirely to invertebrates and microbial activity. This highlights the importance of using exclosures to account for invertebrate activity when quantifying carcass removal due to vertebrates, a contribution that is often overlooked in the literature.

CONCLUSION

Seasonality plays a large role in the diversity and efficiency of scavenger guilds in temperate regions such as the mid-Hudson valley in New York. More research is needed to accurately quantify the impact of season on the ecosystem services provided by scavengers. Studies using exclosures to account for invertebrate activity during different times of year are particularly needed to fully understand the relative roles of vertebrates and invertebrates in carcass removal. This knowledge would provide information to better inform environmental policy and wildlife management regarding vertebrate scavengers in the northeast United States.

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APPENDIX

TABLE 1. Observations of vertebrate scavenger species at camera sites.

	Number of Observations				Percent of Total Observations		
Species	**Summer 2018**	**Summer 2017**	**Winter 2017/2018**	**Total Count**	**Summer (%)**	**Winter (%)**	**Total (%)**
Procyon lotor	84	23	22	129	24.5	34.9	25.9
Lynx rufus	4	1	7	12	1.1	11.1	2.4
Canis latrans	10	43	16	69	12.2	25.4	13.8
Vulpes	0	8	14	22	1.8	22.2	4.4
Urocyon cinereoargenteus	0	2	0	2	0.5	0	0.4
Cathartes aura	51	44	0	95	21.8	0	19.0
Coragyps atratus	2	0	0	2	0.5	0	0.4
Corvus brachyrhynchos	87	0	1	88	20.0	1.6	17.6
Ursus americanus	2	2	1	5	0.9	1.6	1.0
Didelphis virginiana	61	9	2	72	16.1	3.2	14.4
Mephitis	2	0	0	2	0.5	0	0.4
Martes pennanti	0	1	0	1	0.2	0	0.2
Total	**303**	**133**	**63**	**499**	**100**	**100**	**100**

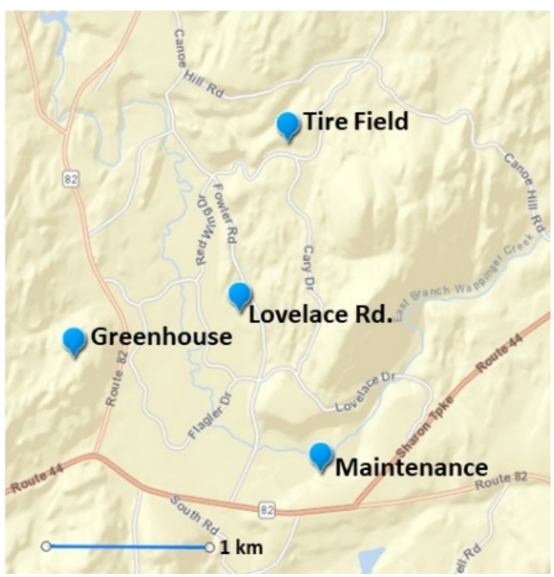

FIGURE 1. Map showing study site locations at Cary Institute of Ecosystem Studies in Millbrook, NY. Sites are shown as blue markers.

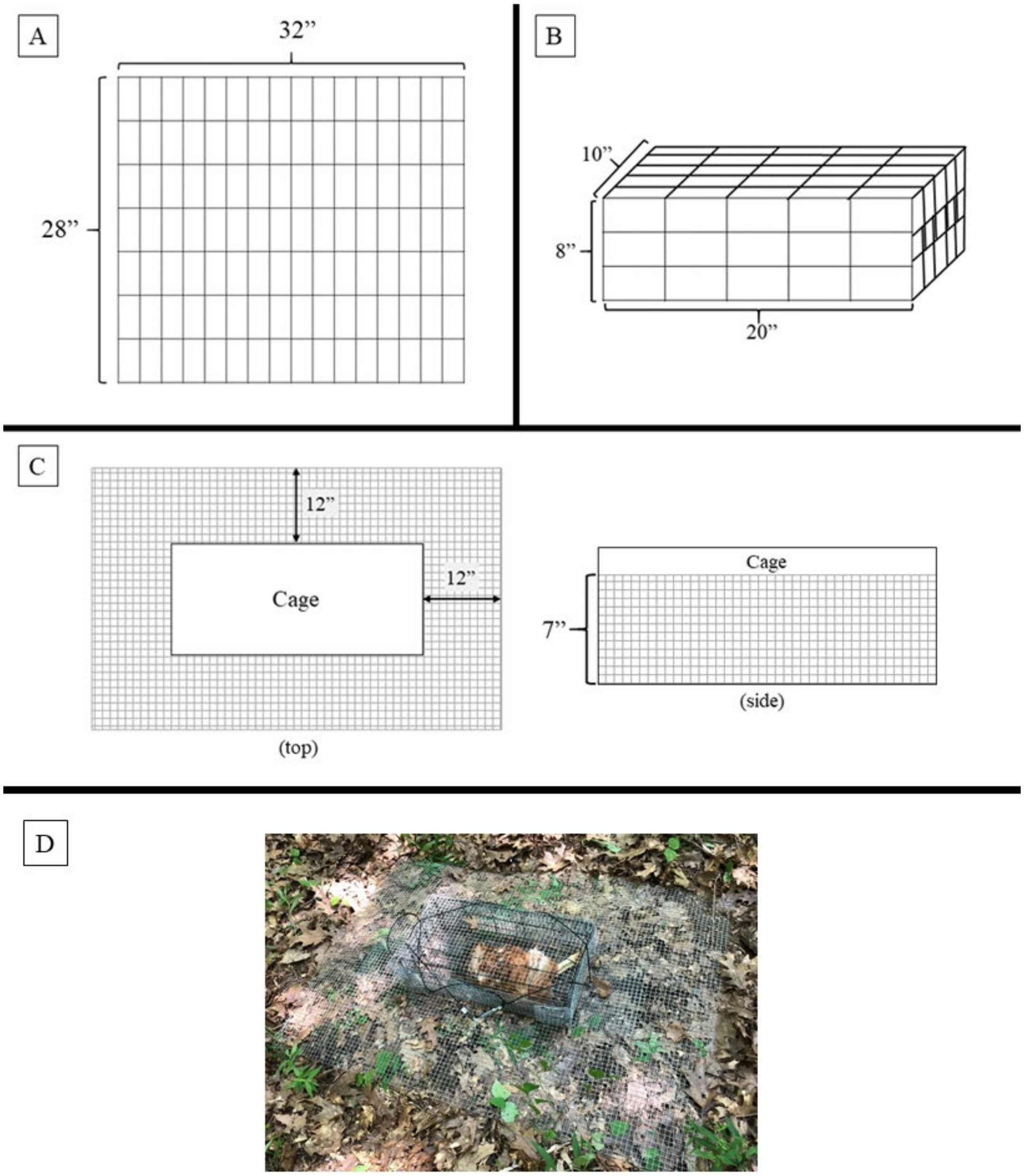

FIGURE 2. Exclosure design. A) The central cage was shaped from a 32” x 28” piece of horse fence. B) The cages were 20” long, 8” tall, and 10” wide, large enough to hold a chicken carcass. The sides of the cage were fastened together using hog rings. After the horse fence cage was built, a second layer made from hardware cloth was attached with hog rings, surrounding the central cage. A 6” x 12” hole was cut out from both layers at the bottom of the cage to ensure the chicken had contact with the ground. C) An additional piece of hardware cloth was used to form an apron around the cage, with 12” on each side of the cage and a hole for the cage in the center. This apron layer was shaped to a height of about 7” on all sides of the cage. D) The exclosure was secured onto the ground using four earth anchors, a cable running between them, and garden staples around the edges of the apron.

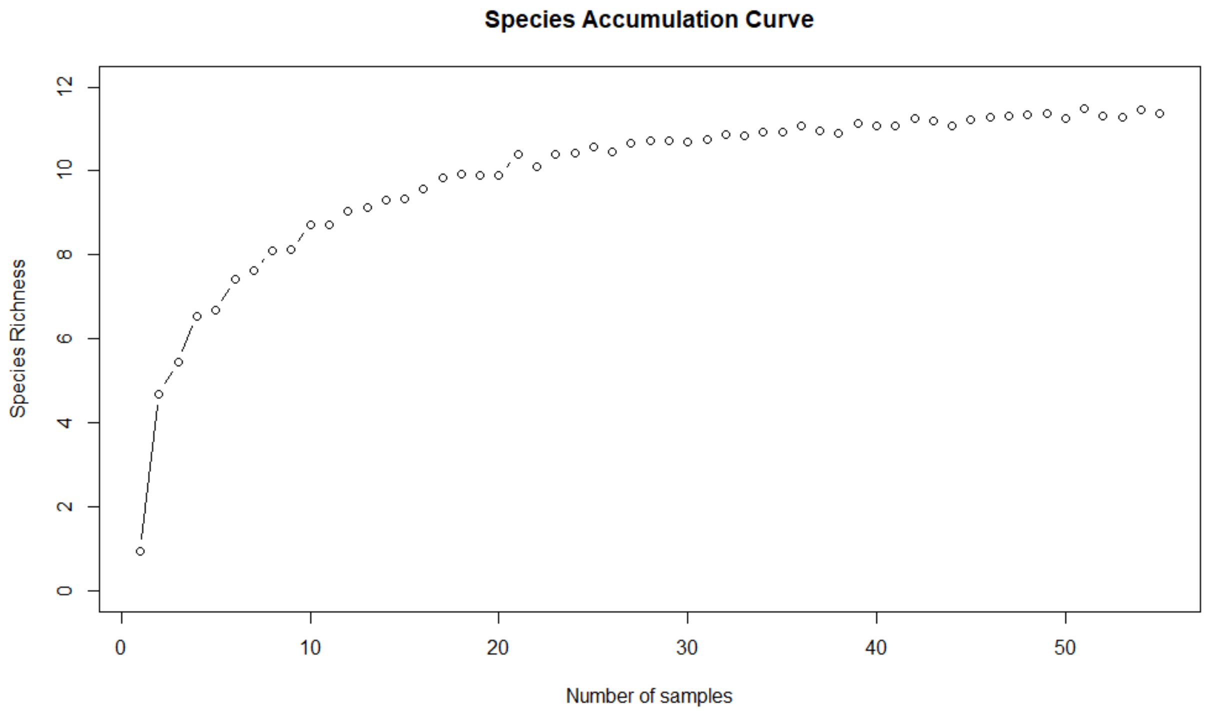

FIGURE 3. Estimated species accumulation curve using bootstrap estimation. This curve shows the number of samples needed to confidently estimate the number of total number of species in the scavenger guild.

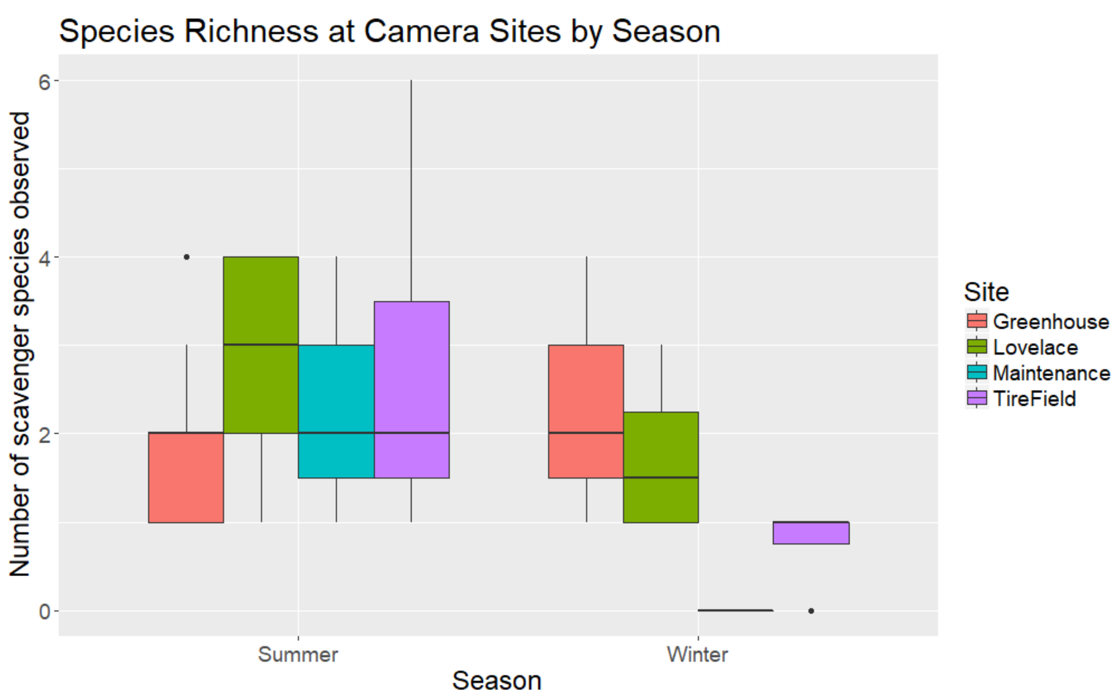

FIGURE 4. Species richness per sample between summer and winter ($p = 0.0039$). Colors represent the four field sites.

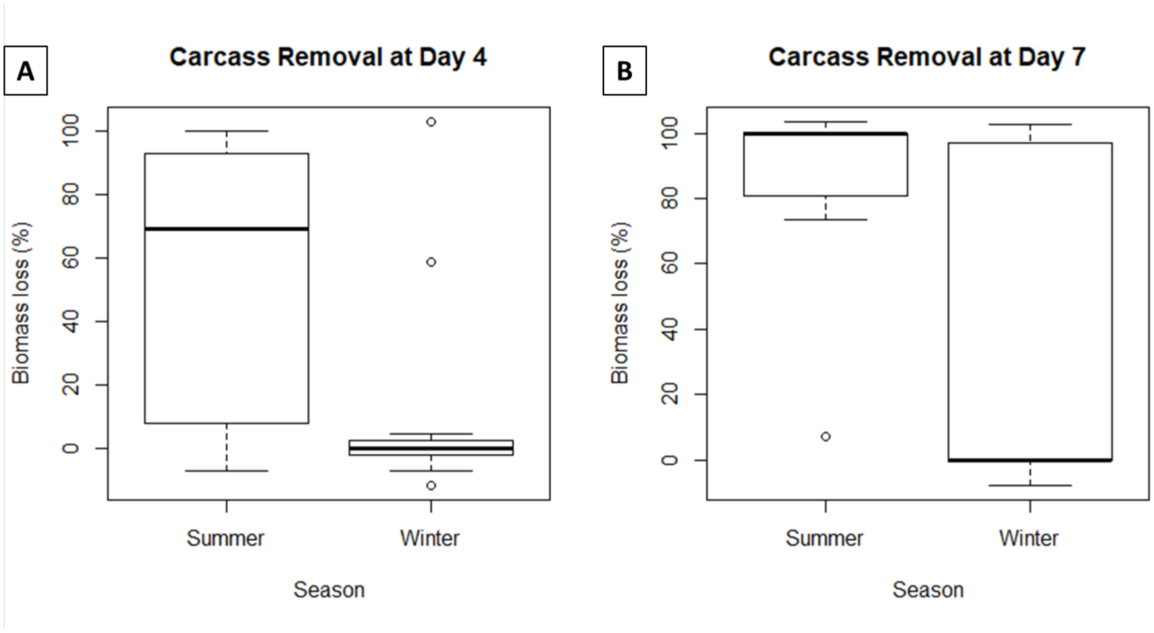

FIGURE 5. Carcass removal between seasons at mid-week (Day 4; A; p = 0.016) and end of week (Day 7; B; p = 0.0016).

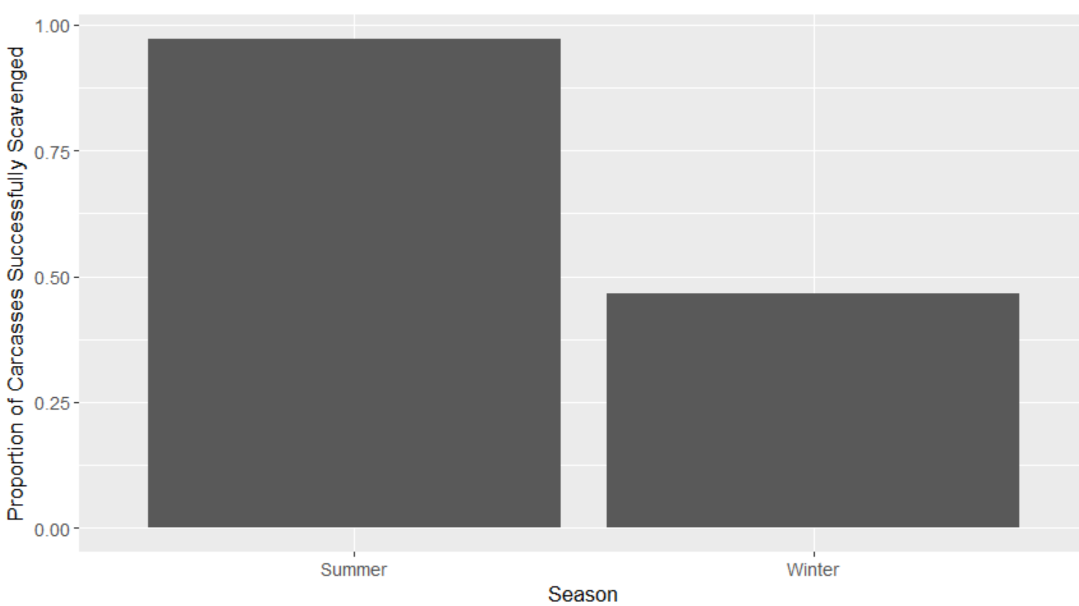

FIGURE 6. Proportion of carcass successfully scavenged in summer and winter.

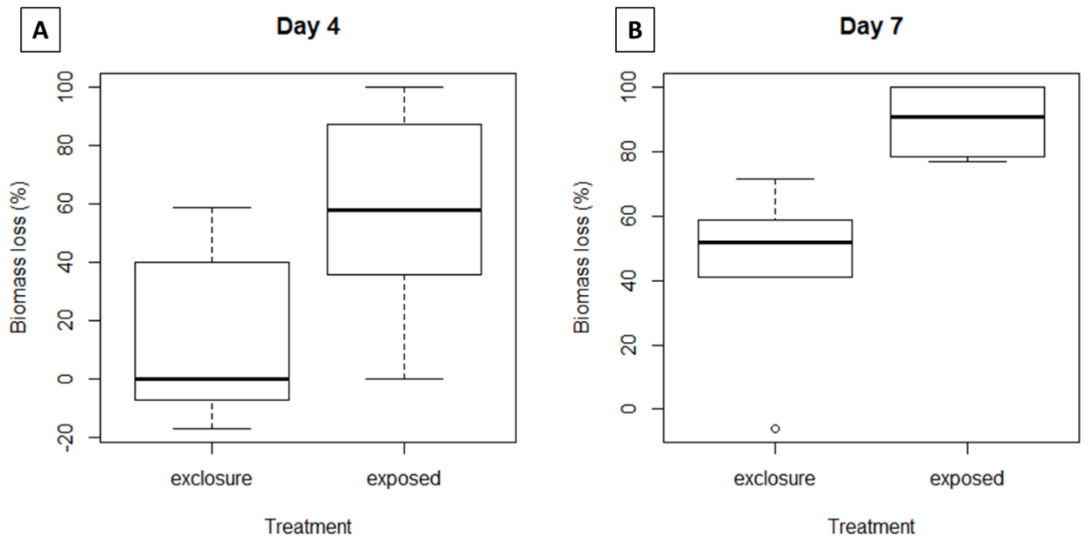

FIGURE 7. Carcass removal between treatments at mid-week (Day 4; A; $p = 0.047$) and end of week (Day 7; B; $p = 0.0062$) during the exclosure experiments.