12-13-2019

Understanding the effects of mass mortality events on plant communities and consumer behavior

Carolina Baruzzi

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Understanding the effects of mass mortality events on plant communities and consumer behavior

By

Carolina Baruzzi

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

December 2019
Understanding the effects of mass mortality events on plant communities and consumer behavior

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Mass mortality events (MMEs) are die-offs that result in increased carrion biomass and sometimes the impairment of functional roles. Concurrently, several vulture species are declining. Carrion is a basal resource in ecosystems and its recycling by vultures is considered an ecosystem service. However, the consequences of simultaneously increasing carrion loads and declining vulture populations are unknown.

I developed a theoretical framework predicting that, with increasing carrion biomass, carrion food web diversity would increase horizontally and vertically, respectively increasing and decreasing carrion recycling efficiency.

Using a manipulative experiment, I investigated the role of bottom-up and top-down forces affecting plant communities during an MME. I selected 5 sites to establish 6 treatments crossing different levels of carrion addition and nutrient addition, and control with vertebrate scavenger and herbivore access. I transplanted six cherrybark oak (*Quercus pagoda*) seedlings to each plot, protecting half of them from herbivory. Carrion biomass shifted dominance of plant functional groups to favor annual plants, an effect reduced by scavenger access. Herbivore access affected plant community response to carrion and limited growth and survival of
transplanted seedlings regardless of treatment. Nutrient addition did not affect plant communities, growth, and survival suggesting that MME effects on plants are likely mediated primarily by top-down forces.

To determine if behavioral plasticity of vultures affects carrion recycling efficiency, I monitored turkey (*Cathartes aura*) and black (*Coragyps atratus*) vulture behavior. Both species increased group size, but only black vultures increased individuals feeding per group and activity overlap between species increased with increasing carrion biomass. As a result, estimated carrion consumption by vultures increased with carrion biomass suggesting behavioral plasticity may alleviate some of the effects of vulture declines on carrion recycling.

Finally, vultures compete with invertebrate scavengers so declining vultures may release their populations to compensate for the loss. However, in one of my experiments, variation in vulture visitation was negatively correlated with the abundance of blowflies parasitized by *Entomophthora* sp. Our observations may suggest that vultures were more likely mediating carrion decomposition affecting parasitism, which may limit blowflies from compensating for declining vultures.

Key words: mass mortality events, resource pulses, scavengers, wildlife die-offs;
ACKNOWLEDGEMENTS

I would like to thank my advisor Marcus Lashley for his mentorship and for always believing in me, even when I was doubting myself. I am also grateful to my committee members for their support and guidance.

This project would have never been completed without the help of numerous graduate and undergraduate students. Their help in the field has been vital and I will forever be grateful to them. I also want to extend my gratitude to the staff of the Panther Swamp National Wildlife Refuge, in particular Seth Swafford, Andy Tauton, Gerald Davis, and Glen Catoe, for their help and support, and also for making me find Theodore.

I am deeply indebted to my friends and family for all their unwavering love and support, which they never failed to show whether they were on this or the other side of the ocean. I have no words to say how grateful I am for that. In particular, I want to thank David, Ashley, Johannah, Juan Andrés, Kelsey, Andrew, Ryo, Conner, Cori, Mariah, Lindsay, and Adrienne for becoming part of my Mississippi family. Also, thank you Shannon for being one of the most inspiring and motivating people I have ever met. To Maya, no words could ever express how grateful I am for our friendship, thank you for being one of my anchors for the past twenty years. Diletta and Martina thank you for always being with me as if there was no distance between us. Finally, thank you Theodore for being always able to bring me happiness.
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CHAPTER I
INTRODUCTION

Mass mortality events (MMEs) are die-offs that cause an abrupt input of carrion into ecosystems. It is relatively unstudied how these large amounts of carrion affect communities, but it is expected that the effects increase as carrion biomass increases (Tomberlin et al. 2017, Baruzzi et al. 2018, Jentsch and White 2019). For example, the relative importance of obligate scavenger groups is expected to shift as a function of increasing carrion biomass (Tomberlin et al. 2017). Moreover, interaction strength between competitors and predation at carrion sites may change as a function of carrion biomass (Baruzzi et al. 2018, Lashley et al. 2018). Because changes in community assembly and the timing of colonization can generate indirect effects of carrion on the community (Heo et al. 2019), understanding how the effects of carrion scale with carrion biomass is an important question to understand the consequences of MMEs.

There is one aspect of MMEs that makes them a unique context in ecology. That is, when MMEs occur they do not just generate a resource pulse, they often also simultaneously impair or remove a functional role. To date, there are numerous studies that investigate MME bottom-up effects (e.g., Sousa et al. 2012, Subalusky et al. 2017) or top-down effects (e.g., Holdo et al. 2009, Ruuhijärvi et al. 2010) but studies that simultaneously do both are almost absent (but see, Hodge 2019). However, because MMEs are increasing in magnitude and occurrence across several taxa, there is a growing need of increasing our knowledge about these phenomena (Fey et al. 2015).
To further complicate our understanding of how the increasing frequency and magnitude of MMEs will affect ecosystems, the only terrestrial obligate vertebrate scavenger group, vultures, is declining globally (Santangeli et al. 2019). Although vulture global decline has been associated with the rise of mesosavengers, vultures are more efficient recyclers than vertebrate mesosavengers (O'Bryan et al. 2019). As such, vulture decline is likely to exacerbate the effects of MMEs on communities, but these effects may be alleviated by vulture behavioral plasticity. Because competition dynamics can be altered during resource pulses (Yang et al. 2010), relaxed competition might lessen the effects of reduced numbers of vultures at carrion sites.

In this study, I employed a theoretical approach to develop predictions about how increasing levels of carrion biomass may affect carrion food webs. I also used an experimental approach to determine if behavioral plasticity of vultures would allow them to increase carrion consumption efficiency and to determine how the effects of carrion on plant communities change as a function of carrion biomass and the role of functional role impairment in those consequences. Finally, I used observations to describe evidence of top-down decomposition regulation by obligate vertebrate scavengers and the effects of relaxed regulation on obligate invertebrate scavenger parasitism. It was my hope that these approaches would increase our understanding of MME ecological consequences.
References


CHAPTER II
EFFECTS OF INCREASING CARRION BIOMASS ON FOOD WEBS

Introduction
In nutrient cycles within ecosystems, organisms can be conceptualized as temporary storage pools of nutrients. At the moment of death, stored nutrients begin mobilizing again in the cycle. Because carrion releases resources that are otherwise unavailable to consumers, death elicits bottom-up effects in food webs. Hereafter, when discussing bottom-up effects of carrion it is in the context of consumers using resources that originate from carrion (i.e. carrion-based food web). While it is widely accepted that carrion is an important resource in ecosystems, and some of the bottom-up effects on scavengers are well documented (e.g. Meehan et al. 2005, Carter et al. 2007, Beasley et al. 2012, Barton et al. 2013, Macdonald et al. 2014), less attention has been paid to how increasing carrion biomass affects the strength of bottom-up and top-down forces. In this paper, we will focus on three important predictions from traditional food web theory about how increasing resource availability and consumer diversity affects food webs from the bottom-up and top-down: 1) increasing resource availability strengthens the bottom-up effects on diversity of primary consumers and across trophic levels (Pace et al. 1999, Shurin et al. 2002, Gessner et al. 2010); 2) increasing primary consumer diversity strengthens top-down control of resource availability (Jonsson and Malmqvist 2000, Hooper et al. 2005, Srivastava et al. 2009, Hector et al. 2009, Tiunov and Scheu 2005); and 3) increasing vertical diversity (i.e. across trophic levels) weakens primary consumer top-down control on resource availability (Wyman...
More directly as it relates to the carrion food web, increasing carrion biomass is predicted to increase scavenger abundance and diversity, and increasing abundance and diversity of scavengers should increase the efficiency of carrion recycling. However, once carrion biomass increases to a level that increases the vertical complexity of the food web, predators of scavengers should decrease the speed of carrion recycling. We acknowledge the importance of the nutrient cycle of carrion for soil bacteria and plants. However, topics regarding soil-based food webs are beyond the scope of this manuscript.

**Does increasing carrion biomass affect food web diversity?**

Previous carrion-based food web studies support the prediction of strengthened bottom-up effects with increasing resource availability (Abrams 1993; Kaunzinger and Morin 1998). To study bottom-up effects, differences in carrion biomass inputs can be generated by manipulating carcass size or quantity, but almost all studies manipulate carcass size. Those studies report that larger carrion size invokes higher scavenger diversity or abundance and lengthens the duration of resource availability (Müller et al. 1990, Nagano and Suzuki 2007, Selva and Fortuna 2007, Sutherland et al. 2013). For example, a study on scavenger assemblages in South Africa detected more species feeding on large (i.e. >100 kg) carcasses than smaller carcasses (i.e. <10 kg; Moleón et al. 2015). They surmised that specialized scavengers were able to quickly capitalize on the smaller carcasses that were available for a shorter period of time, while both specialized and facultative scavengers colonized larger carcasses that persisted longer and were likely easier to detect for less specialized species. Similarly, microbial communities also tend to be more diverse as carcass size is increased (Fontaine and Barot 2005, Bradford et al. 2008). As such,
carrion food web studies support that increasing carrion biomass indeed strengthens bottom-up effects by increasing the scavenger diversity.

While the longer persistence of the resource may contribute to the diversity of consumers by increasing colonization of less specialized species, the decrease in decomposition rate reported in several studies (e.g. Simmons et al. 2009, Spicka et al. 2011, Sutherland et al. 2013) seems to indicate that the increase in consumer diversity did not result in increased recycling efficiency. This pattern is dissimilar to reports in detrital decomposition from aquatic and terrestrial systems, where increasing detritivore diversity increases the efficiency of detrital decomposition (Jonsson and Malmqvist 2000, Srivastava et al. 2009, Hector et al. 2009, Tiunov and Schaeu 2005). Although carrion and leaf detritus are different kinds of resources that attract different consumers, the processes that regulate resource depletion through competition or facilitation among consumers should be similar. So why the different pattern in decomposition rate with increasing consumer diversity in the two systems?

When we compared the systems, we realized differences may result from a confounding factor in the study design of manipulating carrion biomass by altering carcass size. That is, manipulating carrion biomass by increasing carcass size may actually decrease per capita access to carrion by scavengers because of the decreasing surface area to volume ratio of the resource. Empirical evidence that increasing detritivore diversity leads to more efficient decomposition of leaf litter comes from studies that manipulated the litter biomass by changing the number, not the size, of the leaves (Gessner et al. 2010). Also, explicit empirical tests of the top-down effects of consumer diversity come from manipulating access by some detritivores. Thus, a parallel comparison for decomposition rates in carrion food webs would incorporate manipulations of carcass number, instead of size, and scavenger access. To our knowledge only one such data set
has been reported, Lashley et al. (2018a) increased carrion biomass by adding carcasses and also had a partial scavenger exclusion treatment. They concluded carrion recycling became more efficient as carrion biomass increased given that time to full decomposition was relatively similar across the gradient in biomass. In other words, the larger the carrion biomass the faster it had to decompose to reach full decomposition in the same time. Also, their data indicate that efficiency was in part linked to scavenger diversity because excluding vertebrate scavengers consistently delayed decomposition time. Thus, when carrion size is consistent among treatments, results from Lashley et al. (2018a) and various detrital studies suggest similar patterns in the effect of resource biomass and primary consumer diversity on recycling efficiency via facilitation from some organisms providing transportation or access for other organisms to the resource.

The previously observed increases in efficiency associated with scavenger abundance and diversity may be influenced by several mechanisms (e.g. Moreno-Opo and Margalida 2013, Moleón et al. 2014, Abernethy et al. 2016). First, increasing the abundance of scavengers may accelerate decomposition rate simply by attracting more scavengers. Secondly, increasing the diversity of scavengers may increase niche complementarity in the decomposition process. The separation of specialties in decomposing different parts of the same carcass facilitates higher efficiency than would increasing the abundance of a single functional group. For example, dermatophagous species such as skin beetles (Dermestidae) specialize in decomposing skin whereas sarcophagous species such as blowfly larvae specialize in decomposing flesh (Braack 1987). Having the same abundance of decomposers, but with both functional groups represented, would increase efficiency of fully decomposing both skin and flesh. Similarly, another mechanism of efficiency involves indirect effects from species interacting in the carrion food web. For example, vertebrate scavengers facilitate colonization or access of invertebrates or
microbes to carrion by providing transportation or by creating openings to penetrate the epidermis (Meehan et al., 2005). It should also be noted that some authors have reported neutral or negative effects of primary consumer diversity on resource depletion efficiency (McKie et al. 2008, Creed et al. 2009). This normally happens when diversity includes a relatively inefficient species that is dominant because of their activity, density, or aggressive behavior, but could also result from other antagonistic interactions (Gessner et al. 2010).

In most cases, traditional food web theory predicts increases in vertical diversity by adding primary consumer predators should decrease the efficiency of consumers through behavioral- or density-mediated mechanisms (Wyman 1998, Lecerf et al. 2005, Greig and McIntosh 2006, Schmitz et al. 2008). Increasing carrion biomass increases predators of scavengers (Braack et al. 1987), affecting depredation rates and generating other indirect effects (Cortés-Avizanda et al. 2009a and 2009b, Steinbeiser et al. 2017, Lashley et al. 2018a). However, there is, to our knowledge, no empirical evidence of a consistent relationship between predator diversity or abundance and carrion recycling efficiency. In other food webs, increasing vertical diversity may enhance or depress resource exploitation depending on different factors (Gessner et al. 2010). If the predator decreases the abundance or activity of an efficient consumer, or one that is essential in facilitation of other consumers, the predator decreases carrion recycling (Mulder et al. 1999; Schmitz et al. 2008). Alternatively, predators of scavengers could increase recycling efficiency by numerically or temporally regulating competitive dominance of an inefficient consumer in the decomposition process (Duffy et al. 2007) or if the predator is also an efficient scavenger itself.
What happens when biomass is abnormally high?

Recent literature has raised concern over increasing occurrences of mass mortality events (MMEs), which are catastrophic die-offs that differ from background mortality levels in both magnitude and temporal scale (Fey et al. 2015). Depending on cause, MMEs can take place in a relatively short time (e.g. Scorolli et al. 2006) or over several months (e.g. Rijks et al. 2016, Kock et al. 2018), and the number of deaths is widely variable, with some events including hundreds of thousands of individual deaths (e.g. McDowell et al. 2017, Kock et al. 2018). Not only can MMEs be catastrophic to the species affected, but they also generate a unique context in carrion food webs because of the extreme input of resources. Little empirical data are available to evaluate how ecosystem processes are affected by these events but some work suggests that MMEs can have long-lived effects on the productivity of ecosystems. For example, wildebeest (*Connochaetes taurinus*) mass drownings that periodically happen in the Mara River generate a substantial input of bones and soft tissues, which affect nutrient cycling and river food web for years (Subalusky et al. 2017). Based on the idea that extreme resource abundance potentially increases consumer diversity, MMEs could cause a food web expansion to include species that are rarely or not previously documented as participating in the carrion food web.

Lashley et al. (2018a) describe several rare species interacting in the carrion food web, which increased in occurrence with carrion biomass. Thus, MMEs could alter interactions in the carrion food web simply by adding to the number of species interacting. For example, Lashley et al. (2018a) demonstrated this where increasing carrion biomass had a nonlinear exponential increase in soil perturbations from armadillo foraging for blow fly larvae. Also, MMEs may change interaction strength between species by changing the relative importance of scavengers in the decomposition process (Tomberlin et al. 2017). Another unique consequence of MMEs is
due to the fact that there is a finite number of consumers in the ecosystem, and those consumers vary markedly in feeding rates and reproductive capability. Because of those differences, increasing carrion biomass should satiate scavenger populations at different rates and as a result of differing feeding strategies, fundamentally changing the decomposition process. For example, blow fly populations may increase exponentially in weeks but it may take a year or more for vulture populations to respond numerically through reproduction to increased resource availability because of the differing reproductive strategies between organisms. Therefore, the relative contribution of each group to decomposition should change once one consumer becomes numerically satiated.

MMEs could have wide reaching and long-lasting consequences to nutrient cycling if scale effects decomposition rate and the relative contribution scavengers to decomposition (Pechal et al. 2013). They may alter structure of the food web, which affects the transfer of nutrients and energy across trophic levels. If consumption rates moderate the amount of resources reaching soil and this rate differs between scavengers (Keenan et al. 2018), the relative importance of different scavengers could have cascading effects on soil properties, bacterial communities, plant communities, and subterranean fauna (Towne 2000). If decomposers become satiated because of the abnormally high amount of carrion biomass, the ratio of scavenger abundance to carrion biomass will decrease, most likely leading to decreased decomposition rates. Contrastingly, an increase in carrion biomass past the capability of consumers to respond numerically may increase per capita efficiency of scavengers by relaxing intra- and interspecific competition allowing individuals to decompose more efficiently. But even then, per capita increases in scavenger efficiency cannot overcome inundation at extreme levels of carrion biomass.
Empirical observations of bottom-up effects of increasing carrion biomass across trophic levels

We have an ongoing carrion experiment where we manipulated carrion biomass by carcass addition and scavenger access (see Lashley et al. 2018a for study design details). In this experiment, we have been documenting the bottom-up effects on much of the carrion food web. The number of species we documented interacting in the carrion food web increased with carcass biomass (Fig. 2.1). As presented by Lashley et al. (2018a), blowfly larvae attracted secondary consumers as the number of larvae colonizing carcasses increased with carrion biomass. When a single carcass was available, we detected a three-node food web including vertebrate scavengers (vultures), necrophagous decomposers, and their predators (Silphid beetles; Fig. 2.1A). Increasing the amount of carrion biomass by approximately 7-fold resulted in the addition of a fourth node (i.e. insectivorous birds and anoles, Anolis carolinensis; Fig. 2.1B). Quadrupling the carrion biomass yet again (i.e. nearly 30-fold the smallest biomass) further increased the richness within the fourth node with bald-faced hornets (Dolichovespula maculata) and armadillos (Lashley et al. 2018a, Fig. 2.1C). Although, this work is preliminary and only includes 5 points in carrion biomass, these observations are consistent with the prediction that increasing abundance of carrion resources increases the diversity of participation in the carrion food web both within and across trophic levels.

Several common food web interactions documented above, such as vultures and blowflies (Fig. 2.1A), have been frequently reported in the literature (DeVault et al. 2003, Tomberlin et al. 2017). Less common interactions, such as insectivorous birds, anoles, hornets, and armadillos feeding on necrophagous insects, have seldom been reported (Moreno-Opo and Margalida 2013, Lashley et al. 2018a). Also, at the highest biomass, we observed a hummingbird moth (Hemaris
sp.; Fig. 2.1C) feeding on carrion fluids, which to our knowledge, has never been reported in the carrion food web. The increasing diversity of interactions support the prediction of a positive relationship between magnitude and carrion food web complexity. Moreover, diversity increases with nestedness of common and uncommon species similar to that reported in Selva and Fortuna (2007). No species in assemblages at low biomass sites were lost with higher biomass, but novel species were added to the assemblage as carrion biomass increased.

**Theoretical carrion food web, hypotheses, and predictions**

Using empirical observations from our work and previous literature, we developed a conceptual representation of what we predict happens in a carrion food web as carrion biomass increases (Fig. 2.2). Relatively low levels of carrion biomass only attract scavengers (Fig. 2.2A and B). Increasing biomass further increases horizontal food web diversity, and as a result of increased consumer diversity, both levels of carrion reach the end of decomposition in a similar amount of time (Fig. 2.2A and B). Once carrion biomass reaches a level that supports greater vertical diversity in the carrion food web, secondary consumers then limit decomposition efficiency indirectly by numerically and/or behaviorally suppressing scavengers (Fig. 2.2C). At that point, increasing carrion biomass also results in a longer decomposition, which positively feeds back into greater horizontal diversity by allowing less specialized species to detect and invade carrion. Finally, once carrion reaches extreme levels that begin inundating scavengers, decomposition is slowed and horizontal diversity increases including other interactions in the carrion food web (Figure 2.2D).
Moving forward

Because MMEs are increasing (Fey et al. 2015), there is growing concern over the consequences of such large-scale disturbances to ecosystem function. Understanding how ecological interactions respond to increasing biomass will be essential to understand those consequences. Ecosystem responses might depend on the number and density of carrion, and species not previously thought to be involved in carrion recycling might interact at higher levels of biomass. Evaluation of differences between the same biomass quantity and different surface area to volume ratio needs to be investigated so that we can have more generalizable conclusions about the carrion-based food web across study designs. Moreover, our understanding of how vertical diversity affects carrion decomposition and the cycle of nutrients is still weak because of the lack of empirical data. In particular, effects of vertical food web diversity on carrion recycling efficiency are lacking. Also, we were unable to find any data about predator effects on foraging behavior of consumers in a mass mortality context. Interestingly, emerging literature indicates that prey's perception of nutrients changes with predation risk, which could affect how they specialize and when they decide to leave carrion behind (McMahon et al. 2018). Similarly, predators may affect the decomposition process by altering consumer activity patterns, which could also change the way that consumers interact through competition or facilitation. We suggest integrating new techniques such as camera trapping to document rare interactions (e.g., Baruzzi et al. 2017; Cove et al. 2017a and 2017b) or identify factors influencing scavenger activity patterns (Lashley et al. 2018b). Moreover, isotopic labeling of carrion, eDNA, or other emerging technologies may be helpful in understanding how organisms are interacting and how nutrients from carrion are transferring through or across ecosystems. Embracing new
technologies and approaches are critical to expand our understanding of how increasing carrion inputs will affect ecosystems.
Figure 2.1 Increasing biomass and food webs interactions

Interaction strength and number of nodes change with carrion biomass (increasing from panels A-C) in theoretical food webs. Arrow direction indicates positive interactions and line size represents strength. Solid lines represent direct interactions, dotted lines indirect. Reciprocal negative interactions and most indirect interactions are omitted for clarity, but competition between vultures and Calliphoridae larvae are described because this relationship fluctuates with carrion biomass levels. The first panel (a) depicts a single carcass, three node food web with necrophagous insects (Calliphoridae) and vertebrate scavengers (Vultures), as well as predatory beetles (Silphid). Biomass is increased sevenfold in the second panel, resulting in a four-node food web with the addition insectivorous birds and anoles (*Anolis carolinensis*). Interactions in the first food web are strengthened in the second, with the exception of the dampened reciprocal, negative interaction between vultures and fly larvae. The final panel depicts a food web with even more carrion biomass (nearly 30-fold the single carrion treatment) and the addition of armadillos (*Dasypus novemcinctus*) and bald-faced hornets (*Dolichovespula maculata*) to the fourth node. Again, interactions present in previous food webs are amplified.
Figure 2.2   Predicted carrion food web and decomposition time

Predicted responses of the carrion food web (curves) and decomposition time to increasing carrion biomass. The solid line indicates the relative level of carrion biomass where it intersects the y-axis and the relative time for full decomposition where it intersects the x-axis. At low carrion biomass (panel A), horizontal food web diversity and abundance is relatively low. Increasing carrion biomass increases the bottom-up strength which increases horizontal food web diversity and abundance that as a result increases decomposition rate (panel B). At some point, increasing carrion biomass strengthens bottom-up effects so that vertical food web diversity increases (panel C) which results in decreased scavenger efficiency and lengthens the time to full decomposition. Further increasing biomass eventually reaches a level (broken horizontal line) in which consumers become numerically satiated (panel D), which has an additive effect to increasing vertical diversity on lengthening decomposition time and carrion resources persist for enough time that rare species begin interacting in the carrion food web.
References


CHAPTER III
FUNCTIONAL ROLE IMPAIRMENT MEDIATES THE EFFECTS OF MASS MORTALITY EVENTS ON PLANT COMMUNITIES

Mass mortality events (MMEs) are die-offs that generate a substantial input of carrion into an ecosystem (e.g. Subalusky et al. 2017, Kock et al. 2018) and simultaneously impair or remove the functional role of the species affected (e.g. Holdo et al. 2009; but see Kuempel and Altieri 2017). For example, some MMEs have produced hundreds of tons of carrion biomass with the deaths of millions of individuals over relatively short time periods and these events seem to be increasingly common (Fey et al. 2015). Most studies of MMEs focus on causes and population dynamics of the species affected (e.g., Frick et al 2010, De Wit et al. 2014). Of the studies that do consider the ecological effects of MMEs, they tend to focus on the carrion serving as a resource pulse that increases the strength of bottom-up forces (e.g., Subalusky et al. 2017) or on the ecological consequences of the impaired functional role occurring during MMEs (e.g., Schultz et al. 2016). However, to date, literature considering the relative importance of both bottom-up and top-down forces are scant (but see, Hodge 2019). To further complicate the ecological consequences of MMEs, most obligate scavenger species, which are among the most efficient carrion recyclers, are globally declining (Ogada et al. 2012, O'Bryan et al. 2019). Thus, MMEs occurring in the Anthropocene have an added layer of complexity because top-down control in the carrion food web is also impaired, albeit for reasons unrelated to the MME. How
declines in obligate vertebrate scavengers factor into the net effects of an MME remains unknown.

We simulated a mass mortality of herbivores by combining additions of donated feral swine (*Sus scrofa*) carcasses and fencing to impair the vertebrate scavenger and herbivore functional roles. Vertebrate scavenger exclosures were used to simulate vulture decline while herbivore exclosures were used to simulate the effects of an herbivore die-off. We designed this experiment to evaluate the relative importance of strengthening bottom-up forces (i.e., nutrient addition) and simultaneously impaired top-down control (i.e., loss of herbivore functional role and loss of obligate scavenger role) on the indirect effects of carrion on the local plant community. Plants are affected by MMEs directly through carrion-induced mortality (Towne 2000, Carter et al. 2007), and indirectly by affecting primary and secondary consumers that contribute to important processes such as seed dispersal (Steyaert et al. 2018) and potentially altering habitat conditions through soil disturbance (Lashley et al. 2018). Carrion may also cause a resource pulse of nutrients percolating into the soil, which affects plant growth, competition, and herbivore preference (Yang 2008 and 2013, Turner 2014).

We tested four hypotheses to reveal the relative importance of bottom-up and top-down mediated effects of MMEs on the plant community. First, we tested the hypothesis that the effects of carrion on the plant community would increase as the biomass of carrion increased (H1). Second, we tested the hypothesis that, if the effects of carrion on the plant community are primarily from bottom-up control, adding a similar amount of the primary nutrients affecting plant growth (i.e., N, P, and K) to plots would produce the same effects as the carrion (H2). Third, we tested the hypothesis that the net effects of carrion on the plant community would be mediated from the top-down by vertebrate obligate scavengers because they reduce the duration
of carrion and remove nutrients from the site (H3). Finally, we hypothesized that herbivores would mediate the net effects of carrion on plant community by limiting plant growth and reducing survival rates of individual plant species in the community because increased plant nutrient quality could affect herbivore selection. We predicted that carrion would have a greater effect on the plant community as carrion biomass increased and that those effects would be exacerbated by the impairment of the scavenger and herbivore functional roles.

We used a before-after control-impact study design, selecting six plots in each of five loblolly pine (Pinus taeda) forest stands separated by at least 1km (sites) to test each hypothesis. In each site, we established treatments fully crossing carrion addition, nutrient addition, and controls with scavenger and herbivore access to isolate the role of bottom-up and top-down forces on the surrounding plant community. Before adding carrion or nutrients to impact plots, we sampled initial conditions of the plant community at the ground level in all plots (see methods for details). We then added a gradient in carrion biomass (i.e. 25, 60, 180, 360, and 725 kg) to plots across sites to test H1, and the analogous amount of nutrients (i.e. N, P, K) were added across sites to test H2 (see methods for details). In each site, one of the two plots in each treatment pair was fenced to exclude vertebrate scavengers effectively isolating the top-down effects of vertebrate scavengers (i.e., H3). Scavenger fences were removed and plots were split with fencing to exclude herbivores from half of each plot to isolate the top-down effects of an impaired herbivore functional role to test H4 at the beginning of the next growing season (see Supplementary Information 1). We examined the bottom-up and top-down roles of MMEs on plant communities in two ways. First, approximately one, two, and three years post treatment, we resampled plant communities to determine the effects of carrion on changes in plant functional group dominance. Second, we transplanted six 1-year old cherrybark oak (Quercus pagoda)
seedlings to each plot systematically locating 3 inside and three outside of herbivore exclosures all approximately 1m from the nearest seedling and each 1.5 meter from plot center. We measured the growth and survival rate after three years of exposure to the treatment.

Our multivariate regression analyses revealed different forces affected plant functional groups over the years. For the two years following carrion deployment, increasing carrion biomass shifted the dominance of plant functional groups only when interacting with scavenger access ($p = 0.03$; Table A.1) in support of $H_1$ and $H_3$. Univariate regression models for individual functional groups show that perennial vines were positively affected by scavenger access at carrion addition plots ($p = 0.01$; Table A.2). Annual forbs were also positively affected by biomass increase ($p = 0.01$), but irrespectively of scavenger access (Fig. 3.1; Table A.2). Three years after carrion deployment, carrion biomass significantly affected plant functional groups independently ($p = 0.005$) and when interacting with herbivores ($p = 0.02$; Figure 3.2; Table A.3) in contrast to $H_3$ but in support of $H_1$ and $H_4$. While perennial vines decreased at highest carrion biomass levels ($p = 0.015$), annual forbs increased ($p = 0.04$; Figure 3.2; Table A.3). Herbivore access had opposite effects on perennial forbs and grasses. They positively affected perennial forbs ($p = 0.025$) and this effect increased with carrion biomass ($p = 0.045$), while grasses decreased at high carrion biomass levels when herbivores were excluded ($p = 0.02$; Figure 3.2; Table A.4). Scavengers did not have a significant effect on the plant community three years after carrion deployment ($p = 0.39$, Table A.3), although univariate regression models on trees and annual forbs revealed a scavenger effect. Tree seedling abundance decreased at plots without scavengers and their decrease was steeper where herbivores had access to the plots. Annual forb abundance decreased at lower rates at plots where scavengers had access to carrion ($p = 0.035$; Table A.4). Nutrient additions had no effect on plant communities over the years (Table A.1 and
A.3), which supports that the effects of carrion biomass on the plant community are not mediated by the bottom-up effects of nutrients percolating into the soil but by consumer interactions with carrion and the plant community. As predicted, our data collectively indicate that the impairment of the vertebrate scavenger and herbivore functional roles exacerbated the effects of increasing carrion biomass on change in functional role dominance in the plant community. In contrast, carrion addition, nutrient addition nor the presence of vertebrate scavengers affected the survival (Table A.5) or growth of transplanted seedlings (Table A.6). However, herbivore exclosure was related to increased survival (Figure 3.3; Table A.5) and growth (Figure 3.4; Table A.) in support of H4 irrespective of the other treatments.

Our data support the idea that the scale of MME biomass affects the local plant community but that effect was apparently not due to increasing nutrient loads being released from carrion. This suggests that carrion biomass was indirectly changing the plant community by affecting consumer interactions in the food web. Baruzzi et al. (2018) suggested that increasing carrion biomass is expected to increase carrion food web diversity. Similarly, Lashley et al. (2018) suggest one pathway for which this could occur when they reported that blowfly larvae occurrence increased with increasing carrion biomass, which attracted an insectivore causing elevated soil disturbance from foraging. These effects were exacerbated by the exclusion of obligate vertebrate scavengers (Lashley et al. 2018). Interestingly, obligate vertebrate scavengers do not directly affect plants but may do so indirectly by competing with invertebrate obligate scavengers that are prey for secondary consumers. Perennial vines were initially facilitated by scavenger consumption of carrion most likely because soil disturbance was reduced when scavengers had access to remove substantial proportion of the carrion. Similarly, soil disturbance commonly promotes colonization by annual plants (Herben et al. 2018) and annual forbs were
the primary group we observed to increase in dominance as a function of carrion biomass. Differences in top-down influences between 2017-2018 and 2019 might be explained by herbivore site use. In fact, herbivores might initially avoid carrion sites to elude predators (Cortés-Avizanda et al. 2009) or disease transmission (Weinstein et al. 2018). If that was the case, our excluding them from plots would not have a strong overall effect on the community. It is possible that by year three, herbivores were no longer avoiding and may have even been attracted to carrion plots because of the more nutritious plants in the community (Yang 2008). So, restricting herbivore access may have become more important overtime than scavenger access. After three years, the impaired herbivore functional role did directly affect plants. Where herbivores were excluded, grasses decreased and forbs increased in abundance, which likely reflects the selection by the large herbivore species at our sites, white-tailed deer, *Odocoileus virginianus* (Berry et al. 2019). The impairment of the herbivore functional role from herbivore MMEs is likely to produce a primary effect on plant communities as illustrated by growth and survival rate of transplanted seedlings in our study that were only affected by herbivore access.

We acknowledge the lack of replication and relatively small biomass scale for simulating a real MME is a flaw in our study. Though both factors limit the generalizability of our results to all MMEs, we believe our study represents an important initial step in understanding how MMEs affect complex systems. We encourage researchers to further develop studies on MMEs in order to develop a more holistic framework to better understand MMEs within a broader context.
Methods

Study area and experimental set-up

In 2016, we established a carrion deployment experiment in a managed loblolly pine (Pinus taeda) forest, John Starr forest, Starkville, MS. We selected five study sites, each of them including 6 ~20 m² plots (5m diameter). Sites were at least 1km apart. We selected two plots per site with the treatments 1) control, 2) nutrient, or 3) carrion addition, and fenced one plot per treatment preventing access to vertebrate scavengers. Fences were built using wire mesh on the plot circumference, and placing plastic mesh on top. We deployed an increasing amount of feral swine (Sus scrofa) carrion biomass (i.e. 25, 60, 180, 360, and 725 kg) and nutrients (i.e. nitrogen [0.65, 1.53, 4.72, 9.43, and 18.87 kg], phosphorus [0.15, 0.35, 1.08, 2.17, and 4.35 kg], and potassium [0.07, 0.17, 0.53, 1.05, and 2.1 kg]) across sites. Carrion was donated by local landowners conducting feral swine eradication campaigns so no culling was conducted for the purpose of this experiment. We selected nitrogen, phosphorus, and potassium as nutrients because they are present in carrion (Carter et al. 2007, Bump et al. 2009) and they are limiting macronutrients for plants (Bump et al 2009). The amount of nutrients deployed at each plot was calculated based on data provided in Carter et al. (2007), which define the percentage of nitrogen, phosphorus, and potassium available in S. scrofa carrion (respectively, 2.6%, 0.6%, and 0.29%).

In March 2017, for monitoring plant growth and survival, we planted 6 one-year-old cherrybark oak seedlings per plot at approximately 1.5m distance from the plot center. Seedlings were grown in a tree farm in Mississippi during the previous growing season and randomly selected for the transplant. In order to detangle herbivory and scavenger exclusion effects, we removed the fences established in 2016 and we placed wire mesh fencing half of each plot to
exclude vertebrate herbivores (Figure A.1). At every plot, half of the seedlings have been planted inside the herbivore exclosure. Each seedling was marked with flagging tape, which was labelled with a unique identification number.

Data collection

To test $H_1$ through $H_3$, we collected preliminary data on plant communities using three 10m transects staring at the center of each plot and facing north, southeast, and southwest before carrion and nutrient deployment. Marking flags were left at the center of each plot and at the end of each transect in order to signal transect position for future samplings. We recorded every understory plant species touching the transect tape (Figure A.1). Individuals were identified to the lowest taxonomic rank. We sampled plant communities for two years (i.e. 2017 and 2018) after treatments had been applied approximately during the same period the preliminary data have been collected (i.e. between July and August). To test $H_1$ through $H_4$, we collected data on plant growth, survival, and communities. Initial oak seedling height was measured at planting and final height in July 2019, where we also recorded seedling fate (i.e. dead or alive).

Vegetation community was sampled in July 2019 by placing three 80cm² quadrats between 1.5m (n=2, along each side of the diameter) and 1m (n=1, central) from plot center inside and outside of each herbivore exclosure (Figure A.1). We recorded every plant species and number of individuals originating within the quadrat.

Data analysis

All statistical analysis was run in R (version 3.5.1, R Core Team, 2018) and significance level was set at 0.05. To test $H_1$, through $H_3$, we divided sampled individuals in 8 plant functional groups: annual forbs, annual vines, graminoids, perennial forbs, perennial vines,
grasses, shrubs, and trees. We decided to analyze plant functional groups because they ease detection of patterns and generalization of results (Duckworth et al. 2000). Growth form and length of life cycle were verified using the USDA PLANTS Database (https://plants.sc.egov.usda.gov/java/) for every individual. We categorized any species that could exhibit annual life cycles as annual. Species that could adopt both perennial and biannual life cycles were categorized as perennial. In case species could adopt multiple growth forms, we listed that species according to the most common growth form recorded at our study sites. From over 3119 individuals recorded, 7 unknown individuals were removed from the dataset. We also removed Desmodium spp. (n= 24), Galium spp. (n= 5), and Symphyotrichum spp. (n= 4) because they have been identified down the genus level and both annual and perennial species within the genus were present in Mississippi. The mvabund package (Wang et al. 2019) was used to test treatment significance. First, we used the function manyglm, which enabled us to fit a generalized linear model (glm) for every functional group (Wang et al. 2012). We used functional group counts as response variable, and carrion biomass level, nutrient level, scavenger exclosure, and interactions between scavenger exclosure and carrion biomass level or nutrient level as independent variables. To determine which distribution was the most appropriate to fit our data, we compared two models fitting a Poisson and a negative binomial distribution and examined the residual plots. Because the negative binomial distribution was a better fit for our data (Supplementary Information 8), it was used to proceed with hypothesis testing using the anova.manyglm function with restricted permutations, which enabled us to fit glms to multivariate data (Wang et al. 2012). To account for temporal and spatial autocorrelation, we used two level restricted permutations (i.e. site and plot; permute package, Simpson 2019). We set the number of permutations at 1999. Finally, we also used the anova.manyglm function for
testing independent variable effects on individual functional groups in order to determine which functional groups influenced the most vegetation community changes.

We examined the effects of herbivory and carrion deployment on plant functional groups to test \( H_1 \) through \( H_4 \) following a similar procedure from the previous community analysis. Individuals were divided within 8 functional groups and listed according to the most common growth form recorded at our study sites if a case of multiple growth forms per species. Out of 731 observations, 3 unknowns were discarded from the dataset. \textit{Galium spp.} (\( n = 7 \)), \textit{Viola spp.} (\( n = 2 \)), \textit{Symphyotrichum spp.} (\( n = 1 \)), and \textit{Polygala sp.} (\( n = 1 \)) were also removed from the analysis because annual and perennial species were present in Mississippi within the same genus and individuals have been identified up to the genus level. To test our hypotheses, we fitted a Poisson and a negative binomial distribution with the \texttt{mvabund} package using functional group count as response variable and biomass level, nutrient level, scavenger exclosure, herbivore exclosure, and interactions between biomass level and scavenger exclosure and herbivore exclosure as independent variables. Residual plots showed that a negative binomial distribution was more appropriate to model our data (Supplementary Information 8). Hypothesis testing was conducted with the \texttt{anova.manyglm} function, where we used site and plot as levels of restricted permutations to take into account spatial autocorrelation among samples. Number of permutations was set at 1999.

For investigating differences in seedling growth, we built a set of linear mixed models using \texttt{lmer} function in \texttt{lme4} package (Bates et al. 2015). We used a linear model because the difference between final and initial height was used as response variable and some of the seedlings presented negative growth, probably due to herbivory or trampling. Assumptions were tested with residuals and Q-Q plots. All the possible combinations of the following independent
variables were tested: carrion biomass level, nutrient level, scavenger exclosure, herbivore exclosure, and interactions between carrion biomass and scavenger exclosure or carrion biomass and herbivore exclosure. Plot or plot nested within site were treated as random effects, each of them tested with all the possible combinations of independent variables. We compared the models based on AIC weight (model.sel function in the MuMIn package, Bartoń 2019). All models within 2ΔAIC from the first top ranked model were considered as competing models.

Effects of our experimental treatments on seedling survival were tested comparing a set of mixed effect cox proportional hazards regression models (coxme package, Therneau 2019; coxme function). Seedling state was used as the response variable, while biomass level, nutrient level, scavenger exclosure, herbivore exclosure, and interactions between biomass and scavenger exclosure or biomass and herbivore exclosure were treated as independent variables. Plot or plot nested within site were treated as random effects. Models were compared with the model.sel function in the MuMIn package. We considered as competing models all models within 2ΔAIC of the top ranked model.
Figure 3.1 Scavenger and carrion biomass influence on plant functional groups

Changes in plant functional group abundance across carrion biomass levels a) with scavengers and b) without scavengers. The functional groups that responded to carrion biomass increase and scavengers (bolded in the figure) were perennial vines and annual forbs. Annual forbs increased with carrion biomass the year after the deployment. Perennial vines abundance was higher when scavengers were present at carrion plots. Plots were created using the function traitglm in the mvabund package (Wang et al. 2019), which fits a four-corner model using environmental...
variables (i.e. carrion biomass) as independent variables and using model coefficients for coloring the heatmaps.

![Figure 3.2](image)

**Figure 3.2**  Herbivore and carrion biomass influence on plant functional groups

Changes in plant functional groups across carrion biomass levels a) with herbivores and b) without herbivores. Among the functional groups that responded to carrion biomass increase and herbivores (bolded in the figure): perennial vines were negatively affected by increase in carrion biomass either with or without herbivores while annual forbs were positively affected by carrion biomass with or without herbivores. Perennial forbs and grasses showed an opposite pattern: grass abundance decreased while perennial forb abundance increased with greater biomass where herbivores were excluded. Plots were created using the function traitglm in the mvabund package (Wang et al. 2019), which fits a four-corner model using environmental variables (i.e. carrion biomass) as independent variables and using model coefficients for coloring the heatmaps.
Figure 3.3  Cherrybark oak seedling survival

Number of alive seedlings at a) carrion, b) nutrients, and c) control plots across our experimental sites. Herbivore exclosure increased seedlings survival, which was not affected by other variables.

Figure 3.4  Cherrybark oak seedling growth

Growth (cm) differences between fenced and unfenced seedlings in: a) carrion, b) nutrients, and c) control plots across experimental sites. Seedlings exposed to herbivory showed growth, while treatments did not affect seeding growth.
References


Method References


CHAPTER IV
MASS MORTALITY EVENTS AND DECLINING OBLIGATE SCAVENGERS IN THE ANTHROPOCENE: CONSERVATION OF SOCIAL SCAVENGERS THE MAY BE CRITICAL

Introduction

An understudied aspect of global change is the increasing frequency of mass morality events (MMEs) across a wide range of taxa (Fey et al. 2015). Mass morality events are catastrophic demographic events characterized by high numbers of individuals dying in a specific location over a short period of time (Fey et al. 2015). These events are increasing globally in connection with climate change and habitat loss (Wilson and Wolkovich 2011, Fey et al. 2015, DeVault et al. 2016). The carrion pulses produced during MMEs can alter community dynamics, and the magnitude of their indirect effects is largely mediated by carrion consumption by obligate scavengers (Tomberlin et al. 2017, Lashley et al. 2018a). Concurrently, vultures are declining globally (Buechley and Şekercioğlu 2016, Ogada et al. 2012b and 2016, Santangeli et al. 2019), which could exacerbate the effects of MMEs on ecosystems.

New and Old World vultures play a fundamental role in maintaining carrion recycling efficiency (Şekercioğlu 2006, DeVault et al. 2016, Mateo-Tomás et al. 2017). Their behavioral and physiological adaptations allow them to maximize carrion detection and consumption, which in general makes them more efficient recyclers than vertebrate facultative scavengers (Ogada 2012a, Moleón et al. 2014, Hill et al. 2018, O'Bryan et al. 2019). For this reason, the total or
partial loss of the vulture functional role as obligate scavengers from an ecosystem could exacerbate the effects of MMEs on communities despite the potential release of facultative scavenger populations to fill the scavenging role (Ogada et al. 2012a, O'Bryan et al. 2019, Santangeli et al. 2019). Though vultures are declining, their abundance is not the only factor affecting their recycling efficiency. Intra- and inter-specific competition could also affect carrion consumption because resource availability modulates competition (e.g., in plants: Wilson and Tilman 1993, Fynn et al. 2005; in animals: Pimm and Pimm 1982, Odadi et al. 2011, Fattorini et al. 2018). Resource pulses are characterized by short-lived resource peaks (Holt 2008, Yang et al. 2008, Jentsch and White 2019) and the high resource input during these peaks may weaken competition via satiation (Williams and Simon 1995, Satake et al. 2004, Yang et al. 2008) or concentrate consumers intensifying antagonistic interactions (Chesson et al. 2004, Holt 2008, Yang et al. 2013). Behavioral aggregative responses are characteristic of resource pulses (Holt 2008, Yang et al. 2008) and should occur following the abrupt entry of large amounts of carrion produced during MMEs. However, though increasing amounts of carrion may be easier to locate and last longer in the environment leading to increased availability for facultative scavengers (Baruzzi et al. 2018), it is relatively unknown how increasing carrion biomass affects consumption rates among vultures.

We designed a carrion addition experiment with increasing levels of carrion biomass to test the hypothesis that increasing carrion biomass would relax intra and interspecific competition and ultimately lead to more efficient carrion consumption by vultures. In our experiment, black (Coragyps atratus) and turkey (Cathartes aura) vultures were the obligate vertebrate scavengers. Although populations of both species are increasing and listed as least concern on the IUCN Red List of Threatened Species (Ogada et al. 2012b), they may make good
model species to understand the consequences of the global declining trend in this functional role because the differences in their life history encapsulate the feeding behaviors of other threatened vulture taxa (i.e., black vultures are social while turkey vultures tend to feed solitary or in smaller groups; Houston 1986, Holland et al. 2017). We selected three behaviors easily monitored with camera traps that could determine changes in intra-and inter-specific competition affecting carrion consumption: 1) grouping behavior, 2) number of individuals feeding within a group, and 3) diel overlap of activity of carrion use between species. Vulture group size can affect competition and individual foraging (Bosè and Sarrazin 2007, Cortés-Avizanda et al. 2012, Duriez et al. 2012). The number of individuals feeding within groups often indicates the strength of competition because animals have a tradeoff between time spent feeding and monitoring competitors (Beauchamp 2019). Finally, turkey vultures generally avoid feeding with black vultures, especially in large groups (Buckley 1996), so increasing activity overlap of carrion use between the two species indicate a relaxing of interspecific competition due to lower antagonistic interactions (Kronfeld-Schor and Dayan 2003). Because adult vultures lack predators we assumed that their behavior was not driven by avoidance of predation (Kirk and Houston 1995). Furthermore, vultures are diurnal in activity, so there remains little influence of or interactions with nocturnal facultative scavengers (e.g., generalist mesopredators; Houston 1986). We expected black and turkey vultures to be constrained by their life history and would differ in their responses to increasing carrion biomass. As such, we predicted that, with increasing carrion biomass: 1) black vulture group size would increase but turkey vulture group size would not be affected; 2) the number of turkey vultures feeding would not be affected but the number of black vultures feeding would increase due to their solitary and social feeding
habits, respectively; and 3) activity overlap between the two species would increase with increasing carrion biomass because of reduced interspecific antagonism.

Methods

On July 5, 2016, we deployed five levels of feral pig (*Sus scrofa*) carrion biomass (i.e., 25, 60, 180, 360, 725 kg) in five plots (5m diameter) with plots being 3 or more km apart on John Starr Forest located in Oktibbeha County, Mississippi, USA. All plots were located in loblolly pine (*Pinus taeda*) forests between 25 and 30 years old. All feral swine carcasses were donated by local private landowners so no feral swine were euthanized or otherwise harmed for the purposes of this experiment. Feral swine are invasive and cause ecological and economical damage (Barrios-Garcia and Ballari 2012). Private landowners were actively euthanizing feral swine for the purpose of alleviating damages on their property. Carrion was frozen and stored between 3 and 6 months before the deployment. It is probable that each plot was within the same vulture population based on black and turkey vulture home ranges (monthly home range for turkey vultures: ~60 km$^2$ and black vultures: ~30 km$^2$; Holland et al. 2017). Thus, we assumed that any change in vulture behavior was in response to the experimentally manipulated resource availability and not to characteristics unique to a particular population. Moreover, we deployed all carrion on the same day, in similar forests structure, and in the same populations to avoid differences in biotic and abiotic conditions that could have affected vulture responses. We placed a camera trap (Bushnell Trophy Cam, Bushnell Outdoor Products, Overland Park, KS) 0.5m above the ground and 1.5m from carrion to monitor each plot. Camera traps were set to capture still frame images when triggered by motion sensor with 1 min delay, which was determined an appropriate setting to monitor vertebrate scavenger foraging (Turner et al. 2017). From each picture, we recorded time and date, the number of turkey and black vultures present, and the
number of individuals of each species foraging as indicated by their head in contact with carrion. In the case that an individual or the head position was not clearly identifiable, the observation was excluded from analyses.

**Analysis**

We analyzed vulture detections during the first 4 days after carrion deployment. In this period, vultures were detected every day at the 725kg biomass plot, 3 days at the 360kg biomass plot, 2 days at the 180kg biomass plot, and only one day at the 25kg biomass plot. No vultures were detected at day 0 which is in accordance with other studies showing that, depending on canopy cover, carrion is generally detected within a few days from the deployment independent of carrion biomass (e.g., Houston 1986, Rabenold 1987, Houston 1988, Hill et al. 2018). A few vultures sporadically visited some of the plots after day 5. These data were removed in the analyses because active decomposition was already completed. Due to changes in habitat management practices (i.e., forest thinning) that could have affected the ability of vultures to locate carrion, we removed one plot from the analysis (i.e., 60 kg). All statistical analyses were run in R (version 3.5.1, R Core Team, 2018) and \( \alpha \) was set at 0.05.

**Modelling group size responses**

To determine the effects of carrion biomass on group size, we used the maximum number of individuals detected of each species during each hour as our response variable within a periodic regression fitting a Poisson distribution. Using a periodic regression approach allowed us to account for the lack of recognizable individuals, temporal correlation and daily fluctuations (e.g., night and day) among detections. In order to select the set of covariates that better represented our data, we built a set of competing models for each species based on our
experimental design and previous literature investigating vulture behavior (e.g., Prior and Weatherhead 1991, Kirk and Currrall 1994). To account for multicollinearity, we calculated Spearman’s rank correlation coefficient using the ‘Performance Analytics’ package (Peterson and Carl 2019) for each pair of the following independent variables: 1) carrion biomass, 2) turkey or black vulture group size, and 3) days from deployment. We used Spearman’s rank correlation coefficient because the data were non-normally distributed (Hauke and Kossowski 2011). No pairs had $r > 0.5$, which is generally considered as an acceptable threshold for variable correlation (Mukaka 2012), so we used all the possible combinations of the above-mentioned independent variables and hourly periodicity (Figure B.1) in our models. We decided to include days from deployment as one of the covariates to account for variation in carrion biomass due to consumption throughout the data collection period. Number of individuals of the other species present was included to incorporate interspecific competition effects. Finally, to describe the hourly periodicity that better represented each species group size, we used a set of periodicities similar to Engman et al. (2017): 1) no periodicity in group size; 2) 1 peak in group size, with $\sin(h)$ and $\cos(h)$; 3) 2 even peaks in group size, with $\sin(2h)$ and $\cos(2h)$; 4) 2 uneven peaks in group size, with $\sin(h)$, $\cos(h)$, and $\sin(2h)$; 5) 2 uneven peaks in group size, with terms $\sin(h)$, $\cos(h)$, and $\cos(2h)$. We used nlme package (Pinheiro et al. 2018) for building all models (see Table 4.1 and 4.2 for a list of competing models). We ranked all competing models for each species according to their Akaike Information Criterion (AIC) (Akaike 1974), within the ‘AICmodavg’ package (Mazerolle 2017). We considered models to have substantial support if they were within $2 > \Delta AIC$ of the top ranked model.
Modelling feeding responses

An analogous procedure was followed for creating and ranking models for determining the effects of carrion biomass on the number of turkey and black vultures feeding at carrion plots. We used the highest number of individuals per species feeding per hour within a periodic regression fitting a Poisson distribution as the response variable. Candidate models had the following explanatory variables: 1) biomass, 2) days from deployment, 3) the highest number of individuals of the other species present per hour, 4) highest number of conspecifics present per hour, 5) interactions between (1) and (3), and 6) the five periodicity types listed previously. We included number of conspecifics present as an independent variable because it was previously determined to be an important factor determining number of individuals feeding (Houston 1988, Prior and Weatherhead 1991, Buckley 1996). Because Spearman’s rank correlation coefficient was higher than 0.5 for black and turkey vulture group size (Figure B.1) we did not test models simultaneously containing black and turkey vulture group size. All other possible combinations of independent variables were compared and model selection followed the previous information-theoretic approach.

Modelling activity pattern overlap

We performed an overlap analysis to investigate the effect of increasing carrion biomass on diel activity pattern of black and turkey vultures to determine how the species partition resource use temporally as a function of carrion biomass. We estimated an overlap coefficient (Δ) of the daily activity of the two species at each plot, which ranges from 0 (opposite activity cycles) to 1 (identical activity cycles), in the ‘overlap’ package (Ridout and Linkie, 2009). Furthermore, we calculated 95% confidence intervals based on 1000 bootstraps for each overlap coefficient plot.
Cumulative vulture feeding minutes and estimating carrion consumption estimates

We used two methods to estimate how much carrion biomass each species could remove from a plot: 1) we calculated the per species cumulative feeding minutes and 2) we estimated carrion consumption based on the per species minimum number of unique vultures that visited the plots each day (i.e., largest group size detected each day) multiplied by the individual intake. We acknowledge that individual intake could vary markedly among individuals due to several factors such as degree of hunger and social status (Houston 1988). However, we were not able to find any established methodology to better estimate carrion removal, which has been previously defined impossible to measure in the field (Mendelssohn and Leshem 1983). We calculated the per species cumulative vulture feeding minutes by summing the number of detections for the entire sampling period of vultures in a feeding posture and in contact with carrion. A single detection could account for multiple feeding minutes if multiple individuals were detected and feeding. We estimated carrion consumption by multiplying the largest group size detected per day by daily intake. Because we could not uniquely identify individuals, the maximum group size detected was the most conservative estimate of the total number of vultures that visited on a given day. Further, because we could not directly measure consumption, we assumed that individuals consumed 13% of their body weight which was previously indicated as the amount of food consumed by a vulture each day (Hatch 1970, Mendelssohn and Leshem 1983). We used conservative estimates of body weight (i.e., 2kg for black vultures, Mahoney 1983; 1.25kg for turkey vultures, Arad 1988). These metrics should not be interpreted as absolute but instead we aimed to provide an estimate of consumption for comparison of relative consumption across carrion biomass between species. With that said, estimating carrion removal of each species in
this way may provide strong evidence for how the relative importance of the two species in
carrion recycling changes as carrion biomass is increased.

Results

The model best representing black vulture group size included all of our variables (Table 4.3). As predicted, black vulture group size increased with carrion biomass ($\beta = 0.005$, $z = 2.093$, $p = 0.036$). Interestingly, black vulture groups size also continued to increase with days from
deployment ($\beta = 0.17$, $z = 9.014$, $p < 0.001$) and number of turkey vultures present ($\beta = 1.28$, $z = 7.352$, $p < 0.001$; Figure 4.1a). Irregular periodicity (i.e., sin($h$), cos($h$), and cos(2$h$)) was supported in predicting black vulture group size which reflects vulture diurnal habits. However, the effect of turkey vultures on black vulture group size weakened as carrion biomass increased (Table 4.3).

There were three competing models to explain turkey vulture group size (Table 4.4). Each competing model indicated that black vulture group size (top-ranked model: ($\beta = 0.65$, $z = 6.2$; $p < 0.001$) and carrion biomass (top-ranked model: ($\beta = 0.002$, $z = 2.488$; $p = 0.013$) were positively related to turkey vulture group size (Figure 4.1b). The interactive effect decreased, however, with increasing carrion biomass and black vulture group size (top-ranked model: $\beta = -0.001$, $z = -3.332$; $p < 0.001$; Table 4.4). Days from deployment did not have an effect on turkey vulture group size. Two types of periodicities were supported by the competing models (i.e., sin($h$) and cos($h$) or sin($h$), cos($h$), and sin(2$h$)).

Detections of individuals feeding increased exponentially with biomass (i.e., 2, 29, 477, 2820 detections). The competing models for black vulture individuals feeding (Table 4.5) showed that biomass (top-ranked model: $\beta = 0.002$, $z = 3.727$; $p < 0.001$) and black vulture group
size (top-ranked model: $\beta = 0.28$, $z = 11.475$; $p < 0.001$) positively affected the number of black vultures feeding (Figure 3a). Irregular periodicity (i.e., $\sin(h)$, $\cos(h)$, and $\cos(2h)$) was supported to predict black vulture feeding activity, confirming the results obtained with the analysis on black vulture group size. Days from deployment and turkey vulture group size did not affect black vultures feeding.

Turkey vulture group size (top-ranked model: $\beta = 1.08$, $z = 11.445$; $p < 0.001$) was the only independent variable significantly affecting turkey vulture feeding in the competing models (Table 4.6) with a positive association (Figure 4.2). Irregular periodicity was also supported in the turkey vulture feeding model (i.e., $\sin(h)$, $\cos(h)$, and $\cos(2h)$).

We did not calculate overlap at plot 1 (i.e., 25kg) because no black vultures were detected at plot 1. Starting from 180kg of carrion, the overlap coefficient increased across the biomass gradient (i.e., $0.0005$ [95% bootstrapped confidence intervals: $-0.01$ – $0.01$], $0.64$ [95% bootstrapped confidence intervals: $0.59$ – $0.72$], $0.81$ [95% bootstrapped confidence intervals: $0.79$ – $0.85$]; Figure 4.3) indicating that competitive interactions that normally encourage temporal separation of foraging between these species was relaxed. Based on the higher probability density function values throughout the day for each species as carrion biomass increased, the increase in overlap seemed to be a function of both species utilizing carrion for a larger portion of the day as the amount of carrion biomass increased.

The relative contribution to consumption by each species changed as a function of increasing carrion biomass. Using the conservative consumption estimate, the relative importance of black vultures (i.e., 0kg, 1.04kg, 4.16kg, and 10.14kg) compared to turkey vultures (i.e., 0.16kg, 0.16kg, 1.63kg, and 1.95kg) was almost equal at our 25kg and 180kg plots, but approximately doubled and quintupled at the 360kg and 725kg plots, respectively.
Cumulative feeding minutes also show a disproportionate effect of black vultures (i.e., 0, 26, 323, 2242 detections) compared to turkey vultures (i.e., 2, 3, 125, 390 detections) at sites with greater biomass (Figure 4.4).

**Discussion**

The combination of increasing group size and more days of visitation by vultures led to a nonlinear increase in vulture feeding minutes and estimated carrion consumption as carrion biomass increased. This effect was primarily driven by the behavioral plasticity of the more social black vultures which is consistent with simulations by Buckley (1996), where black vultures increased food intake as carrion biomass increased. Buckley also predicted that turkey vulture food intake would be largely mediated by group size because of the more constrained life history traits. Our results may indicate that conservation of social obligate scavengers is particularly important to offset the conservation conundrum of simultaneously increasing MMEs and global obligate vertebrate scavenger declines. It should be noted that turkey vultures also contributed to increase consumption in this study by facilitating the detection of carrion by black vultures, which was not directly captured in our estimates of the relative importance of each species. Thus, while the relaxed life history constraints on feeding behavior allowed the social species to increase consumption with carrion biomass, the solitary species with a more efficient olfactory detection system was important in facilitating quick site colonization to do so.

Similar to predictions from Buckley (1996), group size increased with carrion biomass at lower rates for turkey vultures than black vultures. The same would likely be true for other social feeders such as cinereous (*Aegypius monachus*) and griffon (*Gyps fulvus*) vultures as their group sizes reportedly increases with carrion biomass (e.g., Houston 1988, Moreno-Opo et al. 2010, Duriez et al. 2012). Our data indicates intraspecific facilitation may have been a more important
factor influencing black vulture group size than carrion biomass. Facilitation via local enhancement (i.e. individual attraction to feeding birds) is important to black vultures because they frequently rely on visual detection of other scavengers congregating to locate carrion (Rabenold 1987, Buckley 1996, Jackson et al. 2008). The local enhancement effect may have been more important to explain vulture group size than carrion biomass because black vulture group size continued to increase with days since carrion deployment even though carrion biomass was decreasing over time at the site. If black vulture group size was solely driven by carrion biomass, we would have expected black vulture group size to decrease as carrion biomass decreased over time (Rabenold 1987). Contrastingly, turkey vultures typically rely on olfactory cues to detect carrion and tend to avoid feeding in large groups so they apparently did not respond to local enhancement in our study (Houston 1986, Grigg et al. 2017). Also, the facilitative effects of turkey vultures on black vultures decreased with increasing carrion biomass, suggesting that MMEs may reduce the importance of solitary obligate scavengers in the carrion food web. Likewise, as vulture species that rely on local enhancement for finding carrion decline (Jackson et al. 2008, Ogada et al 2012b), populations might reach a threshold where local enhancement collapses (Jackson et al. 2008). If that occurs, the compensatory effects of behavioral plasticity on recycling efficiency may also be lost. As such, with MMEs increasing, the worldwide trend in decline of obligate vertebrate scavengers should be a major cause of conservation concern (Buechley and Şekercioğlu 2016, Ogada et al. 2016, Santangeli et al. 2019).

Black vultures are tolerant towards conspecifics during feeding bouts (Prior and Weatherhead 1991, Buckley 1996) and this social behavior may allow them to increase feeding rates as carrion biomass increases. The same is likely true in other social feeders (e.g., griffon
vulture), which increase feeding rates as carrion availability increases (Bosè and Sarrazin
2007). Contrastingly, Prior and Weatherhead (1991) reported that turkey vultures are reluctant to
feed in close proximity to others. However, the number of turkey vultures feeding increased with
group size in our experiment but at a reduced rate relative to black vultures. Our observations
may contradict previous reports on turkey vulture behavior because of our experimental design.
That is, most studies focus on individual carcasses and increase carrion biomass by increasing
carcass size, whereas our experiment emulated an MME with a relatively high surface to volume
ratio in carrion biomass because we increased carrion biomass by increasing the number of
individual carcasses deployed. Increasing carrion biomass by increasing the number of individual
carcasses may therefore relax competition resulting in more individuals feeding at the same time.
As an alternative explanation, dominance displays affect the number of individuals feeding
(Duriez et al. 2012) and require more energy when multiple carcasses are present (Prior and
Weatherhead 1991) causing a trade-off between displays and feeding (Kirk and Houston 1995,
Duriez et al. 2012). Therefore, the atypically large amount of carrion biomass and carcasses
resulting from MMEs may relax competition by increasing the cost of dominance displays. In
reality, both mechanisms and possibly others not previously considered are likely contributing to
vulture foraging behavior in the unique context of MMEs.

Black and turkey vultures usually partition carrion use temporally and our observed
increase in activity pattern overlap with increasing carrion biomass further supports the
relaxation of competition. Time spent at a carrion plot is not necessarily associated with relaxed
competition because antagonistic interactions might cause individuals to take longer to satiate
and to spend more time at carcasses (Prior and Weatherhead 1991). However, in our experiment
not only did both species spend more time at carrion sites as carrion biomass increased, a higher
number of individuals were also feeding, which suggests antagonistic interactions did not increase. Although this pattern was consistent across the four levels of biomass in our study, those results should be interpreted with caution given the small sample size in two of the carrion plots (i.e., 25kg: 10 turkey vulture detections, 180kg: 9 turkey vulture and 80 black vulture detections). Lashley et al. (2018b) recommended at least 100 detections to accurately and precisely calculate activity patterns. However, they also reported that their recommendation was based on the diminishing return on the precision of estimates. In their study, activity patterns were relatively accurate down to 10 detections consistently across species but the precision of estimates was poor. Given consistent evidence across behaviors reported herein, we contend that our estimates of activity overlap were accurate even for the low sample size plots, and thus further support that increasing carrion biomass relaxed competition. Interestingly, the heightened overlap appears to be a result of both species spending more time at carrion as opposed to peak activity of each species converging as carrion biomass increased. Spending more time at plots further indicates the relaxation of competition because vultures typically abandon carcasses more quickly to avoid antagonistic interactions when competition intensifies (Bosè et al. 2012).

We acknowledge the lack of spatial and temporal replication and focus on only two scavenger species is a limitation of our study. As suggested by Turner et al. (2017), there is a growing need for a more holistic approach to scavenging research. Factors such as habitat type, season, study species, and scavenger resident and migrant status will certainly affect the outcome of MMEs (Houston 1988, Kirk and Houston 1995, Buckley 1996, Holland et al. 2017, Turner et al. 2017). However, our study does have the strength of isolating the effects of increasing carrion biomass on vulture carrion consumption as a product of behavioral plasticity. Moreover, understanding carrion recycling dynamics in the Anthropocene will further be complicated by
climate change effects on scavenging microbes, fungi, and arthropods (DeVault et al. 2003 and 2016). Because microbe and arthropod contributions to decomposition are predicted to increase with increasing carrion biomass (Tomberlin et al. 2017), the effects of climate change on their function and subsequent carrion recycling efficiency of ecosystems may be exacerbated during MMEs (DeVault et al. 2003 and 2016). Studying all these factors in the context of MMEs proves particularly problematic for logistical and practical reasons (Lashley et al. 2018a), but we urge researchers not to neglect this understudied aspect of global change.

It is predicted that scavenger assemblages in ecosystems will change dramatically in the Anthropocene. For example, the decline in obligate vertebrate scavengers is expected to release facultative scavengers (Ogada et al. 2012a, O'Bryan et al. 2019, Santangeli et al. 2019). This effect may be exacerbated by MMEs because the longer persistence of carcasses during these events will likely increase participation in the carrion food web by species that are rare or novel to scavenging (Baruzzi et al. 2018). However, while primary consumer functional diversity normally increases efficiency in nutrient recycling (Gessner et al. 2010), facultative scavengers are relatively inefficient carrion recyclers and do not replace obligate scavengers in recycling services when they are absent (Ogada 2012a, Moleón et al. 2014, Hill et al. 2018, O'Bryan et al. 2019). Thus, it is unclear if the effects of carrion food web diversity can circumvent an absent or severely impaired obligate scavenger functional role. Our understanding of the role of increased carrion food web diversity on this key ecosystem function is poor but may prove a fruitful avenue of future research given the global trends in obligate scavenger populations.

The increasing prevalence of MMEs (Fey et al. 2015) concurrent with obligate scavenger declines (Sebastián-González et al. 2019) may change carrion recycling dynamics in the Anthropocene. To understand the net effects of global change on this key ecosystem service, a
better understanding of how behavioral plasticity and carrion food web complexity are affected by MMEs is warranted. For example, Lashley et al. (2018a) reported that increasing carrion biomass strengthened the indirect effects of carrion on the local community, and vertebrate scavenger access to that carrion mediated those indirect effects. In their study, vulture access to carrion indirectly decreased soil disturbances from armadillos (Dasypus novemcinctus) that were apparently rooting for pupating blowfly larvae (Diptera: Calliphoridae). Here we further suggest that vulture mediation of the indirect effects of carrion on the community, is not only density-mediated but also behaviorally-mediated with consumer life history constraining those effects. Our study indicates that social feeders provide a fundamental service for promoting resistance to MME disturbances in ecosystems and therefore they are likely the most important vertebrate obligate scavenger group to focus on conserving during the Anthropocene.
Table 4.1  Models compared for testing black vulture group size responses

<table>
<thead>
<tr>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black vulture group size ~ 1 + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Biomass + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Days from Deployment + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Turkey vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Biomass + Days from Deployment + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Biomass + Turkey vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Biomass * Turkey vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Days from Deployment + Turkey vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Black vulture group size ~ Biomass + Days from Deployment + Turkey vulture group size + Periodicity*</td>
</tr>
</tbody>
</table>

*5 types of periodicity were tested: 1) no periodicity in group size; 2) 1 peak in group size, with sin(h) and cos(h); 3) 2 even peaks in group size, with sin(2h) and cos(2h); 4) 2 uneven peaks in group size, with sin(h), cos(h), and sin(2h); 5) 2 uneven peaks in group size, with terms sin(h), cos(h), and cos(2h).
Table 4.2  Models compared for testing turkey vulture group size responses

<table>
<thead>
<tr>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turkey vulture group size ~ 1 + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Days from Deployment + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Black vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass + Days from Deployment + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass + Black vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass * Black vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Days from Deployment + Black vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass + Days from Deployment + Black vulture group size + Periodicity*</td>
</tr>
<tr>
<td>Turkey vulture group size ~ Biomass * Black vulture group size + Days from Deployment + Periodicity*</td>
</tr>
</tbody>
</table>

*5 types of periodicity were tested: 1) no periodicity in group size; 2) 1 peak in group size, with \( \sin(h) \) and \( \cos(h) \); 3) 2 even peaks in group size, with \( \sin(2h) \) and \( \cos(2h) \); 4) 2 uneven peaks in group size, with \( \sin(h) \), \( \cos(h) \), and \( \sin(2h) \); 5) 2 uneven peaks in group size, with terms \( \sin(h) \), \( \cos(h) \), and \( \cos(2h) \).
Table 4.3  Five top-ranked models (based on Akaike’s Information Criterion [AIC]) for black vulture group size.

<table>
<thead>
<tr>
<th>Model description</th>
<th>Δ(AIC)</th>
<th>wi</th>
<th>K</th>
<th>Intercept</th>
<th>Biomass</th>
<th>Deployment days</th>
<th>Turkey</th>
<th>Turkey*Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black ~ p3 +</td>
<td>0.00</td>
<td>0.76</td>
<td>8</td>
<td>-7.65</td>
<td>0.005</td>
<td>0.17</td>
<td>1.28</td>
<td>-0.001</td>
</tr>
<tr>
<td>Deployment days +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turkey*Biomass</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Black ~ p5 +</td>
<td>2.27</td>
<td>0.24</td>
<td>7</td>
<td>-7.13</td>
<td>0.005</td>
<td>-</td>
<td>1.27</td>
<td>-0.001</td>
</tr>
<tr>
<td>Turkey*Biomass</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Black ~ p3 +</td>
<td>18.55</td>
<td>0.00</td>
<td>7</td>
<td>-7.08</td>
<td>0.004</td>
<td>0.139</td>
<td>0.48</td>
<td>-</td>
</tr>
<tr>
<td>Turkey + Biomass Deployment days</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black ~ p5 +</td>
<td>19.27</td>
<td>0.00</td>
<td>6</td>
<td>-6.69</td>
<td>0.004</td>
<td>-</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>Turkey + Biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black ~ p3 +</td>
<td>41.20</td>
<td>0.00</td>
<td>7</td>
<td>-5.08</td>
<td>0.005</td>
<td>0.14</td>
<td>1.5</td>
<td>-0.002</td>
</tr>
<tr>
<td>Deployment days +</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Turkey*Biomass</td>
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</tbody>
</table>

In the model descriptions, Black is black vulture group size, p3 and p5 are different types of periodicity (sin(2h) + cos(2h) and sin(h) + cos(h) + cos(2h), respectively), Biomass is the amount of biomass deployed at each plot, Deployment days is the number of days from the carrion deployment, and Turkey is the turkey vulture group size. Standard error is reported in parenthesis after variable estimates. Bolded variables and interaction coefficients are significant (p<0.05).
Table 4.4  Five top-ranked models (based on Akaike’s Information Criterion [AIC]) for turkey vulture group size

<table>
<thead>
<tr>
<th>Model description</th>
<th>$\Delta$(AIC)</th>
<th>$w_i$</th>
<th>K</th>
<th>Intercept</th>
<th>Biomass</th>
<th>Black</th>
<th>Deployment days</th>
<th>Black*Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turkey ~ p$^4$ + Black*Biomass</td>
<td>0.00</td>
<td>0.38</td>
<td>7</td>
<td>-4.54 (0.57)</td>
<td>0.002 (0.001)</td>
<td>0.65 (0.1)</td>
<td>-</td>
<td>-0.001 (0.00)</td>
</tr>
<tr>
<td>Turkey ~ p$^4$ + Black*Biomass</td>
<td>1.69</td>
<td>0.17</td>
<td>6</td>
<td>-4.2 (0.49)</td>
<td>0.002 (0.001)</td>
<td>0.69 (0.1)</td>
<td>-</td>
<td>-0.001 (0.00)</td>
</tr>
<tr>
<td>Turkey ~ p$^4$ + Deployment days + Black*Biomass</td>
<td>1.85</td>
<td>0.15</td>
<td>8</td>
<td>-4.72 (0.69)</td>
<td>0.002 (0.001)</td>
<td>0.63 (0.1)</td>
<td>0.08 (0.16)</td>
<td>-0.001 (0.00)</td>
</tr>
<tr>
<td>Turkey ~ p$^5$ + Black*Biomass</td>
<td>2.46</td>
<td>0.11</td>
<td>7</td>
<td>-4.43 (0.57)</td>
<td>0.002 (0.001)</td>
<td>0.68 (0.1)</td>
<td>-</td>
<td>-0.001 (0.00)</td>
</tr>
<tr>
<td>Turkey ~ p$^2$ + Deployment days + Black*Biomass</td>
<td>2.99</td>
<td>0.09</td>
<td>7</td>
<td>-4.57 (0.65)</td>
<td>0.002 (0.001)</td>
<td>0.66 (0.11)</td>
<td>0.14 (0.18)</td>
<td>-0.001 (0.00)</td>
</tr>
</tbody>
</table>

In the model descriptions, Turkey is turkey vulture group size, p2, p4, and p5 are three different types of periodicity ($\sin(h) + \cos(h)$, $\sin(h) + \cos(h) + \sin(2h)$ and $\sin(h) + \cos(h) + \cos(2h)$, respectively). Biomass is the amount of biomass deployed at each plot, Deployment days is the number of days from the carrion deployment, and Black is the black vulture group size. Standard error is reported in parenthesis after variable estimates. Bolded variables and interaction coefficients are significant (p<0.05).
Table 4.5  Five top-ranked models (based on Akaike’s Information Criterion [AIC]) for number of black vultures eating.

<table>
<thead>
<tr>
<th>Model description</th>
<th>$\Delta$(AIC)</th>
<th>$w_i$</th>
<th>K</th>
<th>Intercept</th>
<th>Biomass</th>
<th>Black</th>
<th>Deployment days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black feeding $\sim p_5$ + Black + Biomass</td>
<td>0.00</td>
<td>0.49</td>
<td>6</td>
<td>-4.27 (0.59)</td>
<td><strong>0.002</strong> (0.001)</td>
<td><strong>0.28</strong> (0.02)</td>
<td>-</td>
</tr>
<tr>
<td>Black feeding $\sim p_5$ + Black + Biomass + Deployment days</td>
<td>1.56</td>
<td>0.23</td>
<td>7</td>
<td>-4.48 (0.67)</td>
<td><strong>0.002</strong> (0.001)</td>
<td><strong>0.28</strong> (0.03)</td>
<td>0.08 (0.1)</td>
</tr>
<tr>
<td>Black feeding $\sim p_4$ + Black + Biomass</td>
<td>2.58</td>
<td>0.14</td>
<td>6</td>
<td>-3.61 (0.3418)</td>
<td><strong>0.002</strong> (0.001)</td>
<td><strong>0.3</strong> (0.02)</td>
<td>-</td>
</tr>
<tr>
<td>Black feeding $\sim p_3$ + Black + Biomass</td>
<td>4.00</td>
<td>0.07</td>
<td>5</td>
<td>-3.56 (0.34)</td>
<td><strong>0.002</strong> (0.001)</td>
<td><strong>0.3</strong> (0.02)</td>
<td>-</td>
</tr>
<tr>
<td>Black feeding $\sim p_4$ + Black + Biomass + Deployment days</td>
<td>4.65</td>
<td>0.05</td>
<td>7</td>
<td>-3.61 (0.43)</td>
<td><strong>0.002</strong> (0.001)</td>
<td><strong>0.3</strong> (0.03)</td>
<td>0.001 (0.1)</td>
</tr>
</tbody>
</table>

In the model descriptions, Black feeding is the number of black vultures feeding, $p_3$, $p_4$, and $p_5$ are three different types of periodicity ($\sin(2h) + \cos(2h)$, $\sin(h) + \cos(h) + \sin(2h)$ and $\sin(h) + \cos(h) + \cos(2h)$, respectively), Black is black vulture group size, Biomass is the amount of biomass deployed at each plot, and Deployment days is the number of days from the carrion deployment. Standard error is reported in parenthesis after variable estimates. Bolded variables and interaction coefficients are significant (p<0.05).
### Table 4.6  Five top-ranked models (based on Akaike’s Information Criterion [AIC]) for number of turkey vultures eating.

<table>
<thead>
<tr>
<th>Model description</th>
<th>( \Delta(AIC) )</th>
<th>( w_i )</th>
<th>K</th>
<th>Intercept</th>
<th>Biomass</th>
<th>Deployment days</th>
<th>Turkey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turkey feeding ( \sim p_5 + )</td>
<td>0.00</td>
<td>0.27</td>
<td>5</td>
<td>-4.08</td>
<td>-</td>
<td>-</td>
<td>1.08</td>
</tr>
<tr>
<td>Turkey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.1)</td>
</tr>
<tr>
<td>Turkey feeding ( \sim p_5 + )</td>
<td>0.01</td>
<td>0.27</td>
<td>6</td>
<td>-4.49</td>
<td>0.001</td>
<td>-</td>
<td>1.01</td>
</tr>
<tr>
<td>Turkey + Biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.6074)</td>
<td></td>
<td>(0.11)</td>
</tr>
<tr>
<td>Turkey feeding ( \sim p_5 + )</td>
<td>1.84</td>
<td>0.11</td>
<td>6</td>
<td>-4.31</td>
<td>-</td>
<td>0.09</td>
<td>1.08</td>
</tr>
<tr>
<td>Turkey + Deployment days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.72)</td>
<td></td>
<td>(0.1)</td>
</tr>
<tr>
<td>Turkey feeding ( \sim p_5 + )</td>
<td>2.03</td>
<td>0.10</td>
<td>7</td>
<td>-4.6</td>
<td>0.001</td>
<td>0.04</td>
<td>1.01</td>
</tr>
<tr>
<td>Turkey + Biomass + Deployment days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.76)</td>
<td></td>
<td>(0.11)</td>
</tr>
<tr>
<td>Turkey feeding ( \sim p_4 + )</td>
<td>3.75</td>
<td>0.04</td>
<td>5</td>
<td>-3.6971</td>
<td>-</td>
<td>-</td>
<td>1.03</td>
</tr>
<tr>
<td>Turkey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.36)</td>
<td></td>
<td>(0.09)</td>
</tr>
</tbody>
</table>

In the model descriptions, Turkey feeding is the number of turkey vultures feeding, \( p_4 \) and \( p_5 \) are the two types of irregular periodicity \( \sin(h) + \cos(h) + \sin(2h) \) and \( \sin(h) + \cos(h) + \cos(2h) \), respectively. Biomass is the amount of biomass deployed at each plot, Deployment days is the number of days from the carrion deployment, and Turkey is turkey vulture group size. Standard error is reported in parenthesis after variable estimates. Bolded variables and interaction coefficients are significant (p<0.05).
Figure 4.1  Changes in black and turkey vulture group size

Changes in a) black and b) turkey vulture group size. Different biomass levels and days from deployment are shown in separate panels. a) Black vulture group size (y axis) increased with biomass (column panels), turkey vulture group size (x axis), and deployment days (row panels). b) Turkey vulture group size (y axis) increased with biomass (column panels) and black vulture group size (x axis), but not deployment days (row panels).
Figure 4.2  Changes in number of black and turkey vultures feeding

Changes in number of a) black and b) turkey vulture feeding. Separate panel plots have been created for different biomass levels and days from deployment. a) Number of black vultures feeding (y axis) increased with biomass (column panels) and black vulture group size (x axis). Days from deployment (row panels) did not affect the number of black vultures feeding. b) Increased number of turkey vultures feeding (y axis) was caused by increased turkey vulture group size (x axis). Deployment days (row panels), and biomass (column panels) did not influence number of turkey vultures feeding.
Figure 4.3  Activity pattern overlap between turkey and black vultures

Activity pattern overlap between turkey and black vultures at a) plot with 180kg of carrion, b) 360kg of carrion, and c) 725kg of carrion. Activity overlap increased with increasing biomass level indicating relaxed competition.
Figure 4.4  Vulture consumption across carrion biomass levels

Black and turkey vulture cumulative feeding minutes (y axis) throughout the carrion biomass gradient (x axis). Using feeding minutes as a reflection of the contribution to decomposition of each species shows that black vulture contribution becomes increasingly more important than turkey vulture contribution increasing with biomass.
References


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CHAPTER V
EXPLORING CORRELATIONS BETWEEN CARRION DECOMPOSITION RATES, VULTURE VISITATIONS, AND ZOMBIE FLY OUTBREAKS

Mass mortality events (MMEs) are increasing in magnitude and frequency resulting in the abrupt entry of massive amounts of carrion into ecosystems (Fey et al. 2015), while the majority of vulture species are concurrently declining (Ogada et al. 2012a). Little work has been done on these concurrent phenomena, but it is widely accepted that carrion is an important basal resource in ecosystems (Barton et al. 2013) and that obligate vertebrate scavengers provide an important ecosystem service by facilitating the expedient assimilation of carrion nutrients into the ecosystem nutrient cycle (Buechley and Şekercioğlu 2016). The scant literature base on this global change aspect led our research group to execute a series of experiments designed to isolate the ecological effects of simultaneously increasing carrion biomass and impairment of the obligate vertebrate scavenger functional role.

Lashley et al. (2018) documented a remarkable collective dispersal of seemingly endless numbers of blowfly larvae, which generated indirect effects of carrion on the local community. This observation generated numerous hypotheses which inspired our research group to conduct additional experiments. Unpublished data from one such experiment indicated that fly production increased with carrion biomass and that the intentional impairment of vulture access to carrion resulted in more flies produced at a given carrion biomass deployed (Barton et al. unpublished data). Thus, we hypothesized that by elevating fly abundance, carrion may prime the ecosystem
to more efficiently recycle future carrion. If that is the case, the priming effect could be an important mechanism allowing ecosystems to “adapt” to large carrion loads caused by MMEs by becoming more efficient at recycling carrion as it enters the ecosystem over the course of the MME.

In August of 2017, we established an experiment at Panther Swamp National Wildlife Refuge, MS, USA, to test that hypothesis. Our rationale was that each time carrion was placed into the environment, the subsequent background fly abundance would be elevated so that more flies were in close proximity to colonize the next deployment of carrion, a process for which we predicted would lead to faster decomposition. To test that hypothesis, we used feral swine (*Sus scrofa*) carrion that was donated by staff on site. Feral swine are a nuisance invasive species that are commonly removed from federal lands because of potential ecological and economical conflicts (https://www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/operational-activities/feral-swine/feral-swine-program). For this reason, feral swine are continually removed from refuge areas and, in this case, the euthanized animals were donated for the purposes of this research.  

We deployed carrion at 3 sites, with each site having 4 *a priori* established paired plots at least 250m apart. We deployed carrion (i.e., ~150 kg on average per plot) at each site in three consecutive deployments (i.e., t1, t2, and t3) approximately one and two months apart, respectively. One plot at each site received carrion in t1, t2, and t3 and each of the paired plots received carrion in only one time point. A horizontal camera trap was deployed in front of each plot, which allowed us to monitor visitation by vertebrate scavengers (Figure C.1).

On October 14, 2017, approximately 5 weeks after t2, we visited the sites to collect data. Contrary to our prediction of accelerated decomposition rate, carcasses were still decomposing in four of the six plots where carrion was deployed. That was surprising because, in our previous
carrion deployment (i.e. t1), decomposition was completed within 2 weeks so carrion
decomposition rate was apparently slower in t2 than t1 in some plots. Interestingly, the amount
of carrion biomass remaining differed greatly among the six plots that received carrion in t2.
Similar to other methods used to estimate stages of decomposition (e.g. Megyesi et al. 2005,
Keough et al. 2017), we systematically estimated the proportion of different segments of the
body remaining for each carcass (i.e. trunk 35%, head 15%, individual legs 12.5%) and summed
those to get a percentage of carrion remaining at every plot. While at one of the plots, which had
a considerable amount of carrion remaining, we noticed numerous zombie flies (i.e., blowflies
that had been parasitized by the *Entomophthorales* fungus; Figure 5.1). We returned to each of
the 6 plots that day and counted parasitized flies. The zombie flies were perched on plants near
the carrion and, in some cases, on the carrion itself likely allowing conidia (i.e. asexual fungal
spores) to reach other flies congregating at the carrion (Mullens et al. 1987). Also, most infected
flies were in mating pairs with *Entomophthora* fruiting bodies emerging from the abdomen
region (Figure 5.1). We collected three types of data, zombie fly counts, vulture visitation, and
proportion of the carrion remaining at each plot which we used to explore potential relationships
between carrion decomposition, obligate scavengers, and parasites.

Parasitized fly counts ranged from 5 to 80 and whether carrion was previously deployed
in the plots did not apparently affect the number of parasitized flies detected. Also, treatment did
not seem to be linked to decomposition rate of carrion because two of the four plots with carrion
remaining were second time and two were first time deployments. When we examined camera
trap data, black (*Coragyps atratus*) and turkey (*Cathartes aura*) vulture detections differed
among plots even though the sampling window was the same on all plots. A simple correlation
revealed that the number of vultures detected was negatively correlated with the number of
parasitized flies detected (Spearman’s rank correlation coefficient = -0.78; Figure 5.2). We ran two generalized additive models fitting a zero-inflated beta distribution to predict the proportion of remaining carrion: one with the number of zombie flies detected and one with the number of vultures detected. Vulture detections (Cox-Snell R2 = 0.88, p= 0.009) and the number of zombie flies detected (Cox-Snell R2 = 0.76, p= 0.0006) were negatively and positively correlated to the proportion of carrion remaining, respectively. Less zombie flies were detected as vulture detections increased and more carrion was remaining with more zombie flies detected and less vultures detected. Because these were correlative relationships, we discuss a suite of alternative explanations for the correlative relationships we observed. It is important to note, correlations between these variables may simply arise from spurious relationships, but given that vultures and blow flies are two of the most important contributors to carrion decomposition, it is also worth exploring other potential explanations.

**Could Entomophthora regulate carrion decomposition rate?**

Parasitized flies have reduced fecundity and select unsuitable oviposition sites when infected by *Entomophthora* because the fungus highjacks the motor functions directing the infected individual to a suitable perch for conidia dispersal (Watson and Petersen 1993). Because flies consume carrion during their larval stage and fewer flies may successfully oviposit on carrion, which could reduce the number of larvae, consumption rates could have been reduced. Moreover, larval aggregations increase the feeding rate of individuals through intra- and interspecific facilitation by elevating temperature and mass release of digestive enzymes (Rivers et al. 2011) and therefore, the decrease in decomposition rates from fewer larvae could be exacerbated by reduced larval facilitation. Thus, one possibility is that the correlative
relationship between infected flies detected and decomposition rate is explained by a reduction in larvae to decompose carrion.

Alternatively, lower decomposition rates and higher zombie fly detections could have been caused by differences in temperatures across plots because both can be affected by differences in microsite ambient temperature (Parmenter and MacMahon 2009, Kalsbeek et al. 2001, respectively). Decomposition rate of carrion typically declines as ambient temperature decreases. Also, temperature is the main driver of *Entomophthora* activity with activity being greatest during the fall, which was when we observed zombie flies in the experiment on all plots (Watson and Petersen 1993). Thus, variation in temperature between plots could generate a negative correlation between fly infection rate and carrion decomposition rate. When we selected the *a priori* plots, we identified plot areas with similar forest canopy cover, understory plant structure, and elevation. Those edaphic factors being similar likely helped homogenize temperatures across plots. Moreover, temperatures recorded by camera traps were consistent across plots. Thus, differences in microsite temperatures were unlikely driving the correlation between decomposition rate and zombie flies we observed. However, we cannot rule out that other abiotic microsite differences that were not accounted for, such as moisture or wind, could affect our observations.

**Could vultures be regulating carrion decomposition rate?**

The number of vultures detected was negatively correlated with the amount of remaining carrion at each plot. Hill et al. (2018) reported that excluding vultures from consuming carrion decreased decomposition rates. Lower consumption of carrion associated with fewer vulture visitations could explain the correlation between decomposition rate and vulture detections we observed. Although vulture consumption can affect decomposition rates, other factors, such as
other scavenger presence, could have simultaneously caused differences in decomposition rates and vulture detections across plots. Although facultative vertebrate scavenger detections across plots did not seem to be linked to our observation, we cannot rule out that some plot variation could have generated this correlation because animals could have been visited the plots without being detected.

Could vultures or zombie flies be regulating the abundance of the other?

Vultures could have directly caused reduced number of zombie flies through predation or by disturbing the plots causing zombie flies to fall on the ground. Indeed, we have evidence from our camera trap pictures that vultures can predate flies (Figure 5.3). Although these observations are extremely rare in our camera trap pictures, we cannot rule out the hypothesis that increasing number of vultures could have removed or caused a greater number of zombie flies to fall, generating the pattern we observed.

Vultures could have also indirectly regulated fly infection through carrion consumption. Unpublished data from Barton et al. show that vultures reduce blowfly abundance by competing for carrion. Because Entomophthorales infection rates are positively related to host densities (Mullens et al. 1987, Hesketh et al. 2010), a decrease in vulture use, which is likely to be related to decreased consumption, could have caused increased decomposition rates releasing blowfly from competition and increasing their infection rates.

It is also possible that vulture did not indirectly affect Entomophthorales outbreaks but that vultures avoided plots with highest zombie fly abundance. While we cannot rule out this possibility, this scenario is unlikely. Indeed, vultures are known for the cleaning service they provide thanks to their uniquely low stomach pH that kills pathogens (Ogada et al. 2012b) and
we could not find in the literature any indication that vultures avoid parasites of invertebrates, so there is no indication that they should avoid carrion due to parasites.

**Could the correlations be linked by other factors?**

Our observations could have been generated by other processes that we could not test with our experimental design. For example, different zombie fly detections could have been caused by different numbers of infected and susceptible flies colonizing our plots. Moreover, we do not know whether other invertebrates interacted with carrion or zombie flies. We observed zombie flies being eaten by spiders (Araneae; Figure 5.4) so that attributing our observations to a specific cause appears premature and experimental manipulation of different factors is needed to establish causation. However, the potential relationships between carrion decomposition rates, vulture abundance, and factors regulating numerical responses of other obligate scavengers warrant further investigation given the changing interaction with carrion loads, vulture populations, and climate.

**Implications and future directions**

Some authors have posited that MMEs will have unique effects on ecosystems because the effects of carrion scale nonlinearly with biomass. For example, as carrion biomass increases, the relative importance of obligate scavengers is predicted to shift as a result of differing life history constraints on the primary obligate scavenger groups (i.e., microbes, arthropods, and vertebrates; Tomberlin et al. 2017). Moreover, MMEs might generate cascading indirect effects of carrion on the community as previously described in Lashley et al. (2018). Likewise, the impairment or loss of the vertebrate obligate scavenger role may release other vertebrate scavenger populations (Ogada et al. 2012b). However, many facultative vertebrate scavengers
are relatively inefficient carrion consumers and current empirical evidence does not support the premise that vertebrate scavengers overcome the impairment of the vulture functional role (e.g., Hill et al. 2018). Previous work indicated that impairment of the vulture functional role may release blowflies from competition allowing a numerical response that could for the most part overcome the loss of vultures (Barton et al. unpublished data). However, our zombie fly observations herein show that there might be factors that could prevent flies from compensating vulture decline. Decomposition is a fundamental process that allows recycling carrion nutrients into food webs, and future research could explore the relationship among Entomophthorales, vultures, and decomposition rates. Because isolating individual factors for testing the above mentioned hypothesis could be extremely difficult, a germane approach would be to use mathematical models to project how these variables (e.g. vulture detections, edaphic factors) can affect each other and produce similar decomposition patterns to what we observed.
Parasitized flies are directed by *Entomophthora* to the underside of a perch for gravity to disperse the conidia emerging from the abdomen region. Parasitized flies open their wings away from the thorax to better disperse conidia emerging from the intersegmental membranes. It has been suggested that this position is similar to the position adopted by mating females causing males to try to mate with the infected flies (Mullens et al. 1987) thus increasing infection rates and reducing the number of oviposited eggs (Roy et al. 2006).
Figure 5.2  Changes in carrion biomass with number of parasitized flies and vulture detections

Vulture detections is the number of black (Coragyps atratus) and turkey (Cathartes aura) vulture detected at our carrion deployment plots during the period from t2 carrion deployment and zombie fly sampling (~5 weeks after t2). Fly detections is the number of parasitized flies counted at each plot. Carrion biomass is the percentage of carrion biomass still available at each plot. Carrion biomass increased with increasing number of parasitized flies detected and decreased with vulture detections. We suggest lower vulture plot visitations were the main factor affecting carrion biomass remaining at the plots. In turn, longer carrion decomposition time promoted fly aggregations and disease spread.
Figure 5.3  Black vulture (*Coragyps atratus*) vulture pecking on one of our sticky traps.
Figure 5.4  Spider feeding on a parasitized fly at one of our plots.
References


CHAPTER VI  
SYNTHESIS AND CONCLUSION

Mass mortality events are large scale disturbances that are characterized by large carrion inputs abruptly released into the environment. During mass mortality events, several forces that can alter community dynamics originate. The bottom-up carrion pulses are followed by primary and secondary consumers aggregations. How these factors affect ecological responses to mass mortality events is still largely unstudied. Because of the magnitude and unpredictability of these phenomena, research on mass mortality events often focus on their causes, which are often less cumbersome to determine than their effects. However, mass mortality events are increasing in occurrence and magnitude across several taxa and a better notion of their possible ecological consequences is needed.

My results show that top-down forces during mass mortality events largely determine plant community responses. In my experiment, vertebrate scavenger access to carrion and herbivore access to forage changed plant functional group dominance. Herbivory also determined plant growth and survival. In my experiment, vultures consumed the largest amount of carrion. Vulture consumption was mediated by behavioral plasticity, which allowed them to maximize energy intake by releasing them from competition with increasing carrion biomass. My research also provides correlative evidence about the importance of vultures in limiting invertebrate scavenger disease transmission. These results added to previous literature showing that vulture decline is related to the rise of facultative scavengers (e.g., dogs, *Canis lupus*)
familiaris; rats, Rodentia) indicate that vulture decline might pose a threat to human health and ecosystem stability.
APPENDIX A

SUPPLEMENTARY INFORMATION CHAPTER III
Figure A.1  Plot experimental design

Paired plot and vegetation sampling design between 2016 and 2019. Vertebrate scavenger exclosure transects were used to test the effects of vertebrate scavengers on plant communities. Transects were run outside the experimental plots in order to detect any disturbance that could have been caused by primary or secondary consumers. Herbivore exclosures and quadrats were used to test the effects of herbivores on the plant community.
Table A.1  Multivariate regression results for vegetation samplings conducted between 2017-2018

<table>
<thead>
<tr>
<th></th>
<th>Deviance</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrients</td>
<td>6.143</td>
<td>0.93</td>
</tr>
<tr>
<td>Carrion biomass</td>
<td>11.435</td>
<td>0.63</td>
</tr>
<tr>
<td>Scavenger exclosure</td>
<td>17.284</td>
<td>0.16</td>
</tr>
<tr>
<td>Carrion biomass* Scavenger exclosure</td>
<td>16.167</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Results of the multivariate regression for our transect data investigating the influence of vertebrate herbivores and carrion biomass on plant functional groups. Bolded variables are significant.
Table A.2  Univariate regression results for 2017-2018 vegetation community data

<table>
<thead>
<tr>
<th></th>
<th>Annual forbs</th>
<th>Annual vines</th>
<th>Graminoids</th>
<th>Grasses</th>
<th>Perennial forbs</th>
<th>Perennial vines</th>
<th>Shrubs</th>
<th>Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.803</td>
<td>0.758</td>
<td>-1.88</td>
<td>2.074</td>
<td>0.45</td>
<td>2.654</td>
<td>1.407</td>
<td>1.82</td>
</tr>
<tr>
<td>Nutrients</td>
<td>0.001 (0.86)</td>
<td>-0.011 (0.17)</td>
<td>0.002 (0.395)</td>
<td>0.0001 (0.76)</td>
<td>-0.001 (0.595)</td>
<td>-0.00004 (0.96)</td>
<td>0.0001 (0.795)</td>
<td>0.0002 (0.59)</td>
</tr>
<tr>
<td>Carrion biomass</td>
<td><strong>0.003 (0.01)</strong></td>
<td>0.002 (0.24)</td>
<td>0.002 (0.92)</td>
<td>0.00005 (0.575)</td>
<td>-0.003 (0.655)</td>
<td>-0.001 (0.745)</td>
<td>0.00001 (0.625)</td>
<td>0.0001 (0.47)</td>
</tr>
<tr>
<td>Scavenger exclosure (open)</td>
<td>-2.613 (0.055)</td>
<td>-1.36 (0.24)</td>
<td>-0.082 (0.715)</td>
<td>0.276 (0.595)</td>
<td>-0.305 (0.39)</td>
<td>-0.263 (0.085)</td>
<td>-0.142 (0.085)</td>
<td>0.046 (0.89)</td>
</tr>
<tr>
<td>Carrion biomass* Scavenger exclosure (open)</td>
<td>0.003 (0.31)</td>
<td>0.002 (0.615)</td>
<td>-0.150 (0.065)</td>
<td>-0.003 (0.065)</td>
<td>0.003 (0.25)</td>
<td><strong>0.002 (0.01)</strong></td>
<td>-0.0006 (0.42)</td>
<td>-0.001 (0.16)</td>
</tr>
</tbody>
</table>

Univariate regression results for 2017-2018 vegetation community data. Here reported the model coefficients and p-values in parenthesis. Bolded variables are significant (p<0.05). Independent variables that resulted significant in the multivariate test have also been bolded.
Table A.3  Multivariate regression results for vegetations samplings collected in 2019

<table>
<thead>
<tr>
<th></th>
<th>Deviance</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrients</td>
<td>7.51</td>
<td>0.845</td>
</tr>
<tr>
<td>Carrion biomass</td>
<td>45.16</td>
<td>0.005</td>
</tr>
<tr>
<td>Scavenger exclosure</td>
<td>12.98</td>
<td>0.39</td>
</tr>
<tr>
<td>Herbivore exclosure</td>
<td>9.17</td>
<td>0.185</td>
</tr>
<tr>
<td>Carrion biomass* Scavenger exclosure</td>
<td>10.95</td>
<td>0.355</td>
</tr>
<tr>
<td>Carrion biomass* Herbivore exclosure</td>
<td>14.43</td>
<td>0.02</td>
</tr>
<tr>
<td>Scavenger exclosure (open)* Herbivore</td>
<td>11.51</td>
<td>0.105</td>
</tr>
<tr>
<td>Carrion biomass* Scavenger exclosure (open)* Herbivore exclosure (present)</td>
<td>6.44</td>
<td>0.275</td>
</tr>
</tbody>
</table>

Results of the multivariate regression for our quadrats data investigating the influence of vertebrate herbivores and carrion biomass on plant functional groups. Bolded variables are significant.
Table A.4  Univariate regression results for vegetation data collected in 2019

<table>
<thead>
<tr>
<th></th>
<th>Annual forbs</th>
<th>Annual vines</th>
<th>Graminoids</th>
<th>Grasses</th>
<th>Perennial forbs</th>
<th>Perennial vines</th>
<th>Shrubs</th>
<th>Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.843</td>
<td>0.661</td>
<td>-0.564</td>
<td>1.335</td>
<td>-2.473</td>
<td>2.685</td>
<td>0.696</td>
<td>1.885</td>
</tr>
<tr>
<td>Nutrients</td>
<td>0.001</td>
<td>(-0.85)</td>
<td>-0.013</td>
<td>(-0.155)</td>
<td>-0.002</td>
<td>(-0.445)</td>
<td>0.0008</td>
<td>(-0.52)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.155)</td>
<td>(0.445)</td>
<td></td>
<td>(0.585)</td>
<td>(0.65)</td>
<td>(0.88)</td>
<td></td>
</tr>
<tr>
<td>Carrion biomass</td>
<td><strong>0.004</strong></td>
<td><strong>(0.04)</strong></td>
<td>-0.023</td>
<td>-0.002</td>
<td>-0.0003</td>
<td>-0.133</td>
<td><strong>-0.003</strong></td>
<td><strong>(0.015)</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.965)</td>
<td>(0.085)</td>
<td>(0.06)</td>
<td>(0.39)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scavengers</td>
<td>0.743</td>
<td>(0.48)</td>
<td>-1.779</td>
<td>-0.672</td>
<td>0.29</td>
<td>2.529</td>
<td>-0.149</td>
<td>-0.296</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.245)</td>
<td>(0.965)</td>
<td>(0.97)</td>
<td>(0.665)</td>
<td>(0.665)</td>
<td>(0.35)</td>
<td>(0.82)</td>
</tr>
<tr>
<td>Herbivore exclosure</td>
<td>0.137</td>
<td>(0.79)</td>
<td>-0.068</td>
<td>0.156</td>
<td>0.406</td>
<td><strong>3.079</strong></td>
<td>0.399</td>
<td>-0.311</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.715)</td>
<td>(0.565)</td>
<td>(0.94)</td>
<td>(0.665)</td>
<td><strong>(0.025)</strong></td>
<td></td>
<td>(0.61)</td>
</tr>
<tr>
<td>Carrion biomass*</td>
<td><strong>-0.004</strong></td>
<td><strong>(0.035)</strong></td>
<td>0.02</td>
<td>-0.004</td>
<td>-0.001</td>
<td>-0.079</td>
<td>0.001</td>
<td>-0.006</td>
</tr>
<tr>
<td>Scavengers*</td>
<td></td>
<td></td>
<td>(0.35)</td>
<td>(0.82)</td>
<td>(0.63)</td>
<td>(0.855)</td>
<td>(0.49)</td>
<td>(0.955)</td>
</tr>
<tr>
<td>Carrion biomass*</td>
<td>0.001</td>
<td>(0.22)</td>
<td>0.022</td>
<td>-0.196</td>
<td><strong>-0.004</strong></td>
<td><strong>0.131</strong></td>
<td>-0.001</td>
<td>-0.002</td>
</tr>
<tr>
<td>Herbivore exclosure</td>
<td></td>
<td>(0.135)</td>
<td>(0.615)</td>
<td>(0.615)</td>
<td></td>
<td><strong>(0.02)</strong></td>
<td></td>
<td>(0.095)</td>
</tr>
<tr>
<td>Scavengers*</td>
<td>-0.93</td>
<td>(0.3)</td>
<td>-0.658</td>
<td>0.974</td>
<td>-0.259</td>
<td>-2.168</td>
<td>-0.26</td>
<td>0.756</td>
</tr>
<tr>
<td>Herbivore exclosure</td>
<td></td>
<td>(0.505)</td>
<td>(0.255)</td>
<td>(0.4)</td>
<td>(0.2)</td>
<td>(0.205)</td>
<td>(0.09)</td>
<td>(0.05)</td>
</tr>
<tr>
<td>Carrion biomass*</td>
<td><strong>-0.152</strong></td>
<td><strong>(0.19)</strong></td>
<td>0.197</td>
<td>-0.003</td>
<td>0.08</td>
<td>-0.0004</td>
<td>0.008</td>
<td>0.001</td>
</tr>
<tr>
<td>Scavenger*</td>
<td></td>
<td></td>
<td>(0.405)</td>
<td>(0.55)</td>
<td>(0.51)</td>
<td>(0.835)</td>
<td></td>
<td>(0.155)</td>
</tr>
<tr>
<td>Herbivore exclosure</td>
<td></td>
<td></td>
<td>(0.115)</td>
<td>(0.51)</td>
<td>(0.835)</td>
<td>(0.155)</td>
<td></td>
<td>(0.615)</td>
</tr>
</tbody>
</table>

Univariate regression results for vegetation data collected in 2019. Here reported the model coefficients and p-values in parenthesis. Bolded variables are significant (p<0.05).
Table A.5  Competing models for cherrybark oak seedling survival

<table>
<thead>
<tr>
<th>Model description</th>
<th>Δ(AIC)</th>
<th>(w_i)</th>
<th>Herbivory (H)</th>
<th>Nutrients (N)</th>
<th>Fence (F)</th>
<th>Biomass (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surv ~ H + N + (1</td>
<td>Site/Plot)</td>
<td>0.30</td>
<td>0.080</td>
<td>2.998</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Surv ~ H + N + F + (1</td>
<td>Site/Plot)</td>
<td>0.34</td>
<td>0.079</td>
<td>2.984</td>
<td>1</td>
<td>0.3</td>
</tr>
<tr>
<td>Surv ~ H + N + F + (1</td>
<td>Plot)</td>
<td>0.81</td>
<td>0.062</td>
<td>3.031</td>
<td>1</td>
<td>0.32</td>
</tr>
<tr>
<td>Surv ~ H +(1</td>
<td>Plot)</td>
<td>1.00</td>
<td>0.057</td>
<td>3.021</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Surv ~ H + N + B+(1</td>
<td>Site/Plot)</td>
<td>1.14</td>
<td>0.053</td>
<td>3.006</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Surv ~ H + N + F + (1</td>
<td>Plot)</td>
<td>1.17</td>
<td>0.052</td>
<td>3.012</td>
<td>1</td>
<td>0.32</td>
</tr>
<tr>
<td>Surv ~ H + F + (1</td>
<td>Plot)</td>
<td>1.29</td>
<td>0.049</td>
<td>3.002</td>
<td>-</td>
<td>1.367</td>
</tr>
<tr>
<td>Surv ~ H + N + B + F + (1</td>
<td>Site/Plot)</td>
<td>1.49</td>
<td>0.044</td>
<td>2.98</td>
<td>1</td>
<td>1.35 (0.39)</td>
</tr>
<tr>
<td>Surv ~ H + B + (1</td>
<td>Site/Plot)</td>
<td>1.54</td>
<td>0.043</td>
<td>2.997</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Surv ~ H + B + F + (1</td>
<td>Site/Plot)</td>
<td>1.87</td>
<td>0.037</td>
<td>2.98</td>
<td>-</td>
<td>1.36 (0.39)</td>
</tr>
</tbody>
</table>

Competing models (based on Akaike’s Information Criterion [AIC]) for cherrybark oak seedling survival. Competing models had an AIC difference (ΔAIC) from the top-ranked model of less than 2. In the model descriptions, Surv is seedling status (i.e. dead or alive), H is herbivory exclosure, N is nutrient level, F is scavenger exclosure, and B is carrion biomass level. In the results, we report hazard ratios and p-values in parenthesis. Bolded variables are significant (p<0.05).
<table>
<thead>
<tr>
<th>Model description</th>
<th>$\Delta$(AIC)</th>
<th>$w_i$</th>
<th>Intercept</th>
<th>Herbivory (H)</th>
<th>Fence (F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth ~ H + F + (1</td>
<td>Plot)</td>
<td>0</td>
<td>0.237</td>
<td>18.904</td>
<td>-11.245</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(2.663)</td>
<td>(3.389)</td>
</tr>
<tr>
<td>Growth ~ O + F + (1</td>
<td>Site/Plot)</td>
<td>0</td>
<td>0.237</td>
<td>18.904</td>
<td>-11.245</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(2.663)</td>
<td>(3.389)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-1.605</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(3.43)</td>
</tr>
</tbody>
</table>

Competing models (based on Akaike’s Information Criterion [AIC]) for cherrybark oak seedling survival. Competing models had an AIC difference ($\Delta$AIC) from the top-ranked model of less than 2. In the model descriptions, Surv is seedling status (i.e. dead or alive), H is herbivory exclosure, N is nutrient level, F is scavenger exclosure, and B is carrion biomass level. In the results, we report hazard ratios and p-values in parenthesis. Bolded variables are significant ($p<0.05$).
Figure A.2  Residual plots

Residual plots for a) Poisson and b) negative binomials models developed from vegetation transect data collected between 2016 and 2018; c) Poisson and d) negative binomials models developed from vegetation quadrat data collected in 2019.
APPENDIX B

CORRELATION PLOT BETWEEN INDEPENDENT VARIABLE PAIRS USED IN CHAPTER IV
Figure B.1  Correlation plot between independent variable pairs

Black and turkey are black and turkey vulture group size, respectively. Correlation was defined using Spearman’s rank correlation coefficient (indicated above the variable histograms). Bivariate scatterplots are represented below the variable histograms. Because correlation was higher than 0.5, which we considered as a threshold for variable correlation, we did not use model having black and turkey vulture group size as independent variable. The figure was created using PerformanceAnalytics package (Peterson and Carl 2019).
APPENDIX C

VULTURE FIGURE CHAPTER V
Figure C.1  Vultures at carrion deployment plots

Turkey (*Cathartes aura*) and black (*Coragyps atratus*) vultures feeding at one of our carrion deployment plots.