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Scavenger community response to the removal of a dominant scavenger

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The alteration of scavenging communities can reduce basic ecosystem services and increase risks to human and wildlife health. Recent work demonstrated that scavenging communities in agricultural landscapes are extremely efficient: superabundant mesopredators sequestered system energy by dominating scavenging activity. To explore how the disturbance of these communities affects the stability of carrion removal as an ecosystem function, we experimentally manipulated a scavenging community within an agricultural landscape by reducing the abundance of the dominant scavenger, raccoons *Procyon lotor*. We then monitored the fates of 676 mouse *Mus musculus* carcasses placed in 13 control and 13 removal woodlots from June 2007–May 2008. The diversity of vertebrate scavengers did not change between control and removal woodlots and scavenging by invertebrates was unaffected by our experiment. Although Virginia opossums *Didelphis virginiana* and other scavengers exhibited a functional response when raccoons were reduced in abundance, the increases did not change the proportional allocation of carcasses among scavengers. Finally, the reduced abundance of a major scavenger affected system efficiency. More carcasses remained un-scavenged at the end of trials in removal woodlots than in control woodlots. This experiment demonstrates the vulnerability of a critical ecosystem service, carrion removal, to perturbations of the scavenging community and serves to highlight the method by which scavenger communities may respond to perturbations.

There is growing body of literature suggesting that scavengers function as a community: interactions among scavengers are common (Kruuk 1967, Wilmers et al. 2003) and those interactions are not random (Selva and Fortuna 2007, Blázquez et al. 2009). Moreover, intact scavenging communities execute tangible ecosystem services such as the redistribution of energy and reduction of the prevalence of diseases associated with organic decomposition (Şekercioğlu et al. 2004, Jennelle et al. 2009). Thus, the perturbation of scavenging communities potentially has far reaching implications and understanding how scavenging communities function has become a topic of increased significance (Selva and Fortuna 2007). Although a number of studies have investigated the varied forms that competition for carcasses can take between microbes, invertebrates and vertebrates (DeVault and Rhodes 2002, DeVault et al. 2004, Burkepile et al. 2006, Selva and Fortuna 2007, Rozen et al. 2008, Parmenter and MacMahon 2009), they have been conducted primarily within intact scavenger communities in environments with relatively little human disturbance. Human dominated landscapes, on the other hand, tend to harbor different arrangements of habitat attributes and often are characterized by a highly fragmented spatial dispersion of both plant and animal resources (Andrén 1994).

Habitat fragmentation tends to favor the retention of adaptable species (Wiens 1976, Tilman 1994, Gehring and Swihart 2003). Thus, communities within fragmented landscapes, and therefore the scavenging communities in those landscapes (DeVault et al. 2003), tend to be dominated by highly-abundant generalist species (Swihart et al. 2003), particularly generalist mesopredators like those found in the agricultural landscapes of the midwestern United States. The superabundance of mesopredators in such human-altered landscapes has been associated with a growing number of ecosystem-level phenomena (Prugh et al. 2009) as well as the increased edge habitats typical of fragmented agricultural ecosystems (Yahner 1988). Ultimately, however, despite the evidence that scavenging represents an important energy pathway in terrestrial communities (DeVault et al. 2003) and that scavenging communities have direct impacts on ecosystem services and human health, very little is known about the scavenging ecology of agricultural ecosystems, one of the major, and growing, land uses worldwide (Foley et al. 2005).

Recent work by our group revealed that scavenging communities in agricultural ecosystems are comprised of fewer species relative to those found in less disturbed landscapes. However, these communities nonetheless functioned very efficiently as measured by the high proportion of carrion

resources transferred directly from vertebrate carcasses to vertebrate species via scavenging as opposed to that transferred more indirectly to invertebrates or microbes via decomposition (DeVault et al. 2011). This high efficiency was hypothesized to emerge from the structure of the scavenging community itself. Namely, that superabundant mesopredators were sequestering energy in the system by dominating the detrital sub-web of energy flow (DeVault et al. 2011). Mesopredators, therefore, may act as species of large effect (sensu Huston 1997) by driving the function of scavenging communities. Although there is a growing literature investigating the stability of ecosystem function in relation to various species manipulations (Hooper et al. 2005), the stability of scavenging as an ecosystem service has not been empirically evaluated.

Our goal in this research was to test the stability of scavenging as an ecosystem service by altering the structure of the scavenging community. To do this we conducted a one-time removal experiment in which the dominant scavenger, raccoons (*Procyon lotor*; DeVault et al. 2011), were depopulated from a suite of habitat islands (i.e. woodlots). We then quantified the functional (i.e. behavioral) response of the scavenging community to this perturbation by monitoring the fates of experimentally-placed mouse *Mus musculus* carcasses in removal woodlots and a balanced number of control woodlots to identify changes in the efficiency of service delivery and the diversity of the scavenging community.

We addressed two tiers of hypotheses regarding the potential compensatory response of the scavenging community to the reduced abundance of a numerically dominant scavenger (Table 1). Hypotheses based on predictions of interspecific competition for a shared resource (i.e. carrion; Mac Nally 1983) were examined first at the community level (tier 1) to determine the stability of scavenging by measuring the extent of any compensatory scavenging by the manipulated community. Then we examined hypotheses at the level of the scavenger species (or group) to test the form of any apparent functional response among competitors for carcasses (tier 2; Table 1). Given the high abundances, low diversities, and behavioral plasticity symptomatic of the communities of generalist species that persist in agriculturally fragmented landscapes, we predicted full compensation for experimentally reduced raccoon scavenging. In particular, we predicted that a compensatory response would be dominated by another abundant mesopredator, Virginia opossums *Didelphis virginiana*, through an increase in scavenging efficiency. Secondarily, we predicted compensation by invertebrate competitors for carcasses if elapsed time to vertebrate scavenging events increased after raccoons were reduced in abundance.

Methods

Our study area was located in the Upper Wabash River Basin (UWB) of north-central Indiana, USA (Fig. 1). The UWB encompasses 1165 km^2 and approximately 71% of the area is cultivated for agriculture yearly, mainly for the production of corn *Zea mays* and soybeans *Glycine max*; Beasley et al. 2007). Only 13% of the basin is forested, compared to an average of 19% statewide (Moore and Swihart 2005). Forest tracts within the study area are largely confined to drainages where flooding or steep terrain made the land unsuitable for cultivation. The forests, predominantly oak–hickory–maple (*Quercus–Carya–Acer*), are fragmented into woodlots: 75% of these forest patches are $<$5 ha, 50% are $<$2 ha, and only 1% of all forest patches are $>$100 ha (Moore and Swihart 2005). Raccoons and Virginia opossums are the most abundant mesopredators on the landscape; their presence is ubiquitous across the study area (Beasley and Rhodes 2008, Beasley et al. 2010).

Raccoon and Virginia opossum abundances were estimated using capture–mark–recapture (CMR) in 25 control woodlots during March–June of 2003–2007 (detailed methods are in Beasley and Rhodes 2008). In March–June of 2007, an additional 30 woodlots were the focus of an experimental removal of raccoons and simultaneous estimates of opossum abundance. Removal woodlots were saturated with box traps baited with canned cat food and all captured raccoons were euthanized as part of a larger study of mesopredator population dynamics following ASM guidelines and Purdue Animal Care and Use Committee protocol 07-018 (Beasley unpubl.). To ensure complete removal of raccoons, each removal woodlot was trapped continuously until no raccoons were captured and no tracks were observed for four consecutive days. Consequently, the duration of trapping differed among removal woodlots, but was limited to a maximum of 25 days. Raccoons were allowed to naturally recolonize once trapping of the woodlot ceased. During March–June of 2008, one year post-removal, raccoon and

Table 1. Alternative hypotheses designed to indicate the stability of an important ecosystem service, scavenging, via the presence (Tier 1) and form (Tier 2) of compensation in carcass removal by the scavenging community after we reduced the abundance of the numerically dominant scavenger. Null hypotheses were based on no compensation from the scavenging community. All hypotheses indicate the response in removal woodlots relative to levels in control woodlots. Raccoon scavenging was excluded from all analyses but hypothesis IV to avoid spurious conclusions based on a large experimental reduction of raccoon abundance and scavenging.

Tier 1 Identifying a compensatory response at the community level	
hypothesis I:	increase in the total proportion of carcasses scavenged by non-raccoon organisms
hypothesis II:	increase in the diversity of the scavenging community
hypothesis III:	change in the average time from carcass placement to carcass removal
Tier 2 Identifying a functional response below the community level	
hypothesis IV:	increase in carcasses acquisition by members of the scavenging community
hypothesis V:	disproportionate increase in carcass acquisition (i.e., competitive dominance) by a particular scavenger species or group of scavengers relative to others
hypothesis VI:	change in the average time from carcass placement to carcass removal for a specific scavenger species or group of scavengers

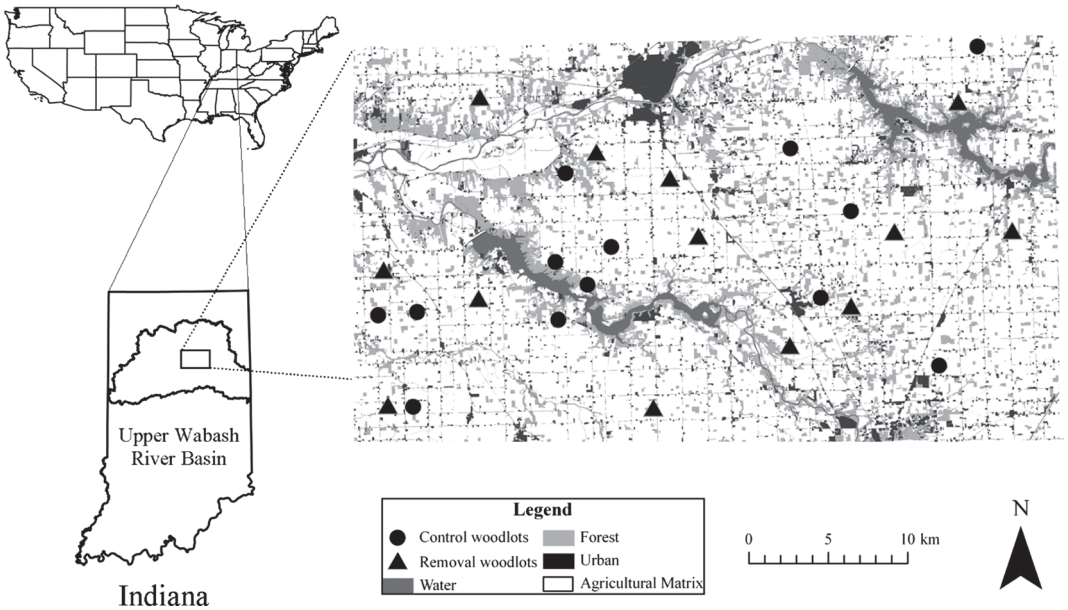

Figure 1. Study area and location of 13 woodlots with intact scavenger communities (Control) and 13 woodlots from which we removed the dominant scavenger, raccoons (Removal). We monitored the fates of mouse carcasses in these woodlots to test the stability of carrion removal, an important ecosystem service, to perturbations of the scavenging community. The Upper Wabash River Basin is representative of many agricultural ecosystems where habitat has been highly fragmented to accommodate intensive agricultural production.

opossum abundances again were estimated in all woodlots using CMR.

We selected 13 woodlots from both the control and removal groups in which to conduct the current study (Fig. 1). Control woodlots (n = 13) retained intact scavenging communities and were selected from the 25 CMR woodlots. Removal woodlots (n = 13) were selected from the 30 raccoon removal woodlots. Woodlots were selected such that woodlot attributes (e.g. size and isolation) were balanced between control and removal groups and represented the range of values present in the landscape (mean study woodlot area = 6.96 ha, range = 2.46–16.32 ha). Woodlots were distributed throughout the study area and all were located a sufficient distance apart (mean distance to nearest study woodlot = 3.7 km, range = 1.6–8.3 km) to minimize the probability that a raccoon would be a resident of any two study woodlots based on raccoon movement behavior in our study landscape (Beasley et al. 2007).

We used remote cameras to monitor the fates of mouse carcasses placed at randomly-assigned locations in all woodlots bi-weekly from 16 June 2007 through 24 May 2008. Each woodlot received one mouse carcass every two weeks. There were 26 trials in each of 26 woodlots incorporating a calendar year following raccoon removal. Thus, we used temporal replicates (i.e. one carcass every two weeks for 26 replicates) rather than multiple carcasses during each trial to measure within-woodlot variance in scavenging community composition.

We modified the remote cameras to capture images when activated by the removal of a mouse carcass from a mechanical trigger (i.e. by a scavenging event). Methods for camera deployment and a description of the trigger mechanism are described in DeVault et al. (2004). Mouse carcasses were obtained frozen from a pet food supplier and were thawed before use. Mice were dark brown in color, and were of similar mass (mean ± SEM; 18.4 ± 0.03 g) to the native mouse in our study area *Peromyscus leucopus*; 17.9 ± 0.16 g; Rhodes unpubl.).

At the completion of each two-week trial, we categorized the fate of each mouse carcass from the camera images as: 1) scavenged – we noted the first scavenger (a vertebrate species or invertebrates as a group) to remove the carcass from the trigger; 2) not scavenged – the whole carcass was present on the trigger mechanism at the end of the trial; 3) missed-detection – the mouse carcass was not present on the trigger mechanism, but a scavenger could not be identified from the images, or; 4) non-trial – carcass fate could not be assigned because of mechanical or human error. Although burying beetles *Nicrophorus* spp. and other invertebrates were visibly responsible for moving some carcasses from the triggers, assigning the event to a single invertebrate species was impossible from our images. However, vertebrates could be described to the species level. Elapsed time from carcass placement to all scavenging events was calculated using the time-stamp imprinted on each image. To evaluate temporal effects on scavenging behavior, we also grouped trials into four discrete seasons. Summer included trials 1–7 (~June–August), fall included trials 8–13 (~September–November), winter included trials 14–20 (~December–February), and spring included trials 21–26 (~March–May).

Data analysis

We began our investigation by validating the success of our removal experiment, first by verifying that there were reduced raccoon numbers in treatment woodlots through the full course of the study, and then by verifying that there was an altered frequency of scavenging by raccoons in those same woodlots relative to our control woodlots (Supplementary material

Appendix A1). Because a numerical response by opossums to the reduced abundance of raccoons would have confounded any inference in our study on a functional response by members of the scavenging community, we verified that opossums did not increase in number over the course of our study (Supplementary material Appendix A1). Further, because the unequal occurrence of missed detections between experimental groups could have represented a systematic bias in our study, we verified that this was not a source of bias in our experiment (Supplementary material Appendix A1).

To assess whether there was an increase in the total proportion of carcasses scavenged in removal woodlots relative to control woodlots (hypothesis I; Table 1), we conducted log-linear analyses in PROC CATMOD on fate categories scavenged (including those fates classified as missed detections) and not scavenged tabulated by treatment (SAS ver. 9.1; SAS Inst.). We eliminated those carcasses scavenged by raccoons from this analysis in order to explicitly examine whether there was a change in carcass acquisition among all non-raccoon scavengers, while controlling for the large, known effect our experiment had on raccoon abundance and carcass acquisition (Supplementary material Appendix A1). Our model parameters included treatment and fate and we used a likelihood ratio test to determine if an association existed between these parameters.

To assess whether there was an increase in the diversity of scavengers in removal relative to control woodlots (hypothesis II), we used frequency data for each scavenger species and invertebrates as a group to calculate separate Shannon-Weiner indices (Krebs 1999) for removal and control woodlots and tested for a difference between experimental groups using a modified t-test (Zar 2002). Because the Shannon-Weiner index is sensitive to species evenness as well as richness (Krebs 1999), we removed all raccoon scavenging events from consideration to minimize the bias associated with our known experimental effect. Additionally, because diversity estimates are not sensitive to the identity of species in the sample, we tested for a difference in the proportion of unique scavenger species in removal versus control woodlots using a χ^2-test in which the proportion of scavengers unique to the control woodlots was the expected value for the removal woodlots.

To assess whether the average time from carcass placement to carcass removal changed between treatments (hypothesis III), we modeled elapsed time (defined as the time from carcass placement to carcass removal for trial fates defined as scavenged) as a function of treatment and season using PROC MIXED in SAS. Treatment and season were fixed effects in our model and we defined random effects based on our split-plot experimental design. Thus, woodlot nested within treatment and the interaction term treatment × season nested within woodlot were included as random effects (Zar 2002). In this analysis we evaluated only the saturated model and we removed raccoon scavenging from the analysis to limit confounding with a density effect caused by our experiment.

For all analyses conducted below the community level, we combined all low-frequency vertebrate scavengers (i.e. those with global frequencies < 10%; Supplementary material Appendix A2) into one category termed 'other vertebrates'. We then compared the contribution of each category of scavenger in the removal woodlots to that observed in the control woodlots using chi square tests (Table 2; hypothesis IV). To assess whether any response by the scavenging community was dominated by a particular scavenger or group of scavengers (hypothesis V) we tested for differences in the proportions of mouse carcasses scavenged by opossums and other vertebrates by treatment and season using log-linear analysis. We examined nested models hierarchically and selected the most parsimonious of those with a non-significant likelihood ratio ($p > 0.05$) for further evaluation. Unfortunately, carcasses scavenged by invertebrates could not be included in this analysis because invertebrates did not scavenge carcasses in all seasons (Fig. 2a). Thus, to accommodate the seasonality of invertebrate scavenging, we constructed an additional log-linear model incorporating treatment and scavenger as main effects but used data only from summer when invertebrates scavenged at their highest frequency (Fig. 2a).

Finally, we modeled elapsed time to carcass removal for opossum and other vertebrates using mixed effect models (hypothesis VI). Fixed effects were treatment, season, and scavenger (i.e. opossum and other vertebrates with invertebrates excluded). Random effects were the same as those used in hypothesis III. We evaluated all potential models ranging from the saturated model through all single-parameter models

Table 2. We conducted separate chi square tests using observed counts from treatment woodlots and expected counts calculated from control proportions (i.e. the % column). Non-trial fates were tested for equality using proportions of the grand total. All other tests were conducted after excluding non-trial fates from consideration.

	Control		Removal					
Fate	Count	%	Count	%	Expected count	Direction of change	χ^2	p
Scavenged								
Virginia opossum	80	28.8%	97	37.7%	74.0	+	7.18	0.007
raccoon	107	38.5%	45	17.5%	98.9	-	29.39	< 0.001
invertebrate	20	7.2%	22	8.6%	18.5	+	0.67	0.414
other vertebrate	14	5.0%	22	8.6%	12.9	+	6.34	0.012
Missed detection	38	13.7%	44	17.1%	35.1	+	2.24	0.134
(sub-total)	(259)	(93.2%)	(230)	(89.5%)				
Not scavenged	19	6.8%	27	10.5%	17.6	+	5.07	0.024
(total)	(278)	(100%)	(257)	(100%)				
Non-trial	60	17.8%	81	24.0%	60	+	7.35	0.007
Grand total	338		338					

and ranked them according to Akaike's information criterion (AIC; Burnham and Anderson 2002). Significant parameters in the best model set (i.e. models with $\Delta AIC \leq 2$) were further evaluated using mean contrasts with p-values adjusted using the Tukey-Kramer method. Again, to accommodate the seasonality of invertebrate scavenging, we constructed an additional mixed-effect model with data from summer only.

To evaluate elapsed time below the community level and include invertebrate scavenging (i.e. using data only from summer when invertebrate scavenging was at its highest frequency) we modeled elapsed time as a function of the fixed effects treatment, scavenger (opossum, other vertebrates, and invertebrates), and the interaction term treatment × scavenger. Random effects were the same as those used in previous analyses. Models were evaluated and mean contrasts were performed as described previously. We did not interpret main effects independently if they were included in a significant interaction term.

Results

Our log-linear model incorporating all non-raccoon scavenging events (which included missed detections) and unscavenged carcasses indicated that the total number of trials attributable to the two fates was greater in the control versus removal woodlots ($\chi^2_1 = 4.37$, $p = 0.036$) and that the overall distribution of trials among the two fates differed

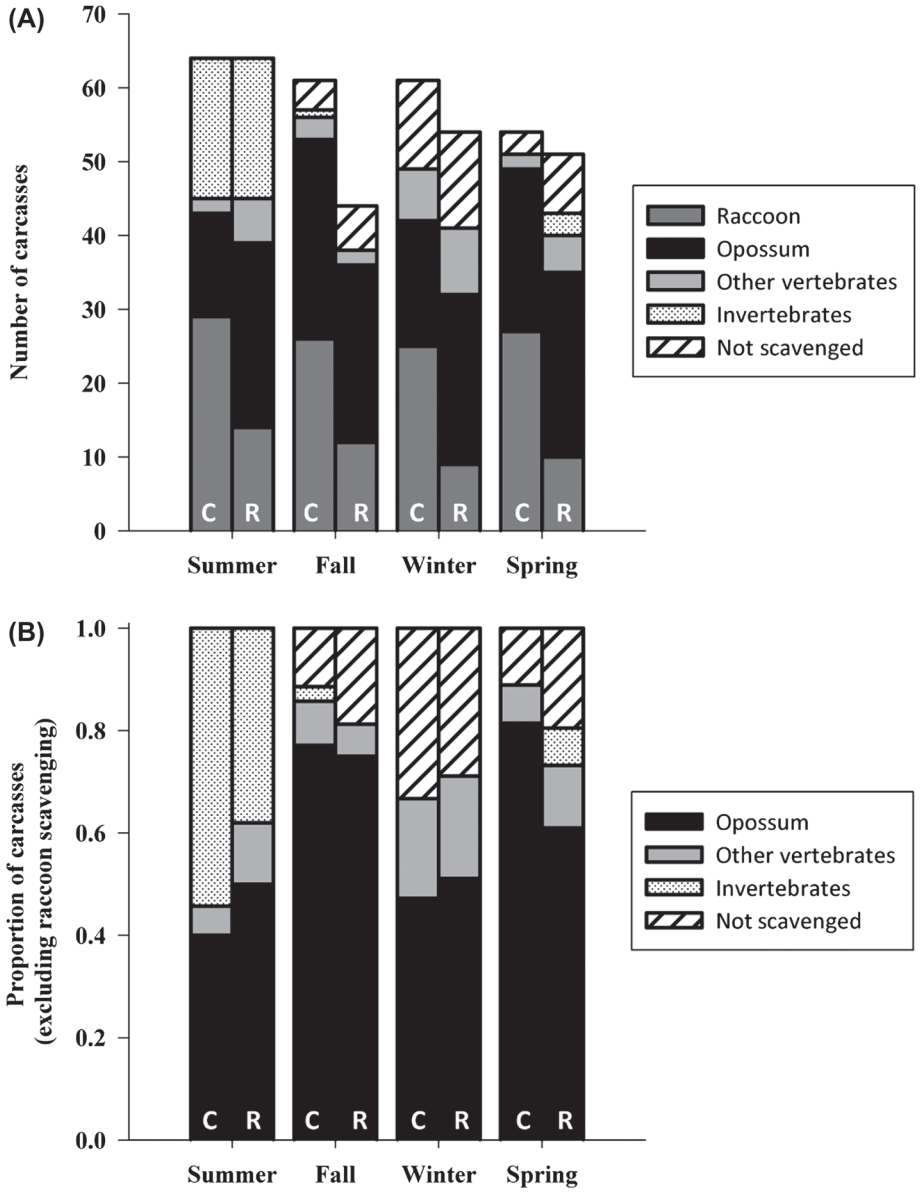

Figure 2. Scavenging of mouse carcasses by season and treatment in north central Indiana, USA, during June 2007 – May 2008. Mouse carcasses were monitored in woodlots with intact scavenger communities (C) and woodlots subjected to a raccoon removal (R) immediately prior to the study. Seasons were roughly: summer (Jun–Aug), fall (Sep–Nov), winter (Dec–Feb), and spring (Mar–Apr). Scavenging by opossums and other vertebrates increased, and carcasses not scavenged were more prevalent after we experimentally reduced the abundance of the dominant scavenger, raccoons (A). However, no scavenger appeared to dominate the compensatory response to reduced raccoon scavenging in terms of an increased proportion of carcasses acquired (B).

($\chi^2_1 = 160.52$, $p < 0.001$). However, the distribution of trials among the fates did not differ between the control and removal woodlots (likelihood ratio $\chi^2_1 = 0.24$, $p = 0.626$; hypothesis I). In addition, the diversity of scavengers in removal woodlots (H' = 0.48 decits) was not different from the diversity of scavengers in control woodlots (H' = 0.45 decits; $t = -0.527$, DF = 248, $p = 0.701$). Nor was there a difference in the number of unique scavengers (hypothesis II) between removal woodlots and control woodlots (4 vs 2, respectively; $\chi^2_1 = 2.00$, $p = 0.157$).

Our model of elapsed time indicated no effect of treatment ($F_{1,247} = 0.04$, $p = 0.849$) on the elapsed time to scavenging (hypothesis III), although elapsed time did vary by season ($F_{3,247} = 14.20$, $p < 0.001$; treatment × season, $F_{3,247} = 0.80$, $p = 0.496$). After correction for multiple comparisons, elapsed time from carcass placement to carcass removal was shorter in summer (mean ± SE; 1.23 days ± 0.23) than in spring (2.87 ± 0.28, $p < 0.001$) and winter (3.30 ± 0.28, $p < 0.001$), but was no different than that in fall (1.69 ± 0.27, $p = 0.553$). Elapsed time did not differ between spring and winter ($p = 0.683$), but elapsed times in both of these seasons were longer than that in fall ($p = 0.017$ and $p < 0.001$, respectively).

The results of our individual chi-square tests revealed that the overall proportions of carcasses classified as scavenged by opossums, scavenged by other vertebrates, and 'not scavenged' increased significantly in removal woodlots as compared to our controls (Table 2; hypothesis IV). Interestingly, the proportion of trials attributed to invertebrate scavenging in removal woodlots did not increase beyond that expected from control woodlots (Table 2). In our analysis designed to detect disproportionate responses of non-raccoon scavengers to our treatment (hypothesis V), the most parsimonious log-linear model of opossum and other vertebrate scavenging incorporated scavenger as the single model parameter ($\chi^2_1 = 75.89$, $p < 0.001$, Fig. 2b). Notably excluded from this model were the main effects treatment and season along with all interaction terms (likelihood ratio $\chi^2_{14} = 17.64$, $p = 0.224$, Fig. 2b). Similarly, the most parsimonious log-linear model of opossum, other vertebrate, and invertebrate scavenging using data from summer included scavenger as the only model parameter ($\chi^2_1 = 17.91$, $p < 0.001$), again excluding the main effect treatment and the treatment × scavenger interaction term from the model (likelihood ratio $\chi^2_3 = 5.24$, $p = 0.155$).

The best model of elapsed time to carcass removal by opossums and other vertebrates across experimental groups and seasons was the saturated model (AIC = 909.7; competing models had ΔAIC > 10). However, the only significant parameter in the model was season ($F_{3,197} = 4.56$, $p = 0.004$), whereas treatment ($F_{1,197} = 0.13$, $p = 0.718$), scavenger ($F_{1,197} = 0.79$, $p = 0.376$), and the interaction terms (all $p > 0.05$) explained little variation in the model (hypothesis VI). After correction for multiple comparisons, elapsed time to carcass removal was shorter in summer (mean ± SE; 1.17 ± 0.49) than during winter (3.06 ± 0.33, $p = 0.008$) and spring (2.95 ± 0.49, $p = 0.051$), but did not differ for other seasonal comparisons. Using data only from summer and including invertebrates as scavengers, the best model of elapsed time to carcass removal again was the saturated model (AIC = 275.4; competing models had ΔAIC > 4), though in this model none of the parameters explained a significant amount of variation (treatment $F_{1,41} = 1.17$, $p = 0.286$; scavenger $F_{2,78} = 2.08$, $p = 0.132$; treatment × scavenger $F_{2,78} = 2.30$, $p = 0.107$).

Discussion

The scavenging community as a whole exhibited a broad response to perturbation as multiple groups of scavengers compensated for reduced raccoon scavenging. Yet, the response was not fully compensatory such that the stability of an important ecosystem service, carcass removal by scavengers, was affected by our manipulation of the scavenging community. We detected a significant effect of treatment on the frequency of scavenging overall as our removal experiment altered the proportional contributions of scavengers acquiring carrion. However, a majority of the carrion was still sequestered within the mesopredator assemblage. Twenty-five of 35 (71%) trial outcomes that we observed as numerical increases in scavenging in the removal versus control woodlots were attributable to vertebrates as opposed to scavenging by invertebrates or those carcasses remaining un-scavenged. Thus, primarily opossums but also 'other vertebrates' clearly exhibited a functional response as they acquired more carcasses in removal woodlots relative to their counterparts in control woodlots; counterparts that presumably were experiencing higher levels of competition with raccoons for carrion resources. Alternatively, our data provided no evidence that the scavenger communities in removal woodlots increased in diversity or numbers of unique scavengers relative to control woodlots. This outcome likely is a function of the highly-truncated scavenging community in this fragmented agricultural ecosystem (DeVault et al. 2011). Variance in elapsed time to carcass removal at the community level and among scavengers was driven by seasonal variation, not by our experiment: results that reinforce previous research suggesting that scavenging is a process mediated primarily by temperature (DeVault et al. 2004), weather (Selva et al. 2005), and chemical processes (DeVault et al. 2003, Burkepile et al. 2006).

Contrary to our prediction, the frequency of scavenging by invertebrates did not increase when the decline in vertebrate scavenging resulted in more available carcasses. Further, no vertebrate scavenger dominated the increase in carcass acquisition when competition with raccoons for carcasses should have been reduced as a result of their experimentally reduced abundance. Thus, although non-raccoon vertebrates in the manipulated community increased their utilization of carrion and exhibited a functional response, the relationships among those species in terms of relative proportions of carcasses claimed remained unchanged. These results, an apparent non-response by invertebrates to increased carcass availability and no disproportionate response by any vertebrate scavenger to putatively reduced competition, provide robust evidence in agreement with recent work indicating that factors other than competition (e.g. the spatial or temporal dispersion of carcasses) serve to structure the scavenging community as a whole (Selva and Fortuna 2007).

Intriguingly, the number of carcasses that remained un-scavenged at the end of our trials in removal woodlots

(n = 27) increased 42% beyond baseline levels calculated from control woodlots (n = 19). This result indicates that even though the scavenging community responded to an increased availability of carrion, primarily through increased scavenging by non-raccoon vertebrates, the perturbed scavenging community was less efficient in removing carcasses than was the undisturbed community. This finding is significant because the efficiency with which scavenger communities consume carrion is a critical ecosystem service that has wide implications (Cortés-Avizanda et al. 2009, Wenny et al. 2011), even for the health of human populations (Jennelle et al. 2009).

Many studies have solidified a link between ecosystem function and overall species diversity (Loreau et al. 2001, Duffy 2002, Hector and Bagchi 2007). However, the removal or addition of a single species also can have cascading effects on ecosystem function (Duggins et al. 1989). The relative impact of a single species on the function of an ecosystem can range from very high for 'brittle' (sensu Dobson et al. 2006) ecosystem functions (e.g. apex predators regulate herbivory; Ripple et al. 2001) to low in situations where the ecosystem function involves numerous species exhibiting niche-redundancy (e.g. primary productivity in grasslands; Tilman et al. 2001).

Although the effects of a single species on the function of scavenging communities previously received little attention, the near extirpation of vultures as a guild from much of South Asia highlights the scope of impact associated with the disturbance of scavenging communities. Cascading effects of increased carcass availability included an explosion in feral dog numbers, an associated increased incidence of rabies among humans, and an estimated cost of over US $34 billion (Pain et al. 2003, Oaks et al. 2004, Markandya et al. 2008). Even in our highly fragmented agricultural landscape, where most species that persist are generalists and likely to exhibit functional redundancy as facultative scavengers (DeVault et al. 2003), the reduced abundance of a single species disrupted system efficiency and left more carrion unclaimed than was the case in our control environments. Thus, our study experimentally demonstrated the vulnerability of an important ecosystem service, carrion removal, to perturbations of the scavenging community. Further, our study system may serve as a model highlighting the method by which scavenging communities respond to perturbations. Future research should strive to more fully elucidate the function of scavenging communities in relation to services in a variety of ecosystems.

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Supplementary material (available online as Appendix O19771 at <www.oikosoffice.lu.se/appendix>). Appendix A1 and A2.