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Interactions between a detrital resource pulse and a detritivore community

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Abstract Detritivore communities influence the decomposition of detrital resources in virtually all natural systems. Conversely, detrital resources can also have considerable bottom-up effects on detritivore communities. While many investigations have examined detritivory and decomposition processes, few have considered interactions between detritivores and detritus as concurrent processes in the same system, or in the context of natural detrital pulses. In many systems, resource pulses contribute substantial detrital inputs to belowground systems. These detrital pulses may influence interactions between the detritivore community and detrital decomposition. I conducted field experiments to investigate interactions between detrital resource pulses of periodical cicada (*Magicicada* spp.) carcasses and scavenging detritivorous macroarthropods. Cicada litterfall pulses influenced several broad groups in the macroarthropod community, including relatively specialized necrophilous taxa and relatively generalized detritivores, omnivores and predators. Conversely, detritivore activity increased the rate of cicada carcass decomposition by 4,082% compared to caged control carcasses. These results suggest that interactions between pulses of cicada detritus and the detritivore community influence both the persistence of ephemeral detrital resources, and the distribution, abundance and behavior of detritivore populations.

Keywords Detrital resource pulses · Detritivore communities · Dynamic food webs · Decomposition · Periodical cicadas (*Magicicada* spp.)

Introduction

Detritivores influence the decomposition of detrital resources in virtually all natural systems, with broad consequences for community structure and ecosystem function (Seastedt and Crossley 1984; Moore et al. 2004). By shredding, consuming and transforming organic detritus, detritivores accelerate microbial decomposition and nutrient cycling (Edwards et al. 1970; Kitchell et al. 1979; Swift et al. 1979; Vossbrinck et al. 1979; Seastedt and Crossley 1984; Seastedt 1984; Lussenhop 1992). The cumulative effect of these detritivore actions is extensive: up to 95% of primary productivity cycles directly through detritus-based foodwebs in diverse grassland, desert and forest systems (Seastedt and Crossley 1984; Coleman 1996). By initiating the process of detrital decomposition, detritivore communities mediate substantial fluxes between the aboveground and belowground components of terrestrial ecosystems.

Conversely, detrital resources often have considerable bottom-up effects on detritivore communities. Investigations in diverse systems have documented generally positive effects of detrital resource enrichment on detritivore immigration, activity and reproduction (McBrayer et al. 1977; Seastedt 1984; Chen and Wise 1997, 1999; Reynolds et al. 2003). For example, Chen and Wise (1999) demonstrated that populations of forest litter detritivores increased under experimentally pressed supplementation with mushrooms, potatoes and fruit fly medium. These observations are consistent with conceptual and theoretical models suggesting broad resource limitation of detritivore populations in most ecosystems (Hairston et al. 1960; Pimm 1982; Nisbet et al. 1997).

Both experimental and theoretical investigations have examined detritivory and decomposition processes.

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However, few studies have considered both the bottom-up effects of detrital resources on detritivores and the effects of detritivores on the persistence of detrital resources in the same natural system. It may be particularly important to consider decomposition as the result of these simultaneous and reciprocal interactions. Although most models of detrital food webs assume a constant renewal rate for an unchanging detrital pool (Moore et al. 2004), many natural systems are characterized by reciprocal interactions between dynamic detritivore communities and temporally variable detrital resources (Moore et al. 2004).

In many systems, resource pulses may influence interactions between the detritivore community and detrital decomposition. Resource pulses are uncommon events of ephemeral resource superabundance that occur in wide-ranging ecosystems (Ostfeld and Keesing 2000; Yang 2004). Although considerable resource variability exists in all natural systems (Sears et al. 2004), notable examples of resource pulses include oak and beech masts (Zackrisson et al. 1999; Ostfeld and Keesing 2000), spawning salmon (Helfield and Naiman 2003), hurricane-mediated greenfalls (Whigham et al. 1991; Lodge et al. 1991, 1994) and insect outbreaks (Lovett and Ruesink 1995; Yang 2004). In recent years, ecologists have begun to describe some general patterns of community responses to diverse resource pulses (Ostfeld and Keesing 2000).

These observations suggest three broad consumer groups that may be especially likely to experience direct effects from resource pulses: widespread, generalist consumers, relatively specialized and highly mobile consumers, and detrital consumers (Curran and Leighton 2000; Ostfeld and Keesing 2000; Yang 2004). Widespread generalist consumers are able to survive long interpulse intervals because of their broader diets and opportunistically utilize pulsed resources when they become available. For example, many generalist small mammals shift their diets to consume ephemerally available seeds and fruits during mast events (Curran and Leighton 2000; Ostfeld and Keesing 2000). Relatively specialized and highly mobile consumers may also be important consumers of resource pulses. For example, long-tailed parakeets (*Psittacula longicauda*) travel long distances to consume mast fruit crops in Indonesian tropical forests (Curran and Leighton 2000), and passenger pigeons *Ectopistes migratorius* may have filled a similar role during acorn mast events in North America (Blockstein 2002). These species may be able to utilize patchy and ephemeral resources by foraging over larger spatial scales. Finally, many resource pulses satiate predators and other aboveground consumers (Karban 1982; Sweeney and Vannote 1982; Williams et al. 1993), yielding detrital inputs of uncommon magnitude, duration, phenology, composition and spatial scale to detritivore communities. The resulting detrital pulses can influence diverse belowground communities and ecosystem processes (Ben-David et al. 1998; Zackrisson et al. 1999; Yang 2004). However, the effects of pulsed

detrital inputs on scavenging detritivore communities are not well understood.

Periodical cicadas (*Magicicada* spp.) provide a natural context to investigate the effects of resource pulses on detritivore communities and decomposition. Periodical cicadas are large insects (adult mass 0.25–0.75 g) that feed on plant roots belowground for 13 or 17 years before emerging synchronously at densities of 0–350 individuals m^{-2} (Brown and Chippendale 1973; Williams and Simon 1995). Adult cicadas are a conspicuous part of the aboveground community for 4–6 weeks. Cicada distributions are often patchy on scales of < 1 km, while synchronous cohorts occur on scales of 10^5 km^2 (Marlatt 1907; Dybas and Davis 1962; Williams et al. 1993). Although their role in forest communities is largely unrecognized due to their long belowground life history, periodical cicadas may be the most common herbivores in the wide range of North American deciduous forests in both number and cumulative biomass (Dybas and Davis 1962; Dybas and Lloyd 1974). A large proportion of this cicada biomass enters belowground foodwebs as detrital litterfall during the summer of emergence, due to predator satiation at high densities (Karban 1982; Williams et al. 1993). Although arthropod bodies are a small component of biomass fluxes in most terrestrial systems (Seastedt and Crossley 1984), the unusual life history of these insects suggests that they may represent a substantial temporally stored resource pulse across a large area of this forest ecosystem (Wheeler et al. 1992; Whiles et al. 2001; Yang 2004). In particular, previous studies have shown that the decomposition of these detrital cicada pulses increases belowground microbial biomass and soil nitrogen availability, with indirect effects on seed mass in at least one forest plant species (Yang 2004).

In this study, I investigate reciprocal interactions between detrital resource pulses of periodical cicada carcasses and communities of scavenging macroarthropods. I ask two questions: (1) how do resource pulses of cicada detritus affect these detritivore communities? and (2) how do these detritivore communities effect the decomposition of periodical cicada detrital pulses?

Methods

Macroarthropod detritivore experiment

I conducted a field supplementation experiment using a range of natural cicada carcass deposition densities in order to investigate the effects of cicada carcasses on macroarthropod communities. I collected approximately 17,000 *M. septendecim* and *M. cassini* adults during the 2003 emergence of Brood IX at Concord College (37°25'25.0"N, 81°0'23.9"W), Athens Lake (37°24'36.8"N, 81°0'27.5"W) and Pipestem State Park (37°31'18.3"N, 80°59'8.6"W) near Athens, WV, USA. Cicadas were collected with insect nets and by hand, and included male and female *M. septendecim* and *M. cassini*

individuals in naturally occurring proportions across a variety of adult life stages. These collections were composed of 58% *M. septendecim* and 42% *M. cassini* in an approximately 1:1 sex ratio, and included adults that were newly emerged, chorusing, ovipositing, dying due to faulty eclosion, and recently killed due to stormy weather events or incomplete depredation. Cicadas in advanced stages of decomposition were not collected. These collections represent well-documented sources of nonpredation cicada mortality in a system with strong predator satiation (White et al. 1979; Karban 1982, 1983, 1984; Williams et al. 1993; Williams and Simon 1995). Cicadas were frozen within 1–4 h after collection and used in experiments 1–14 days later. These collections represented approximately 12.4 kg of cicada biomass, or 4.5 kg dry mass, with a C:N ratio of 4.76.

Eighty-eight 1 m² forest plots in Glen Alton, VA, USA (Jefferson National Forest, USDA Forest Service, 37°26'12.3"N, 80°32'25.1"W) were randomly assigned to receive four levels of manipulated cicada litterfall density: 0 (control), 60, 120 or 240 cicadas m⁻² with 22 replicates in each treatment group. These cicada litterfall densities correspond to 0, 16, 32 and 64 g of dry cicada biomass m⁻², or 0, 8, 16, 32 g of carbon input m⁻², respectively. Plots were distributed in a > 10 m interval grid chosen to minimize habitat variability and between-plot interactions. A more complete description of the soil and physical characteristics of this study site is provided in Yang (2004). Treatment levels were chosen to reflect a well-documented range of naturally occurring cicada densities (Dybas and Davis 1962; Williams et al. 1993; Rodenhouse et al. 1997; Whiles et al. 2001). For example, Williams and Simon (1995) cite several references documenting emergence densities ranging between 3 and > 350 cicadas m⁻². A census of 25 haphazard 1 m² quadrats in 2002 recorded cicada densities ranging from 6 to 504 emergence holes m⁻² (mean = 95.92, SD = 104.81) and a conservative census of cicada deposition showed litterfall densities between 0 and 1,840 cicadas m⁻² (mean = 56.94, SD = 134.63) (Yang 2004).

The Glen Alton site includes a low-slope region of *Quercus* and *Acer*-dominated deciduous forest located within the broad geographic range of the Brood IX cicada emergence. This site was less than 1 km from an active cicada chorus, but plots received < 1 cicada m⁻² of ambient litterfall due to the spatial patchiness of these emergences. These conditions provided a biologically relevant context for experimental litterfall supplementation. Cicada carcasses were hand-delivered to experimental plots on June 1, 2003.

Macroarthropods were censused in each experimental plot using two unbaited, circular 7 cm diameter pitfall trap subsamples. Although the utility of pitfall trap sampling for absolute measures across different habitats or for particular taxa is limited (Topping and Sunderland 1992), pitfall trap capture rates can provide an index of relative arthropod behavioral activity and population density levels (i.e. "activity-density") in

controlled experimental plots (Baars 1979; Ericson 1979; Loreau 1991). Terrestrial macroarthropods from pitfall traps in control and treatment plots were collected and preserved in ethylene glycol solution 0–7 days and 14–21 days after the carcasses addition. A single cumulative collection was made at the end of each period, to minimize disturbance to the plots. In all quantitative analyses, specimen collections were identified to family (Coleoptera: Carabidae, Silphidae, Histeridae, Scarabaeidae, Geotrupidae, Staphylinidae; Hymenoptera: Formicidae), suborder (Opiliones: Palpatores, Araneae: Labidognatha) or order (Orthoptera, Blattaria, Diplopoda, Chilopoda, Dermaptera). These levels of taxonomic resolution were chosen to provide approximate information about broad trophic relationships. Subsequent generic (Coleoptera: Silphidae: *Nicrophorus* sp. and *Necrophila* sp., Coleoptera: Histeridae: *Marginotus* sp., Coleoptera: Scarabaeidae: *Onthophagus* sp., Geotrupidae: *Geotrupes* sp.) and specific identifications (Coleoptera: Carabidae: *Carabus goryi*, *Platynus decentus*, *Pterostichus coracinus*, *Pterostichus mutus*, *Sphaeroderus stenostomus*, *Sphaeroderus canadensis*) within groups facilitated interpretations of the observed results.

I used repeated-measures multivariate analysis of variance (MANOVA) to investigate the overall effect of cicada supplementation level (0, 60, 120 and 240 cicadas m⁻²), time (0–7 days and 14–21 days after supplementation), and level × time interactions on the activity-density of 14 macroarthropod taxa. I assessed the univariate normality of residuals in each taxon as a proxy for multivariate normality (Scheiner 2001). Square root transformations improved normality in this generally Poisson-distributed dataset, but the assumption of normality was not met in all taxa due to the high frequency of zeros. In order to improve normality and reduce the overall dimensionality of these data, I employed principal components analysis (PCA) to identify five principal components with eigenvalues greater than unity. I conducted a second repeated-measures MANOVA using these data to test for community level effects from cicada supplementation level, time and level × time interactions. The residuals of these principal components were normally distributed. Although the conclusions of these two MANOVA approaches were identical, the analysis of principle components is more appropriate because of its consistency with normality assumptions. MANOVA is generally robust to deviations from multivariate normality and homoscedasticity (Scheiner 2001), and tests for homoscedasticity in MANOVA are often oversensitive to departures from multivariate normality. Under these circumstances, I employed Pillai's Trace as the most appropriate test of significance because of its robustness (Scheiner 2001; Harris 2001) and power (Seber 1984) under deviations from the assumptions of MANOVA.

I conducted subsequent univariate Kruskal–Wallis analysis of variance (ANOVA) tests in order to investigate the effects of cicada supplementation level and time within each taxon. I assessed level × time interactions

using a Kruskal–Wallis test to examine treatment effects in a dataset composed of plotwise differences between the observations at the two periods. This test is a non-parametric analog to a parametric repeated measures analysis when looking at the level \times time interaction. In taxa with significant interaction effects ($n=3$), I used separate Kruskal–Wallis tests to investigate the effects of cicada supplementation level in each collection time period. I also conducted least-squares polynomial regressions to examine the form of arthropod responses to increasing cicada supplementation in each collection period. Regression analyses provide an alternative approach to investigate the relationship between cicada supplementation and arthropod activity-density on continuous axes. Arthropod activity-density data were rank-transformed prior to regression to create a distribution-free analysis (Iman and Conover 1979; Conover and Iman 1981). The conclusions of this analysis were consistent with regressions of untransformed data. I used lack-of-fit tests to determine the simplest model order. All univariate analyses were conducted in a protected framework after significant overall effects were detected in MANOVA to control the probability of Type I error in multiple comparisons (Scheiner 2001).

Cicada decomposition experiment

I conducted a second experiment to investigate the effects of detritivores on cicada carcass decomposition using a comparison of detritivore-exclusion and open control carcasses. I collected live periodical cicadas during the 2004 emergence of Brood X at the Blandy Experimental Farm near Boyce, VA, USA (39°3'47.0''N 78°3'39.7''W). These cicadas were frozen within 1 h of collection, and used in these experiments 7–14 days later. At the beginning of this experiment, an initial population of 520 female cicadas (*M. cassini*) was thawed to room temperature, then individually massed without oven drying and tethered using dental floss tied with a clove hitch around the thorax. Cicadas were randomly assigned to detritivore exclusion and control groups with five cicada carcass subsamples in each experimental replicate. Detritivores were excluded with 10 \times 20 cm (height \times diameter) aluminum insect screen (1.3 mm mesh) cages. Cages were constructed without floors to allow natural soil contact and cicada carcass microhabitats. Control cicadas were placed in sham exclusion cages with 4 cm wide openings in the walls and top to allow detritivore access. Decomposition was measured as the remaining dry mass of the cicada carcass attached to the tether at five time intervals (0, 18, 60, 144, and 360 h). The thoracic attachment of these tethers effectively retained identifiable carcass units while allowing decomposition and disintegration. Because the final mass measurements required carcass drying, repeated measures of the same carcass would present potentially unrealistic decomposition conditions. Instead, I collected independent samples of exclusion and control

carcasses at each time period over the course of the experiment to avoid repeated measures of the same carcasses (Underwood 1997). Decomposition trials were conducted in the context of natural cicada litterfalls (approximately 45.4 ± 38.3 cicadas m^{-2} , mean \pm SD) at a low-slope mixed deciduous forest near Milldale, VA, USA (Stonebridge Farm, 39°0'33.6''N 78°4'13.9''W) between June 13 and June 30, 2004.

To investigate the effect of detritivore shredding on the rate of cicada carcass decomposition, I fit negative exponential functions to control and detritivore exclusion decomposition data using an iterated Gauss–Newton method based on least squares criteria. Previous studies have suggested that negative exponential functions provide a robust model for many organic decomposition processes (Minderman 1968; Vossbrinck et al. 1979; Seastedt and Tate 1981). A one-component fitted negative exponential regression estimates a constant proportional decay rate (k) in the model $B_t = B_0 e^{-kt}$, where B_t represents the fraction of carcass mass remaining at time t . I used Mann–Whitney U -tests to investigate the difference between control and detritivore exclusion carcasses at each time period with a Bonferroni correction for multiple comparisons.

Results

Macroarthropod detritivore experiment

A multivariate analysis of 14 macroarthropod taxa suggests that this community was influenced by both cicada supplementation level ($P=0.0017$) and time since supplementation ($P<0.0001$). Cicada supplementation level did not influence the overall density ($P=0.618$) of these macroarthropod taxa, suggesting that these MANOVA results indicate quantitative changes in community composition, rather than overall increases in macroarthropod density. Similarly, a multivariate analysis of principal components from this dataset also indicates community-level effects of cicada supplementation level ($P=0.0038$) and time since supplementation ($P<0.0001$). The effect of cicada carcass availability on the broad macroarthropod community did not vary significantly between the two time periods (level \times time, MANOVA, $P=0.0648$; PC MANOVA, $P=0.1041$), although observed patterns suggest that some specific taxa may have responded to the cicada pulse differently during the two time periods (Fig. 1, see also univariate analyses below). The results of these parallel multivariate analyses suggest that pulses of cicada carcass litterfall are a substantial transient influence on the macroarthropod community and provide a protected framework for subsequent univariate analyses of particular taxa.

This diverse macroarthropod community included specialized detritus-associated groups, as well as several generalist detritivores, omnivores, and predators.

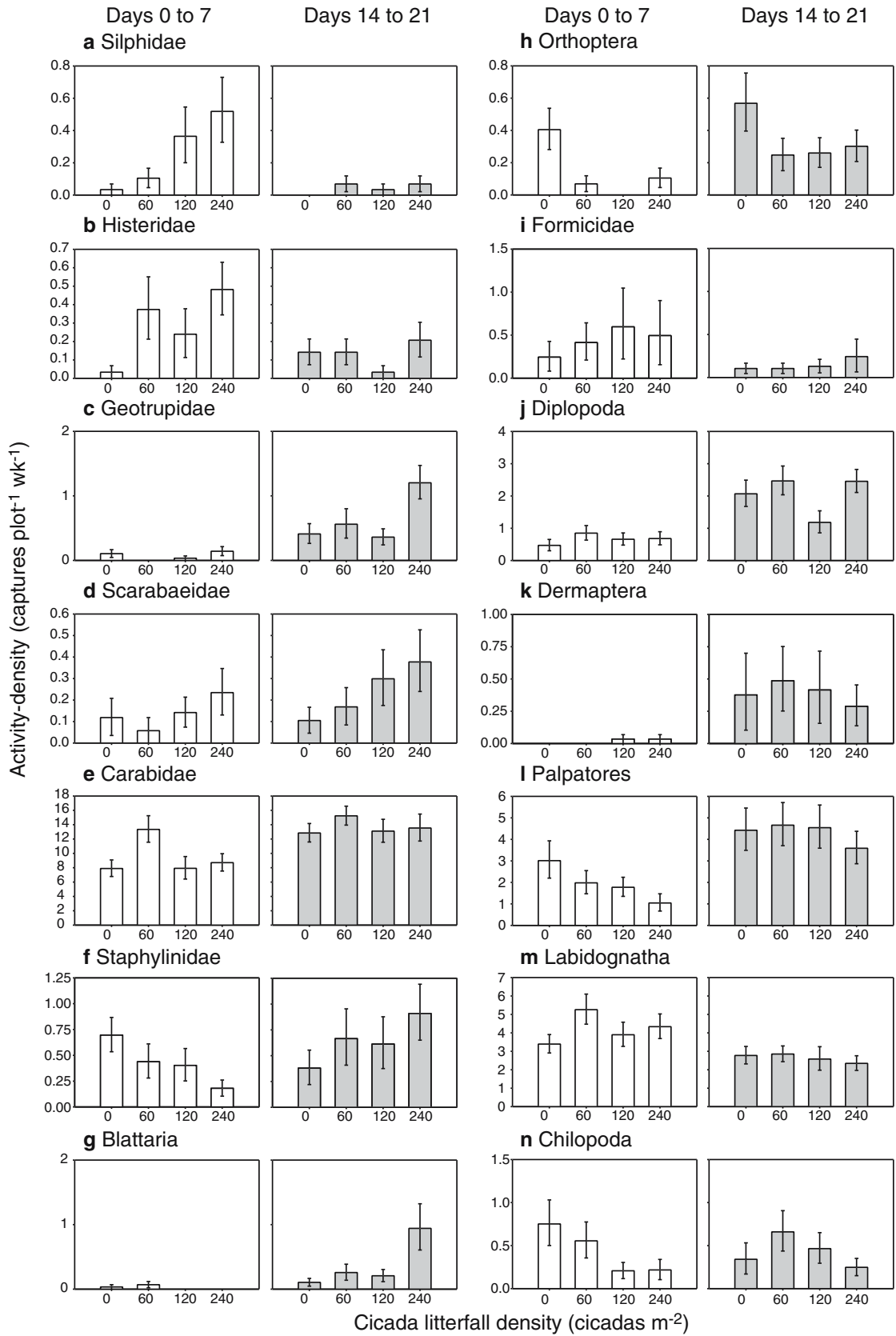


Fig. 1 Activity-density of 14 macroarthropod taxa (a-n) in response to four levels of cicada litterfall supplementation (0, 60, 120 and 240 cicadas m⁻²) at two time periods: days 0-7 (open bars) and days 14-21 (shaded bars). Activity-density is reported as individual captures per plot per week (mean \pm SE)

Carrion beetles (Silphidae), hister beetles (Histeridae), and dung beetles (Scarabaeidae and Geotrupidae) were among the relatively specialized detritus-associated taxa in this community. The assemblage of relatively polyphagous detritivores, omnivores, and predators in this community included ground beetles (Carabidae), rove beetles (Staphylinidae), cockroaches (Blattaria), grasshoppers and crickets (Orthoptera), millipedes (Diplopoda), earwigs (Dermaptera), ants (Formicidae), and harvestmen (Palpatores). Spiders (Labidognatha) and centipedes (Chilopoda) were included as strictly predaceous taxa.

The silphid and histerid genera observed in these experiments (Silphidae: *Nicrophorus* sp. and *Necrophila* sp., Histeridae: *Marginotus* sp.) are commonly found in association with vertebrate carrion. These silphid genera are necrophagous detritivores and predators, whereas these histerids are predators of early-colonizing diptera eggs and larvae in detritus (Borror et al. 1989; Arnett and Thomas 2001). Increasing cicada carcass availability had a positive effect on the activity-density of both silphids (Fig. 1a, $P=0.031$) and histerids (Fig. 1b, $P=0.022$). These responses were characterized by rapid colonization of supplemented plots in days 1–7, with diminished activity-density during days 14–21 (Fig. 1a, b). Mean silphid activity-density increased by > 1,400% in maximally supplemented plots compared to control plots during the earliest stages of decomposition (Dunnnett's test, $P<0.05$). Mean histerid activity-density increased by > 1,300% in the same comparison (Dunnnett's test, $P<0.05$).

In contrast, the saprophagous and coprophagous earth boring dung beetles (Geotrupidae: *Geotrupes* sp.) showed a delayed response to increasing cicada carcass availability (level \times time, Fig. 1c, $P=0.0428$). Geotrupid activity-density did not respond to the cicada carcass pulse in days 1–7 (Fig. 1c, linear regression, $P=0.3215$; Kruskal–Wallis, $P=0.1424$), but showed a generally positive response to cicada supplementation in days 14–21 (Fig. 1c, linear regression, $P=0.0046$; Kruskal–Wallis, $P=0.0141$). The activity-density of geotrupid beetles increased by 193% in maximally supplemented plots compared to control plots during the later time period (Fig. 1c, Dunnnett's test, $P<0.05$). These analyses were unable to detect effects of cicada carcass availability on the activity-density of generally coprophagous scarab dung beetles (Scarabaeidae: *Onthophagus* sp., Fig. 1d, $P=0.1194$), although observed trends in both time periods suggest the possibility of undetected positive effects.

Cicada supplementation influenced the activity-density of carabid ground beetles in this community (Fig. 1e, $P=0.0449$). Carabid activity-density increased by 69% in plots supplemented with 60 cicada carcasses m^{-2} compared to controls during days 1–7 (Dunnnett's test, $P<0.05$), but did not differ from control levels at increasing levels of cicada availability. No effect of cicada supplementation was detected in days 14–21. Staphylinid rove beetles showed different responses to

cicada supplementation in each time period (level \times time, $P=0.0093$). Staphylinid activity-density decreased with increasing cicada carcass availability during days 1–7 (Fig. 1f; linear regression, $P=0.0122$; Kruskal–Wallis, $P=0.0724$), but showed a nonsignificant positive relationship with cicada carcass availability in days 14–21 (linear regression, $P=0.0808$; Kruskal–Wallis, $P=0.3488$). Nearly all known carabid and staphylinid beetles are polyphagous predators, though supplemental scavenging and detritus-associated predation is widespread in these diverse groups (Lovei and Sunderland 1996; Bohac 1999; Toft and Bilde 2002).

Cockroaches showed a delayed positive response to cicada supplementation during the later stages of decomposition (level \times time, Fig. 1g, $P=0.0337$). No effect of cicada carcass availability was observed in days 1–7 (linear regression, $P=0.2011$, Kruskal–Wallis, $P=0.2894$). In days 14–21, cockroach activity-density increased with increasing cicada carcass availability (linear regression, $P=0.0063$; Kruskal–Wallis, $P=0.0460$). This response was largely driven by an approximately 800% increase in cockroach activity-density in maximally supplemented plots compared to control plots during the later decomposition stages (Dunnnett's test, $P<0.05$). Nearly all cockroaches are opportunistic generalist detritivores with broad diets (Borror et al. 1989).

Responses to cicada supplementation were often negative or variable among phytophagous, omnivorous, and primarily plant-detritus-feeding taxa. Grasshoppers and crickets showed a negative response to cicada supplementation (Fig. 1h, $P=0.0064$). This effect was particularly strong in the initial time period: activity-density in unsupplemented control plots was approximately 600% greater than in each of three cicada supplementation levels during days 1–7 (Dunnnett's test, $P<0.05$). Cicada supplementation did not have any detectable effect on ants (Fig. 1i, $P=0.8571$), millipedes (Fig. 1j, $P=0.1377$), earwigs (Fig. 1k, $P=0.7072$) and harvestmen (Fig. 1l, $P=0.2375$), though observed trends suggest the possibility of negative initial responses in harvestmen.

Strictly predaceous taxa showed relatively weak or negative responses to increased cicada supplementation in these experiments. Spiders showed no response to different levels of cicada carcass availability (Fig. 1m, $P=0.5662$). The activity-density of centipedes showed an inconsistent and nonsignificant response to cicada supplementation across both time periods (Fig. 1n, $P=0.2019$), though patterns of activity-density observed in days 1–7 suggest the possibility of weak negative trends (linear regression, $P=0.0216$, Kruskal–Wallis, $P=0.0965$).

Cicada decomposition experiment

Cicada carcass decomposition followed a pattern of negative exponential decay in the presence of

detritivores (Fig. 2, $R^2_{\text{adj}}=0.83$). The fitted decay rate in the presence of detritivores (k_{control}) was -0.046 h^{-1} (97.5% CI = -0.060 h^{-1} to -0.035 h^{-1}). This decay constant indicates that the expected mass of a cicada carcass decreased by approximately 5% during each hour in the field. By comparison, the decay constant of cicada carcasses in detritivore exclusion cages ($k_{\text{exclusion}}$) was -0.0011 h^{-1} (Fig. 2, $R^2_{\text{adj}}=0.32$, 97.5% CI = -0.0019 h^{-1} to -0.0005 h^{-1})—a reduction of 4,082% compared to the control decay constant ($P < 0.0001$). The estimated half-life of a cicada carcass in the absence of macrodetritivores is 608 h, whereas the expected half-life of a carcass exposed to detritivores is 15 h. The mean mass of detritivore exclusion carcasses was 54% greater than open control carcasses after 18 h in the field ($P = 0.0007$). This paired comparison was also significant at 60 h ($P < 0.0001$), 144 h ($P < 0.0001$), and 360 h of detritivore exposure ($P < 0.0001$). In the absence of detritivores, 83% of the expected initial carcass mass remained intact after 360 h in the field.

Discussion

Cicada pulses influenced several broad groups in the macroarthropod community, including relatively specialized necrophilous taxa and relatively generalized detritivores, omnivores and predators. Although individual detritivore taxa showed varied responses to cicada carcass pulses, these results suggest a few broad patterns: (1) relatively specialized and highly mobile carrion-associated detritivores (e.g. carrion beetles and hister beetles) were most likely to show rapid, strong and positive responses to pulsed inputs of cicada detritus, (2) many generalist detritivores also responded positively to cicada supplementation (e.g. ground beetles and cock-

roaches), sometimes showing increased activity-density at later decomposition stages, and (3) some predaceous, phytophagous, and omnivorous taxa showed negative responses to cicada supplementation (e.g. grasshoppers and crickets), while several other such groups showed no response to cicada supplementation (e.g. spiders and earwigs).

The response of scavenging macroarthropods to cicada resource pulses supports a general observation that resource pulses may commonly have strong direct effects on detrital-based communities. These results also suggest that the two recurrent consumer types that often utilize pulsed resource availability in nondetrital systems, widespread trophic generalists and relatively specialized mobile taxa, may also be important consumer strategies within the detrital community. These findings expand upon the general patterns of consumer responses to resource pulses found in other systems (Ostfeld and Keesing 2000; Curran and Leighton 2000).

The temporal patterns of observed responses suggest that cicada litterfall pulses represent a changing resource throughout the process of decomposition. These patterns are consistent with a dynamic view of food webs where transient temporal niches arise throughout the succession of a detrital resource (Moore et al. 2004). Notably, some detritivore responses persisted well beyond the duration of identifiable cicada carcasses, and several taxa responded most strongly to the profoundly disintegrated detrital fragments at advanced stages of decomposition. Several taxa in this macroarthropod community appeared to show strong bottom-up responses to pulses of cicada litterfall. Effects were varied and complex within this community, including both positive and negative responses to cicada litterfall.

Most of the positive and negative numerical responses observed on the timescale of this investigation are likely to have resulted from primarily behavioral, rather than reproductive, mechanisms. Rapid behavioral responses are likely to be especially important in the context of naturally patchy and transient phenomena, such as cicada pulses. Observed increases in activity-density could be due to immigration, increased movement, or both. Likewise, observed decreases in activity-density could result from mortality, emigration, decreased movement, or a combination of these factors. Indirect effects may also have contributed to these observed responses. For example, apparent negative responses of some taxa to cicada carcasses may have resulted from the trait-mediated effects (i.e. intimidation and crowding) of immigrating taxa (Schmitz et al. 2004; Preisser et al. 2005). In particular, spatially patchy cicada pulses favored rapid positive behavioral responses by mobile specialists and widespread generalists. Mobile detrital specialists may be particularly adapted to utilize patchy and short-lived resources. More generally, these results suggest that if the timescale of resource duration is much shorter than the timescale of consumer generations, behavioral mechanisms will probably be an important component of the population response. On

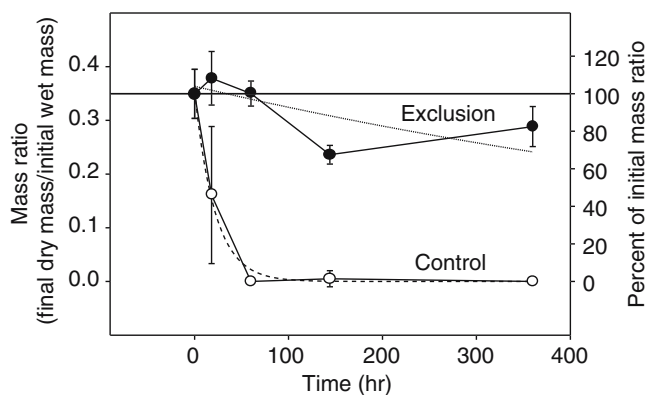


Fig. 2 Cicada carcass decomposition with detritivores excluded (filled circles) and in open controls (open circles). Each replicate represents the mean (\pm SE) of five individually massed subsample carcasses ($N_0=9$, $N_{18}=8$, $N_{60}=10$, $N_{144}=5$ and $N_{360}=3$ exclusion replicates, and $N_0=9$, $N_{18}=12$, $N_{60}=12$, $N_{144}=17$ and $N_{360}=19$ control replicates). The dotted lines represent fitted negative exponential regressions. The solid horizontal line represents the initial mass ratio (final dry mass/initial wet mass)

the relatively short timescales of many resource pulses, both behavioral and reproductive responses are likely to be relevant components of population responses (Ostfeld and Keesing 2000). However, these processes may occur at different scales: behavioral responses may generally be local in space and ephemeral in time, whereas reproductive responses may commonly be more diffuse in space and delayed in time.

Observed patterns of detritivore succession on large magnitude cicada pulses are similar to patterns observed in studies of vertebrate carcass decomposition (Payne 1965; Hanski 1987; Doube 1987; Schoenly and Reid 1987; Watson and Carlton 2003; Archer 2003). Both of these resources attract a diverse, specific and often overlapping detritivore community. From a detritivore's perspective, both large cicada litterfall pulses and vertebrate carcasses may represent relatively large inputs of spatially patchy and temporally ephemeral animal detritus.

By comparison, several investigations have described rapid scavenging of arthropod carcasses by generalist detritivores in diverse habitats under nonpulsed conditions (Jeanne 1979; Seastedt and Tate 1981; Seastedt et al. 1981; Fellers and Fellers 1982; Young 1984; Rosenheim 1990; Retana et al. 1991). In many of these systems, arthropod carcasses are rapidly scavenged by widespread resource generalists, often wasps and ants. For example, Retana et al. (1991) observed ants scavenging arthropod carcasses in 285 ± 282 s (mean \pm SD) in a Mediterranean grassland, Fellers and Fellers (1982) describe ant scavenging of dead flies and moths in 405 ± 461 s (mean \pm SD) in a North American deciduous forest, and Seastedt et al. (1981) report that bagged and tethered cricket carcasses were discovered by vespid wasps within minutes and were completely consumed when observed 24 h later in a North American oak-hickory forest. Similar phenomena have been described in alpine and postvolcanic environments where wind-borne arthropod detritus supports generalist detritivore populations in the absence of local resources (Spalding 1979; Ashmole et al. 1983; Edwards 1986, 1987, 1988; Ashmole and Ashmole 1987; Swan 1992; Edwards and Sugg 1993; Sugg and Edwards 1998). The observed response of the detritivore community to small magnitude cicada pulses may be more similar to the patterns documented in these nonpulsed systems: specialized necrophilous taxa were less abundant and widespread generalist taxa were more common at lower levels of cicada supplementation. These observations indicate that the magnitude and spatial distribution of detrital inputs may influence the nature of consumer responses.

Studies demonstrating the rapid scavenging of invertebrate carcasses under nonpulsed conditions suggest that decomposition rates in the cicada system may be reduced under conditions of detrital superabundance. Although the concept of "detritivore satiation" is probably more limited than predator satiation, it may be useful to investigate the possibility of reduced decomposition rates under pulsed resource conditions in a

context where both pulsed and nonpulsed resource dynamics occur.

Theoretical studies have considered the effects of behavioral responses (immigration and emigration) on detritivore dynamics under spatially patchy resource distributions (e.g. Nisbet et al. 1997), though few have investigated the effects of resource pulses. However, this study presents a more complex system that includes both spatial and temporal variation. Because of this large temporal variability, transient dynamics incorporating both behavioral and reproductive timescales may be particularly relevant in descriptions of pulsed systems (Hastings 2004).

Identifying the persistence of resource pulse effects in natural systems remains an important open question. Possible mechanisms of persistent effects include biomass storage in some long-lived component of the community, time-lagged indirect effects ramifying through the broader community, or changes in the community composition, such as local invasions or extinctions. However, few studies have investigated the persistence of direct and indirect effects from large, transient resource perturbations across a diverse natural community. This is a formidable task beyond the scope of the present investigation, though studies in specific systems such as this one contribute incrementally to this effort.

While pulses of cicada detritus influenced the detritivore community, detritivores also dramatically increased the rate of cicada carcass decomposition. These results parallel previously reported investigations of vertebrate carrion and plant litter decomposition in the presence and absence of detritivores (Payne 1965; Edwards et al. 1970; Vossbrinck et al. 1979; Beare et al. 1992; Reynolds et al. 2003). In this system, the mechanisms of detritivore action are likely to include both direct consumption of detritus and facilitation of microbial penetration, transportation, and decomposition (Kitchell et al. 1979; Seastedt 1984; Moore et al. 1988; Beare et al. 1992; Coleman 1996; Bengtsson et al. 1996; Wall and Moore 1999). Detritivore-mediated decomposition of cicada litterfall pulses may accelerate substantial nutrient and biomass fluxes between the aboveground and belowground components of a large ecosystem (Yang 2004).

In the absence of detritivores, cicada carcasses showed a temporary increase in mass after 18 h in the field. This pattern appears to have resulted from the rapid colonization of many intact carcasses by unidentified larval diptera oviposited through the enclosure mesh (personal observation). No maggots were observed on fragmented cicada carcasses open to detritivores. The proliferation of maggots on caged carcasses illustrates a particularly rapid reproductive response on an ephemeral resource. These observations also suggest parallels to the biocontrol of Australian bush fly populations living in cattle dung pads through the introduction of exotic dung beetles (Wallace and Tyndale-biscoe 1983; Tyndale-biscoe and Vogt 1991, 1996). In both of these

systems, detritivores may limit fly populations through direct predation, habitat modification, and competition.

Detritivore communities are often described as donor-controlled systems because detritivores do not directly affect the renewal rate of detritus (Pimm 1982; Setälä 2002; Moore et al. 2004). Although this system is likely to be donor-controlled, detritivores commonly influence the persistence and character of detrital resources (Edwards et al. 1970; Seastedt and Crossley 1984; Moore et al. 2004). In this system, the availability and character of detrital resources is variable in space and time. The results of this study indicate that detritivore consumption and shredding dramatically reduces the persistence of cicada carcasses, even under conditions of pulsed superabundance. The behavioral responses of mobile detritivores may be especially important in these pulsed and patchy systems. For example, rapid detritivore responses may limit the availability of ephemeral resources to saprophagous flies and decomposer microbes through consumption and comminution.

Taken together, these results suggest reciprocal interactions between detritivore communities and detrital persistence during cicada litterfall pulses: detritivores affect detrital resource availability while detrital resources influence the composition of the detritivorous macroarthropod community. These processes operate concurrently during natural cicada pulse events (personal observation). Detritivore behavioral responses to pulsed resource availability leads to a shift in the macroarthropod community composition, which contributes to the rapid consumption and comminution of the pulsed resource. In turn, this consumption and comminution substantially reduces the persistence of the detrital resource. The findings of this study are consistent with the idea that detritus–detritivore interactions influence both the aboveground persistence of cicada biomass pulses, and the distribution, abundance and behavior of detritivore populations.

The spatially patchy and temporally pulsed nature of the perturbation provides a particularly apt opportunity to document this reciprocal interaction—this pulsed perturbation has direct effects on the activity and distribution of detritivores on short spatial and temporal scales, and indirect consequences for detritivore-mediated decomposition. The spatial extent of cicada emergence events suggests that this pulse may influence detritivore communities across a landscape scale in North American forest ecosystems.

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