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ALLOCHTHONOUS SUBSIDY OF PERIODICAL CICADAS AFFECTS THE DYNAMICS AND STABILITY OF POND COMMUNITIES

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Abstract. Periodical cicadas emerge from below ground every 13 or 17 years in North American forests, with individual broods representing the synchronous movement of trillions of individuals across geographic regions. Due to predator satiation, most individuals escape predation, die, and become deposited as detritus. Some of this emergent biomass falls into woodland aquatic habitats (small streams and woodland ponds) and serves as a high-quality allochthonous detritus pulse in early summer. We present results of a two-part study in which we (1) quantified deposition of Brood X periodical cicada detritus into woodland ponds and low-order streams in southwestern Ohio, and (2) conducted an outdoor mesocosm experiment in which we examined the effects of deposition of different amounts of cicada detritus on food webs characteristic of forest ponds. In the mesocosm experiment, we manipulated the amount of cicada detritus input to examine if food web dynamics and stability varied with the magnitude of this allochthonous resource subsidy, as predicted by numerous theoretical models. Deposition data indicate that, during years of periodical cicada emergence, cicada carcasses can represent a sizable pulse of allochthonous detritus to forest aquatic ecosystems. In the mesocosm experiment, cicada carcass deposition rapidly affected food webs, leading to substantial increases in nutrients and organism biomass, with the magnitude of increase dependent upon the amount of cicada detritus. Deposition of cicada detritus impacted the stability of organism functional groups and populations by affecting the temporal variability and biomass minima. However, contrary to theory, stability measures were not consistently related to the size of the allochthonous pulse (i.e., the amount of cicada detritus). Our study underscores the need for theory to further explore consequences of pulsed allochthonous subsidies for food web stability.

Key words: allochthonous subsidy; aquatic food webs; detritus; mesocosm; periodical cicadas; resource pulse; stability; woodland ponds; zooplankton.

Introduction

The emergence of periodical cicadas (Homoptera: Cicadidae: *Magicicada*) is a spectacular event in North American forests. Periodical cicadas are one of the most abundant animals in eastern United States forests, with peak densities of >300 individuals/m^2 (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001). The synchronous emergence of a geographic brood of periodical cicadas every 13 or 17 years is composed of 10^6–10^9 individuals across thousands of hectares (see Plate 1). The coordinated movement of relatively large numbers of individuals from below ground to above ground represents a large and infrequent translocation of biomass and nutrients (Whiles et al. 2001). Even at modest emergence densities, the majority of individuals in a local population avoid predation through predator satiation, leaving the overwhelming portion of individuals to breed, die, and become deposited as detritus (Williams et al. 1993).

The deposition of periodical cicada carcasses at the end of an emergence event represents a sizable resource pulse, affecting soil nutrient cycling, the performance of herbaceous vegetation, and the demography of terrestrial consumer populations (Wheeler et al. 1992, Yang 2004, Koenig and Liebhold 2005, Yang 2006). In forest ecosystems, headwater streams and small ponds are intimately connected to the terrestrial landscape, receiving nutrients and energy from soils and through the deposition of leaf litter and terrestrial arthropods (Wallace et al. 1997, Wipfli 1997, Rubbo and Kiesecker 2004). During years of cicada emergence, woodland aquatic ecosystems may receive a pulse of detritus when cicada populations senesce in early summer (Vokoun 2000). The impact of this potentially large and

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infrequent pulse of allochthonous detritus on forest aquatic ecosystems has not been previously investigated.

Allochthonous resource subsidies (i.e., the movement of prey, nutrients, or energy into one ecosystem from another) are ubiquitous, affecting the productivity, food web structure, and stability of a wide variety of ecosystems (Polis et al. 1997, Pace et al. 2004, Polis et al. 2004, Carpenter et al. 2005). Ecological theory predicts that allochthonous resource subsidies can stabilize or destabilize food webs by affecting the variability and minimum size of recipient populations and ecosystem components (Rosenzweig 1971, DeAngelis 1992, Huxel and McCann 1998, Huxel 1999). Theory suggests that the precise effects of subsidies on food web stability depend on subsidy quality, timing, and magnitude, as well as recipient food web configuration (Rosenzweig 1971, DeAngelis 1992, Huxel and McCann 1998, Huxel 1999, Takimoto et al. 2002). In particular, theoretical models focusing on manipulations of allochthonous input demonstrate that low to moderate levels of allochthonous subsidy tend to stabilize food webs by diffusing intense food web interactions, while large magnitude subsidies lead to lower stability of recipient populations through the decoupling of consumer–resource interactions (Huxel and McCann 1998, Huxel et al. 2002). Most models examining the effects of allochthonous subsidies of different magnitudes treat subsidies as temporally constant inputs (Huxel and McCann 1998, Huxel et al. 2002), and some allochthonous subsidies to ecosystems can be relatively constant across a diversity of time scales (Caraco and Cole 2004, Vanni and Headworth 2004). Yet empirical studies have demonstrated that many subsidies also occur as temporal pulses (Carlton and Goldman 1984, Naiman et al. 2002, Anderson and Polis 2004, Yang 2004). Currently there is limited theoretical exploration of the effects of pulsed allochthonous subsidies on communities and ecosystems (but see Huston and DeAngelis 1994, Takimoto et al. 2002). Theoretical predictions of the effects of constant and pulsed subsidies have provided insight into the importance of allochthonous subsidies to the stability of food webs and ecosystems, but most of these predictions remain untested (Jeffries 2000). Thus there is a need for empirical assessment of the theoretical predictions of the effects of allochthonous resource subsidies on food web and ecosystem stability.

Food web responses to allochthonous inputs depend on the immediate fate and the point at which inputs enter the recipient food web (Huxel and McCann 1998, Huxel et al. 2002). Thus the specific effects of a pulse of cicada detritus on aquatic ecosystems may depend on the fate of energy and nutrients in cicada corpses. Cicada litter is relatively high quality (Brown and Chippendale 1973, Yang 2004) and may quickly release dissolved nutrients for uptake by bacteria, phytoplankton, and periphyton. Alternately, cicada litter may be consumed directly by larger metazoans (e.g., crayfish and fish), whose subsequent digestive and excretory activities will determine the fate of nutrients and energy derived from cicada detritus. In order to understand the effects of a pulse of periodical cicadas on aquatic food webs, the pathway by which nutrients and energy from cicadas enter aquatic food webs must be elucidated.

In this study, we examined the input of a pulse of periodical cicada detritus to forest aquatic ecosystems and determined the effects of cicada detritus deposition on aquatic food webs and ecosystems. We estimated periodical cicada detritus deposition into forested aquatic ecosystems (low-order streams and woodland ponds) during the emergence of Brood X periodical cicadas in southwestern Ohio, USA, in the summer of 2004. In addition, we conducted a mesocosm experiment in which we examined the effects of cicada detritus on food webs typical of forest ponds. In the mesocosm experiment, we manipulated the magnitude of cicada detritus input in order to examine if ecosystem dynamics and stability vary significantly with the magnitude of a pulsed allochthonous subsidy. This study represents one of the first experimental assessments of the effects of a pulsed allochthonous detritus subsidy on the stability of ecosystem components (Anderson and Polis 2004).

Materials and Methods

Deposition of Brood X periodical cicada detritus in aquatic ecosystems

Cicada litter deposition into woodland aquatic ecosystems was estimated with open plastic litterfall baskets (0.08 m^2 surface area; Yang 2004) in 10 temporary and semipermanent woodland ponds and six 30-m reaches of first- and second-order streams located within 10 km of Oxford, Ohio, USA. Baskets were placed in ponds and streams several days prior to the start of the emergence of Brood X periodical cicadas in the summer of 2004 (early May) and left in place until after the end of the emergence period (early July). All pond and stream sites were selected before the cicada emergence period and were located in lowland areas with abundant woody vegetation. To determine if periodical cicada emergence densities were within the range used in our mesocosm experiment, we additionally estimated periodical cicada emergence densities in 16 wooded locations in southwestern Ohio (woodlots, fencerows, and riparian areas; Appendix A).

During the cicada litter collection period, individual ponds contained 2–10 baskets, with each pond containing at least one basket per 5 m^2 of pond surface area. Pond surface areas ranged from 6 to 50 m^2 with maximum depths of 5–33 cm. Pond baskets were elevated above the water surface on metal or wooden poles. Each stream reach had 10 baskets regularly placed along the stream bed (elevated on metal poles) or secured onto metal rebar supports driven into the stream bank and extended above the stream surface. On several occasions, we temporarily removed baskets from within streams because of sudden large stream flows caused by storms (typically removed ~72 h per storm event).

We collected cicada litter from baskets every three to six days during the emergence period. Litter from each basket was sorted and counted by type, dried at 60°C for 48 h, and weighed to determine dry mass deposition (g/m^2). Litter was categorized into the following types: whole adults, whole nymphs, molted nymphal exoskeletons (exuviae), severed wings, and severed heads with wings attached (a result of bird predation; Williams et al. 1993). Cicada litter fluxes to aquatic systems during the emergence period were transformed to areal nutrient loadings ($mmol/m^2$) of carbon (C), nitrogen (N), and phosphorus (P) by multiplying the number of specific litter items falling into an individual litter basket by the amount of C, N, and P in the litter type (based upon nutrient content analysis of each litter type; see Appendix B).

Mesocosm experiment

Description and experimental design.—We coupled observations of the deposition of cicada litter into natural ecosystems to a controlled and replicated mesocosm experiment. Mesocosms are excellent tools for exploring ecological interactions and have been used in numerous studies (Drenner and Mazumder 1999); however, it is likely that we sacrificed some environmental heterogeneity and community diversity by using mesocosms. The use of mesocosms allowed us to keep environmental variables and community composition constant while solely manipulating the magnitude of cicada detritus inputs.

Sixteen polyethylene tanks (2.0-m^2 surface area, 900-L capacity) at the Miami University Ecological Research Center were filled with water from a nearby fishless pond. Water was filtered through a 500-μm screen to prevent addition of large invertebrates. Each tank received 340 g (dry mass) of sycamore (*Platanus occidentalis*) leaf litter. This leaf litter mass was used because it covered the bottom of mesocosm tanks to a level that was visually comparable to leaf litter cover on the bottoms of local woodland ponds. Sycamore trees are abundant in riparian areas in southwestern Ohio, and leaf litter was collected from a riparian area in January 2004 and dried in the lab until it reached constant mass. Water and leaf litter were added to mesocosms in mid-May 2004 and were allowed to "equilibrate" for ~one week before food webs characteristic of small woodland ponds were assembled. Sixteen tows of a 63-μm Wisconsin plankton net from the same fishless pond were collected and diluted to 20 L, and 1 L of this (containing zooplankton, phytoplankton, and bacteria) was added to each tank. Each tank also received 47 snails (*Helisoma* spp.), 80 amphipods (*Gammarus* sp.), and two to three crayfish (*Orconectes rusticus*; mean ± 1 SD wet mass in each mesocosm = 17.4 ± 4.1 g). Mesocosm community composition and organism densities were based on invertebrate communities in permanent, semipermanent, and temporary ponds (Harris 1995). Mesocosms were covered with mesh (50% shade cloth) to limit organism migration and to reduce light intensity to levels more characteristic of woodland ponds.

The experimental design consisted of four levels of cicada detritus addition, with each treatment replicated four times: 0, 75, 150, and 300 cicadas/m^2. Cicada addition levels were initially based upon literature values of emergence densities (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001), and our estimates of Brood X emergence densities in summer 2004 in forests immediately adjacent to woodland ponds and low-order streams in southwestern Ohio were within this range (Appendix A). We collected approximately 15 000 live Brood X adult periodical cicadas over a three-day period at a location adjacent to the Miami University campus and immediately froze them. Cicadas were used within two weeks of collection. Cicadas were thawed and added to mesocosms on four dates over an eight-day period, with each addition representing 25% of the total amount a treatment would receive. Cicadas were added to mesocosms over this time interval because populations gradually senesce over several weeks at the end of the emergence period, but a majority of individuals typically die during a one- to two-week period (Williams et al. 1993; W. H. Nowlin, *unpublished data*). One species (*Magicicada cassini*) represented ~90% of the total added detritus, and male and female cicadas were added at ambient sex ratios (~1:1). Based on nutrient content of adult cicadas (Appendix B), C loadings into the three treatments receiving cicadas were 756, 1512, and 3023 mmol C/m^2 in the 75, 150, and 300 individuals/m^2 treatments, respectively. N loadings were 133, 266, and 532 mmol N/m^2, and P loadings were 4, 8, and 16 mmol P/m^2 in the 75, 150, and 300 individuals/m^2 treatments, respectively.

Sampling and response variables.—Nutrient concentrations and the biomass of organisms in mesocosms were measured once prior to the addition of cicadas and then at various frequencies (depending on the response variable) for seven weeks after the start of cicada detritus additions. Water column components (nutrients, bacteria, phytoplankton, and zooplankton) were obtained with an integrated tube that collected samples (~2 L per sample) from the water's surface to near the bottom. Soluble reactive phosphorus (SRP), ammonium (NH_4^+), total phosphorus (TP), total nitrogen (TN), and phytoplankton biomass were measured twice per week after the start of cicada detritus additions. SRP and NH_4^+ were measured on a Lachat QuikChem® FIA+ 8000 Series autoanalyzer (Lachat Instruments, Loveland, Colorado, USA). TN and TP were measured as NO_3^- and PO_4^{3-}, respectively, on the autoanalyzer after persulfate digestion. Phytoplankton biomass was estimated by filtration onto Pall A/E glass fiber filters (Pall Corporation, East Hills, New York, USA), and chlorophyll *a* concentration was measured with a fluorometer after extraction with acetone at 4°C in the dark for a minimum of 8 h. Pelagic bacteria and zooplankton biomass were determined once per week after addition of cicada detritus. Bacteria biomass was estimated by epifluorescent microscope counts after staining with DAPI (4′,6-Diamidino-2-phenylindole dihydrochloride; Sigma-Aldrich, St. Louis, Missouri, USA) and filtration onto black membrane filters (0.2-μm pore size). Densities were converted to carbon biomass assuming 15 fg C/cell (Cotner and Biddanda 2002). Zooplankton were collected with three integrated samples which were pooled, preserved in buffered sugar-formalin, and counted and measured with a dissecting microscope. Crustacean zooplankton densities were converted to dry mass using published length–mass equations (Bottrell et al. 1976, Rosen 1981, Culver et al. 1985), and rotifer biomasses were calculated using biovolume (Ruttner-Kolisko 1977). A minimum of 60% of the total sample volume was counted. Cladocerans and rotifers were identified to genus, and copepods were identified to order (calanoid or cyclopoid). Zooplankton taxa were grouped into herbivorous or predaceous functional groups based upon general taxonomic feeding preferences (Thorp and Covich 1991). Six rotifer genera (*Brachionus*, *Hexarthra*, *Platyias*, *Monostyla*, *Mytilina,* and *Lecane*), all cladoceran genera (*Alona*, *Chydorus*, *Daphnia,* and *Scapholeberis*), and calanoid copepods were classified as herbivores. Cyclopoid copepods and the rotifer *Asplanchna* were classified as predators. We acknowledge the diversity of feeding preferences within some of these taxonomic groups, especially within the copepod orders; however, we did not observe large-bodied predaceous calanoid copepod taxa (i.e., *Epischura*) in samples, and most cyclopoid copepod taxa exhibit some predatory feeding behavior (Thorp and Covich 1991). Periphyton biomass was measured every two weeks after cicada addition. Unglazed ceramic tiles (9.43 cm^2 surface area) were placed in a shallow plastic tray on the bottom of mesocosms immediately after water was added. Individual tiles were removed on sampling dates, immediately placed in black plastic vials, and stored in a −10°C freezer. Acetone was added to vials, and chlorophyll *a* was extracted in the dark at 4°C for 8 h and measured on a fluorometer.

The experiment was conducted for 51 days after the first addition of cicada carcasses (7 June–28 July), and at the end of this period, mesocosms were drained and all macroinvertebrate populations (crayfish, snails, and amphipods) were assessed. (See Appendix C for detailed methods.)

Data analyses.—In order to assess the impacts of deposition of different levels of cicada detritus, we examined the responses of nutrient concentrations and organism biomasses. Responses of nutrient concentrations and the biomass of organism functional groups to different levels of cicada detritus were analyzed with univariate repeated-measures ANOVA with SPSS (Statistical Programs for the Social Sciences; SPSS 2004). All post-cicada deposition sampling dates for each response variable (SRP, NH_4^+, TP, TN, and the biomasses of bacteria, phytoplankton, herbivorous and predaceous zooplankton, and periphyton) were used for analyses. Cicada abundance was treated as a categorical variable in analyses, and a Greenhouse-Geisser correction was applied in cases where the assumption sphericity was not met (von Ende 1993). Significance (α) was initially set at $P \leq 0.05$, and a sequential Bonferroni procedure was performed to adjust α for multiple comparisons (Rice 1989, Moran 2003). In this procedure, we ranked all response variable *P* values from least to greatest and then compared the lowest *P* value to α/k, where k is the number of individual tests (in this scenario $0.05/9 = 0.0056$). Significance was inferred if the *P* value of this response variable was lower than the adjusted α. We then progressively compared the increasingly greater *P* values to $k - 1$, $k - 2$, and so on until the *P* value of a response variable exceeded the adjusted α.

We quantified the stability responses of food web and ecosystem components in two ways. First, we compared the temporal variability of nutrient concentrations and planktonic and benthic organisms following the addition of cicada detritus to mesocosms. We examined the stability responses of bacteria, phytoplankton, zooplankton, and periphyton because these functional groups could be repeatedly sampled over multiple generations. We did not destructively sample crayfish, amphipod, and snail populations repeatedly because it is unlikely that these organisms would produce as many generations as planktonic organisms; thus we did not address the stability responses of benthic organism populations to different levels of cicada detritus and only examined their responses at the end of the experiment. Temporal variability of nutrient concentrations and biomasses were estimated by calculation of the temporal coefficient of variation (CV; Gaston and McArdle 1994, Fagan 1997, McCann 2000, Halpern et al. 2005) where, CV is equal to 100 multiplied by the standard deviation of all post-addition sampling dates/mean of all post-addition sampling dates. We compared treatment effects on CVs with one-way ANOVA, using each mesocosm CV as an observation. We confirmed assumptions of homogeneity of variances with the SPSS default version of Levene's test. Again, significance was set at $P \leq 0.05$, and α was adjusted with a sequential Bonferroni procedure. If a significant treatment effect on a CV was detected, homogeneous subsets were determined with Tukey's honestly significant difference (hsd).

CVs provide information on the relative variability of ecosystem components after a pulse of cicada detritus, but increased temporal variability alone does not necessarily denote lower probability of persistence within a food web (May 1973). Therefore, our second stability measure was based on the minimum biomass of organisms following cicada deposition (Pimm et al.

1988, Huxel and McCann 1998). Biomass minima for organism functional groups were designated as the minimum observed biomass value of a functional group across all dates following the addition of cicadas. Functional group biomass minima were compared by determining the minimum post-addition biomass of each functional group in each mesocosm within each treatment and comparing treatments with one-way ANOVA. Levene's test was performed prior to analyses to confirm the assumption of homogeneity of variances. Significance was a priori set at $P \leq 0.05$, and a sequential Bonferroni procedure was performed to adjust α. When a significant overall treatment effect on a minimum biomass was detected, homogeneous subsets were determined with post hoc comparisons (Tukey's hsd).

Most theoretical examinations of allochthonous subsidy effects assess the stability of homogeneous populations of "trophospecies" (Rosenzweig 1971, DeAngelis 1992, Huxel and McCann 1998, Huxel 1999, Huxel et al. 2002, Takimoto et al. 2002), but responses of an aggregate group (e.g., functional group) to resource perturbations may be different than the constituent species within the group (Tilman 1996, Cottingham et al. 2001, Persson et al. 2001). Thus we also examined the temporal variability of biomass (temporal CV) of 13 zooplankton taxa, representing 93% ± 3% of total zooplankton biomass. These 13 taxa were selected because they occurred in most mesocosms and collectively comprised an overwhelming portion of the total zooplankton biomass. Comparison of CVs of individual zooplankton taxa among treatments was performed in the same fashion as for the functional group analyses. Significance was set at $P \leq 0.05$, and a sequential Bonferroni procedure was performed to adjust α.

We also assessed the biomass minima of the 13 zooplankton taxa; however, the use of simple biomass minima for individual taxa was unsuitable because population densities frequently dropped below detection limits (i.e., densities in samples were too low to be detected, given the number and volume of subsamples counted) and then rebounded above detection limits. If a taxon dropped below the detection limit, its biomass would consequently be calculated as "zero" on that date. Thus population minima calculated as zero do not reflect the actual minima, preventing accurate determination if minima differed among treatments. To circumvent this problem, we used logistic regression to test whether the proportion of dates a taxon was below detection limits was a function of the level of cicada detritus. Presumably a higher proportion of dates in which a taxon was below detection limits indicates that the density of the taxon was relatively lower (e.g., increased rarity) or underwent a greater number of density oscillations that dropped below detection limits. Polynomial contrasts were performed to determine whether data contained significant linear or quadratic components. Significance was inferred at $P \leq 0.05$, and α was subsequently adjusted with a sequential Bonferroni procedure.

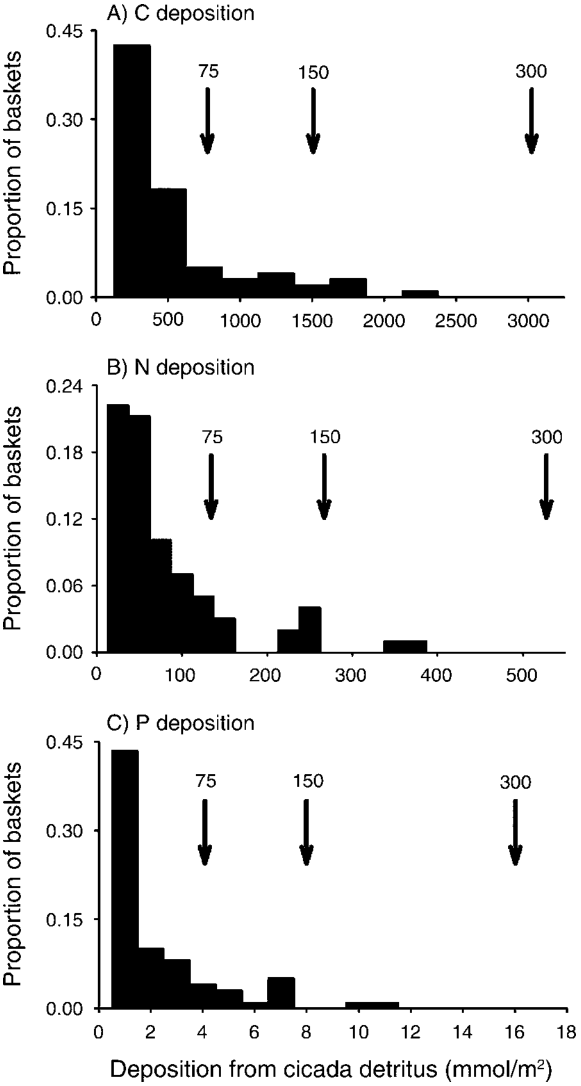

FIG. 1. Frequency distributions of Brood X periodical cicada detritus areal loading of (A) C, (B) N, and (C) P into woodland ponds and low-order streams. Distributions are calculated as the proportion of the total number of litterfall baskets ($N = 99$) in 250 (for C), 25 (for N), or 1 (for P) mmol/m^2 intervals. Arrows on each panel indicate the areal nutrient loadings associated with the treatments of 75, 150, and 300 cicadas/m^2 in the mesocosm experiment.

RESULTS

Brood X detritus deposition into woodland aquatic ecosystems

Cicada litter C deposition into aquatic ecosystems ranged from 6 to 2046 mmol C/m^2 (Fig. 1A; median = 160 mmol C/m^2), N deposition varied from 1.3 to 388 mmol N/m^2 (Fig. 1B; median = 31 mmol N/m^2), and P loading ranged from 0.009 to 11 mmol/m^2 (Fig. 1C; median = 0.9 mmol P/m^2). The frequency distribution of

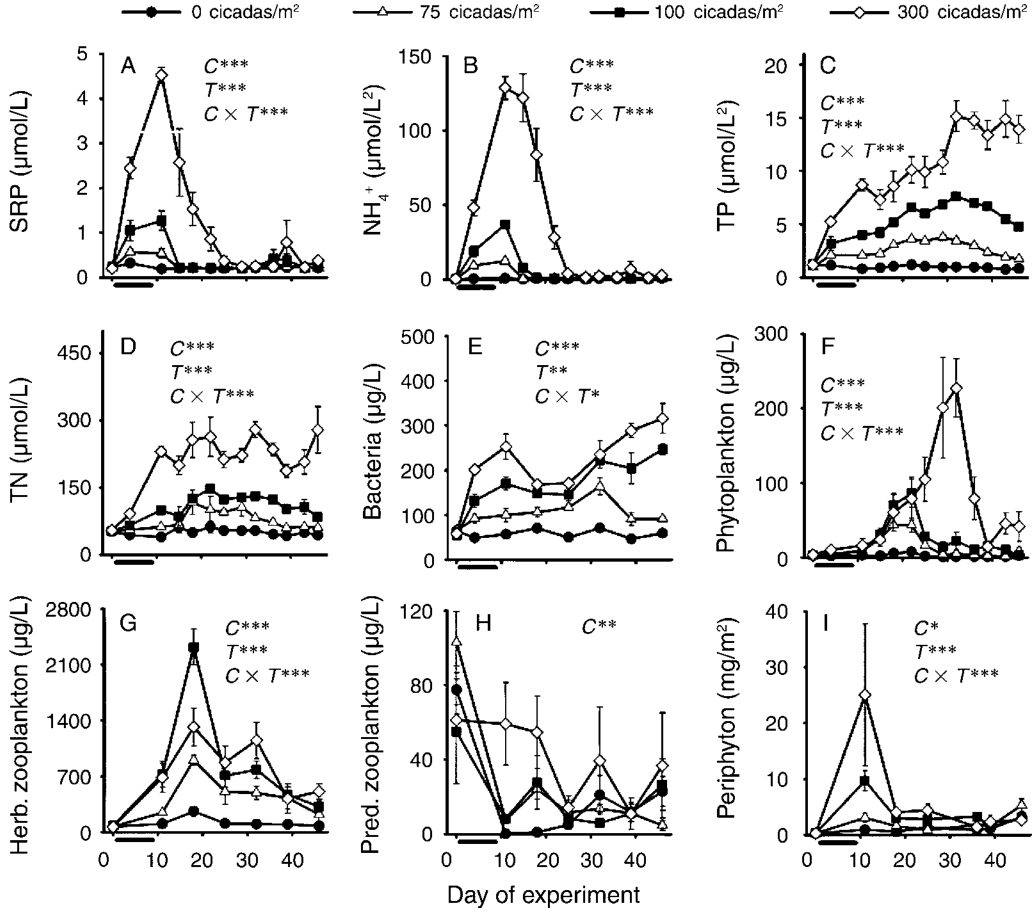

FIG. 2. Response of (A–D) nutrient concentrations and (E–I) the biomass of organism functional groups to different levels of cicada detritus (0, 75, 150, and 300 cicadas/m^2). The short horizontal line immediately below the *x*-axis of each panel indicates the interval during which cicada detritus was added. Asterisks indicate significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) for the overall treatment effect (*C*), the time effect (*T*), and the treatment × time interaction (*C* × *T*). In panel (H), *T* and *C* × *T* effects were not significant ($P > 0.05$). Error bars are ±SE. Abbreviations are: SRP, soluble reactive phosphorus; TP, total phosphorus; TN, total nitrogen; Herb. zooplankton, herbivorous zooplankton; Pred. zooplankton, predaceous zooplankton.

cicada deposition amounts into forest aquatic ecosystems was highly peaked, and ~60% of all baskets received <500 mmol C/m^2, <100 mmol N/m^2, and <1 mmol P/m^2 during the emergence period. When nutrient inputs from cicada litter deposition into pond and stream sites are compared, stream sites tend to have higher C (16–2046 mmol C/m^2; median = 307 mmol C/m^2), N (3–388 mmol N/m^2; median = 58 mmol N/m^2), and P (0.009–11 mmol P/m^2; median = 2 mmol P/m^2) inputs than pond sites (C: 6–308 mmol C/m^2, median = 16 mmol C/m^2; N: 1–58 mmol N/m^2, median = 3 mmol N/m^2; P: 0.009–2 mmol P/m^2, median = 0.02 mmol P/m^2). Nutrient loading in the mesocosm experiment associated with cicada detritus in the 75 and 150 individuals/m^2 treatments fell within the observed distributions in forest aquatic ecosystems. Nutrient loading in the high treatment (300 individuals/m^2) corresponded to the high cicada densities we observed and reported in the literature (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001), but was higher than nutrient loading rates observed in our field survey. We saw evidence of scavenging from litterfall baskets (e.g., litter baskets molested; see *Discussion*), so the cicada litter nutrient deposition amounts presented in Fig. 1 are probably underestimates of actual deposition amounts.

Mesocosm experiment

In experimental mesocosms, cicada detritus addition rapidly increased water column nutrients (Fig. 2A–D). Dissolved inorganic nutrient concentrations (SRP and NH_4^+) quickly increased and then declined, apparently through decomposition of cicada carcasses and subsequent assimilation by bacteria, phytoplankton, and periphyton. Total nutrient concentrations (TP and TN), which include all dissolved and particulate forms, increased with the level of cicada detritus and persisted until the end of the experiment (Fig. 2C, D). Maximum

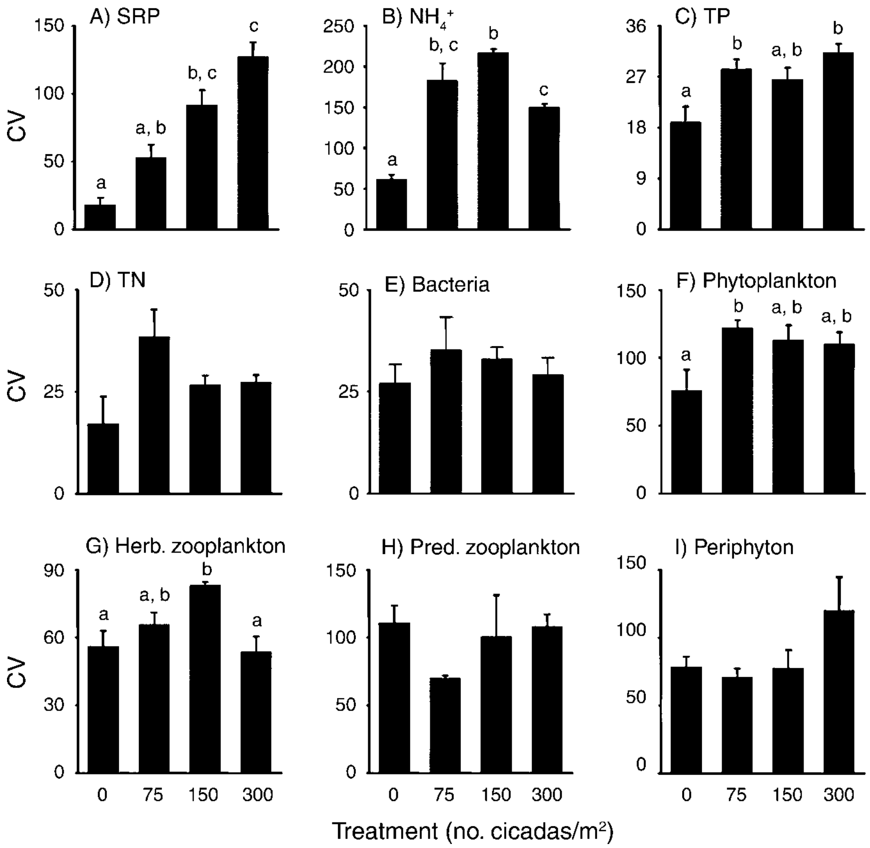

FIG. 3. Response of the temporal coefficient of variation (CV) of (A–D) nutrient concentrations and (E–I) the biomass of organism functional groups following the addition of different levels of cicada detritus (0, 75, 150, and 300 cicadas/m^2). Homogeneous treatment groups (based on post hoc Tukey's hsd tests) are presented for response variables in which a significant overall treatment effect was detected. Homogeneous groups of treatments are distinguished with the same letter (a, b, or c). Error bars are +SE. Abbreviations are the same as for Fig. 2.

water column TP and TN concentrations represented 33, 36, and 42% of P and 37, 17, and 23% of N added as cicada litter in the 75, 150, and 300 cicadas/m^2 treatments, respectively.

The nutrient pulse associated with cicada detritus rapidly propagated to planktonic and benthic organisms. The biomass of bacteria, phytoplankton, herbivorous zooplankton, predatory zooplankton, and periphyton was significantly higher in treatments receiving cicada detritus (Fig. 2E–I). In addition, the magnitude of biomass enhancement of functional groups increased with the amount of cicada detritus. However, the timing and temporal trajectories of biomass responses to cicada detritus differed among functional groups. Bacteria were the first organisms to increase in response to cicada detritus additions and remained elevated until the end of the experimental period. Phytoplankton and herbivorous zooplankton exhibited slightly lagged biomass increases after cicada detritus additions and declined by the end of the experiment. Predatory zooplankton biomass was at a maximum in all treatments preceding the addition of cicada detritus, but mesocosms receiving cicada detritus had significantly higher biomasses throughout the experiment. Similar to bacteria, periphyton biomass rapidly increased after cicada additions, but periphyton declined to pre-addition levels within two weeks.

Cicada deposition significantly affected the temporal variability of nutrient concentrations and the biomass of two functional groups (Fig. 3A–I). The CV of SRP concentration increased linearly (i.e., SRP was more variable) with increasing cicada subsidy. The CVs of NH_4^+ and TP were significantly higher in treatments receiving cicada detritus, but both response variables exhibited nonlinear responses to increasing cicada detritus levels. Phytoplankton and herbivorous zooplankton were the only organism functional groups whose CVs were significantly affected by cicada input, and the highest variability occurred at low and intermediate levels of cicadas, respectively.

At the population level, two of 13 zooplankton taxa exhibited significant responses in CV to additions of cicada detritus (Appendix D: Table D1). The herbivore *Chydorus* exhibited significant nonlinear responses to the level of cicada addition with the lowest variability exhibited at the highest levels of cicada addition. The

TABLE 1. Minimum biomass response of organism functional groups following addition of cicada detritus to mesocosms in each treatment (0, 75, 150, and 300 cicadas/m^2).

Functional group and treatment	Mean ± SE	$F_{3,12}$	P	HGs
Bacteria				
0	37.8 ± 1.9	4.96	0.018*	A
75	64.2 ± 3.6			B
150	54.8 ± 8.4			A, B
300	58.4 ± 4.0			A, B
Phytoplankton				
0	0.6 ± 0.1	4.62	0.023*	A
75	0.6 ± 0.3			A
150	1.3 ± 0.2			B
300	1.0 ± 0.7			A, B
Herbivorous zooplankton				
0	0.8 ± 0.3	3.99	0.035*	A
75	2.1 ± 1.3			A, B
150	5.0 ± 2.1			B
300	2.7 ± 1.2			A, B
Predaceous zooplankton				
0	69.0 ± 14.6	1.59	0.244	
75	176.1 ± 108.0			
150	321.2 ± 144.0			
300	259.6 ± 123.2			
Periphyton				
0	0.7 ± 0.1	2.61	0.099	
75	0.86 ± 0.2			
150	1.61 ± 0.12			
300	12.0 ± 11.0			

Notes: Biomass units for functional groups are the same as for Fig. 2. The P value for the overall ANOVA is reported for each group (* $P < 0.05$). Homogeneous groups (HGs), based upon post hoc Tukey's hsd tests, are presented for groups in which a significant treatment effect was detected. Homogeneous groups of treatments are designated with the same letter (A or B).

biomass of *Hexarthra* (an herbivorous rotifer) exhibited a linear increase in variability with increasing cicada detritus.

The minimum observed biomasses of bacteria, phytoplankton, and herbivorous zooplankton were influenced significantly by addition of cicada detritus (Table 1). These three functional groups exhibited significantly higher biomass minima in treatments receiving cicada detritus, and in these cases, the highest biomass minima occurred at low or intermediate cicada additions. Thus according to this metric, low or intermediate cicada subsidies stabilized these functional groups. We also assessed this response at the population level using the 13 zooplankton taxa. Only one taxon exhibited significant minimum population density responses to the level of cicada detritus (Appendix D: Table D2); the herbivorous rotifer *Mytilina* became significantly rarer in the treatment that received the largest cicada pulse.

Addition of cicada litter led to significantly higher snail numbers at the end of the experiment (Fig. 4A; one-way ANOVA: $F_{3,12} = 5.98$, $P = 0.010$). The magnitude of the increase in snail populations was a function of the amount of cicada detritus, with the highest snail numbers observed in the 300 cicadas/m^2 treatment.

Crayfish biomass at the end of the experiment was not affected by the addition of periodical cicada detritus (Fig. 4B; one-way ANOVA: $F_{3,12} = 0.227$, $P = 0.876$). In all treatments, crayfish biomass increased, on average, by ~30%. The lack of a significant effect on the percentage increase in crayfish biomass may be due to the duration of the experiment (~60 days) relative to the lifespan, growth rates, and reproductive frequency of crayfish.

DISCUSSION

In the study presented here, we show that aquatic ecosystems in eastern North American forests receive a pulsed allochthonous subsidy of highly labile detritus during periodical cicada emergence. Results from our mesocosm experiment demonstrate that deposition of periodical cicada carcasses had rapid and persistent effects on nutrient concentrations and the biomass of organism functional groups and populations. Energy and nutrients from cicada detritus quickly spread to benthic and pelagic populations, and these effects lasted for multiple generations of several trophic levels. Detritus pulses associated with senescence of primary-producer tissues or the death of semelparous animal populations have been shown to affect ecosystem

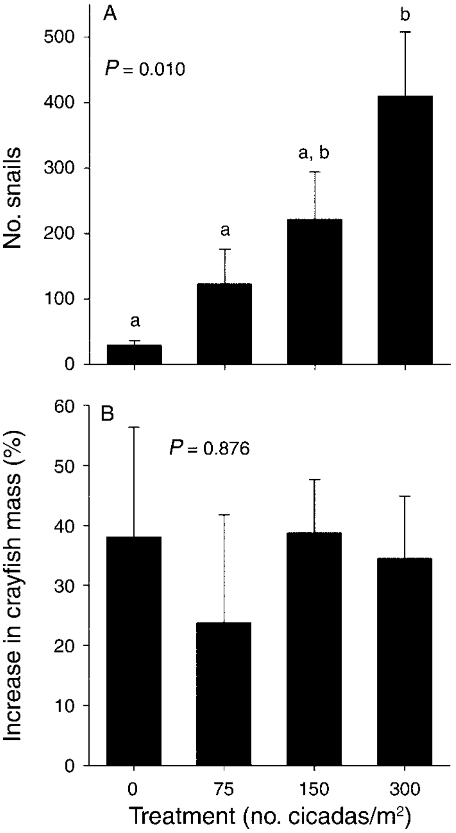

FIG. 4. (A) Total number of snails in the pooled bottom and wall samples at the end of the mesocosm experiment in experimental treatments (0, 75, 150, and 300 cicadas/m^2). The reported *P* value is the result of the overall one-way ANOVA. Homogeneous treatment groups are indicated with the same letter (a or b). (B) Percentage change in the total biomass of crayfish at the end of the mesocosm experiment in experimental treatments (0, 75, 150, and 300 cicadas/m^2). The reported *P* value is the result of the overall one-way ANOVA. Error bars in both panels are +SE.

productivity and food web structure (Wallace et al. 1997, Helfield and Naiman 2001, Yang 2004). Detritus pulses in freshwater ecosystems often come from externally derived or allochthonous organic matter sources (i.e., anadromous salmon carcasses, terrestrial leaf litter), and a large number of studies have examined the effects of allochthonous detritus pulses on nutrient dynamics, ecosystem productivity, and food web structure (Carlton and Goldman 1984, Wallace et al. 1997, Jurgens and Sala 2000, Naiman et al. 2002, Pace et al. 2004, Rubbo and Kiesecker 2004). However, few studies have experimentally addressed the effects of allochthonous detritus pulses on the stability of ecosystems components, food webs, or populations. Anderson and Polis (2004) examined the effects of pulses of allochthonously derived nutrients (via seabird guano) on the stability of plant, herbivore, and predator populations on arid islands in the Gulf of California and found that plant and herbivore populations on islands that received pulsed nutrient inputs from guano tended to exhibit greater temporal variability (i.e., greater instability) than islands that did not receive guano inputs. Our results are consistent with many of the aforementioned studies in that a pulse of allochthonous organic matter had large impacts on food web dynamics; however, we additionally demonstrate that a pulsed allochthonous subsidy affected the stability of nutrient concentrations, organism functional groups, and populations and that these effects generally varied with the size of the allochthonous pulse.

Ecosystem and population responses to the addition of cicada detritus in our mesocosm experiment were rapid, indicating that cicada detritus subsidies act similarly to an input of dissolved inorganic nutrients, rather than a subsidy of relatively poor-quality detritus (e.g., leaf litter). The rapid release of dissolved nutrients from cicada carcasses in mesocosms may have been enhanced by freezing cicadas prior to addition to mesocosms; however, short-term, lab-based experiments indicate that decomposition and mass loss rates are not substantially different between fresh (unfrozen) and frozen cicadas carcasses (C. L. Pray and W. H. Nowlin, *unpublished data*). Our analyses of cicada detritus nutrient content indicate that cicada litter is relatively high quality and contains higher mass-specific nutrient concentrations than other allochthonous subsidies to forest aquatic ecosystems. In general, cicada litter contains 10–13% N and 0.06–0.8% P, by mass (Appendix B). In comparison, the nutrient concentration of senesced leaf litter (the major allochthonous detritus source to woodland ponds and streams) is lower than cicada bodies. Based upon analyses we performed (Appendix B) and values reported in the literature (Killingbeck 1996), the nutrient content of senesced leaf litter from trees commonly found in riparian forests in southwestern Ohio (our analysis = *Platanus occidentalis*; literature = *Acer rubrum*, *Fagus* spp., *Liriodendron tulipifera*) are ~1% N and ~0.08% P, by mass. In addition, cicada bodies are relatively rich in lipids (mostly triglycerides) and soluble protein (Brown and Chippendale 1973), while energy and nutrients in leaf litter are generally in more recalcitrant forms (i.e., complex polyphenolic compounds).

While the nutrient content and quality of periodical cicada litter is relatively high, it is critical to examine the magnitude of periodical cicada litter pulses in the context of other allochthonous organic matter pulses to forest aquatic systems (e.g., autumnal leaf litter inputs and rainfall events). Based upon litterfall basket surveys, cicada litter total dry mass inputs to woodland ponds and streams in southwestern Ohio range from 0.14 to 46.4 g dry mass/m^2 ($\bar{x}$ = 8.08 g dry mass/m^2; W. H. Nowlin, *unpublished data*). Total autumnal leaf litter dry mass inputs to these same ecosystems (measured with the same litterfall baskets) are much higher, ranging from 124.5 to 520.78 g dry mass/m^2 ($\bar{x}$ = 305.07 g dry mass/m^2; W. H. Nowlin, *unpublished data*). Even though cicada litter inputs to woodland ponds and streams represent a fraction of the total mass entering these systems in leaf litter, the higher nutrient content of cicada litter indicates that it can represent a substantial nutrient pulse to woodland aquatic systems during the growing season. Assuming leaf litter is 1% N and 0.08% P by mass, leaf litter inputs translate to N and P loadings of 88.30–369.35 mmol N/m^2 ($\bar{x}$ = 305.07 mmol N/m^2) and 3.12–13.06 mmol P/m^2 ($\bar{x}$ = 7.65 mmol P/m^2). Cicada litter N and P inputs to these systems ranged from 1.27–387.87 mmol N/m^2 and 0.009–11.22 mmol P/m^2 (Fig. 1C, D). Therefore, N and P derived from periodical cicada litter can represent from 1.4% to 105% ($\bar{x}$ = 31%) of the N and 0.3% to 86% ($\bar{x}$ = 25%) of the P that is annually deposited into woodland aquatic systems in southwestern Ohio through autumn leaf senescence.

The amount of cicada litter deposition we observed in woodland aquatic ecosystems tended to be lower than the cicada additions in our mesocosm experiment. It is likely that nutrient fluxes determined from our litterfall baskets are conservative estimates because of scavenging from baskets (Yang 2004). Yang (2004) used precisely the same baskets to estimate cicada litter deposition on eastern North American forest floors and reported average scavenging losses of 72% of cicada litter over a 48-h period. If we "correct" our cicada litterfall amounts by the minimum scavenging loss from baskets (30%) reported by Yang (2004), the highest nutrient loadings to ponds and streams are only ~10% lower than the largest additions in the mesocosm experiment. In addition, we have evidence that scavengers (mostly raccoons) molested litterfall baskets at some field sites (pulled them down, chewed on the plastic) between litter collections, further suggesting that scavenging from baskets was common. Thus it is highly probable that the treatment levels used in the mesocosm experiment were within the range of cicada litter deposition amounts observed in aquatic ecosystems in forests in southwestern Ohio and elsewhere within the Brood X range.

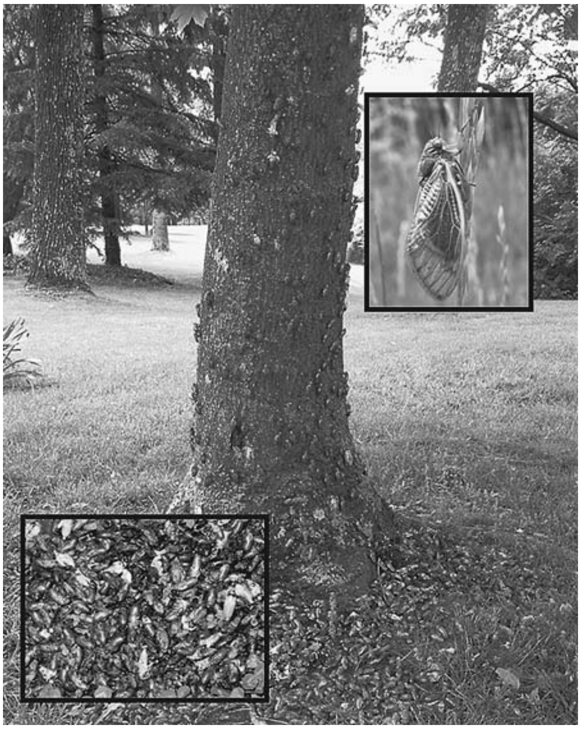

PLATE 1. Photographs of periodical cicadas near the Miami University campus in southwestern Ohio, USA, in summer 2004. The larger photograph shows nymphs emerging and climbing up a tree to molt into adults. The lower left photograph is a close-up of high densities of nymphs emerging from the ground, and the upper right inset photograph is of an adult cicada after molting. Photo credits: larger photograph and upper right inset, W. H. Nowlin; lower left inset, M. W. Fields.

To our knowledge, this study is the first controlled experiment testing whether a pulsed allochthonous detrital subsidy affects the stability of ecosystem components and populations. Several ecological models predict the effects of allochthonous subsidies on food web and ecosystem stability; however, none of these models are directly applicable to the allochthonous subsidy in our mesocosm experiment. Most models that manipulate subsidy magnitude consider subsidies as temporally constant inputs, predicting that large subsidies decrease population minima, but also decrease temporal variability of populations (Huxel and McCann 1998, Huxel et al. 2002). In contrast to these predictions, we found that nutrient concentrations, organism functional groups, and populations exhibited idiosyncratic responses to the largest pulsed subsidy of cicada detritus: the largest additions of cicada detritus increased, decreased, or had no effect on temporal variability and biomass minima of the various populations, functional groups, or ecosystem components. Models exploring pulsed subsidies are less common, but theory predicts that pulsed subsidies should decrease temporal variability and increase biomass minima of recipient populations as long as subsidy pulses are (1) temporally asynchronous with one another and (2) not spaced too far apart temporally such that recipient populations do not experience periods of low resource availability (Takimoto et al. 2002). In our mesocosm experiment, addition of cicada litter was the only manipulated resource pulse; therefore, we do not know if deposition of different amounts of cicada litter would have a stabilizing or destabilizing effect if pulses of other resources were also manipulated (e.g., autumnal leaf litter deposition). However, because cicada senescence and leaf fall occur several months apart (early June for cicadas vs. late October for leaf litter), it is likely that most pelagic biomass enhancements induced by cicadas will have dissipated by the time leaf fall has an effect; however, due to the relatively long life spans of many larger benthivorous organisms, the effects of a pulse of cicada detritus on benthic communities are more likely to persist beyond a single season. In addition, pulsed allochthonous subsidies often vary in magnitude (Polis et al. 2004); therefore emerging allochthonous resource theory should be expanded to include pulsed subsidies that vary in magnitude.

Virtually all current models that examine the influence of allochthonous subsidies on food web stability examine dynamics of homogeneous populations in simple food webs (Rosenzweig 1971, DeAngelis 1992, Huxel and McCann 1998, Huxel 1999, Huxel et al. 2002, Takimoto et al. 2002); however, empirical studies indicate that responses of aggregate groups to resource perturbations often differ from the responses of the species contained within aggregate groups (Tilman 1996, Cottingham et al. 2001, Persson et al. 2001). Aggregation is inherent at some level in all ecosystems, for instance, as multiple genotypes within a species may result in functional heterogeneity (Yoshida et al. 2003). As a consequence, it remains unclear precisely how or when models with homogeneous populations apply to natural systems. Both modeling and empirical studies suggest that the biomass stability of aggregate groups to a resource perturbation should be higher than that of individual species within groups because of species-level compensatory dynamics (Tilman 1996, Cottingham et al. 2001, Persson et al. 2001). In the present study, the herbivorous zooplankton functional group exhibited its highest biomass variability and lowest biomass minima (e.g., the lowest stability) at the largest level of cicada addition. However, within the herbivorous zooplankton functional group, two of 11 taxa exhibited significant CV responses, and only one taxon displayed a significant population minimum response to cicada detritus deposition. Thus while the variability and minimum biomass of the herbivore functional group exhibited a clear response to inputs of cicada detritus, a majority of individual taxa within the group did not exhibit significant stability responses. Cottingham and Carpenter (1998) similarly found that temporal variability of populations of individual phytoplankton taxa were less reliable indicators of resource perturbation (whole-lake enrichment) than total phytoplankton biomass (an aggregate measure). In contrast in the present study, neither the predatory zooplankton functional group nor any of the individual taxa within the group exhibited significant variability of population minima responses to subsidies of cicada detritus. Thus our results imply that differences in the stability responses of functional groups vs. individual constituent populations can be idiosyncratic, depending upon the specific functional group and populations in question.

The emergence of periodical cicadas has been shown to be an important resource pulse in North American forests, yet the long-term effects of these pulse events are poorly understood. Yang (2004) and Yang (2006) observed increased herbaceous vegetation seed size and foliar N content and increased activity of detritivorous macroarthropods in response to pulses of cicada detritus; however, the persistence of these effects (i.e., for more than one growing season) in aboveground communities is unknown. Koenig and Liebhold (2005) determined that periodical cicada emergences affected the demography of 15 North American bird species, with some avian population responses persisting for up to three years after the emergence of a periodical cicada brood. In our study, the effects of a pulse of cicada detritus on planktonic communities were relatively persistent, influencing ecosystem productivity and dynamics across multiple generations within a single growing season. If deposition of cicada carcasses increased propagule production (spores, resting eggs, seeds), recruitment, or dispersal rates of long-lived pond organisms (e.g., amphibians), periodical cicada effects could also persist for many years between emergence events.

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APPENDIX A

Methods and results of a survey of Brood X periodical cicada emergence densities in southwestern Ohio (*Ecological Archives* E088-130-A1).

APPENDIX B

Methods and statistical analysis of mass-specific nutrient concentrations and nutrient ratios of material associated with the emergence of Brood X periodical cicadas (*Ecological Archives* E088-130-A2).

APPENDIX C

Detailed sampling and analytical methods for macroinvertebrate abundances at the end of the mesocosm experiment (*Ecological Archives* E088-130-A3).

APPENDIX D

Zooplankton population responses to experimental manipulation of cicada detritus (*Ecological Archives* E088-130-A4).