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Acute resource pulses from periodical cicadas propagate to belowground food webs but do not affect tree performance

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Abstract

Acute resource pulses can have dramatic legacies for organismal growth, but the legacy effects of resource pulses on broader aspects of community structure and ecosystem processes are less understood. Mass emergence of periodical cicadas (*Magicicada* spp.) provides an excellent opportunity to shed light on the influence of resource pulses on community and ecosystem dynamics: the adults emerge every 13 or 17 years in vast numbers over much of eastern North America, with a smaller but still significant number becoming incorporated into forest food webs. To study the potential effects of such arthropod resource pulse on primary production and belowground food webs, we added adult cicada bodies to the soil surface surrounding sycamore trees and assessed soil carbon and nitrogen concentrations, plant-available nutrients, abundance and community composition of soil fauna occupying various trophic levels, decomposition rate of plant litter after 50 and 100 days, and tree performance for 4 years. Contrary to previous studies, we did not find significant cicada effects on tree performance despite observing higher plant-available nutrient levels on cicada addition plots. Cicada addition did change the community composition of soil nematodes and increased the abundance of bacterial- and fungal-feeding nematodes, while plant feeders, omnivores, and predators were not influenced. Altogether, acute resource pulses from decomposing cicadas propagated belowground to soil microbial-feeding invertebrates and stimulated nutrient mineralization in the soil, but these effects did not transfer up to affect tree performance. We conclude that, despite their influence on soil food web and processes they carry out, even massive resource pulses from arthropods do not necessarily translate to NPP, supporting the view that ephemeral nutrient pulses can be attenuated relatively quickly despite being relatively large in magnitude.

KEYWORDS
decomposition, *Magicicada* spp., microbial feeding soil fauna, nematode community, pulsed detrital subsidy, resource limitation and NPP, tree performance, trophic interactions

INTRODUCTION

A growing number of studies has tried to unravel the impacts of mass mortality events, including acute resource pulses—rare but substantial inputs of new resources over short time periods—on organismal growth and broader aspects of community and ecosystem level processes (Fey et al., 2019; Kristensen et al., 2020; Le Mellec et al., 2011; Yang et al., 2010). Notable pulses like seed and fruit masting, carrion and carcasses, and herbivore outbreaks, can directly stimulate short term production of consumers, but also indirectly affect food webs and nutrient dynamics (Yang et al., 2010). However, the influence of massive insect outbreaks on ecosystem dynamics, especially on belowground processes, is not well known. While early theoretical models predict that such resource pulse effects attenuate with increasing trophic distance due to thermodynamic constraints and stochastic environmental variation (Schoener, 1993; Wootton, 1994), a recent meta-analysis by Kristensen et al. (2020) provides evidence that increased insect herbivory during outbreaks alters belowground fauna and soil biogeochemistry in a variety of forest ecosystems worldwide. In terrestrial ecosystems, such outbreaks are one of the most spatially broad forms of resource pulses. Less common, but similar in their potential ecosystem effects, are arthropod populations with highly synchronized development, culminating in mass emergence followed by mass mortality. The two best known examples are the train millipede (*Parafontaria laminata armigera*, Diplopoda: Xystodesmidae) in Japan, with an 8-year life cycle (Niijima et al., 2021), and the periodical cicadas (Homoptera: Cicadidae) in North America emerging every 13–17 years. Periodical cicadas cause one of the largest resource pulses in North American forests, with up to 3,000,000 individuals per hectare coming to the surface from belowground (Dybas & Davis, 1962). Despite being of enormous significance to predators, the overwhelming majority of cicadas perish and fall to the forest floor uneaten. These corpses then become an acute resource pulse for both above- and belowground producers and consumers (Brown & Chippendale, 1973; Whiles et al., 2001).

Empirical investigations suggest that dead bodies of adult cicadas represent an important flux of nutrients and energy via stimulating soil microbial biomass (Yang, 2004), influencing community composition of mobile, epigeic soil macroarthropods (Yang, 2006), and increasing plant-available nutrients in surface soils (Yang, 2004, 2008). At least some of these cicada-derived effects have been shown to translate into enhanced biomass production of herbs (Yang, 2004) and tree seedlings (Yang & Karban, 2019), and also affect the productivity and dynamics of woodland ponds and streams (Nowlin et al., 2007; Pray et al., 2009).

Despite the recent advances in unraveling the potential influences of insect resource pulses on ecosystem dynamics (Lovett & Ruesink, 1995; Kristensen et al., 2020; Fey et al., 2019), virtually nothing is known whether this resource input, or other resource inputs showing periodicity, transfers up to trophic levels beyond soil microbes in the soil food web. Food web theory (de Ruiter et al., 2005; Hunt et al., 1987) suggests, and empirical evidence (Coleman et al., 2017; Forge et al., 2008; Treonis et al., 2010) shows, that a substantial part of enrichment at the primary decomposer level, i.e., soil bacteria and fungi, of the decomposer food web translates into changes of microbial feeders, such as soil micro- and mesofauna. Furthermore, as increased biomass of soil microbial feeders generally results in stimulated decomposition and nutrient turnover rates (Bardgett & Wardle, 2010; Scheu et al., 2005; Setälä, 2002), the rate of net primary production (NPP) is, in part, regulated by the quality and quantity of trophic interactions below the ground (Setälä & Huhta, 1991; Wardle et al., 2004). Changes in soil nutrient dynamics can manifest themselves as increased plant nutrient levels and thus can influence the performance of foliar herbivores (Wardle et al., 2004; Zehnder & Hunter, 2009). However, it is not known whether the increased soil nutrient concentrations (Le Mellec et al., 2011; Yang, 2004, 2008) and improved plant growth (Yang, 2004; Yang & Karban, 2019) after resource pulses were due to feeding interactions that enhanced nutrient turnover within the entire soil food web, or resulted mostly from direct leakage of soluble N from herbivore bodies. Furthermore, studies on the effects of resource enrichment on one of the fundamental ecosystem processes, the decomposition of soil organic matter, are lacking.

Yang (2004) reported increased soil microbial biomass and inorganic N concentrations in experimental plot soils 4 weeks after cicada addition. The coincidence of high microbial biomass with enhanced nutrient mineralization is not self-evident, because (1) soil fungi and bacteria can efficiently immobilize nutrients reducing soil nutrient concentrations (Swift et al., 1979) and (2) low microbial biomass typically associates with stimulated nutrient mineralization under high grazing pressure by soil fauna (Coleman et al., 2017; Mikola & Setälä, 1998; Trap et al., 2016). Consequently, assessment of soil fauna, i.e., trophic groups positioned higher up in the soil food web, provides a holistic way to explore how far resource pulses, derived from aboveground sources, propagate in the plant–soil system. For example, based on feeding habits, soil nematodes (Nematoda, or roundworms) can be classified into functional groups (Yeates et al., 1993), the abundance of which can be used to depict consumer-induced compositional and functional alterations (Bongers, 1990;

Ferris & Bongers, 2006). Due to the low C/N ratio of fresh arthropod corpses (5.5; Pray et al., 2009), the energy/nutrient channel theory predicts that soil biota within the bacterial-based energy channel should dominate immediately following resource pulses, while the relative proportion of decomposers within the fungal-based channel should increase in time with lowered quality of the arthropod carcasses. This ecosystem/food web approach can be adopted to unravel the pathways through which arthropod-derived resource pulses propagate through the plant–soil system; a major knowledge gap highlighted by Kristensen et al. (2020).

The aim of our field study, using cicada-derived resource pulse as a model system, was to explore the spatiotemporal extent to which resource enrichment influences the plant–soil system. Specifically, we investigated the responses of soil microbial-detritivorous fauna (Nematoda, Acari, and Collembola), soil nutrient concentrations, decomposition activity, and the performance of young sycamore trees (*Platanus occidentalis*). Furthermore, we assessed whether the impact of this resource pulse is transient or lasts until the end of the growing season and beyond. We hypothesized that (1) carcasses of adult periodical cicadas (*Magicicada* spp.) will boost the abundances of consumers (microbial-detritivorous and predatory soil fauna) in the soil food web; this shift will manifest in (2) enhanced decomposition rate of plant litter due to enhanced feeding interactions and/or priming effect by the cicada corpses and (3) increased soil nutrient concentrations and NPP. We expected this influence to increase towards the end of the growing season due to the slow decomposition of the relatively recalcitrant, chitin-rich exoskeleton of adult cicadas (Brown & Chippendale, 1973).

METHODS

In 2016, we collected ~3000 live Brood V cicadas in western Maryland and immediately placed them into a freezer (−20°C). Brood V consists of three species, *Magicicada septendecim* (L. 1758), *M. cassini* (Fisher, 1851), and *M. septendecula* (Alexander & Moore, 1962), which we did not attempt to separate.

We performed this study in the BiodiversiTREE experimental forest plantation at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland, USA. The experiments were installed into one 35 × 35 m monoculture stand containing 255 American sycamores planted in 2013 (*Platanus occidentalis* L.) (detailed description of BiodiversiTREE in Appendix S1). Trees were uniformly aged (past the sapling stage), uniformly sized, and evenly spaced on similar soils, creating an ideal common garden experiment. Trees growing in the first three rows on the northeast and southwest facing sides of the sycamore stand were randomly selected and assigned as cicada addition ($N = 10$ trees) or control ($N = 10$ trees), with the two sides of the stand considered experimental "blocks." Under each block we created four cage enclosures surrounding the stem. One such set is considered a "plot." Cages had a wooden frame (dimensions 60 cm long × 30 cm wide × 6 cm deep) and a wire mesh (0.5 cm opening) on the top and bottom. Cicadas were enclosed in a finer mesh bag (0.8 mm polyester mosquito netting). The wire and polyester mesh prevented access by both vertebrate and large-bodied invertebrate consumers. To determine initial cicada dry mass, 75 randomly chosen specimens were placed in a drying oven at 70°C for several days and individually massed. Mean initial dry mass was 230 ± 12 mg ($N = 75$; mean ± SE). A total of 60 cicadas were placed into each cage, resulting in a density of 240 individuals/m^2, or a dry mass of 55.2 g, under each tree, which is within the range of densities observed in the field (295 ± 33 individuals/m^2 in upland forests; Dybas & Davis, 1962). Cages and bags without cicadas were also placed under control trees (Figure 1). Cages were established in June 2016 and remained in place until May 2017. In May 2017, all remaining cicadas were collected and oven dried (70°C for 4 days) and weighed. Soil temperature and moisture were also measured in the field on various occasions when sampling took place (Appendix S2: Table S1). In the mid-Atlantic region, annual precipitation is around 800–1000 mm, distributed evenly throughout the seasons. While some of the one-time soil moisture readings fell on the lower range, there was sufficient precipitation preceding the two major sampling campaigns (174 mm between day 0 and day 50; 152 mm between day 50 and day 100; Chitra-Tarak et al., 2019) to maintain biochemical activity.

To assess potential cicada effects below- and aboveground, we collected a diverse set of physical, chemical, and biological data (Appendix S3). For belowground changes, we analyzed soil carbon (C), nitrogen (N), δ^{13}C, and δ^{15}N at different depths at the beginning and end of the experiment. We determined plant available nutrients using ion exchange resin capsules after 50 and 100 days. Litter decomposition rates were estimated by burying nylon teabags filled with green tea leaves as a common substrate. Remaining litter material was determined after 100 and 200 days. To explore changes in the soil food web, we compared nematode and microarthropod communities between cicada addition and control plots. Sampling, extraction, and preservation followed standard protocols (Appendix S1). Nematodes were sampled from 0 to 2 and 2 to 5 cm soil depths in both August and October 2016. Microarthropods were sampled from 0 to 5 cm depth in November 2016. In all of the three soil fauna sampling events, soil samples were taken under cages in all 20 plots.

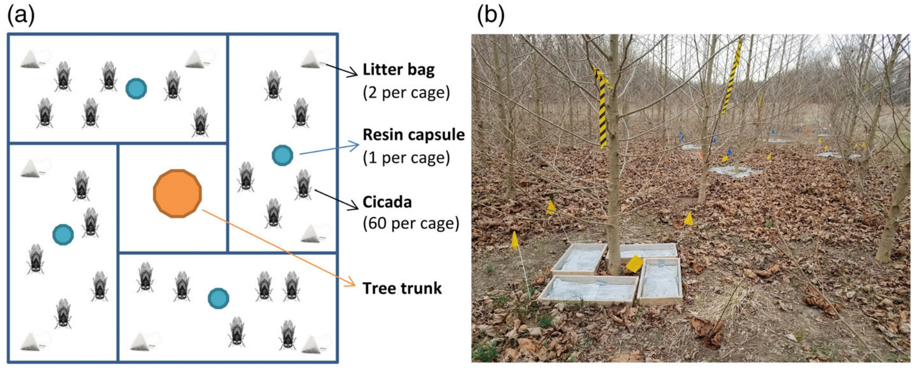

FIGURE 1 (a) Plot diagram and (b) a photo of study plots in an American sycamore tree monoculture during the 2016–2017 winter. The plot (1 m^2 in size, either with or without cicada bodies) consists of four cages around the tree trunk. Two litter bags and one resin capsule were installed under each cage.

For potential effects on aboveground tree performance, we collected height, diameter at breast height (DBH), herbivore damage, and C, N, $\delta^{13}C$, $\delta^{15}N$, and chlorophyll content index of the sycamore leaves. We measured these parameters several times between June 2016 and August 2017, with final tree DBH measured in September 2021.

All statistical analyses were conducted in R v4.1.0 (R Core Team, 2021). Packages used include *lme4* (Bates et al., 2015) for mixed effect models, *mvabund* (Wang et al., 2012) for multiple generalized linear models, *vegan* (Oksanen et al., 2016) for ordination and β diversity, and *ggplot2* (Wickham, 2016) for visualization. Normality of the data was examined using the Shapiro test and Q-Q plot. In mixed effect models, significance was evaluated using likelihood ratio tests.

The effects of cicada addition on soil C content, N content, $\delta^{13}C$, and $\delta^{15}N$ after 100 days were analyzed using mixed effect models, with "plot" as a random effect and "block," "soil depth," "cicada," and their interactions as fixed effects. The effects of cicada addition on soil nutrients (NO_3^-, NH_4^+, phosphorus, and potassium) and tea bag mass loss were analyzed using analysis of variance (ANOVA), taking into account the effect of "block." Separate analyses were conducted for data from day 50 and day 100.

The effects of cicada addition on American sycamore growth (change in DBH and tree height from the initial measurement), leaf chemistry (chlorophyll content index, percent C, percent N, C:N ratio, $\delta^{13}C$, and $\delta^{15}N$) and insect damage were analyzed using ANOVA, taking into account the effect of "block." Separate analyses were conducted for data from different sampling events.

The effects of cicada addition on the abundance of each nematode functional group (bacterial feeder, fungal feeder, plant feeder, and predator + omnivore) were analyzed using mixed effects models, with "plot" as a random effect and "block," "soil depth," "season," "cicada," and their two-way and three-way interactions as fixed effects. For three-way interactions, we tested only those containing both "block" and "cicada." Due to low numbers of predatory and omnivorous nematodes in our samples, these two groups were combined for analyses. Nematode abundance data were first standardized for 10 g of dry soil and then log-transformed to improve normality. Multiple generalized linear models (GLMs) with negative binomial distribution were conducted simultaneously to examine the effects of cicada addition on the abundance of individual nematode genera. The *p* values were adjusted for multiple testing via a free stepdown resampling procedure (Wang et al., 2012). Different seasons and soil depths were analyzed separately. Nematode community structure was visualized using nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distance. PERMANOVA (Anderson et al., 2006) with 999 permutations distinguished the effect of cicada addition on nematode community structures. The effect of cicadas on β diversity was examined by testing the homogeneity of multivariate dispersions (Anderson et al., 2006, 2011) using the Bray-Curtis distance and PERMDISP (Anderson et al., 2006) with 999 permutations.

For microarthropods, total Acari were tallied. The effects of cicada on total abundance of Acari were analyzed using ANOVA, taking into account the effect of "block." NMDS, PERMANOVA, PERMDISP, and GLMs were conducted to investigate cicada effects on Acari communities (identification done to the family level). We did not analyze Collembola data because only 20 individuals were collected in our samples.

RESULTS

Soil C and N, plant-available nutrients, and decomposition

At the end of the experiment, the mean remaining cicada dry mass under each tree was 15.7 ± 0.4 g, corresponding to 72% mass loss. Cicada plots tended to have higher % soil carbon (C), % nitrogen (N), and δ^{15}N values as well as lower δ^{13}C values compared to the control plots (Figure 2). These trends were consistent throughout all the three soil depths. However, except for a significant interaction between cicada addition and soil depth for δ^{15}N, these trends were not statistically significant (Appendix S2: Table S2).

Cicada addition had a clear effect on the content of some of the elements in the resin capsules 50 and 100 days after the start of the experiment (Figure 3; Appendix S2: Table S3). In August (day 50), contents of NH_4^+, NO_3^-, P, and K were significantly elevated in cicada soils compared to control soils. In October (day 100), NH_4^+ and NO_3^- remained elevated (Figure 3; Appendix S2: Table S4).

Cicada addition did not have statistically significant effects on decomposition (estimated as the percentage of tea bag mass loss) on day 100 (October 2016; $F_{1,16} = 2.509$, $p = 0.133$) or day 200 (February 2017; $F_{1,16} = 0.526$, $p = 0.479$; Appendix S3: Figure S1).

American sycamore trees

American sycamore trees showed apparent temporal decrease in leaf δ^{13}C values in both the cicada and control plots (Appendix S3: Figure S2). Cicada addition did not have statistically significant effects on sycamore DBH or height, nor did it have significant effects on leaf insect damage, chlorophyll content index, percent C, percent N, C:N ratio, δ^{13}C, and δ^{15}N (Appendix S2: Tables S5–S6; Appendix S3: Figure S3).

Nematode functional groups and community structure

Numbers of bacterial feeders ($\chi^2 = 14.02$, df $= 1$, $p < 0.001$), and fungal feeders ($\chi^2 = 5.36$, df $= 1$, $p = 0.021$) were significantly increased by cicada addition (Figure 4; Appendix S2: Table S7). These groups were also significantly more abundant in August than in October (bacterial feeders: $\chi^2 = 4.26$, df $= 1$, $p = 0.039$; fungal feeders:

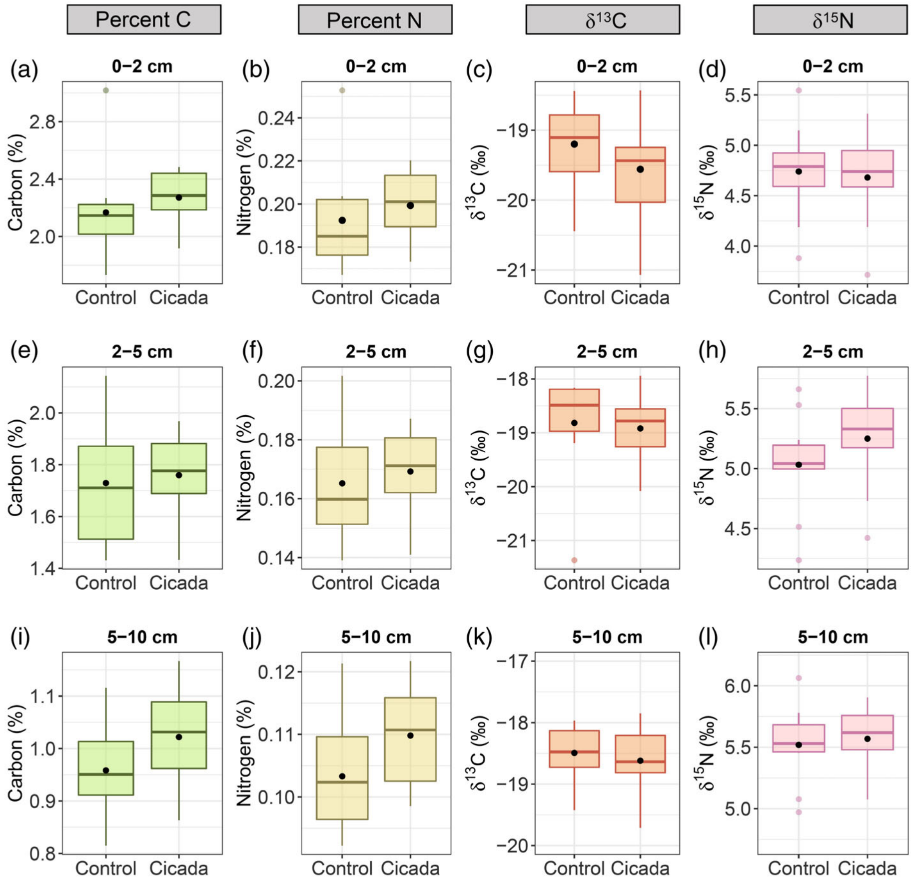

FIGURE 2 Soil C, N, δ^{13}C, and δ^{15}N at three soil depths (0–2, 2–5, and 5–10 cm) in the control and the cicada plots on day 100 in October 2016. A clear trend of increasing soil C and N and decreasing δ^{13}C, though not statistically significant, can be seen throughout the three soil depths. Box plots show medians (horizontal lines inside the boxes), means (black dots), first and third quartiles (lower and upper edges of the boxes), 1.5× interquartile ranges (lines extending from the boxes), and outliers (colored dots). Note the different scales on the *y*-axes.

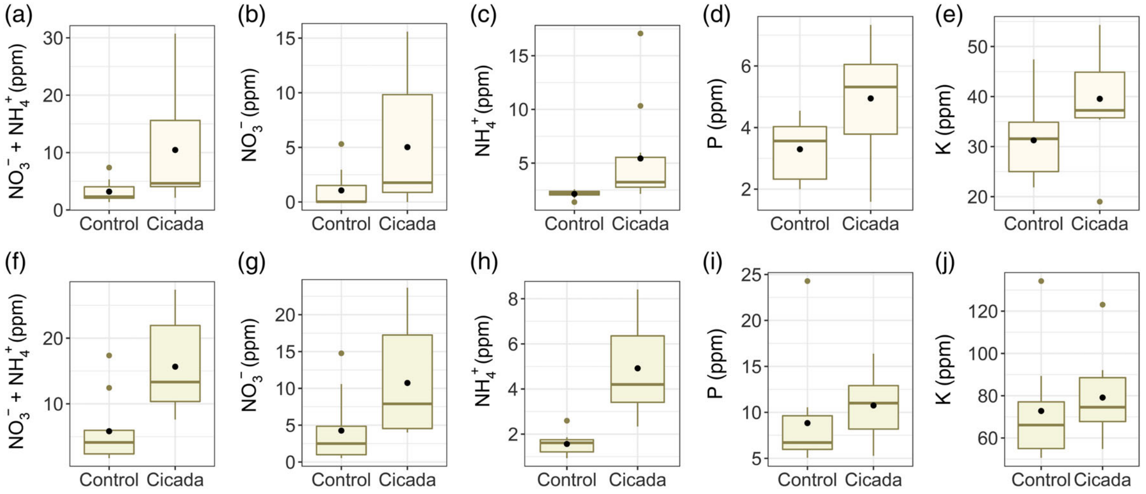

FIGURE 3 The influence of cicada carcasses on plant-available nutrients inferred from the resin capsule method 50 days (top, panels (a)–(e)) and 100 days (bottom, panels (f)–(j)) after the start of the experiment. In general, cicadas increased plant available nutrients. The cicada effect is statistically significant ($p < 0.05$) in panels (a)–(h) but not in (i) and (j). Box plots show medians (horizontal lines inside the boxes), means (black dots inside the boxes), first and third quartiles (lower and upper edges of the boxes), 1.5× interquartile ranges (lines extending from the boxes), and outliers (dots outside the boxes). Note the different scales on the *y* axes.

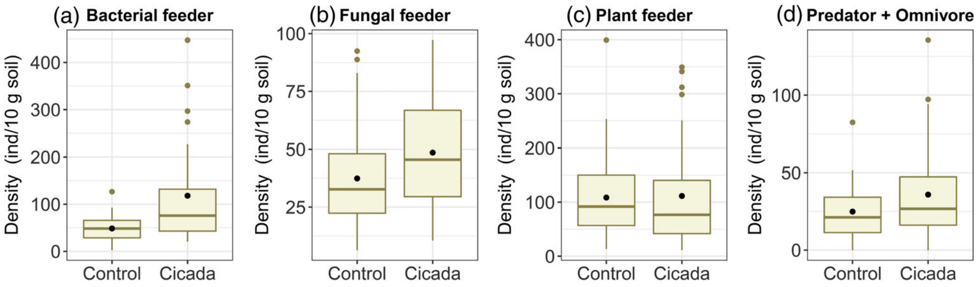

FIGURE 4 The influence of cicada carcasses on the numbers (individuals per 10 g dry soil) of different nematode feeding groups. Cicada addition significantly increased the abundance of (a) bacterial-feeding nematodes ($p < 0.001$) and (b) fungal-feeding nematodes ($p = 0.0206$), while it had no effect on the abundance of (c) plant-feeding nematodes ($p = 0.6728$) and (d) predatory and omnivorous nematodes ($p = 0.4384$) in mixed-effect models. Data from the two soil depths and seasons are pooled. Box plots show medians (horizontal lines inside the boxes), means (black dots inside the boxes), first and third quartiles (lower and upper edges of the boxes), 1.5× interquartile ranges (lines extending from the boxes), and outliers (dots outside the boxes). Note the different scales on the *y* axes.

$\chi^2 = 5.57$, df = 1, $p = 0.018$) and in surface soils (0–2 cm depth) compared to deeper soils (2–5 cm depth) (bacterial feeders: $\chi^2 = 49.71$, df = 1, $p < 0.001$; fungal feeders: $\chi^2 = 23.25$, df = 1, $p < 0.001$). In contrast, the abundances of plant feeders and omnivores + predators were not influenced by cicada addition. The "cicada × block" and "block × season" were significant in the bacterial-feeder analysis ($\chi^2 = 6.70$, df = 1, $p = 0.010$ and $\chi^2 = 11.21$, df = 1, $p < 0.001$, respectively), but all other interactions were not significant.

Soil nematode community structure was significantly different between cicada and control plots in both August and October (Figure 5; PERMANOVA, $p < 0.001$ in both seasons). β diversity was significantly higher in cicada plots than in control plots in August (PERMDISP, $p = 0.006$) but not in October ($p = 0.44$; Appendix S3: Figure S4).

The overall effects of cicada addition on individual nematode genera were significant or nearly significant in all four data sets (multiple GLM p values: 0.027 for the 0–2 cm soils in August, 0.062 for the 2–5 cm soils in August, 0.001 for the 0–2 cm soils in October, and 0.023 for the 2–5 cm soils in October). In August, the bacterial feeder *Rhabditis* spp. ($p = 0.006$ and 0.003 for 0–2 cm and 2–5 cm soils, respectively) and the fungal feeder *Tylencholaimus* spp. ($p = 0.047$ for 0–2 cm soils) increased significantly in cicada plots (Appendix S3: Figure S5). In October, numbers of the bacterial feeder

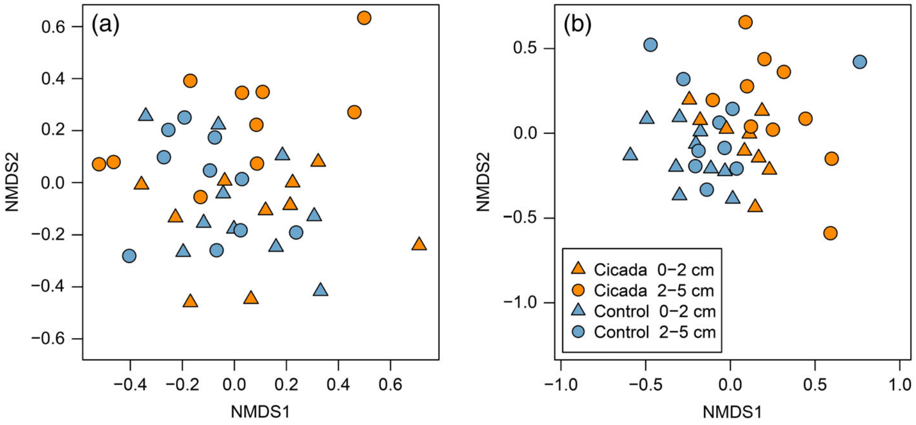

FIGURE 5 The influence of cicada carcasses on the community structure of soil nematodes (a) in August and (b) in October visualized using nonmetric multidimensional scaling. The Bray-Curtis distance was calculated using the density of each nematode genus. Orange symbols represent the cicada plots; blue symbols represent the control plots. Circles represent the deeper soil (2–5 cm); triangles represent the shallower soil (0–2 cm). Compared to the control plots, the cicada plots had higher β diversity in August ($p = 0.006$, PERMDISP) and different community composition in October ($p < 0.001$, PERMANOVA), as in August (panel a), the orange symbols can be seen more spread from each other than the blue symbols, and in October (panel b), the orange and the blue symbols form two groups that are generally separated from each other.

Panagrolaimus spp. were higher ($p = 0.001$ for 0–2 cm soils). In contrast, numbers of the two plant/fungal feeders *Filenchus* spp. and *Tylenchus* spp. were significantly lower in cicada soils than in control soils ($p = 0.039$ and 0.002, respectively).

Microarthropod community structure

For microarthropods, 19 Acari families were collected (Appendix S2: Table S8). The effect of cicadas on total Acari abundance was not statistically significant ($F_{1,16} = 0.487$, $p = 0.495$). In multiple generalized linear models, the cicada effect was not significant ($p = 0.233$). However, while cicada addition did not have a significant effect on overall community structure of Acari (PERMANOVA, $p = 0.107$), cicada plots had significantly higher β diversity than control plots (PERMDISP, $p = 0.048$) (Appendix S3: Figures S6 and S7).

DISCUSSION

Using cicada corpses as a model system, we hypothesized that arthropod resource pulses would alter the soil detrital food web by stimulating decomposition of organic matter, enhancing soil nutrients, and ultimately influencing tree performance. We found evidence for much of the former but not the latter. Both bacterial and fungal feeding nematodes were more abundant in cicada plots than in control plots. This clearly suggests that soil microbial production was higher, i.e., enough to promote greater abundance of the consumers, in cicada addition than in control plots, and highlights that arthropod-derived resource pulses can propagate up through the bacterial and fungal energy channels (sensu de Ruiter et al., 1995; Hunt et al., 1987) and thereby influence a variety of biota in these complex soil food webs. We acknowledge that the response of the microbial biomass to the resource pulse was quantified only indirectly through the response of their consumers.

Moreover, in terms of nematode community composition, the high β diversity (i.e., species turnover) in the cicada plots in August suggests that cicada impact on soil microbes transfers to their consumers rather early after the resource pulse. Our findings agree with those of Yang (2004) and further suggest that the impact of arthropod corpses on the structure of the soil food web can last until the end of the growing season. Our findings also show that, contrary to Yang (2008), cicada corpses need not be fragmented by epigeic soil macrofauna to induce changes belowground.

The stimulating effect of the cicada corpses on the soil food web likely continued until the end of the growing season (day 100), as indicated by the higher densities of both bacterial and fungal feeding nematodes in the cicada plots and the divergent functional group composition between the cicada and the control plots in October. It has been suggested (Fey et al., 2019; Nowlin et al., 2007) that consumer responses to resource pulses in terrestrial habitats should be slow relative to aquatic habitats, due to widespread differences in the structure and dynamics of these two ecosystem types. In general, slow consumer response in terrestrial food webs is explained by the relatively long generation times of the biota and by the reduced effects of top-down control in these systems (Shurin et al., 2006; Strong, 1992). The rapid response of microbial-feeder communities in our study does not support this hypothesis. Density and biomass of soil microbes, the second largest and functionally dominant biomass after plants in terrestrial systems (Whitman et al., 1998), can be top-down controlled (Mikola & Setälä, 1998; Moore et al., 2003), thus it is not surprising that consumers of soil microbes, as well as the processes they carry out, responded rapidly to cicada resource pulse. In our study, biota with small body size occupying the basal levels of decomposer food webs were more responsive to resource addition compared to their consumers. This is in line with predictions in the meta-analysis by Yang et al. (2010), and a theoretical model by Holt and Polis (1997), according to which consumers at higher trophic positions may not respond to changes in prey densities when the resource pulse is quick and the predator satiated. As most carbon and energy fixed by primary producers is processed by soil decomposer microbes and their consumers (Townsend et al., 2000), we suggest such a rapid response to resource pulses at the base of food webs could be a general pattern.

Opposite to microbial feeding nematodes, neither plant feeding nematodes nor predatory and/or omnivorous nematodes responded to cicada addition. It is unclear why the latter groups, which are known to control the abundance of their nematode prey (Allen-Morley & Coleman, 1989; Mikola & Setälä, 1998), did not benefit from the increased nematode numbers relative to the control soils. The same was observed for predatory and microbial-detritivorous soil microarthropod groups. It remains open whether taxa within these two consumer groups, which have longer generation times than their prey (see Persson et al., 1980; Siepel, 1994), would respond to cicada resource pulses later on. Furthermore, the very low density of collembolans is surprising and can indicate one or a combination of these factors: (1) these former agricultural soil might have been unsuitable, (2) relatively low soil moisture at the time of sampling, and (3) absence of leaf litter and other types of detritus underneath the cages.

The cicada-induced increase in soil fungi and bacteria (Yang, 2004) and their consumers (our study) can be expected to stimulate ecosystem processes such as litter decomposition. It is well established that, by grazing on soil fungi and bacteria, microbivores can stimulate microbial activity, which enhances decomposition rate of organic matter (Beare et al., 1995; Moore et al., 2003). However, it is not known whether aboveground consumer-based resource pulses influence decomposition rate of soil organic matter, either directly, via stimulating soil microbial biomass and activity, or indirectly, through increasing densities of microbial feeders (Kristensen et al., 2020). We found some tentative evidence for aboveground resource pulse effects on organic matter dynamics: green tea litter mass loss after 100 days was 10% higher in the cicada plots than in the control plots, while this difference was only 2% after 200 days. However, mineralization of N, P, and K, a process also indicating stimulated microbial activity, in the soils was significantly enhanced by the presence of cicada bodies. For example, plant-available N (NH_4^+ and NO_3^- combined) in the soil increased fourfold due to cicada addition, which is in line with Yang (2004) and Le Mellec et al. (2011), reporting stimulated N-fluxes following cicada addition in the US, and a moth outbreak in Germany, respectively. It is interesting that N-mineralization seemed to exceed immobilization throughout the growing season in our study and in that by Yang (2004); this may result from the low C:N ratio of cicada corpses compared to our soils (5.2 and 11, respectively). However, as resource inputs with high N content do not necessarily boost N mineralization, which also depends on element stoichiometric ratio of the substrate and the soil microbial community (Sistla & Schimel, 2012; Zhu et al., 2018), more work is needed to unravel the mechanisms behind the clearly activated, invertebrate induced mineralization processes in the soils.

Despite the significant input of cicada (commonly exceeding 200 kg dry mass/ha or 22 kg N/ha; Dybas & Davis, 1962, Luken & Kalisz, 1989) and other arthropod necromass that accumulates on the soil after a resource pulse, no previous studies have quantified the influence of this input on soil C and N contents. In his seminal paper, Yang (2004) was the first to establish controlled experiments to assess the effects of cicada carcass deposition on soil biota and processes, but the influence of this resource pulse on soil C and N contents was not studied. The results of our study suggest that cicadas can, albeit slightly, increase the contents of both total C and total N in the soil in <3 months after cicada addition. This slight increase is consistent with a decrease in soil $\delta^{13}C$, an indicator of cicada-derived C in the soil of our experimental plots and may appear unexpected given the facts that (1) not all cicada bodies were decomposed by the time of soil sampling and (2) litter decomposition, i.e., C loss, was slightly stimulated in the cicada soils. However, as the cicada-derived C can only be a very small portion of soil total C in the cicada-treated plots, the decrease of $\delta^{13}C$ values, i.e., increased soil C-content due to cicada addition, is necessarily very small and transient. The same holds with soil total N.

As net primary productivity (NPP) is often limited by N and P in terrestrial ecosystems (Vitousek & Howarth, 1991), the enhanced concentrations of NO_3^- and NH_4^+, as well as PO_4^{3-} detected in the cicada influenced soils can be expected to increase plant nutrient uptake and biomass production. Indeed, Yang (2004) reported that a forest herb, the American bellflower (*Campanulastrum americanum*), produced foliage with 12% greater N content and seeds with 9% larger size relative to controls. Similarly, Yang and Karban (2019) reported that corpses of periodical cicadas (*Magicicada* spp.; ~300 individuals m^{-2}) increased the height and trunk diameter of sycamore seedlings by 5% and 14%, respectively, in the year of cicada addition. As the authors did not survey soil nutrient dynamics in their study plots, they hypothesized that the improved growth of the tree seedlings likely stems from the fertilization effect by decomposing cicada corpses (see Yang, 2004). However, despite the clear, cicada-induced changes in soil biota and soil nutrient dynamics observed in our study, none of the parameters, including foliar damage measured from the sycamore trees, was responsive to cicada addition. This can be attributable to the relatively large size (height ~5 m, DBH of ~47 mm in August 2017) of the trees and thus the insignificant amount of N stored in cicada bodies (~5 g N m^{-2}) relative to that in the uppermost 0–10 cm soils (~170 g N m^{-2}) and American sycamore trees (210–462 g N $tree^{-1}$; estimated using data by Domec et al., 2017). Whether such fertilization manifests as enhanced growth of mature forest trees under natural conditions is not yet known; however, a tree dendrochronological survey showed that the growth of some, but not all, tree species increased but not until 5 years after cicada emergence (Speer et al., 2010). It is worth noting that the density of cicada corpses used in our experiment and those of previous studies may overestimate the actual deadfall due to the fairly wide dispersal of adult cicadas (Whiles et al., 2001, 2019).

In summary, our study using resource pulses by periodical cicadas provides evidence that massive, rapidly occurring arthropod resource inputs can have substantial direct bottom-up effects on soils and ecosystem dynamics (Yang and Gratton, 2014; Kristensen et al., 2020; McCary et al., 2021; Yang et al., 2010). The amount of N (ranging from 10 to 70 kg ha^{-1}) entering the soils in adult cicada bodies every 17 years is relatively small compared to other N-sources, such as annual atmospheric N deposition (~10 kg N ha^{-1} $year^{-1}$ during the past two decades) in Maryland, USA (Burns et al., 2021; Driscoll et al., 2003). As such an amount of atmospheric input is unlikely to increase forest growth in temperate ecosystems (Nadelhoffer et al., 1999; Solberg et al., 2009), this raises the question of the extent to which periodic, pulse fertilizations by cicadas or other arthropods can influence site productivity. The effect is more likely indirect; input of arthropod corpses induces priming, i.e., the stimulation of decomposition and nutrient mineralization of "old" soil organic matter by inputs of fresh organic material (Paterson et al., 2008; Paterson & Sim, 2013). In terms of cicadas, the clearly higher soil NH_4^+ and NO_3^- in the cicada plots relative to the control plots observed in our study and in that by Yang (2004) may indicate the existence of cicada-derived priming effects. The lack of tree performance enhancement in our study supports the view that the effect of ephemeral nutrient additions is largely determined by edaphic factors (Beauregard & de Blois, 2014). Thus, episodic resource pulses may not stimulate NPP in the short-term, but rather the long-term legacies of these pulses may instead be manifested mostly as alterations to belowground food webs and nutrient dynamics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Setälä et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.16802128.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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