

## Periodical cicada emergence resource pulse tracks forest expansion in a tallgrass prairie landscape

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**Abstract.** Understanding factors that influence resource pulses is an important aspect of ecosystem ecology. We quantified below- to aboveground energy and nutrient fluxes during the 2015 periodical cicada emergence from forest habitats in a tallgrass prairie matrix and compared results to our prior studies of the 1998 emergence in the same watershed. We estimated 35.2 million cicadas emerged across 159 ha in 2015, almost 2× more than the 19.6 million across 98 ha in 1998. The 2015 emergence resulted in below- to aboveground fluxes of 9.4 metric tons of ash-free dry mass and 1.12 metric tons of N, both ~2× greater than 1998. This corresponds to 59 kg C/ha and 7 kg N/ha in and adjacent to forested areas in 2015. Increased emergence in 2015 was a result of spatial expansion of cicadas, not higher densities. Periodical cicadas are expanding with forest habitats in this region. Cicadas expand into and oviposit in ~40% of available forest habitat during each emergence. Accordingly, we predict the 2032 emergence will span ~245 ha. Our study demonstrates how human alterations to a landscape, in this case forest expansion linked to fire suppression and reduced grazing, can alter the magnitude and extent of a resource pulse.

**Key words:** ecological subsidy; forest expansion; insect; landscape ecology; resource pulse.

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### INTRODUCTION

Ecologists increasingly recognize the significance of linkages between ecosystems and the fluxes of energy and materials between them. These fluxes, or ecological subsidies, can be driven by physical processes such as water and air movements (e.g., Junk et al. 1989), or biological events such as insect emergences and animal migrations (Polis et al. 1997, Baxter et al. 2005). Energy and nutrients associated with subsidies

can be significant to recipient systems, fueling productivity, and effects can cascade through food webs and into adjacent habitats. For example, Ben-David et al. (1998) found that marine-derived nutrients associated with salmon migrating from the ocean to streams were detectable in adjacent forests because of the movements of piscivorous predators that consumed salmon. Large, episodic events such as salmon migrations and other events where ephemeral resources become abundant are resource pulses, with

associated energy and nutrient subsidies affecting multiple trophic levels and eliciting both top-down and bottom-up cascading effects (Nowlin et al. 2008, Yang et al. 2008).

The appearance of adult periodical cicadas is among the most spectacular insect emergence events and represents classic examples of resource pulses. Periodical cicadas are relatively large insects, and their massive, synchronized emergences every 13 or 17 yr provide substantial fluxes of biomass and associated energy and nutrients from below- to aboveground habitats (Whiles et al. 2001, Nowlin et al. 2007). Positive ecological responses to deposited cicada biomass (i.e., carcasses) have been documented in both terrestrial and freshwater systems (Yang 2004, Nowlin et al. 2007, 2008, Pray et al. 2009), as cicada biomass can represent a significant pool of limiting nutrients including nitrogen (Whiles et al. 2001, Yang 2013). Effects of periodical cicada emergences are generally considered confined to the vicinity of the emergence, as adults rarely disperse more than ~50 m (Karban 1981), although movements of predators that feed on emerging cicadas could increase the ecological footprints of these events (e.g., Ben-David et al. 1998).

Periodical cicadas feed by tapping into xylem vessels in tree roots, and this limits their distribution to forested areas. However, they can be locally abundant in grassland regions where they inhabit forest patches (Whiles et al. 2001). The tallgrass prairie regions of North America, although dominated by grasses and forbs, often have patches of well-developed forest, particularly along streams and rivers. Forest habitats have been expanding in the tallgrass prairie over the past century, mainly due to fire suppression and loss of native grazers (Briggs et al. 2002a, b, Veach et al. 2014), and these forest patches can harbor dense populations of periodical cicadas (Whiles et al. 2001). As forests expand in this region, it is possible that periodical cicadas will also expand, although their opportunity for dispersal is limited to once every 13 or 17 yr during adult emergence, as nymphs are sedentary on tree roots located underneath the trees where their eggs were deposited.

We previously quantified (emerging adult abundance, biomass, and associated N fluxes) the 1998 Brood IV periodical cicada emergence

from riparian forests in a tallgrass prairie watershed in eastern Kansas. Our objective for this study was to quantify emergence of the same brood in the same watershed in 2015, using the same methods, to compare the two emergence events and assess whether periodical cicadas are expanding with the riparian forests in the region. Because we observed cicadas ovipositing in forested areas where no adults had emerged in 1998, we hypothesized that the spatial extent of the cicada emergence would expand along with forest expansion as new oviposition habitat became available to each new generation of adults. We further hypothesized that expansion of forest habitat and cicadas would increase the overall below- to aboveground flux of energy and nutrients in the watershed.

## METHODS

### Study area

We quantified the Brood IV 17-yr periodical cicada emergence in the gallery forest area of the Kings Creek drainage on the Konza Prairie Biological Station (KPBS) in northeastern Kansas. KPBS is located in the Flint Hills, which is characterized by shallow, rocky soils. This region is primarily tallgrass prairie, dominated by warm-season grasses and diverse forbs. The Kings Creek catchment is 1630 ha, consisting mostly of native tallgrass prairie, with gallery forest along stream reaches. Dominant trees in the gallery forest include bur oak (*Quercus macrocarpa*), chinquapin oak (*Q. muehlenbergii*), elms (*Ulmus* spp.), and hackberry (*Celtis occidentalis*). Like the rest of the Flint Hills, woody vegetation is expanding on KPBS due to fire suppression and changes in grazing (Briggs et al. 2002a, b, Riley and Dodds 2012).

### Emergence traps

We established five emergence trap transects in the gallery forest along lower Kings Creek. Each transect consisting of 10 traps (each 2500 cm<sup>2</sup> sampling area, 0.9 m high) placed 10–20 m apart in a line. Traps consisted of metal mesh screening (3-mm aperture) formed into a cylinder, fastened with rivets, and secured to the ground with landscape staples (10 cm in length). Lids constructed from the same material were placed on top of each with the edges folded to

grip the trap bodies. Transect locations were approximately the same as used during the 1998 emergence (see Figure 1 in Whiles et al. 2001).

We placed traps in the field 9–11 May and checked them every three days until evidence of cicada emergence (an exuvium) was observed in the vicinity of the traps on 17 May. The first adult cicadas were observed on 18 May, and the first cicada in an emergence trap was collected the same day. Cool and wet weather limited emergence during 19–23 May. All traps were checked daily during peak emergence (24 May–14 June), and every two to three days as the emergence waned (14–19 June). Adult cicadas and nymphal exuviae collected in traps were sexed, counted, and frozen until they were processed for mass and body size analyses. While all cicadas collected in our traps were *Magicicada cassini*, *M. septendecim* was also identified on KPBS for the first time during this study.

#### *Individual mass and nitrogen content estimates*

We processed 21 female and 21 male cicadas to obtain sex-specific dry mass (DM) and ash-free dry mass (AFDM) estimates. Individuals were dried at 50°C for four days, weighed to obtain DM, placed in a muffle furnace at 500°C for four hours, and re-weighed to obtain AFDM; exuvia AFDM values from the 1998 study were used for 2015 estimates. Adult male and female AFDM estimates from 2015 were compared to those from 1998.

Mass estimates were applied to emergence hole count data (see below) to estimate biomass flux associated with the emergence across the watershed. We used a sex ratio estimate obtained from the emergence traps (54.5% male and 45.5% female) to apply gender-specific mass and N estimates to emergence hole counts, and mass and N values for an exuvium were added to each individual estimate. We used % N estimates from the 1998 cicada collections (males = 11.2%, females = 10.9%, and exuviae = 7.9%; Whiles et al. 2001) and applied them to gender-specific DM estimates to calculate N flux associated with emergence.

#### *Emergence hole counts*

We used 0.1-m<sup>2</sup> rectangular sampling frames to estimate emergence densities across the entire Kings Creek gallery forest. The ~150 ha of gallery forest in the Kings Creek drainage was divided

into 106 sections that ranged in size from 0.1 to 8 ha, and investigator teams were assigned to sections. Before hole count surveys, investigators calibrated methods as a group. Our sampling approach focused on walking along streams because forests in this region are primarily riparian. Teams of 2–4 investigators walked assigned sections of the forest during 22 June–2 July, after the emergence ended. Teams dropped a sampling frame at ~5-m intervals in a random direction. Vegetation and detritus were then removed, and all emergence holes within the frame were counted. Each hole corresponds to the emergence of 1 individual (Dybas and Davis 1962). Cicada emergence holes are distinct from those of other large burrowing invertebrates at KPBS, and periodical cicadas emerge prior to other cicadas found in this region (Callaham et al. 2000). A total of 8883 frame counts were made during the sampling period.

We digitized woody vegetation sections into a GIS, and average density of holes (=average number of individuals emerging/m<sup>2</sup>) was calculated for each section of the wooded area using inverse distance-weighted interpolation. Total emergence from each woody vegetation section was then calculated as the product of the average number of emergence holes/m<sup>2</sup> and section area. Individual mass and nitrogen estimates (see *Individual mass and nitrogen content estimates*) were then applied to emergence density estimates for each section.

#### *Woody vegetation cover*

Area of woody vegetation was estimated as a proxy for estimating forest expansion between emergence events. Woody vegetation was mapped by tracing areas of woody cover on transparent mylar sheets overlaid over printed aerial images. Available images dated as close to the year of an emergence were selected for mapping. Images selected were 1978, 2003, and 2015 for the 1981, 1998, and 2015 emergences, respectively. Effort was made to restrict mapping to more mature woody vegetation and exclude sparse shrubby areas as much as possible. However, it is impossible to fully differentiate between shrub and forest cover in gray scale images, so resulting maps include both mature forest and early seral stages of woody expansion. Mylar traces were scanned and geo-rectified using a minimum of five control points in a GIS

for further analysis. Area of woody vegetation coincident with emergence years was estimated by interpolated values using linear regression ( $R^2 = 0.996$ ).

## RESULTS

### Emergence traps

A total of 719 males, 601 females, 36 non-molted nymphs, along with 1317 exuvia, were collected in traps during the emergence (Fig. 1). Traps collected an average of  $105.6 \pm 13.1$  adult individuals/m<sup>2</sup> (SE,  $n = 50$ ) during the course of the emergence. Mean density based on just exuvia collected in traps was not significantly different from actual adults (paired  $t$ -test, two-tailed,  $df = 49$ ,  $t = 0.094$ ,  $P = 0.92$ ). Based on traps, density of males ( $57.5 \pm 6.8$  individuals/m<sup>2</sup>) was higher than that of females ( $48.1 \pm 6.7$  individuals/m<sup>2</sup>; paired  $t$ -test, two-tailed,  $df = 49$ ,  $t = 3.44$ ,  $P = 0.0012$ ). The overall sex ratio based on trap catches was 1.2:1 M:F.

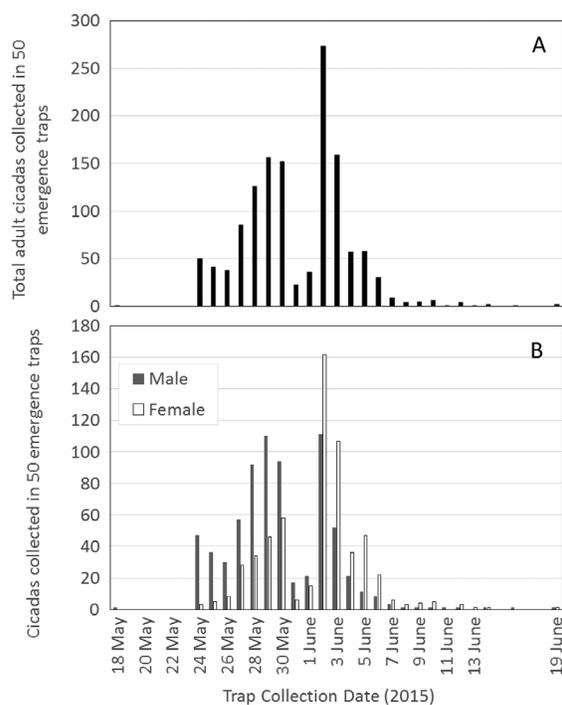


Fig. 1. Total (A) and number of adult male and female (B) cicadas collected in 50 emergence traps located along 5 transects in the gallery forest of KPBS on each collection date.

### Emergence phenology

The emergence lasted 32 d (18 May–19 June). However, due to unusually cool weather, emergence was limited during 19–23 May. From 24 May on, daily numbers of emerging cicadas (adult males and females) roughly followed a bell-shaped curve with the exception of 31 May–1 June, where again cool weather reduced emergence rates (Fig. 1). Emergence peaked on 2 June and then dropped sharply until 7 June, with a long attenuation (4–6 total individuals across all 50 traps from 8 to 10 June; 1–4 on collection dates between 11 and 19 June). 98% of individuals emerged during the 14-d peak of the emergence (24 May–7 June); 60.5% emerged during the six-day peak (29 May–3 June), a period that included two days of low emergence.

There was a phenological difference in the emergence between the sexes (Fig. 1B), with male emergence peaking earlier than females. However, with the exception of the lone cicada captured on 18 May, the first females emerged at the same time as the first males.

### Emergence production patterns

There were no differences in body masses between emergence years for males (1998 =  $0.149$  g AFDM  $\pm$   $0.009$ , 2015 =  $0.15$  g AFDM  $\pm$   $0.005$  g) or females (1998 =  $0.264 \pm 0.009$ , 2015 =  $0.26 \pm 0.01$ ;  $t$ -test,  $P > 0.05$ ). Emergence density in each of the surveyed sections during 2015 ranged from 1.1 to 92.7 individuals/m<sup>2</sup>, with an average of 24.9 m<sup>-2</sup>. This was similar to the 27.2 m<sup>-2</sup> average across parcels in 1998. Corresponding average emergent cicada biomass and N flux values across the wooded area in the watershed during 2015 were 5.8 g AFDM/m<sup>2</sup> and 0.697 g N/m<sup>2</sup>, respectively, similar to the 6.3 g AFDM/m<sup>2</sup> mass and 0.63 g/m<sup>2</sup> N average estimates from 1998.

Estimated total number of individuals emerging in 2015 was 35.2 million cicadas emerging over 159 ha (Fig. 2). This was 1.8 times as many cicadas and 1.6 times the area of emergence estimated in 1998 (98 ha in 1998). This corresponded to 9.4 metric tons of AFDM and 1.12 metric tons of N during the 2015 emergence in the Kings Creek watershed.

While the overall abundance and biomass of emerging cicadas in the watershed increased from 1998 to 2015, and the spatial extent of the emergence increased by 62%, emergence was

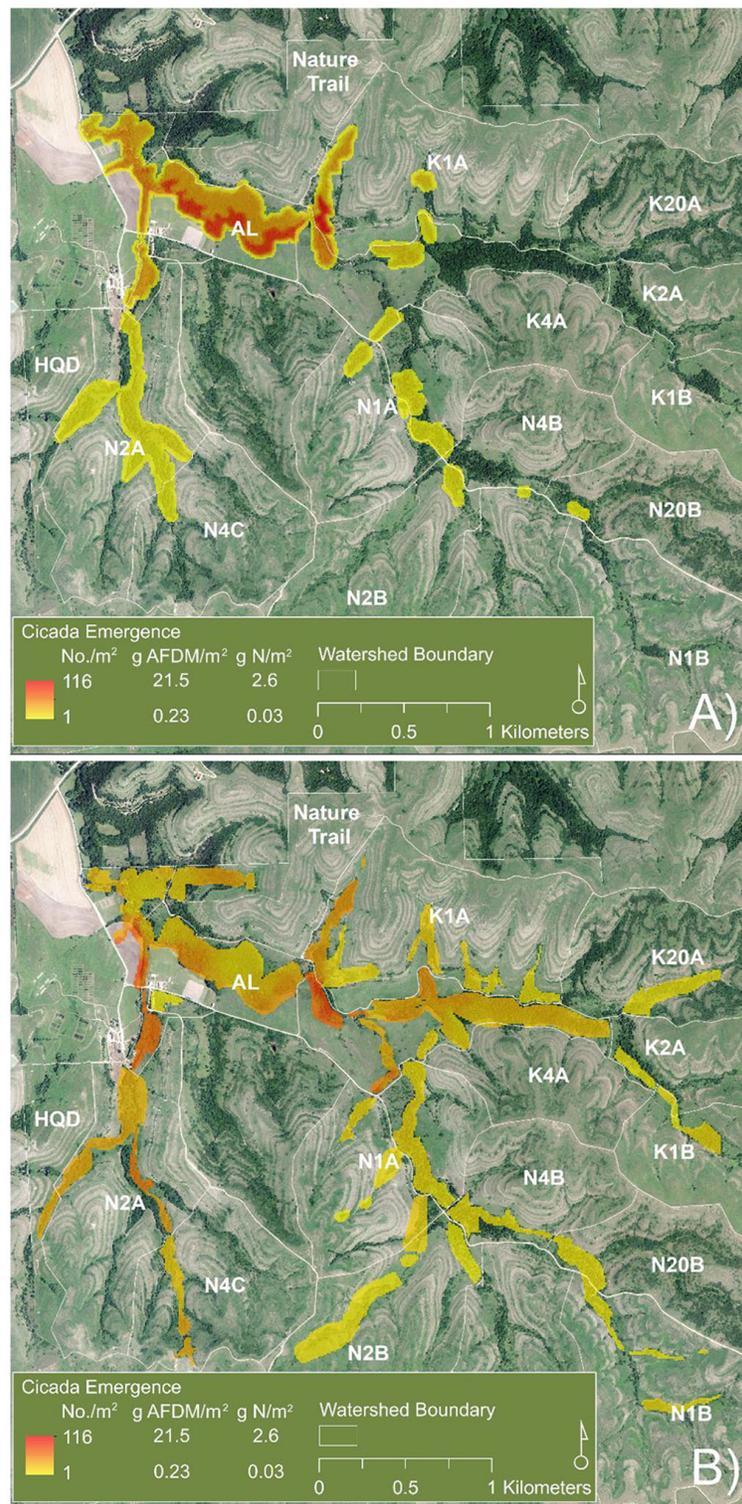


Fig. 2. Spatial distribution of cicada emergence, ash-free dry mass, and nitrogen in 1998 (Panel A) and 2015 (Panel B) in the Kings Creek drainage.

lower than 1998 in some areas, particularly heavily forested parcels in the lower portions of the watershed (Fig. 3). The overall larger emergence flux in 2015 was a function of spatial expansion of cicadas in the watershed, rather than increased densities.

Cicadas in 1998 emerged from ~39% of woody vegetated area that was available to adults in 1981 and ~28% of the total emergence area in 1998 was in areas that were adjacent to woody areas but did not have woody vegetation in 1981. During the 2015 emergence, cicadas emerged from a similar portion of woody vegetation habitat that had been available to adults in 1998 (~38%), with ~34% of the total emergence area in marginal areas that did not have woody vegetation in 1998 (Fig. 4).

## DISCUSSION

Our results indicate that forest expansion in the tallgrass prairie region is increasing the spatial extent of periodical cicada populations and thus the below- to aboveground resource pulses associated with their emergences. There were nearly 2× more cicadas in the Kings Creek watershed in 2015 compared to the prior emergence in 1998 because the emergence area expanded by >60%. Forest expansion related to human activities is occurring in many grassland regions globally (Bowman et al. 2001, Scholtz et al. 2018), and likely influencing similar animal-mediated energy and nutrient fluxes. Our analyses of images over time indicate that woody vegetation cover on KPBS increased by ~100%

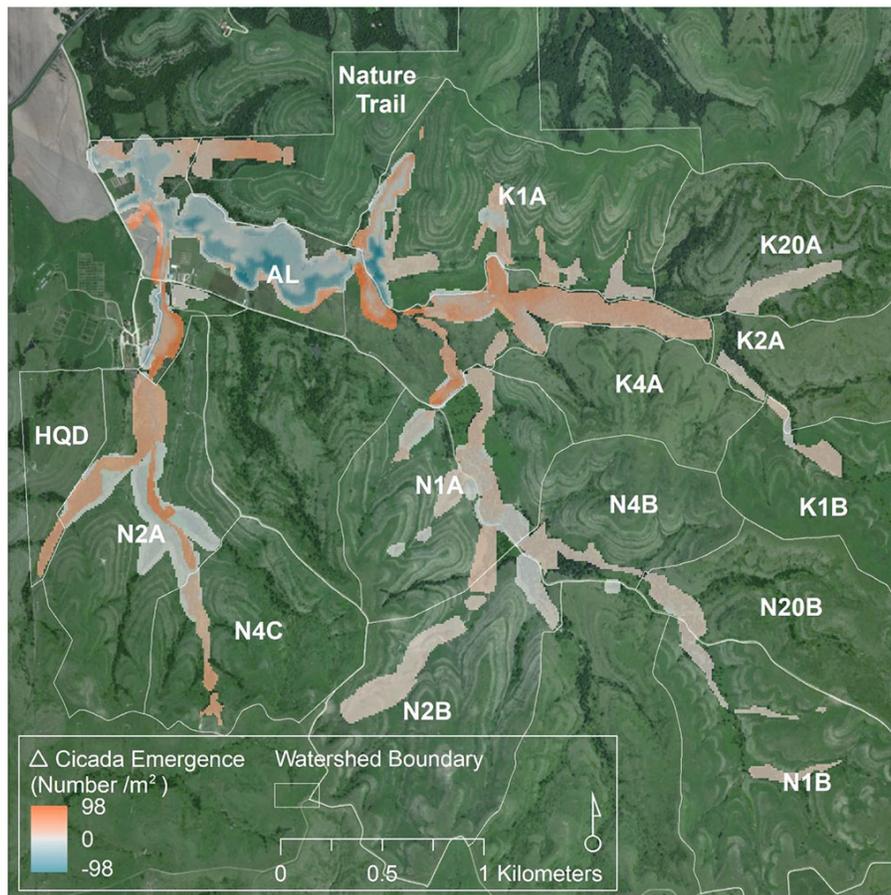


Fig. 3. Change in density of cicada emergence in the Kings Creek drainage from 1998 to 2015. Intensity of blue shades indicates decreased emergence between the two sampling years, and intensity of red shades indicates areas of increases in emergence.

from 1981 to 2015, which translates to ~3%, or ~5.4 ha, per year from 1981 to 2015.

Periodical cicada range expansion in the tall-grass prairie is important because it represents the spatial expansion of a significant below- to aboveground flux of energy and nutrients that was historically limited to a small percentage of the landscape. Woody vegetation in this region was mostly confined to relatively narrow riparian or gallery forests adjacent to rivers, but human activities, in particular the extirpation of native ungulate grazers and fire suppression, have facilitated significant forest expansion in the last century (Briggs et al. 2002*a, b*, Veach et al. 2014). Whiles et al. (2001) estimated that the average N flux associated with the 1998 periodical cicada emergence was ~40% of annual bulk precipitation N inputs on KPBS; this percentage per unit area was about the same for 2015, but the spatial extent of this significant N flux was much greater, such that the total below- to aboveground N flux across the watershed was ~2.2 times greater in 2015 compared to 1998.

The increased emergence in 2015 was not a function of higher population densities in wooded habitats. In fact, cicadas were overall less concentrated in many wooded areas in 2015 compared to 1998, with overall average densities across the extent of woody vegetation habitat 8% lower in 2015 compared to 1998. This reduction in densities may be because the adults in 1998 had more woody vegetation habitat to spread across and oviposit in but could also be due to any number of factors that influence oviposition site selection, egg production, hatching success, and/or larval survival. Male periodical cicadas form chorusing centers in certain trees, and this can lead to clumped distributions because of females concentrating in these trees and ovipositing in or near them. Historically, when only narrow parcels of wooded habitat were available in this region, chorus centers were likely very concentrated. With woody vegetation expansion, chorus centers have likely spread out across the watershed, leading to declining densities over time.

The N flux associated with the periodical cicada emergence in this region is ecologically significant and likely influences multiple trophic levels. Yang (2004) performed experimental periodical cicada carcass additions to forest plots and

plants using carcass densities that would correspond to the range of adult cicada densities we observed in both our 1998 and 2015 studies. Yang (2004) found that cicada carcass additions increased soil microbial biomass, and soil ammonium and nitrate availability, and increased American bellflower (*Campanulastrum americanum*) foliage nitrogen content and seed size. Responses like these can have cascading effects, both bottom-up and top-down, such as increased plant growth rates, increased herbivory rates, and changes in plant community competitive hierarchies (Yang 2008, 2013).

To efficiently estimate cicada emergence densities across an expanding area of woody vegetation, we sampled emergence holes across the area. Hole counts are rapid and accurate because the emergence holes are unique (Dybas and Davis 1962, Whiles et al. 2001). An advantage of the hole count method is that it accounts for high spatial variability across the gallery forest. Periodical cicadas, due to their root feeding as nymphs, are likely to emerge in a somewhat clumped spatial pattern at small spatial scales. Our study also provided a unique opportunity to compare hole count density estimates those from emergence traps deployed at the same time and in the same area. Hole counts in the closest areas where emergence traps were located estimated half or less of the densities of emergence traps. This may simply be due to spatial variability, but it also suggests that values based on hole counts produced conservative estimate of the resource pulse. If actual emergence rates were double the hole count estimates across the entire watershed, as suggested by emergence trap values, the pulse may have been closer to 19 metric tons of AFDN and 2.3 metric tons of N.

The cicadas at KPBS do not appear very efficient at expanding with the forest in the region, and this may be due to limited dispersal capabilities in both time and space. Dispersal is limited to once every 17 yr for the species we examined, and studies indicate that adults do not move far from where they emerge, generally less than 50 m (Karbon 1981). Reports of limited dispersal are consistent with patterns we observed. Emergence patterns from 1998 indicate that adults in 1981 oviposited in only 39% of the wooded habitat available to them, and a similar pattern was evident in 2015, with adults in 1998 ovipositing

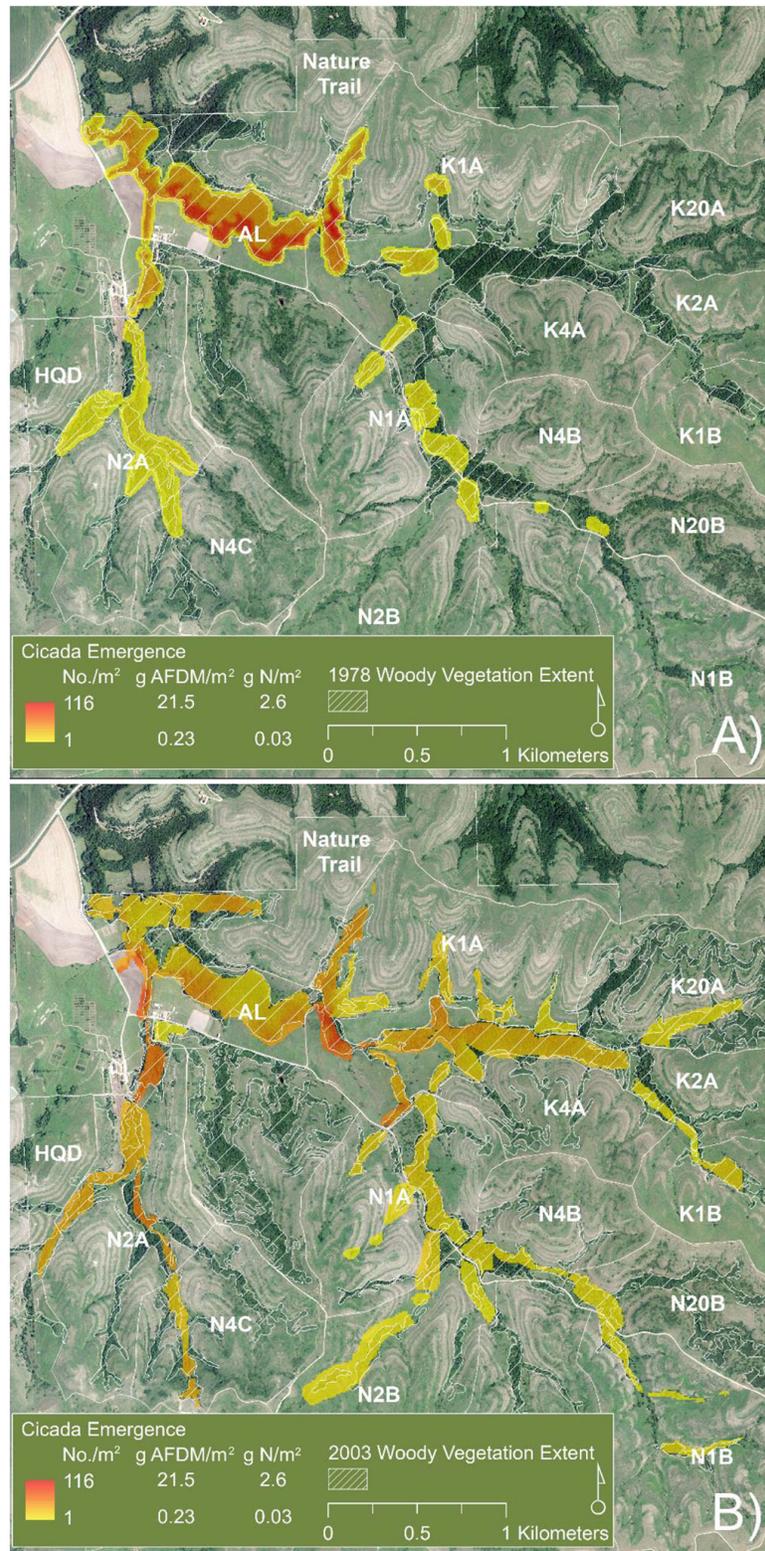


Fig. 4. (A) Periodical cicada emergence densities and N flux in 1998 compared to available woody habitat in

(Fig. 4. *Continued*)

1978 (crosshatched region), which is the approximate forest habitat that was available when adults emerged and oviposited in 1981. Area of emergence was ~39% of available woody habitat. (B) Periodical cicada emergence densities and N flux in 2015 compared to available forest habitat in 2003 (crosshatched region), which is the approximate forest habitat that was available when adults emerged and oviposited in 1998. Area of emergence was ~38% of available woody habitat.

in just 38% of wooded habitat available. Although it is possible cicadas did oviposit in other areas and eggs or nymphs did not survive, it seems most likely that the absence of cicadas from a given wooded area is because they simply did not oviposit there. Some areas that we classified as woody vegetation habitat may have been unsuitable for oviposition because they had transitioned and were dominated by shrubby vegetation rather than large trees. Likewise, the emergence of cicadas from areas that were not classified as woody when adults were present is likely because they attached to roots of woody vegetation that expanded beyond the canopy; others have noted that periodical cicadas, particularly *M. cassini*, show a preference for forest edge habitats (Lloyd and Karban 1983, Rodenhouse et al. 1997).

Whatever the underlying mechanisms, periodical cicadas in this region are expanding with woody vegetation, albeit inefficiently because of dispersal limitations. Woody vegetation covered ~353 ha in 2015; assuming an average oviposition area of 38.5% of woody habitat available and 30.9% along margins of woody habitat based on 1998 and 2015 emergence patterns, we can predict cicada emergence in 2032 will expand to ~245 ha in the Kings Creek watershed.

Considering the natural history of periodical cicadas, the spread of woody vegetation is the most feasible explanation for their range expansion on KPBS. We did not directly test this relationship experimentally, but periodical cicadas are generally considered obligate root feeders on woody vegetation (White and Strehl 1978). There are a few cicada species found on KPBS, and stable isotope studies indicate all either feed exclusively on herbaceous vegetation or woody vegetation; isotopic analyses of periodical cicadas during this study indicated they fed on roots of woody vegetation (Callaham et al. 2000). Even if some periodical cicadas could feed on roots of grasses or forbs, their distribution would still be

limited to areas with woody vegetation because females oviposit in twigs of woody plants (Williams and Simon 1995).

It is hypothesized that the temporal patterns of periodical cicada emergences keep predators from adapting to and efficiently exploiting these massive, but infrequent resource pulses. The sudden appearance of so many individuals leads to predator satiation, and for many insectivores, the life spans of many individuals will not include a periodical cicada emergence event. As woody vegetation and periodical cicada emergences expand into habitats that were historically mostly devoid of both, this is likely even more so the case. Periodical cicada emergences did not occur in at least the recent evolutionary history of many populations of predators occupying these grassland habitats. In contrast, predator populations in historically forested regions have likely exploited and benefitted from these resource pulses for many generations.

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