



Use of tree species by three species of *Magicicada* (Hemiptera: Cicadidae) in an Appalachian forest

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Abstract Periodical cicadas (*Magicicada* spp.) are endemic to deciduous forests in the eastern United States. In successional forests, they must partition resources such as host trees to coexist. We measured tree size, emergence holes, oviposition scar bundles, and chorusing center abundances of *Magicicada* species on 12 common tree species in a deciduous forest to understand host-tree use. We predicted that the abundance of periodical cicadas and use of specific host-tree species would change depending on the *Magicicada* species and tree life stage. We considered the size of the tree (diameter at breast height) as a covariate to control for tree size and collected eggs for a greenhouse experiment to assess whether nymphs prefer to feed on *Quercus rubra* or *Acer saccharum*. More emergence holes were found below *Quercus* species than any other tree species. The abundance of periodical cicadas on host trees used for chorusing centers varied depending on the *Magicicada* species, but were most abundant on *Quercus* species. Oviposition scar bundles were also more frequent on *Quercus*. More nymphs were found on *Quercus* than *Acer* in the nymph preference study. Though periodical cicadas used *Quercus* hosts more than other tree species, their abundances on different host tree sizes and

species differed significantly. Periodical cicada species may use specific host species and life stages as a way to partition resources and minimize competition among the *Magicicada* species during emergence years.

Keywords Ecological succession · Habitat partitioning · Periodical cicadas · Successional forests

Introduction

Periodical cicadas (*Magicicada* spp.) have long intrigued scientists (e.g., Walsh and Riley 1868; Marlatt 1907; Simon et al. 2022). Early American entomologists such as Walsh and Riley (1868) and Marlatt (1907) marveled at the extended juvenile period and periodicity of these insects. Indeed, they have the longest juvenile development time reported of any insect (Marlatt 1907; Kritsky 2004; Simon et al. 2022). Periodical cicadas emerge in broods that are geographically contiguous and temporally isolated from other broods (Dybas and Lloyd 1974). They display 13- and 17-year life cycles and occasionally experience development accelerations and decelerations, allowing a switch in life-cycle period (Cooley et al. 2018). The nymphs spend developmental years belowground feeding on root xylem (White and Strehl 1978). At the end of the 13- or 17-year cycle, they emerge as adults in synchrony with others of their brood.

Natural history of periodical cicadas

There are seven recognized species of periodical cicadas: *Magicicada cassini*, *M. septendecim*, *M. septendecula*, *M. tredecassini*, *M. tredecim*, *M. tredecula*, and *M. neotredicim* (Alexander and Moore 1962; Dybas and Davis 1962).

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Within periodical cicada broods, several species emerge in synchrony and are partially separated by habitat (White 1980; Yang 2006; Simon et al. 2022). The species-specific physiological behaviors of cicadas have been used to explain distribution patterns and sympatric-segregation patterns within habitats (Sanborn et al. 2004).

During emergence years, periodical cicadas display the largest insect emergence known, with densities as high as 372 cicadas m^{-2} (Dybas and Davis 1962; Karban 1982, 2014). Such dense emergences can have wide-ranging effects on the ecology of the habitats and tree hosts (Yang and Karban 2019; Perkovich and Ward 2022). For example, Yang and Karban (2019) found that tree growth significantly increased during the year of an emergence due to the excess nutrients deposited in the ecosystem by accumulation of dead adults. Additionally, Perkovich and Ward (2022) found that there were significant changes in forest tree phytochemistry before, during, and after periodical cicada emergences. Furthermore, oviposition damage causes the ends of branches to wither, and sometimes break, and also become more susceptible to disease (Zwet et al. 1997). Moreover, periodical cicada emergences have a significant effect on the soil communities of host trees (Setälä et al. 2022). For example, Setälä et al. (2022) found that resource pulses from periodical cicada emergence significantly changed the community composition of soil nematodes.

Extended periodicity in a dynamic environment

Periodical cicadas are exclusive to deciduous forests in eastern North America (Williams and Simon 1995; Simon et al. 2022). Much of the forested area where they emerge is part of the Appalachian Mountains. These forests are experiencing rapid changes in tree compositional architecture due to anthropogenic factors (Angel et al. 2017; Cooley et al. 2018) and successional processes (Tuttle et al. 2019; White et al. 2018). Appalachian forest dynamics suggest that succession is causing a shift away from *Quercus* spp. (oak)-dominated forests to *Acer* spp. (maple)- and *Fagus* spp. (beech)-dominated forests (McEwan and Muller 2006; Chapman and McEwan 2016; Allen et al. 2018).

There has been extensive research done on the effects of periodical cicadas on tree growth (e.g. Karban 1982; Koenig and Liebhold 2003; Yang and Karban 2019), oviposition preference (Dybas and Lloyd 1974; White 1980; Clay et al. 2009), and habitat/ tree host preference (Dybas and Lloyd 1974; Lloyd and White 1980). More recent studies have focused on mapping the distributions of the various broods based on geographic validations and are focused on understanding population dynamics (Cooley et al. 2011, 2018), while mapping studies sought to reveal biogeographical patterns of emergences (Cooley 2015). For example, Clay et al. (2009) demonstrated that periodical cicadas were more

likely to emerge from primary forests than secondary (or successional) forests but preferred to oviposit in successional sites. It is not surprising that periodical cicadas emerge more from primary forests due to the extended life cycle. That is, a tree must be of an appropriate size for a female to oviposit eggs and must survive for the next 17 years for the next generation of periodical cicadas to emerge from underneath the tree. Findings by Clay et al. (2009) suggest that successive cicada generations could indicate shifting mosaics of dominant plant species and plant ontogenies in these forests. Furthermore, understanding how host trees are being used and partitioned in forested areas will help provide information about microhabitats that are most likely to be affected by the emergences. The goal of this study was to analyze the use of host tree species by periodical cicada species and the life stage for specific cicada behaviors (i.e., emergence, oviposition, chorusing) in a successional forest.

We used a successional forest to analyze periodical cicada behavior and host-tree use at the beginning of their emergence. We made three predictions based on the life-history strategies of periodical cicadas: (1) Because of the extended developmental period of cicada nymphs, there would be a greater number of emergence holes located below large (> 35 cm diameter at breast height (DBH)) trees (Clay et al. 2009). (2) In relation to the previous prediction, oviposition attempts should be more abundant in small (< 35 cm DBH) trees to ensure that the tree survives the next 17 years during offspring development. (3) Periodical cicada species are more abundant in specific species and sizes of host tree, and their abundance will vary depending on tree-host species and size. We made no a priori predictions about which host-tree species would be favored by a specific periodical cicada species, but that variations in host-tree use may act as a potential mechanism to partition host-tree resources.

Materials and methods

Study site

Periodical cicada chorusing only occurs for 3–4 weeks during an emergence (Williams and Simon 1995). Because the peak of the emergence usually occurs from late May to early June (Williams and Simon 1995; Kritsky 2004; Simon et al. 2022), we sampled over 4 days during peak emergence (3–6 June 2019). We analyzed Brood VIII 17-year periodical cicadas (Marlatt 1907; Gossard 1917) in Keystone State Park (Westmoreland County, PA, USA). The park is ~485 ha and is part of the Appalachian mixed-mesophytic forest. We sampled a quadrant within the following GPS coordinates: 40.3772, -79.3920; 40.3757, -79.3921; 40.3755, -79.3857; and 40.3770, -79.3859. This forest contains a wide array of tree species but is dominated by *Quercus alba* (white oak)

and *Quercus rubra* (red oak) in the overstory, with *Acer saccharinum* (silver maple), *Acer saccharum* (sugar maple), and *Fagus grandifolia* (beech) in the subcanopy (McCarthy et al. 2001). The park's landscape is a combination of patches of old-growth forest and disturbed areas with new-growth (secondary) forest. Cicadas began emerging in the area in late May 2019. We conducted our sampling 1 week after cicadas began emerging due to the teneral period (i.e., state of the insect immediately after molting during which the exoskeleton has not hardened) (Karban 1981; Cooley and Marshall 2001).

Without completing a tree survey a priori, it is difficult to separate preference from tree availability. To avoid bias from less abundant trees, we sampled from 12 dominant tree species: *A. negundo* (box elder), *A. saccharinum*, *A. saccharum*, *F. grandifolia*, *Fraxinus americana* (American ash), *Juglans nigra* (American black walnut), *Liriodendron tulipifera* (tulip poplar), *Q. alba*, *Q. palustris*, *Q. rubra* (red oak), *Sassafras albidum* (sassafras), and *Ulmus americana* (American elm). Each of these species had at least 30 reproductively active individuals within the sampled quadrant. Only trees with actively chorusing males were selected (aside from *J. nigra*, in which no male cicadas were chorusing). Despite not finding any activity in *J. nigra*, this species was not excluded from this study because we were able to find enough trees to sample. *J. nigra* was previously recorded as a favored host-plant of periodical cicadas (Clay et al. 2009). Trees were randomly selected throughout the forest. However, all chosen trees were at least 2 m apart, and no two trees from the same species were sampled next to each other. We measured DBH as an index of size and formed two classifications of trees. Continuous height data were used as a covariate in analyses (discussed later in the *Statistical analyses* section), but were grouped subsequently to elucidate overall patterns in host-plant size usage. Due to the positive correlation between DBH and tree age (Fulton 1999; Oladi 2005; Liu et al. 2018), we used DBH to differentiate between old trees (large trees with DBH > 35 cm; cf. Johnson 1992) and young trees (small trees with a DBH 10 < 35 cm). Due to height limitations, we only sampled from trees that had canopy foliage that was readily accessible with our telescoping net (described below). In the area we sampled, trees were closely spaced. However, we selected trees that were at least 3 m away from one another to avoid overlap.

Adult cicada host-tree usage: emergence holes and oviposition scar bundles

During an emergence year, periodical cicada nymphs emerge from holes or will sometimes form chimneys that are emergence-hole constructs built up like a cone or tower. Chimneys and holes can be used to estimate cicada emergences

(Dybas and Davis 1962). Under individual trees, we counted structural chimneys and emergence holes. We use the term "emergence hole" to describe any instance (chimney or hole) where a periodical cicada nymph exited the soil. To standardize counting methods for all trees, a 2-m radius (starting from the center of the tree) was measured around each trunk, and the leaf litter was carefully removed from the area to reveal emergence holes. All emergence holes within the 2-m radius were counted and assumed to be from that tree. Some individuals may have emerged from under the same tree, but were more than 2 m away. However, we used the 2-m radius to avoid counting emergences that may have come from neighboring trees. Each chimney corresponds to the emergence of one cicada and is distinct from other burrowing invertebrate holes (Dybas and Davis 1962). We conducted qualitative assessment of terminal twigs for oviposition scar bundles and oviposition scar damages for each tree and averaged per tree. Females slide their sheathed ovipositors along branches, piercing the branch every few centimeters, locating a place to lay their eggs (Kritsky 2004). "Flagging" occurs when a branch is severely injured from oviposition and the branch tip breaks and terminal leaves turn brown (White 1981). Flagging does not always occur with each ovipositional attempt. We examined trees in the field for these scars. Because the scars are generally grouped together, we called each group "oviposition scar bundles". For consistency, entire trees were visually surveyed for these oviposition scar bundles.

Adult cicada host-tree usage: adult densities in chorusing centers and species identification

A telescoping BioQuip insect net (46 cm handle, 30 cm diameter net opening; BioQuip, Compton, CA, USA) was used for sweep net collections of cicadas from each tree. The collections took place over the 3 days, between 12:00 and 16:00 h when chorusing males were the most active. Samples were collected from 10 strokes of the sweep net through the crown foliage at a height of ~4 m on each tree. Each swipe was taken at a different location on the tree for a total of 10 locations per tree. The cicadas were sealed in a plastic container until the 10 swipes were taken from the tree. The cicadas were then identified to species and sex determined before releasing.

We analyzed an emergence, containing three of the seven species that are endemic to the northeastern United States (*M. cassini*, *M. septendecim*, and *M. septendecula*) (Alexander and Moore 1962; Marshall and Cooley 2000). For identification, we used the *Magicicada* species key published by Kritsky (2004). In general, *M. cassini* (described by Cassin 1851; Fischer 1851) is much smaller than *M. septendecim* and *M. septendecula*. Additionally, *M. septendecula*

(described by Alexander and Moore 1962) is distinguishable by its orange abdominal bands. In all three species, males and females are easy to differentiate.

Nymph preference experiment

Weeks before cicada emergence, one sapling of *Q. rubra* (red oak) and one of *A. saccharum* (sugar maple) were planted at opposite ends (~ 1 m apart) in each of 10 plastic containers (65-L) in a greenhouse. On 6 June 2019, *Magicicada* eggs were collected from trees at the study site by removing the end portion of branches that had oviposition scar bundles. Ten branches with cicada eggs were collected from red oak trees, and 10 branches with cicada eggs were collected from sugar maples. The collected branches were taken to the greenhouse, the cut end of the branches was placed in a centrifuge tube with water to maintain branch vigor and prevent desiccation, then one branch was placed in the center of each plastic container so that cicada nymphs, once hatched, would fall directly between the red oak and sugar maple. Average placement between the two tree saplings forced nymphs to travel a small distance to begin feeding. The first eggs hatched on 26 June. The last set of eggs hatched on 4 August. Saplings from the plastic containers were harvested 2 weeks after the eggs hatched and nymphs were counted. To count individual nymphs, we carefully sifted through the soil. Each tree was first removed and combed over for any attached nymphs. We used a small trowel to remove the soil. Each shovel full was carefully sifted to find the small white nymphs. Only the first 7.5 cm of soil was removed because newly hatched nymphs do not dig much deeper.

Statistical analyses

Effects of tree species and size on adult cicada abundance and partitioning

Adult cicada data were analyzed using a multivariate analysis of covariance (MANCOVA) to minimize Type I statistical error due to testing the significance of multiple dependent variables (i.e., periodical cicada emergence holes, oviposition scar bundles, and periodical cicada counts in chorusing centers [total, by species, and male and female]). For significant dependent variables, a univariate analysis of covariance (ANCOVA) was run with Scheffe's post hoc test of the main effects tree species, tree life stage [large (i.e., old) vs. small (i.e., young) as a covariate] and the interaction between tree species and tree life stage (as a covariate). Pearson's correlations were run between cicada abundance data and DBH for each tree species to assess the relationship between these variables. Tests of variance and correlations were run using R version 3.6.0 (R Core Team 2019).

Hartigan's dip test of unimodality (Hartigan and Hartigan 1985; Maechler 2015) was performed on cicada abundance (total and individual species) and tree life stage for each tree species to measure multimodality. If a tree species was multimodal, histograms were created to visualize the peaks. For these analyses, we used the R package *diptest* (Maechler 2015). However, it may be difficult to find trees that express the intermediate growth sizes and potentially bias sampling efforts for individuals that are smaller or larger than the intermediate developmental stage. To ensure there was no bias from disproportional sampling in tree species with bimodal distributions, we also ran a nonparametric Kolmogorov–Smirnov two-sample test to compare the proportion of cicadas in each size class to the proportion of trees in each size class.

Statistical analysis of nymph preference

A χ^2 test was used to determine whether the cicadas preferred *Q. rubra* (red oak) or *A. saccharum* (sugar maple). If there was no preference, we expected observation values would be 50% on *Q. rubra* and 50% on *A. saccharum*. If preference did exist, there would be an increase in observed values for the preferred tree species. Because we had multiple dependent variables (i.e., the number of cicada nymphs on oak roots and the number of cicada nymphs on maple roots), we ran a MANOVA to determine whether the “home” tree species (i.e., the tree species on which the cicada eggs hatched) played a role in the nymphs' preference. Both tests were performed using R version 3.6.0 (R Core Team 2019).

Results

Adult host-tree usage and partitioning

Adult cicada abundances (measured as the number of emergence holes, the number of oviposition scar bundles, the number of males for each species, the number of females for each species, and the total number of each periodical cicada species in chorusing centers) were significantly affected by tree species (MANCOVA: Wilk's $\lambda = 0.001$, $F = 26.172$, $P < 0.001$, error df = 2087), tree size (i.e., large trees vs. young trees) (MANCOVA: Wilk's $\lambda = 0.222$, $F = 26.172$, $P < 0.001$, error df = 267), and the interactive effects of tree species and stage (MANCOVA: Wilk's $\lambda = 0.007$, $F = 26.172$, $P < 0.001$, error df = 2087). ANCOVA results are discussed in greater detail below.

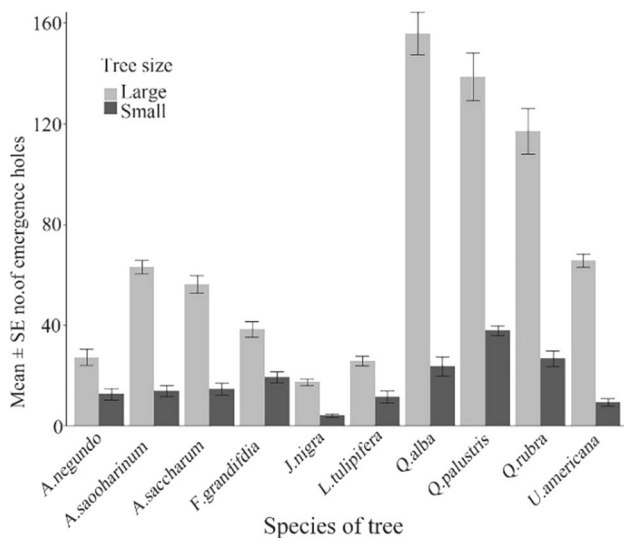
Emergence holes

Emergence holes were most abundant under large oak trees (Table 1, Fig. 1). *Quercus* species had significantly

Table 1 Univariate analysis of covariance for effects of tree species and life stage on abundance of periodical cicadas by species

Variable measured	Tree species			Tree life stage (covariate)			Tree species × life stage		
	df	F	P	df	F	P	df	F	P
Emergence holes	10	19.66	<0.001	1	89.79	<0.001	10	3.36	<0.001
Oviposition scar bundles	10	11.3	<0.001	1	797.65	<0.001	10	4.78	<0.001
total cicadas	10	236.65	<0.001	1	13.63	<0.001	10	179.9	<0.001
<i>M. cassini</i> (total)	10	380.71	<0.001	1	0.03	0.869	10	88.53	<0.001
<i>M. cassini</i> males	10	179.13	<0.001	1	0.03	0.869	10	40.57	<0.001
<i>M. cassini</i> females	10	179.75	<0.001	1	0.01	0.989	10	47.94	<0.001
<i>M. septendecim</i> (total)	10	160.53	<0.001	1	7.85	0.009	10	201.11	<0.001
<i>M. septendecim</i> males	10	77.33	<0.001	1	2.51	0.115	10	107.55	<0.001
<i>M. septendecim</i> females	10	66.28	<0.001	1	6.09	0.01	10	67.27	<0.001
<i>M. septendecula</i> (total)	10	77.87	<0.001	1	6.83	0.01	10	41.44	<0.001
<i>M. septendecula</i> males	10	36.54	<0.001	1	5.42	0.021	10	41.44	<0.001
<i>M. septendecula</i> females	10	43.8	<0.001	1	3.47	0.064	10	72.97	<0.001

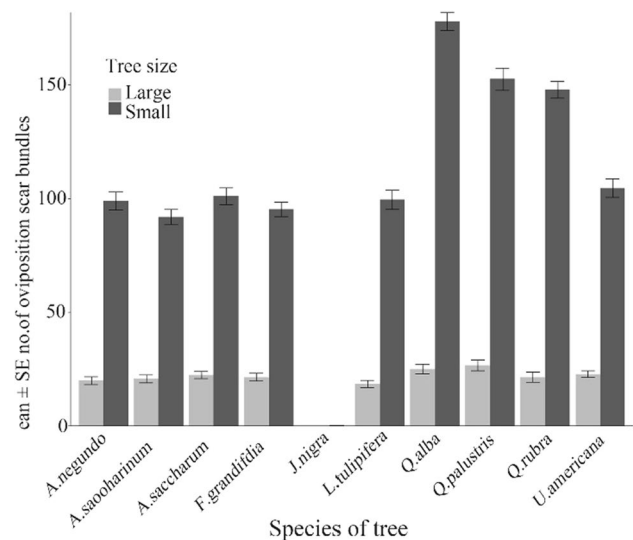
*Bolded values indicate significant differences by Scheffe post hoc test ($P < 0.05$)

**Fig. 1** Mean number of cicada emergence holes under each tree

more emergence holes than any other tree species (Table 1, Fig. 1). There were significantly more emergence holes under large trees than young trees, regardless of species (Table 1, Fig. 1).

Oviposition scar bundles

Quercus species had significantly more oviposition scar bundles than other tree species (Scheffe's post hoc test: $P < 0.001$). *J. nigra* was generally avoided by female cicadas and rarely had oviposition scar bundles (Scheffe's post hoc test: P range < 0.001). Across all tree species, small trees were preferred over large trees (Table 1). There were significantly more oviposition scar bundles on small *Quercus* trees

**Fig. 2** Mean number of oviposition scar bundles on each tree

(Table 1, Fig. 2) than on large *Quercus* trees, indicating that female cicadas preferred to oviposit on these trees.

Host trees used as chorusing centers

Abundance of the *Magicicada* species in the two life stages of trees assessed varied depending on the species of the tree (Table 1, Fig. 3a). In general, *Magicicada* preferred *Q. alba* (regardless of size) and small *F. americana* for chorusing centers (Scheffe's post hoc test: P range < 0.001 and P range < 0.001 to 0.015, respectively). The abundance of the different *Magicicada* species varied across the tree species; *M. cassini* preferred to chorus in small *Q. alba* trees (Table 1, Fig. 3b) and generally avoided *F. americana* and *J. nigra* trees (Fig. 3b). *M. septendecim* preferred to chorus in

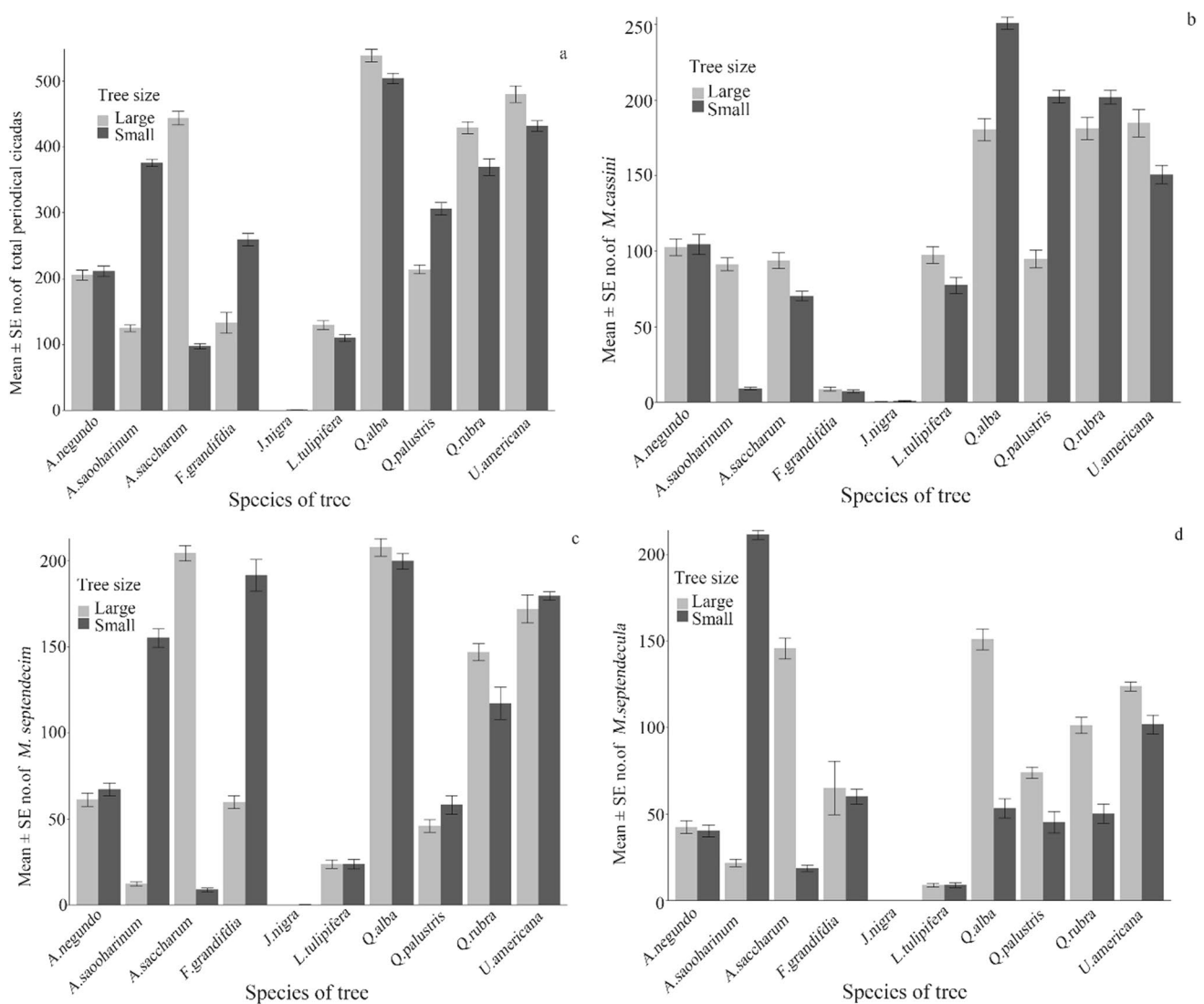


Fig. 3 Mean distribution of periodical cicadas on each tree species. Mean number of individuals of **a** all *Magicicada* species, **b** *Magicicada cassini*, **c** *M. septendecim*, and **d** *M. septendecula* on each tree species

small *F. americana* (Table 1, Fig. 3c) and avoided *L. tulipifera* and *J. nigra* (Fig. 3c). *M. septendecula* had several preferred species for chorusing centers: small *A. saccharinum*, small *F. americana*, and large *Q. alba* (Table 1, Fig. 3d) and avoided *L. tulipifera* and *J. nigra* (Fig. 3d).

Pearson's correlations between tree size (DBH) and the number of cicadas demonstrated positive or negative associations depending on the tree species (Table 2). Periodical cicadas had a strong negative correlation between tree size (DBH) and the number of cicadas with *A. saccharinum*, *F. americana*, *F. grandifolia*, and *Q. palustris* trees (Table 2), but a strong positive correlation with *A. saccharum* and *Q. rubra* (Table 2). Interestingly, there were three tree species that showed bimodality of cicada abundances in each tree size: *A. saccharinum* (Table 3, Fig. 4a), *A. saccharum* (Table 3, Fig. 4c), and *F. americana* (Table 3,

Fig. 4e). Individual *Magicicada* species abundances also showed bimodality for the same three tree species (Table 3). Correlations between individual *Magicicada* species abundance and tree size (DBH) showed bimodal distributions (Fig. 4b, d, and f). Proportions of periodical cicadas sampled in each tree size class were not statistically different (Kolmogorov–Smirnov two-sample test: $P = 0.699$, $P = 1.000$, respectively) during the beginning of the emergence when we sampled.

Cicada nymph preference

There was a significantly greater proportion of cicada nymphs on *Q. rubra* saplings than on *A. saccharum* saplings (χ^2 test: $n = 3185$, $\chi^2_{17} = 162.89$, $P < 0.001$). The home tree that the cicada egg was laid on did not significantly

Table 2 Pearson's correlations between tree size (DBH) and abundance of periodical cicadas in chorusing centers

Tree species	<i>r</i>	<i>P</i>
<i>Acer negundo</i>	0.04	0.856
<i>A. saccharinum</i>	-0.90	<0.001
<i>A. saccharum</i>	0.85	<0.001
<i>Fraxinus americana</i>	-0.77	<0.001
<i>Fagus grandifolia</i>	-0.78	<0.001
<i>Juglans nigra</i>	-0.17	0.36
<i>Liriodendron tulipifera</i>	0.41	0.026
<i>Quercus alba</i>	0.42	0.021
<i>Q. palustris</i>	-0.69	<0.001
<i>Q. rubra</i>	0.65	<0.001
<i>Sassafras albidum</i>	0.30	0.105
<i>Ulmus americana</i>	0.43	0.017

*Bolded values indicate significant differences by Scheffe post hoc test ($P < 0.05$)

influence the number of cicada nymphs on *Q. rubra* roots or *A. saccharum* roots (MANOVA: Wilk's $\lambda = 0.880$, $F = 1.027$, $P = 0.382$, error df = 15).

Discussion

Previous studies have reported two contrasting views on cicada habitat partitioning and use (Alexander and Moore 1958; Dybas and Lloyd 1962; Brown and Zuefle 2009). Alexander and Moore (1958) reported that *M. cassini* and *M. septendecim* showed no division of habitats except for local congregations due to chorusing males. However, another study done on the same brood in the same region found that *Magicicada* species partitioned space by habitat type (Dybas and Lloyd 1962). A potential reason for the contradicting reports may be related to habitat partitioning by *Magicicada* species and specific host-tree species (Clay et al. 2009; Dybas and Lloyd 1974). Tree community organization is driven by niche partitioning and trade-offs that potentially enable trees to coexist in several different types of habitats (Salas et al. 2006; Hao et al. 2007). As diversity and dominance shift in successional forests, tree host abundance also shifts, potentially changing the availability and use of

specific host trees (Flinn et al. 2018; White et al. 2018; Tuttle 2019).

Emergence holes and oviposition scar bundles

We found significantly more cicada emergence holes located beneath species of *Quercus* than any other tree species. There are several explanations regarding the proportion of emergence holes under species of *Quercus*. (1) Tree species' abundances may have biased female oviposition toward more dominant tree species. A tree species that is more common may have a higher probability of becoming a host because it is more "apparent" (Feeny 1976). *Quercus* are still a dominant species, but their dominance is quickly being replaced by other tree species (Flinn et al. 2018; White et al. 2018; Tuttle 2019). Previous studies suggest that periodical cicadas frequented *Quercus* species (Marlatt 1907; Clay et al. 2009) so their persistence in the forest community may be the cause of their "apparency" to the periodical cicadas. Furthermore, Clay et al. (2009) found that frequency of a tree species was not correlated with oviposition rates. (2) The greater number of emergence holes below *Quercus* species may be due to a higher survival rate of cicada nymphs on *Quercus*. Cicada nymphs preferred *Quercus* over *Acer*, regardless of their home tree species. *Quercus* species allocate nonstructural carbohydrates to belowground storage when their aboveground tissues are injured (Perkovich and Ward 2021a, b); the excess sugars in root tissues may provide an advantage for young nymphs. Alternatively, *Quercus* saplings may have greater root biomass, sustaining a greater number of nymphs and improving their survival. (3) In a forest transitioning from *Quercus* dominance to *Acer* dominance (Flinn et al. 2018), it is possible that *Quercus* species are older (larger) or that they are located on less-disturbed soil. Succession is a type of disturbance that often alters soil biology and characteristics (Sadaka and Ponge 2003; Hofmeister et al. 2004), which may have significant impacts on cicada nymphs (Robinson et al. 2007; Moriyama and Numata 2015), especially during the 17 years of *Magicicada* nymphal development. (4) A final consideration is that the higher cicada abundances on *Quercus* may be caused by a variable not directly linked to the *Quercus*. For example, previous literature suggests that shade is necessary for chimney construction (Howard 1911; Andrews 1955). It is possible

Table 3 Hartigan's dip test for bimodality of periodical cicada species' abundance

	<i>A. saccharinum</i>		<i>A. saccharum</i>		<i>F. americana</i>	
	<i>D</i>	<i>P</i>	<i>D</i>	<i>P</i>	<i>D</i>	<i>P</i>
<i>M. cassini</i>	0.123	<0.001	0.094	<0.001	0.090	0.041
<i>M. septendecim</i>	0.151	<0.001	0.182	<0.001	0.203	<0.001
<i>M. septendecula</i>	0.207	<0.001	0.141	<0.001	0.102	0.010

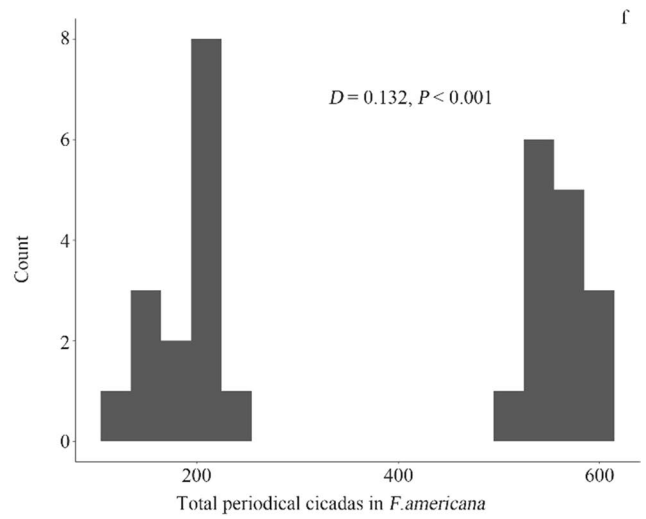
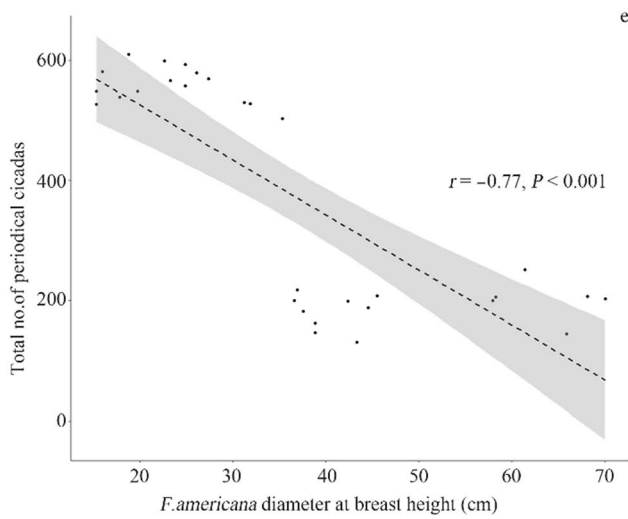
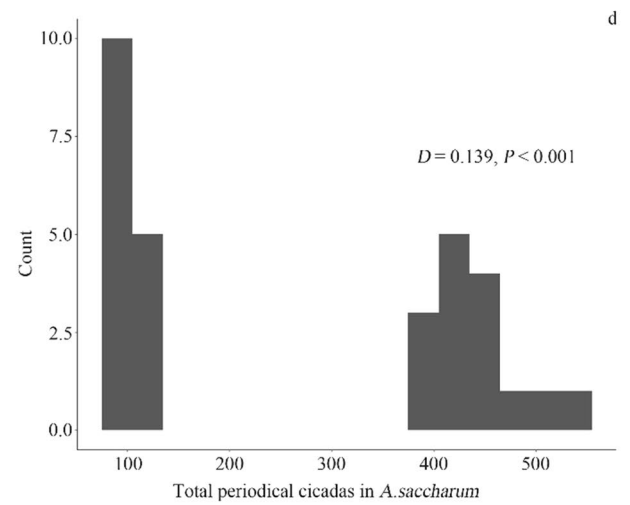
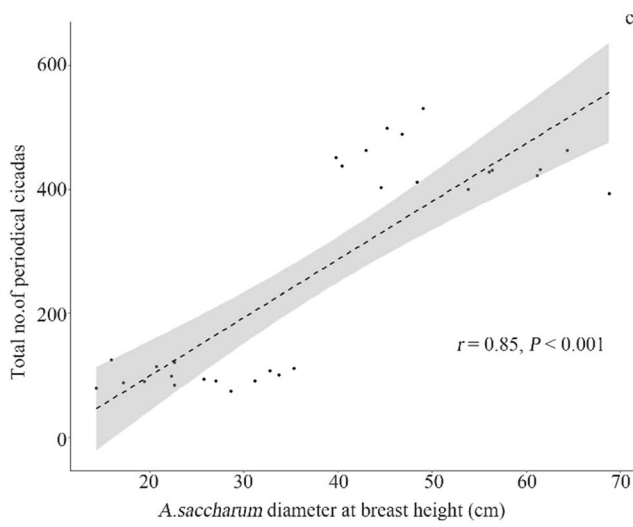
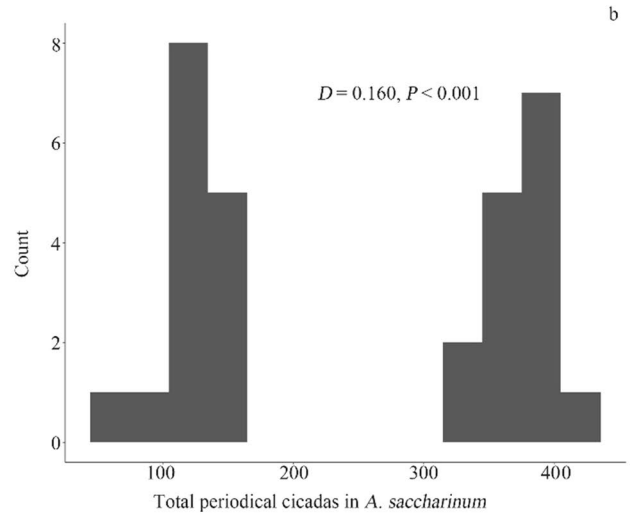
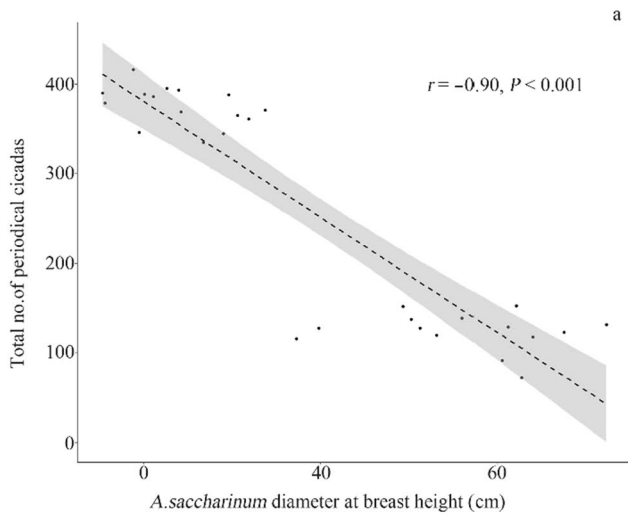


Fig. 4 Bimodal distributions of periodical cicada abundance and correlations with tree size. **a** Abundance of *Magicicada* individuals on *A. saccharinum*, **b** correlation between number of cicadas on *A. saccharinum* and tree diameter at breast height, **c** abundance of *Magicicada* individuals on *A. saccharum*, **d** correlation between number of cicadas on *A. saccharum* and tree diameter at breast height, **e** abundance of *Magicicada* individuals on *F. americana*, and **f** correlation between number of cicadas on *F. americana* and tree diameter at breast height

that large *Quercus* provide a greater amount of shade, which was not examined.

The random arrangement of tree species within a forest (Hao et al. 2007) may be causing the co-occurrence of periodical cicada species within a forest. However, the three periodical cicada species differ in their abundances, indicating preference differences. All three species of periodical cicada were present within the same forested area, but we found that *M. cassini* chorusing was more abundant in small *Q. alba* trees and was never in *F. grandifolia* and *J. nigra*. *M. septendecim* chorusing was more abundant in small *F. americana* and not found in *L. tulipifera* and *J. nigra*. *M. septendecula* chorused in multiple tree species and life stages (small *A. saccharinum*, small *F. americana*, and large *Q. alba*), but not in *L. tulipifera* and *J. nigra*. In earlier studies, the habitats of the three species often overlapped in disturbed areas (Lloyd and White 1976; White 1980), whereas we found periodical cicadas inhabited the same general areas (our personal observation). However, we found differences in their use of host tree. Chorusing centers of *M. cassini* were more abundant on *Quercus* species and chorusing centers of *M. septendecim* were more abundant on *F. americana*, as was also documented by previous studies (Dybas and Lloyd 1962; Lloyd and White 1976). Dybas and Lloyd (1974) found *M. septendecim* to be less host-specific than *M. septendecula*. Interestingly, we found *M. septendecula* had multiple chorusing host species (Fig. 3d). Our study was performed at one site to understand host-tree use and partitioning among the periodical cicada species, whereas Dybas and Lloyd (1974) may have captured variations between upland and lowland environment types. Alternatively, the difference in abundance on specific hosts of *M. septendecim* and *M. septendecula* recorded in previous studies may be due to a breakdown in reproductive isolation caused by succession (White 1980). Reproductive isolation of periodical cicada species due to habitat use can be disrupted by disturbance (White 1980). In disturbed areas, all three species may compete for host trees for chorusing and oviposition (Lloyd and White 1980; White 1980; Lloyd 1984). We observed a greater diversity of acceptable tree hosts for chorusing *M. septendecula*, which may be due to this competition. *M. septendecula* is considered the rarer of the three species and often suffers more severely from competition (Lloyd and White 1983).

Previous studies suggested that *J. nigra* was a common host species for periodical cicadas (e.g., Dybas and Lloyd 1974; Lloyd and White 1976), yet we found that in the 30 *J. nigra* trees we sampled, there were generally no signs of periodical cicada activity. In fact, we only found 12 emergence holes under *J. nigra* and no chorusing centers in any of the sampled trees. We are unable to determine whether *J. nigra* is avoided or whether there is a lower probability of these trees in the environment. However, we were able to find a sufficient abundance of this species in the area. If *J. nigra* is a common host, the periodical cicadas would have been able to locate this host-tree species as well. Several other studies have also found *J. nigra* to be less utilized than previously reported (see Brown and Zuefle 2009; Clay et al. 2009). Brown and Zuefle (2009) found that cicadas were more likely to oviposit on native plants. However, when the native *J. nigra* was compared to the invasive *J. regia*, they found a preference for the invasive over the native. It is plausible that as *J. nigra* population densities decline due to replacement by *Acer* and *Fagus* (Moser et al. 2020), periodical cicadas are adapting and using different hosts.

Periodical cicadas demonstrate a lek mating system where females disperse from the chorusing center to mate (Yang 2006). Karban (1984) found that nymph mortality rates increased nearest to chorusing centers and that females often leave chorusing centers when ready to oviposit (Karbon 1984; Williams and Simon 1995). Therefore, *ex post facto* scars left behind from ovipositional attempts have been repeatedly used to determine the use of tree hosts for oviposition (e.g., White 1980; Yang 2006; Clay et al. 2009). Using this method, we found significantly more oviposition scar bundles on *Quercus* species than any other tree species, indicating *Quercus* species are commonly used for oviposition. We cannot definitively determine which *Magicicada* species were responsible for the oviposition scars, but we can confirm that more female cicadas attempted to oviposition on *Quercus* species.

Ontogeny of tree host in periodical cicada use and resource partitioning

We found that emergence holes are more common below large *Quercus* trees than small trees of this genus or on any other tree species; however, oviposition scar bundles are more common on small *Quercus* than on large *Quercus* or on any other tree species. Considering the 17-year life cycle, ovipositing on small (i.e., younger) trees could be an evolutionary adaptation for female cicadas to ensure that the tree will survive while the next generation of cicadas develop underground. However, younger trees do not always have a high survival rate (Lines et al. 2010). There may be other characteristics associated with tree ontogeny such as defense mechanisms (Barton and Boege 2017; Ochoa-Lopez et al.

2020) and physiology (Erbilgin and Colgan 2012; Voitsek-hovskaja and Tyutereva 2015) that make them more susceptible to periodical cicada oviposition. Furthermore, adult chorusing in small rather than large trees is dependent on the tree species.

Species-specific ontogenetic changes in tree-host usage may be a mechanism that promotes partitioning of resources between the periodical cicada species in disturbed areas such as successional forests. We would then expect to find a positive correlation between tree size (DBH) and the number of cicadas because larger trees have more space. Analyzing individual tree species, we found that some tree species had a positive correlation between tree size and cicada abundance (Table 2). However, several tree species had a negative correlation between tree size and cicada abundance (*A. saccharinum*, *F. americana*, *F. grandifolia*, and *Q. palustris*). Tree size can be positively correlated to tree life stage (Fulton 1999; Oladi 2005; Liu et al. 2018), so that older trees are larger in size. In contrast, cicada use of younger trees may be due to ontogenetic changes in tree phytochemistry (Donaldson et al. 2006; Holeski et al. 2012). Multiple tree species have been shown to increase concentrations of phenolic glycosides, an insect herbivore deterrent, as the tree ages (Boeckler et al. 2011; Holeski et al. 2012). Additionally, periodical cicadas have been shown to significantly upregulate defense production in some tree species with increasing age (Perkovich and Ward 2022).

Even more perplexing than the tree species-dependent correlations between tree size and periodical cicada density is the bimodality of periodical cicada abundance in the different ontogenetic stages of *A. saccharinum*, *A. saccharum*, and *F. americana*. Considering the correlations (Fig. 4), there are two groupings of cicada population sizes at different tree sizes. The two clusters in the cicada abundance and tree size (DBH) correlations (Fig. 4) were congruent with the bimodal peaks in the abundance histograms (Fig. 4), suggesting that the bimodal peaks are due to exclusive uses of two different tree sizes. There are several scenarios that could explain this bimodal distribution. (1) The growth rates of plants, including many trees species, demonstrate a Gompertz distribution due to accelerated growth rates during intermediate developmental stages (Weiner 2004). Individual trees could potentially spend a smaller amount of time in the intermediate part of the Gompertz curve, where growth is rapid (Shi et al. 2017). Bimodal distributions could have been formed by sampling biases. Gompertz and related distributions of plant growth rates such as Michaelis–Menten curves explain how two size classes could exist with few intermediate samples (Weiner 2004; Shi et al. 2017; Abdelhady and Amer 2021). However, there is a roughly continuous sampling of trees from 15 to 70 cm (Fig. 4a), indicating no bias of tree size that could be causing the periodical cicadas' bimodal distribution. (2)

Large trees could hold more periodical cicadas than small trees. However, we found a negative correlation between cicada abundance and tree size (DBH) for *A. saccharinum* and *F. americana*. (3) There could be a physiological or behavioral mechanism that is causing the bimodal distribution. For example, *M. neotredecim* was distinguished as its own species by female preferences for different chorusing pitches (Marshall and Cooley 2000). More research is needed to determine if behaviors are occurring that could be causing the bimodality of life-stage preference in these three tree species (i.e., *A. saccharinum*, *A. saccharum*, and *F. americana*). If there is, in fact, a selective mechanism behind the use of different-sized trees for chorusing, then it could be a potential mechanism for speciation within the *Magicalicada* genus. However, this scenario is highly speculative and has not been proposed for this group of insects.

Conclusions

We found that *Quercus* trees are commonly used by periodical cicadas throughout their life cycle; nymphs (emergence holes), adults (chorusing centers) and for oviposition (oviposition scar bundles). As *Quercus* populations decline in the Appalachian forests (Radcliffe et al. 2021), periodical cicadas will need to tolerate and/or adapt to the new environments. Recent studies further suggest that urbanization of Appalachian forests is disrupting the 17-year life cycle of periodical cicadas (Beasley et al. 2017). Beasley et al. (2017) found that periodical cicadas from urban areas were larger than those from forested settings, indicating that periodical cicadas may be able to adapt to changing environments, but the long-term consequences of these adaptations are yet unknown. Other members of the cicada family are being used as bioindicators to analyze ecophysiological responses of cicadas to climate change (Moriyama and Numata 2019). Periodical cicadas may offer scientists an opportunity to study long-term effects of habitat and climate change due to their unique longevity.

Our results and discussion are strictly based on a snapshot of the beginning of periodical cicada emergence. Protandry and differences in budburst of varying tree species can change the dynamics of insects and plant hosts over time (Toji et al. 2020). Additionally, a male bias may have also occurred because males are more active flyers (Dybas and Lloyd 1974; Oberdörster and Grant 2007). Furthermore, changes in periodical cicada behavior reported previously could be a consequence of different methodologies or different sampling locations. The main point of this study was to analyze how periodical cicada species used different tree species in a successional forest. If environments are changing, then the conditions during previous studies cannot be replicated. However, our results add to the numerous other

studies that suggest changes in periodical cicada use of tree species (e.g., Clay et al. 2009; Cooley et al. 2013). In our discussion, we were careful to note possible differences in methods and sampling area that may account for results that differ from those of older studies. However, we also reported important new observations of high abundances and avoidances of tree hosts (mainly *J. nigra*). The changes of tree-host use and partitioning may produce further insight about the ability of periodical cicadas to adapt to a changing environment.

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