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Advances in the Evolution and Ecology of 13- and 17-Year Periodical Cicadas

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Abstract

Apart from model organisms, 13- and 17-year periodical cicadas (Hemiptera: Cicadidae: *Magicicada*) are among the most studied insects in evolution and ecology. They are attractive subjects because they predictably emerge in large numbers; have a complex biogeography shaped by both spatial and temporal isolation; and include three largely sympatric, parallel species groups that are, in a sense, evolutionary replicates. *Magicicada* are also relatively easy to capture and manipulate, and their spectacular, synchronized mass emergences facilitate outreach and citizen science opportunities. Since the last major review, studies of *Magicicada* have revealed insights into reproductive character displacement and the nature of species boundaries, provided additional examples of allochronic speciation, found evidence for repeated and parallel (but noncontemporaneous) evolution of 13- and 17-year life cycles, quantified the amount and direction of gene flow through time, revealed phylogeographic patterning resulting from paleoclimate change, examined the timing of juvenile development, and created hypotheses for the evolution of life-cycle control and the future effects of climate change on *Magicicada* life cycles. New ecological studies have supported and questioned the role of prime numbers in *Magicicada* ecology and evolution, found bidirectional shifts in population size over generations, quantified the contribution of *Magicicada* to nutrient flow in forest ecosystems, and examined behavioral and biochemical interactions between *Magicicada* and their fungal parasites and bacterial endosymbionts.

INTRODUCTION

Periodical: an organism with a synchronized emergence and a fixed time from egg to adult of *k* years, where $k > 1$ (9, 54)

Truly periodical organisms, where adults emerge at a particular location only once in a set number of years and not at any other time, are rare and fascinating (e.g., 54, 57, 58, 118). The most well-known periodical insects are the seven species of North American periodical cicadas in the genus *Magicicada*; in addition, in northeast India, the World Cup cicada *Chremistica ribhoi*, traditionally known as the Niangtaser, emerges every four years, coinciding with the football (soccer) World Cup (51), and in Fiji, the Nanai, *Raiateana knowlesi*, has a perfectly periodical eight-year cycle (36, 146). *Magicicada*, Nanai, and Niangtaser were prized as food, ornaments, and/or gifts by indigenous peoples long before scientists took notice of them (36, 50, 71, 146).

Magicicada have earned a worldwide following due to their spectacular, recklessly theatrical emergences in tremendous numbers, their gentle nature, and their bright red eyes. Their popularity makes *Magicicada* an excellent flagship taxon for public outreach and citizen science projects (3, 19, 20, 30, 73) (see the sidebar titled Crowdsourcing as a Valuable Tool and the Related Resources). Scientists have been fascinated by their biology, and large numbers of *Magicicada* papers have been published, including in disciplines not covered in this review but as varied as nanofabrication of hydrophobic and bactericidal surfaces (125) and entomophagy (81).

In the last major review of *Magicicada*, Williams & Simon (155) summarized periodical cicada ecology and evolution, including juvenile development, emergence, xylem feeding, habitat

CROWDSOURCING AS A VALUABLE TOOL

As early as 1834, Gideon B. Smith used what today would be called crowdsourcing to solicit records of cicada emergences from postmasters, editors, and the general public (72). Marlatt's (97) 1907 maps made use of data from Smith, agricultural agents, and similar crowdsourcing efforts (20). Simon's (128) 1988 revision of the Marlatt maps solicited and gathered information from magazine and newspaper articles, postcards, telephone calls to agricultural extension agents, field work, museum records, older literature, and notes in the Cooperative Plant Pest Report/Cooperative Economic Insect Report. These records were at the county level only and thus poorly distinguished low- versus high-density records and off-cycle stragglers (98). Recent next-generation maps have focused on GPS point data and include crowdsourced efforts as well as verification of perimeters and odd localities by trained experts (e.g., 19, 20, 22, 27, 30, 73). One unexpected outcome of this effort was the discovery of more disjunct populations than were previously known (20). The first internet-enabled crowdsourcing efforts were carried out via email messages; later efforts made use of web pages and forms designed to be filled out at a computer. Records collected by these means were hard to verify and sometimes hard to interpret. As powerful mobile technology became ubiquitous, the next generation of crowdsourcing emerged in the form of the Cicada Safari App, which allows users to upload photos or short videos to provide verification of their records. This app is freely available in the app stores of most major mobile operating systems. Raup et al. (124) used data from the app and weather stations to demonstrate how to track patterns of cicada emergence.

BROODS

Periodical cicadas are named according to their year of emergence or brood. All cicadas emerging in 2012 are members of Brood I, those emerging in 2013 are members of Brood II, those emerging in 2014 are members of Brood III, and so on. Broods were numbered by various authors and then renumbered (to clear up confusion) to the Roman numeral system that we currently use (96). The 17-year broods were numbered I–XIII, while the 13-year broods were numbered XVIII–XXX (**Figure 1*b*,*c***). The year 1893 was chosen arbitrarily for Broods I and XVIII. Multiple independently derived populations that emerge in the same year all belong to a single brood. Some broods do not exist, either because they never formed or because they became extinct. For example, New England Brood XI (not included in **Figure 1**) went extinct in the mid-twentieth century (29, 95). Brood VII from upstate New York has significantly shrunk in geographic extent during the past half-century and may be nearing extinction (28, 46, 119, 120). The existence of various other broods recorded in the past (97) is difficult to determine because off-year straggler individuals can emerge four years early or late or, less commonly, one year early or late (20, 98, 100). There are currently 12 recognized extant broods of 17-year cicadas and three extant broods of 13-year cicadas (**Figure 1*b*,*c***). Most broods contain all three *Magicicada* species groups.

preferences, oviposition behavior, host-plant damage, predation, fungal infections, the evolution of long life and periodicity, and the evolution of the year classes (known as broods; see the sidebar titled Broods). In this review, we update developments in our understanding of *Magicicada* evolution and ecology over the past 27 years.

The complex life cycle of *Magicicada* can best be explained in pictures (**Figure 1**). *Magicicada* occurs only in the United States east of the Great Plains and contains species with both 13- and 17-year life cycles (**Figure 1*a***), roughly occupying the northeastern and southeastern deciduous forest biomes, respectively. The seven named species (**Figure 1*b***) fall into three species groups: Decim, Cassini, and Decula (155). These three groups are morphologically, behaviorally, and genetically distinct (136) but appear identical to predators (156). Decula and Cassini have two species each (one of each life cycle), whereas Decim has three species (one 17-year and two 13-year species) (31, 99, 132). All three species groups overlap geographically to a large extent within both 13- and 17-year broods (**Figure 1*c***; see the sidebar titled Broods). Cassini and Decula split from each other approximately 2.5 Mya, and their ancestor is estimated to have split from the ancestor of Decim approximately 3.9 Mya (45, 136) (**Figure 1*b***). Decim, Cassini, and Decula are largely prezygotically isolated from each other by their different calling and courtship songs (23, 38), although occasional interspecific mating pairs are found (155), and forced mating among them results in viable eggs that hatch (44, 153). Although *Magicicada* emerge synchronously at any given location within just a few days of each other, *Magicicada* juveniles (nymphs) grow at different rates underground (93, 154) (**Figure 1*d***). This is discussed in more detail when we describe the evolution of the life cycle.

Broods: year classes of periodical cicadas

Species group: a subgeneric clade or lineage of sister species; there are three species groups in *Magicicada*: Decim, Cassini, and Decula

EVOLUTION OF *MAGICICADA*

Seven Species of *Magicicada*

Alexander & Moore (2) named six species of *Magicicada*. Lloyd & Dybas (84) countered that, with no known morphological or behavioral differences between the 13- and 17-year sibling pairs, the six entities should be considered three species. Later, Martin & Simon (107) found a genetic discontinuity in Decim-group 13-year cicadas between northern and southern parts of the range (**Figure 1*a***) of what was then considered to be an entirely *Magicicada tredecim* population. This

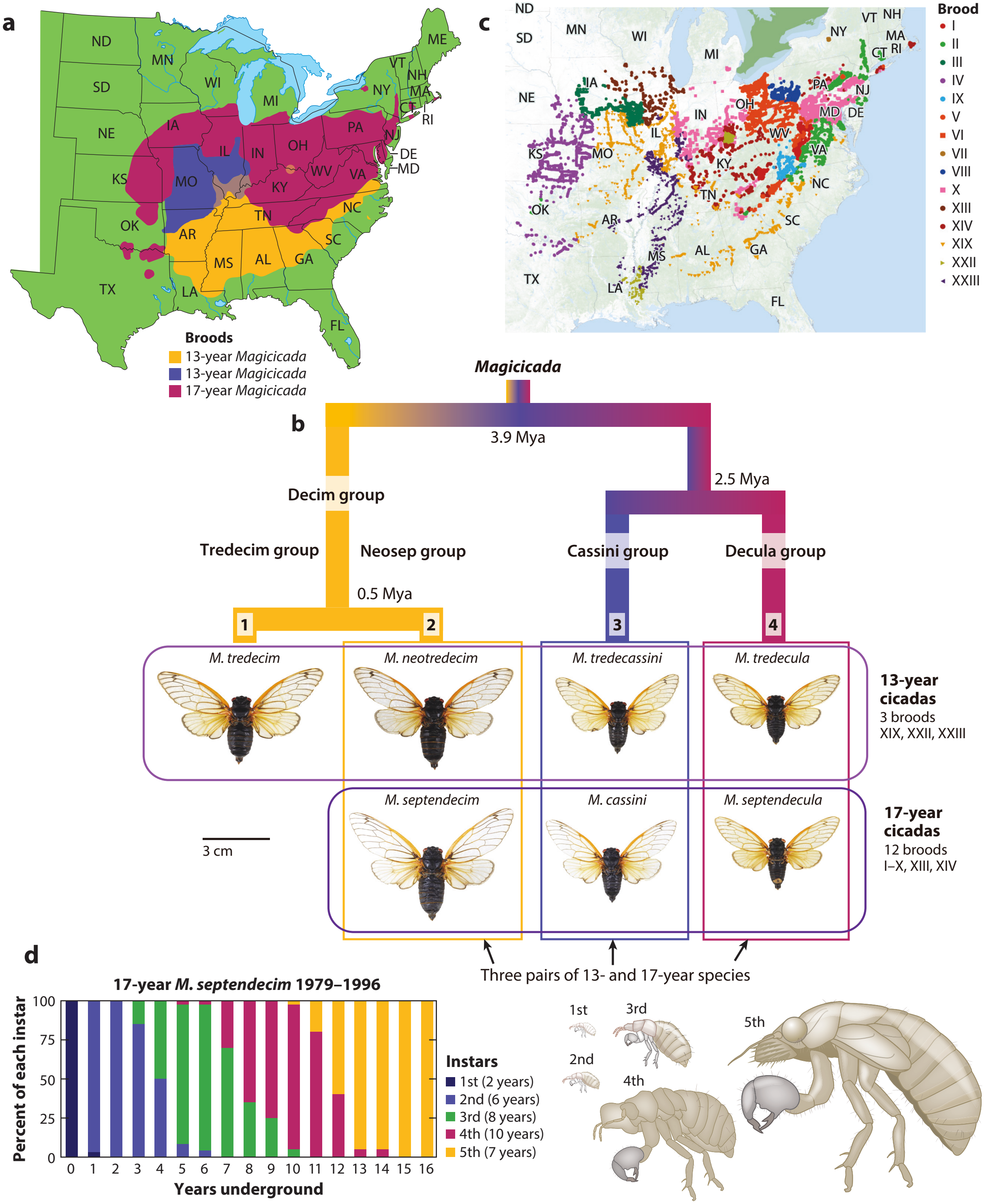

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Figure 1 (*Figure appears on preceding page*)

Magicicada basic biology. (*a*) Approximate distribution of 17-year cicadas (*magenta*) and all 13-year cicadas, including *Magicicada neotredecim* (*purple*) and *Magicicada tredecim* (*gold*). Both *Magicicada tredecassini* and *Magicicada tredecula* are found throughout the ranges of *M. tredecim* and *M. neotredecim*. Overlaps between *M. tredecim* and *M. neotredecim* (*brown*) and between all 17-year cicadas and *M. tredecim*, *M. tredecassini*, and *M. tredecula* (*orange circle* at the OH–KY boundary) are also shown. Note that 17-year species in Texas and Oklahoma are exclusively *Magicicada cassini*, and those in Massachusetts and far-upstate New York are exclusively *Magicicada septendecim*. Note also that many areas inside the distributional range do not host periodical cicadas due to habitat degradation. (*b*) Species lineages, life cycles, numbers of broods, divergence times, and phylogenetic relationships of the four reproductively isolated lineages—① Tre, ② Neosep, ③ Cassini, and ④ Decula—and the seven named species of *Magicicada*. Panel *b* modified from Reference 45 under CC BY 4.0. (*c*) Verified presence records of 13- and 17-year broods, based on data collected in the field by Simon laboratory personnel and collaborators over the past 40 years and stored at **https://cicadas.uconn.edu**. Absence of records should not necessarily be interpreted as absence of cicadas. (*d*) Distribution of the five nymphal instars over 17 years in a single population of 17-year cicadas from Southington, Connecticut, showing the number of years over which each instar can be found. Data taken from Reference 93.

discontinuity was seen in abdominal color (2, 67, 107, 132), allozyme frequencies (85, 107), wing morphometrics (129), and mitochondrial DNA (mtDNA) (107, 108, 132). Marshall & Cooley (99) used behavior (male song pitch and female song preferences) and abdomen-color evidence to show that the southern and northern lineages overlapped in sympatry (see the brown area in **Figure 1*a***) and were reproductively isolated, evidence that led them to describe the northern form as a new 13-year species, *Magicicada neotredecim*. Cooley et al. (31) demonstrated that there was a correspondence among the song, the abdomen color, and the mitochondrial genotypes by examining individual mating pairs collected in the *M. tredecim*–*M. neotredecim* overlap zone.

Species Phylogeny

Molecular phylogenetic analyses imply that all extant lineages shared a common ancestor approximately 3.9 Mya (136). The Cassini and Decula species groups diverged from each other 2.5 Mya (the earliest Pleistocene). Later in the Pleistocene, Decim-lineage cicadas (now called *M. tredecim* or Tre) diverged from the common ancestor of *Magicicada septendecim* and *M. neotredecim* (Neosep lineage) approximately 500,000 years ago. Similarly, genomic-scale molecular phylogenetic analyses by Sota and colleagues (35, 45, 67, 136) consistently recovered four reproductively isolated lineages within *Magicicada* (not the three, six, or seven suggested by previous authors) (**Figures 1*b*** and **2*a***). Koyama et al. (67) and Fujisawa et al. (45) found no evidence of introgressive hybridization among any of the four lineages, despite that fact that interlineage mating pairs (mostly a Cassini male and a Decim female) are occasionally found in the field (83), and the eggs of hybrid crosses between pairs of all species lineages do hatch (44, 153). *Magicicada tredecim* is more genetically divergent from its sister taxon (Neosep) than any of the other three 13–17-year pairs (45, 136).

The two life cycles within each of the Neosep, Cassini, and Decula lineages show only a limited genomic sequence divergence despite the clear spatial and temporal segregation between 13- and 17-year cicada sister clades. Although the sister taxa within each of these three lineages differ in life cycle, there are no separate monophyletic 13- versus 17-year clades found via maximum-likelihood phylogenetic analyses, even using genomic-scale sequence data (35, 45, 67, 136) (**Figure 2*a***). In contrast, a coalescent simulation analysis of the transcriptome data found that present-day 13- and 17-year broods represented separate monophyletic groups (or, alternatively, the divergence of a monophyletic group of all 13-year broods from a 17-year brood), but that gene flow has occurred between the 13- and 17-year brood pairs within each species group (not including *M. tredecim*) after the 13–17-year splits 200,000–100,000 years ago before the Last Glacial Maximum (LGM) (45) (**Figure 2*b***). This extensive gene flow explains why maximum-likelihood phylogenetic analysis was not able to distinguish separate monophyletic 13- and 17-year groups within the Neosep, Cassini, and Decula lineages.

Monophyletic: having a single evolutionary origin; a monophyletic group contains all living descendants of a common ancestor

Coalescent simulation analysis: a type of phylogenetic analysis that attempts to recover species history rather than gene history by tracing inheritance backward in time to a common ancestor

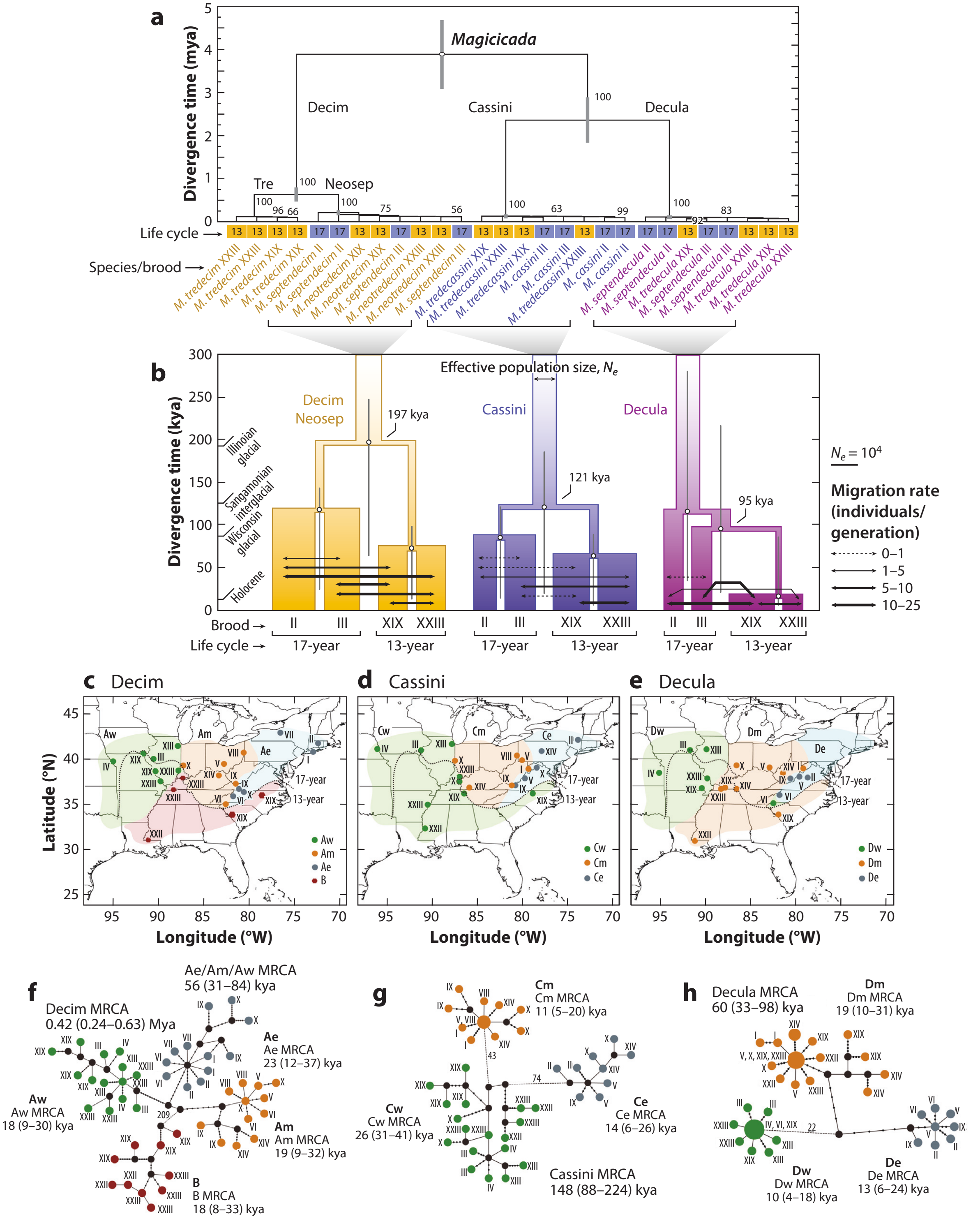

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Figure 2 (*Figure appears on preceding page*)

Relationships among and demographic history of periodical cicada broods. (*a*) Maximum-likelihood tree (dated) showing the relationships among individuals from representative broods. Numerals show bootstrap percentages of node recovery (shown only when >50%). (*b*) Demographic history of broods in each species lineage reconstructed using fastsimcoal2 (42). Divergence of broods is shown with divergence times and effective population sizes (N_e; width of column). Vertical bars for divergence times show 95% confidence intervals. Estimated gene flow (N_eM) between broods is shown by arrows of different thicknesses with an embedded key. (*c–e*) Geographic distribution of samples of (*c*) Decim, (*d*) Cassini, and (*e*) Decula. (*f–h*) Median-joining network of mitogenomic haplotypes in (*f*) Decim, (*g*) Cassini, and (*h*) Decula, with western haplotype region in green, middle haplotype region in pale orange, eastern haplotype region in light blue, and southern haplotype region in light red. Solid circles are colored to match the colors of the phylogeographic regions. Brood numbers are indicated by Roman numerals next to the circles. The broken line indicates the boundary between 13- and 17-year cicadas. A indicates Neosep and includes Ae, Am, and Aw; B indicates Tre; C indicates Cassini and includes Ce, Cm, and Cw; and D indicates Decula and includes De, Dm, and Dw. For the networks (*bottom*), colored circles (matching the map colors) represent haplotypes, and black circles represent missing haplotypes that were not observed. Solid lines between each of two linked haplotypes correspond to one mutation. Cases in which there are 20 mutations or fewer are represented by solid lines with small black dots. Cases in which there are more than 20 mutations are indicated by dashed lines with numerals. The area of the circle is proportional to the number of haplotypes. Panels *a* and *b* modified from Reference 45 under CC BY 4.0; panels *c–h* modified from Reference 35 under CC BY-NC 4.0.

The Species Question in Periodical Cicadas

Butlin et al. (10), synthesizing previous literature on speciation mechanisms, promoted a speciation framework consisting of three stages of indeterminate length: (*a*) initiation of reproductive isolation, (*b*) strengthening and increased differentiation across each of the genomes, and (*c*) completion of reproductive isolation. Differentiation can occur along a continuum from complete allopatry (no range overlap; no gene flow) through parapatry (adjacency; some degree of gene flow) to sympatry (range overlap; no gene flow despite high opportunity for gene flow). Based on the evidence, Tre, Neosep, Cassini, and Decula species lineages each appear to be in the third stage; the degree of gene flow prior to reaching this stage is unclear, but the data surrounding the relationships between the most recent 13–17-year species pairs provide one plausible scenario (discussed below).

Evidence that *M. tredecim* is in the completion stage of speciation comes from the strong reproductive character displacement in calling song pitch that takes place when *M. tredecim* individuals are confronted with sympatric or parapatric *M. neotredecim* (18, 99). Experimental matings suggest that undisplaced *M. neotredecim* outside the contact zone may not be fully prezygotically isolated from *M. tredecim* and *M. septendecim* (26), although they never encounter these taxa in time or space. However, experiments in other organisms suggest that reproductive character displacement could arise after less than a dozen generations of secondary contact (55). This is a definite possibility in periodical cicadas given that *M. tredecim* and undisplaced *M. neotredecim* and *M. septendecim* satisfy the requirement for character displacement to evolve, i.e., that differences in calling song pitch already exist and, presumably, hybrids are less fit (99).

The three newest 13–17-year pairs within Neosep, Cassini, and Decula, respectively (**Figures 1*b*** and **2*a***), appear to be in the strengthening phase (the second stage) of reproductive isolation; genomic analyses suggest that there has been considerable recent gene flow between the members of each pair (45, 67). This gene flow was thought to be limited in scope because 13- and 17-year life cycles can only meet once every 221 years, and geographic overlap is currently small. However, off-cycle emergences could increase the frequency of gene flow, and past overlap could have been greater (although there is no evidence for or against this). This isolation, enforced by mismatched cycles and currently limited geographic overlap, may well be facilitating a gradual increase in genomic divergence, even though phylogenomic analysis cannot yet detect it (45, 67). The question arises of whether we should recommend retaining the seven species of *Magicicada* that we have now, or reduce them to four species (*M. tredecim*, *Magicicada* "decim" *Magicicada*

Reproductive character displacement: divergence in the mean trait value of a mate-recognition character that is caused by competitive natural selection

Endosymbiont: an organism (e.g., a bacterium, fungus, or alga) that resides inside a host organism

Jump: a collective term for either early or late emergences

cassini, and *Magicicada* "decula"). Given that (*a*) there is currently very little, if any, contact between the recent 13–17-year pairs, (*b*) this is not likely to change; (*c*) many well-recognized species (past and present) have reticulate phylogenetic histories (94); and (*d*) the species names are useful in understanding and discussing *Magicicada* evolutionary relationships, we suggest retaining the seven current species names. More important than what we call them is understanding how they evolved.

Phylogeography

Phylogeographic studies of the seven *Magicicada* species have helped elucidate their post-Pleistocene history (35, 136). Sota et al. (136) used a combination of nuclear and mitochondrial genes to create a phylogeny for *Magicicada*; as is typical of recent divergences, the information in the tip clades was almost exclusively supplied by mtDNA. These data suggest that the Neosep (mtDNA lineage A), Cassini (mtDNA lineage C), and Decula (mtDNA lineage D) species lineages are divided into eastern (east of the Appalachian Mountains; e), middle (just west of the Appalachian Mountains; m), and western (Mississippi Valley and eastern edge of the Great Plains; w) segments. No *M. tredecim* have e, m, or w haplotypes; all are members of a separate southern mtDNA haplotype lineage B (**Figure 2*c***). The southern distribution of *M. tredecim* is now also occupied by western Cassini (*Magicicada tredecassini*) and middle and western Decula (*Magicicada tredecula*) (**Figure 2*c*–*e***). These biogeographic subdivisions, similar to those seen in other North American animals and plants (134), were verified and clarified by Du et al. (35), who sequenced whole mitogenomes for 125 of the same specimens (**Figure 2*c*–*h***). Interestingly, data from maternally inherited *Magicicada Hodgkinia* endosymbiont variants from *M. septendecim* reflected exactly the same geographic patterns as the mtDNA (11, supplemental figure S2).

The most recent common ancestor of the e, m, and w haplotypes in each phylogeographic lineage existed 26–10 Kya (i.e., from the LGM to the beginning of the Holocene) (**Figure 2*b*–*h***). Patterns of phylogenetic relatedness and gene flow among e versus m versus w differ among Decim, Cassini, and Decula lineages (35, figures 3 and 4) (**Figure 2*b***). Demographic inference with mitogenome data indicated that a population bottleneck occurred during the last glacial period, followed by rapid population expansion from approximately 10,000 years ago in all lineages except *M. tredecim* (35). Thus, it is supposed that non-Tre lineages were confined to three refugia in the LGM, with nothing resembling the present-day brood structure. Present-day broods (**Figure 1*c***) were created after the migration from the Pleistocene refugia, likely after the establishment of forests roughly resembling the current northeastern and southeastern deciduous forest biomes approximately 10,000 years ago. We can envision the broods being stamped out as if by a cookie cutter from the e, m, and w haplotypes (albeit not all at the same time because the process is hypothesized to be triggered by localized climate anomalies) (2, 20, 39, 84, 99, 101, 155).

Simon et al. (132) pointed out that the two largest 13-year broods, XIX and XXIII, are separated in time by four years; both broods contain *M. neotredecim* (in the north) and *M. tredecim* (in the south). Brood XXIII is largely embedded within Brood XIX in the Mississippi River Valley. They proposed two hypotheses for the existence of multiple species in each brood, both based on entrainment into pre-existing *M. tredecim*: (*a*) A single *M. neotredecim* population was formed from *M. septendecim* by a four-year life-cycle switch (or repeated four-year life-cycle switches over many generations) in the northern Mississippi Valley in the current range of the combined Broods XIX plus XXIII, and later, the current Broods XIX and XXIII split throughout their Mississippi Valley range (from Louisiana to Illinois); or (*b*) two separate populations of *M. neotredecim* were formed at different times by four-year jumps from *M. septendecim* in the northern Mississippi Valley and joined the pre-existing Broods XIX and XXIII to the south, independently, by entrainment. Brood XXII was independently derived from Brood XXIII by a one-year straggling event around the

LGM (35). The coalescent simulation by Fujisawa et al. (45) suggests that the process described in hypothesis *a* (*M. neotredecim* forming prior to Broods XIX and XXIII splitting) occurred in the Neosep pair of the Decim species group. Hypothesis *a* also seems to describe the Cassini species group because all *M. tredecassini* that co-occur with *M. tredecim* are derived from the Cw mtDNA haplotype lineage. In contrast, hypothesis *b* seems to better describe patterns in the Decula species group. Decula that co-occur with *M. tredecim* are derived both from Dw and from Dm haplotype lineages (35). Thus, 13-year Cassini and Decula may have entered Broods XIX and XXIII (already occupied by *M. tredecim*) in different ways (i.e., Cassini from one area but Decula from two areas). Multiple species could have been entrained into the southern brood via four-year early and late emergences (see the section titled Life Cycle Shifts by Four-Year Jumps), aided by natural selection due to predator satiation and longer growing seasons.

Polyphyletic Broods

Studies by Du et al. (35), Sota et al. (136), and Cooley et al. (20) suggest that many 17-year broods are polyphyletic (i.e., have mixtures of two or more of the e, m, and w mitochondrial haplotypes). Using the cookie cutter analogy, sometimes the cutter straddled the boundary between e and m haplotypes (but, interestingly, not w).

Traditionally, the brood concept has been more of a bookkeeping tool than an intentional statement about evolutionary history (96). Broods are merely year classes (see the sidebar titled Broods). Many broods have odd disjunct populations far from their main ranges (19, 20, 30, 131). Some of these disjuncts seem best explained as having formed independently due to regional climatic events and as emerging on a schedule that is coincidentally synchronic with another population, despite the lack of any recent shared evolutionary history with that population. The Long Island populations (131) are the best examples of such independent brood formation events (20). In contrast, other disjuncts may be best explained as relicts of a once geographically larger brood. For example, the disjunct population of 13-year Brood XXII in northern Kentucky and southern Ohio is surrounded completely by 17-year cicadas. It could not have formed by life-cycle switching from its neighbors because it contains individuals that are genetically, morphologically, and behaviorally identical to *M. tredecim*, rather than to *M. neotredecim* or *M. septendecim*; this disjunct population seems best explained as a relict of a once-larger distribution of 13-year broods that are currently found far downriver in the Ohio and Mississippi river valleys (73).

The Origin of *Magicicada*

Magicicada has no known close relatives in North America; the geographically closest relative is a species collected in Guatemala that is known only from two specimens collected in the late nineteenth century (115). *Magicicada* were originally, incorrectly, thought to be allied to the North American genus *Okanagana* and its European sister genus *Tibicina* in the tribe Tibicinini (subfamily Tibicininae) (116). Superficially, all three genera look alike, with similarly sized, slim, black bodies; orange wing veins; and exposed timbals (singing organs). Inspection of other *Magicicada* morphological characteristics convinced Moulds (116) that *Magicicada* were instead closely allied to genera in the *Abricta* complex from Australia, Guatemala, Mauritius, and the Afrotropics (Cicadettinae: Taphurini) (115). Molecular analysis based on a combination of nuclear and mitochondrial genes (105) confirmed the relationship between *Magicicada* and the *Abricta* complex and strongly supported the groups' inclusion in the larger worldwide Lamotialnini (now 18 genera), rather than in Taphurini. The former Taphurini subtribe (Tryellina) containing these genera was elevated to become the separate tribe Lamotialnini (105).

EVOLUTIONARY ECOLOGY

Behavior

Magicicada males gather and sing in chorusing trees in large groups (155). Species in this genus have unusually complex courtship sequences, involving multiple species-specific songs and tactile behaviors (23, 38). Males engage in call–fly behavior, alternating short flights with bouts of calling. As pair formation progresses, males use different mating songs and stop signaling once they begin copulating; copulation lasts for several hours (24). Like some New Zealand (37, 79) and Australian (49, 122) cicadas, *Magicicada* females indicate receptivity by responding to males with sharp wing flicks timed to cues in the male song. Female wing flick signals have been found in *Okanagana* (17) and many New Zealand cicadas (56, 102, 104, 106). The discovery of wing-flick signaling allowed detailed examination of mate choice in periodical cicada aggregations. The discovery of reproductive character displacement in calling song pitch, where *M. neotredecim* is sympatric with *M. tredecim*, and the general unresponsiveness of females of either species to males of the other (99) demonstrated that female periodical cicadas have, at minimum, the ability to exercise mate choice favoring conspecifics. Karban (61) demonstrated a correlation between body size and mating success in *M. cassini*, but Cooley & Marshall (24) found little evidence for this. *Magicicada* appear to exercise threshold-based choice, with the threshold being species identity. While *Magicicada* aggregations have long been described as having the qualities of mating leks (1, 2), to date, females have not been demonstrated to choose among conspecific males as in traditional leks.

Wing-flick signaling in female *Magicicada* is a potent indicator of readiness to mate, and thus, the signaling system is ripe for exploitation. Courting males are in danger of being usurped by males who may land nearby and to whom the receptive female may respond. As a defense, courting males produce acoustical interference sounds that jam the signals of their potential rivals, who, receiving no response, leave and search elsewhere (23). *Magicicada* wing-flick signals are also exploited by parasites (see below).

Fungal Parasites and Signal Exploitation

While periodicity and predator satiation have been invoked as characteristics that limit opportunities for specialist predators (84), this is not the case for parasites with long resting spores, like some fungi. *Magicicada* nymphs from all seven species can be infected by the entomopathogenic fungus *Massospora cicadina* (Peck) (Zygomycota: Entomophthorales) (135). *Massospora* is cicada specific and has 11 described species known to infect at least 15 cicada species across three Cicadidae subfamilies; *Mas. cicadina* is found exclusively in *Magicicada* species (90). Its sister species is *Massospora diceroproctae* (found in *Diceroprocta*), and sister to this pair is *Massospora levispora* (found in *Okanagana* and *Platypedia*). *Massospora tettigatis* (found in *Tettigades*) is sister to the entire group. These fungal relationships mirror the phylogenetic relationships of the host cicadas. The other eight *Massospora* species have yet to be studied phylogenetically (90).

As they emerge from the ground, *Magicicada* fifth-instar nymphs encounter *Mas. cicadina* fungal spores in the soil. The life cycle of *Massospora* includes two life stages. In the first stage, resting spores germinate, fill the cicada abdomen with hyphae and conidia, and sterilize but do not kill the host cicadas. In the second stage, resting spores are produced and dispersed. The fungus produces chemicals that presumably alter the behavior of the cicada. *Massospora cicadina* produces the psychoactive amphetamine cathinone (identical to the plant-derived substance in Khat leaves, *Catha edulis*, chewed in the Middle East by humans), which is hypothesized to be involved in behavioral takeover (7). The fungus modifies the behavior of conidia-infected male *Magicicada* males so that they produce female-like wing-flick receptivity signals (23) in addition to their calling songs, making them extremely attractive to other cicada males in the chorus and increasing the odds of conidiospore transmission (25). While this host–parasite system has many similarities to other examples in the zombie insect literature, it is unusual in that it involves active transmission by a living host, rather than passive transmission by a host that has succumbed to the parasite (87).

The only other known example of predators or parasites exploiting cicada wing-flick signals is the aggressively mimetic Australian katydid *Chlorobalius leucoviridis*, which imitates female wing-flick signals to lure in male cicadas and eat them (102). North American *Okanagana rimosa* are infected by the acoustically orienting sarcophagid fly parasitoid *Emblemasoma auditrix* (66, 78, 126), but no similar parasitoid exploitations have been discovered in *Magicicada*, even though *M. cassini* have been experimentally infected with *E. auditrix* (77).

Predator foolhardy: an organism that has less-than-enthusiastic escape behavior

Stragglers: individual cicadas that emerge off cycle, generally four (or, less often, one) years before or after an emergence

Quasicycling: a repeated pattern that is less than evenly spaced

Periodicity and Prime Numbers

The change from *Magicicada* nymph to adult is age based rather than size based; adults appear periodically in any given location once every 13 or 17 years (and occasionally after 9 or 21 years; see the sections titled Life Cycle Shifts by Four-Year Jumps and Straggling). The evolution of periodicity in *Magicicada* is inextricably linked to the evolution of synchronicity, long life cycle, large population size, complex courtship, and their predator foolhardy behavior. These traits have been hypothesized to strengthen over time through natural selection feedback loops (109). This combination of traits underlies the spectacular, dense, and dramatic emergences characteristic of *Magicicada* and allows them to persist in the face of predators (83, 155). Cicadas emerging in small numbers or off cycle (stragglers) usually do not survive to reproduce (60, 82, 156). We summarize and synthesize hypotheses on the evolution of *Magicicada* life cycles in **Supplemental Table 1**.

Supplemental Material >

Martin & Simon (109) were the first to suggest that the switch from a size-based development strategy to an age-based strategy requires the lengthening of the life cycle. Toivonen & Fromhage (140) focused on this strategy and predicted that unstable environments favor the development of synchronous periodicity, suggesting that a periodical competitor can only invade such an environment if it has a longer life cycle, a condition that they dubbed an evolutionary ratchet (because increases are irreversible). Other mathematical modelers suggest that both 13 and 17 are prime numbers, and that this is related to the evolution of periodicity in organisms with long life cycles (e.g., 34, 47, 139, 147, 165). Webb (147) suggested that the 13- and 17-year prime-numbered life cycles arise as resonances of emergences with two- and three-year quasicycling predators. Nonspecialist quasicycling vertebrate predators have differential reproduction every two or three years, which, according to the model, favors periodical prey with prime-numbered life cycles. Imperfect predator cycling is a requirement because no periodical predators are known (e.g., all periodical insects are herbivores; 54). This idea is elegant mathematically but begs for further modeling to accommodate these additional factors: (*a*) the abundance and cycling of below-ground predators and (*b*) the importance of four-year early and late life-cycle switches, which sometimes produce non-prime-numbered (e.g., 9- or 21-year) life cycles. Other explanations are needed to understand life-cycle evolution in the majority of periodical insects that have two-year life cycles and appear in even versus odd years in nonoverlapping broods (54), as well as the evolution of periodical cicadas in India (51) and Fiji (146) that have four- and eight-year periodicity, respectively.

Yoshimura et al. (165) followed up on the frequently suggested idea (e.g., 32, 33, 164) that prime-numbered life cycles are favored in *Magicicada* due to selection against nonprime hybrid life cycles during the Pleistocene because prime cycles have fewer opportunities for hybridizing with other cycles, which is assumed to be maladaptive. However, the advantage of prime cycles in avoiding hybridization holds only if all populations with different cycle lengths start at the same time (i.e., all populations are age zero at time $t = 0$), which is a special case (141). In addition, the lack of examples of individuals with the nuclear DNA of one species and the mtDNA of another, as has been observed in other hybridizing cicadas (104, 144), argues that the hybridization required for such a scenario has not occurred in *Magicicada*. In addition, more than 100 years of mapped locality observations (128) (**Figure 1*c***) suggest that the intermediate life cycles expected from hybridization do not exist and that hybridization is not involved in triggering life-cycle changes (101). Grant (48) also critiqued the idea that the 13–17-year life-cycle switches that occurred during the Pleistocene involved intermediate life cycles, given that no evidence for such life cycles has yet been discovered.

Acceleration: an early emergence

Deceleration: a late emergence

Nymphal Growth

White & Lloyd (154) established that underground nymphal growth rates are higher in warmer areas that have longer growing seasons, characteristic of regions typically occupied by 13-year cicadas. Koyama et al. (68) demonstrated that, for all three species groups, 13-year cicadas grow faster than 17-year cicadas, even those in nearby locations with similar mean annual temperatures.

Periodicity is intimately tied to the evolution of stereotypical nymphal growth timing, since all nonperiodical cicadas show variable emergence timing. The ancestors of *Magicicada* must, like all other nonperiodical cicadas, have had nymphs that grew at variable rates, such that the offspring of any one female likely emerged over a period of three or more years (**Supplemental Table 2**). Ancestral populations of *Magicicada* had to evolve fixed-length life cycles, likely in one of two ways: Either all nymphs could develop at exactly the same rate, or those that reached the fifth and final instar first could wait (but not necessarily stop growing) for laggards to catch up before emerging. Pioneering studies of growth rates of nymphs of multiple ages from multiple localities (for a review, see 155) were followed in later years by a heroic study by Maier (93), who sampled approximately 100 *M. septendecim* nymphs per year over a 17-year period at a single location in Connecticut. This comprehensive study showed that the brief first instar lasted, on average, a year or less. The second to fifth instars each had an average duration of approximately four years but with an increasingly large variance as laggards fell further and further behind. Second instars were found over a 6-year period, third instars were found over an 8-year period, fourth instars were found over a 10-year period, and fifth instars were found over a 7-year period (digging ceased after the brood emerged in the 17th year) (**Figure 1*d***). We do not know what proportion of laggard nymphs never emerged.

Supplemental Material >

Evidently, *Magicicada* do not achieve synchronization by having uniform nymphal growth rates; rather, they compensate for unequal growth rates. This compensation requires that the counting mechanism for determining emergence year be decoupled from developmental rates and cueing of transitions between nymphal instars. This decoupling is not as surprising as it seems because the timing of nymphal instars is decoupled from adult emergence in other insects (e.g., 121) and because growth rates of individuals could be influenced by many factors including variation in growth rates among genotypes, the species of host plant, patchy distribution of nutrients or sunlight for host plants, and the quality of the cicadas' bacterial endosymbionts. Periodical cicada adults vary substantially in size (127), likely as a result of the mix of fast- and slow-growing nymphs in each emergence.

Life Cycle Shifts by Four-Year Jumps

Lloyd & Dybas (84) suggested that the four large 17-year broods that overlap in mosaic fashion (sympatric only in rare instances) were derived from each other by four-year life-cycle changes. Because four-year-late emergences had not been observed, much of the subsequent literature focused on four-year-early emergences (termed accelerations), including in 13-year cicadas (103). Since that time, several four-year decelerations have been documented (e.g., 20, 92, 103), including in 13-year cicadas (100). Lloyd & Dybas (84) suggested that smaller broods that were

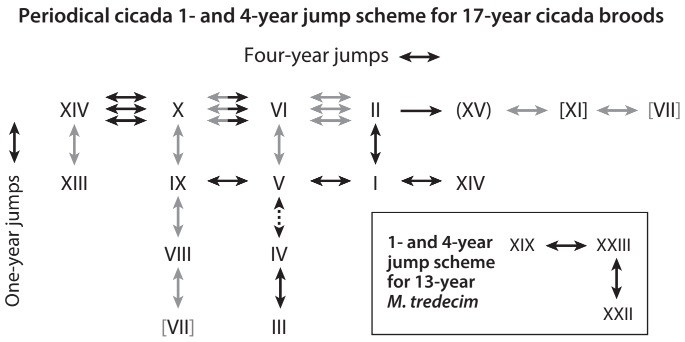

Figure 3

Formal scheme for deriving all 17-year periodical cicada broods from the postulated ancestor, Brood XIV, by a combination of four-year and one-year changes in the life cycle. Broods for which there are doubtful or no historical records are excluded. Double-headed arrows have been added to show derivation of broods from both early- and late-emerging populations, depending on climatic conditions. Triple arrows indicate the possibility of continuous migration through time between geographically overlapping or adjacent populations over generations. Black arrows indicate high-probability jumps. Gray arrows indicate life-cycle jumps that are rare or do not occur today but may have occurred in the past. Dashed arrows indicate derivations that are doubtful or impossible due to lack of geographic continuity. Brood XV is in parentheses because it is not self-reproducing at present but may have been in the past. Broods in square black brackets are extinct, and broods in square gray brackets are nearly extinct. One-year-early and one-year-late emergences are less commonly observed and contain many fewer individuals than are observed for four-year accelerations or decelerations of the life cycle. Figure based on information updated from References 20, 84, and 131.

nonoverlapping were derived from others by a one-year change in the life cycle. Cooley et al. (20) refined this scheme, introducing the term four- or one-year jumps to refer to temporary life-cycle acceleration or deceleration by which broods of the same life cycle could be derived from each other. We further update the scheme in this review in line with our current thinking (**Figure 3**). It has been suggested that periodicity and four-year jumps evolved prior to the common ancestor of all extant broods because all four species lineages exhibit these behaviors, suggesting shared genetic architecture (135).

The prevalence of four-year (early and late) stragglers suggests that they have some relationship to permanent shifts between 13- and 17-year life cycles. Lloyd & Dybas (84) suggested that the 13-year life cycle evolved prior to the 17-year life cycle because other cicadas have shorter life cycles and that 17-year cicadas were derived from 13-year cicadas during cooler climatic conditions that created shorter growing seasons and required more time for development. Permanent four-year life-cycle shortening would be adaptive if it decreased competition among underground nymphs of the source brood (assuming that not all individuals participate in the four-year shift) (85, 132), while permanent four-year extensions of the life cycle would be adaptive if they fostered periodicity by ensuring that slower-growing nymphs have time to catch up with enough of their brood mates to satiate predators (109).

Straggling

Straggling events are generally one- or four-year changes in timing and are temporary. Straggling may involve only a few cicadas, or it may involve enough individuals to allow chorusing of the off-cycle cicadas (39, 100, 131). The hypothesis of periodical cicada brood formation within a life cycle via mass numbers of cicadas undergoing temporary life-cycle jumps (**Figure 3**) does not explicitly address the possibility that brood boundaries may be somewhat dynamic (69) and that one brood may gradually replace another over time via a process involving successive waves of small numbers of stragglers (70, 75, 86). Kritsky (69) used historical records to demonstrate that this replacement has been occurring recently. It is a fair—and almost unresolvable—question whether straggling events, large or small, that occur in the same areas in multiple generations represent new instances of straggling or are the offspring of successfully reproducing stragglers from previous cicada generations. The phenomenon of shadow brooding, in which straggler populations appear not to be self-maintaining, but rather are continuously replenished by new stragglers before they can be driven extinct (21, 86, 98), may in fact be another route to permanent brood formation if such shadow broods eventually reach a tipping point where they are able to persist and perhaps even replace their parent broods (5, 76, 89).

Canalization: another name for genetic assimilation

The persistence of straggling is difficult to understand. For periodical cicada populations to persist, they must be of sufficient densities to satiate predators; put another way, a quorum, not a majority, is required for periodical cicadas to achieve permanence, where a quorum is defined as the minimum number of cicadas required to satiate predators. Thus, periodical cicadas are expected to face strong selection to avoid off-cycle emergences. At the same time, if cicadas do compete for resources, then periodical cicadas that have the ability to switch to a different schedule may be favored by selection; thus, straggling may open new avenues for dispersal and emigration in these species. How periodical cicadas will maintain their periodicity in the face of climate change is an open question; four-year-early straggling events may possibly become more common as growing seasons lengthen in any given area, and with repetition, these events could lead to canalization of alternative life cycles, i.e., 13-year from 17-year cicadas and 9-year from 13-year cicadas (84, 99, 132, 148).

The Ecology of Broods

In any given woodlot, overlaps between broods appear rare or small in extent (22). Theoretical work by Blackwood and colleagues (5, 76, 89) predicts that overlap may only be ephemeral. Coexistence of two broods has been observed only when year classes are separated by at least four years (155). Most cases of overlapping broods are mosaics (**Figure 1*c***), with only rare instances in which members of different broods occupy the same individual trees (130). Several straggling models include different assumptions, but all come to the conclusion that a combination of predator satiation and/or competition between nymphs of different broods is sufficient to prevent brood overlap (5, 76, 80, 89). Those individuals that emerge at a time and place that does not include at least a quorum of other cicadas are unlikely to survive predation (60) or mate successfully (117), although Karban (59) found that *Magicicada* were able to find each other and mate rapidly even at low density. Asymmetric competition between nymphs of different broods is hypothesized to favor older, more established nymphs over younger, newly established ones (85), and there are data to suggest that forests with overlapping broods four years apart can support more cicada biomass (130). Although this hypothesis suggests that broods remain stable once formed, historical records suggest that brood boundaries can shrink or grow due to temporal migration between adjacent or overlapping broods (69, 74, 138).

Control of the Life Cycle

Although control of timing of the day of emergence is relatively well understood to be related to ground temperature (53, 124), the control of timing of the year of emergence is not. The 13–17-year life-cycle length difference clearly has a genetic basis because it persists under similar environmental conditions at the geographic boundary between 13- and 17-year life cycles. The genetic life-cycle difference probably includes control of juvenile growth or development rate, which appears to be faster in 13-year than in 17-year cicadas under the same climatic conditions (68). The different growth rates and resultant time required to reach some threshold body size (e.g., critical body weight) may interact with some internal year-counting mechanism to determine the timing of emergence to adulthood.

Given the difficulty of crossing experiments that involve raising offspring to maturity, comparison of genomic sequences between life cycles is a practical way to explore the genetic basis of the life-cycle difference. However, previous analysis with approximately 2,600 orthologous transcriptome sequences from all seven species showed that the sequence differences were extremely small between 13- and 17-year species within species groups, and an attempt to find candidate genes for the life-cycle differences failed (44). A thorough comparison of whole genome sequences between 13- and 17-year species within species groups and exploration of possible epigenetic controls are needed to reveal factors responsible for the control of life-cycle length.

Plasticity: a plastic trait is one that can respond to the environment in which it finds itself

Genetic assimilation: the transition from a plastic trait to a genetic trait gradually over time due to a selective advantage

It is unknown how periodical cicadas count 13 or 17 years, although they seem to be able to keep track of at least a few years by counting host seasonal cycles as they feed on plant root xylem fluid (63). They may keep track of a relatively small group of years or, alternatively, a long sequence of years using some epigenetic mechanism such as a DNA methylation time counter, as has been suggested for long-lived periodical bamboos (166).

Hayes (52) suggested that periodical cicadas might count years in intervals of four as $13 = 1 + 4 \times 3$ and $17 = 1 + 4 \times 4$, but later in his paper, he cautioned that this hypothesis is weakened by the fact that nymphs grow at variable rates underground. In support of this hypothesis, each nymphal stage has an average duration of four years (93), and the number four is important in *Magicicada* biology, since it represents the difference between the two life cycles and is involved in the four-year jump phenomenon. Perhaps, then, it is not a coincidence that the only two other known instances of periodical cicadas have life-cycle lengths of four (51) and eight (146) years. If, in *Magicicada*, the decision whether to emerge is made at the end of each four-year period (after reaching the fifth instar and becoming mature or competent to emerge), then we suggest that laggard or incompetent nymphs will wait for the next window so that synchronized emergence can occur once every four years. Waiting four years between emergences has the selective advantage of allowing more cicadas to catch up (109) so that the subsequent emergence can satiate predators. If periodical cicadas do have a four-year clock and genetic variation, as well as environmental variation (plasticity), in juvenile growth rate, then the mechanisms of the synchronized emergence, as well as the four-year jumps and life-cycle canalization via genetic assimilation (84, 99, 132, 148), could be explained (see the Future Issues).

THE ECOLOGY OF PERIODICAL CICADAS

High Abundance, Herbivory, and Tree Growth

Periodical cicadas are one of the primary herbivores of eastern deciduous forests, with densities exceeding 300 individuals/m^2 in continuous forest (40) and 600 individuals/m^2 in fertilized areas (62). Despite their potential as foundation species, the relationship between periodical cicadas and their host trees is still not completely understood, in part because of the difficulties of accurately determining below-ground nymph density. Since cicada nymphs move little underground, ovipositional scars in twigs have been used to estimate the number of underground nymphs, although Smits et al. (133) found that egg-nest density was not a predictor of below-ground nymph density, at least on a small scale. Cook & Holt (16) found no relationship between egg nests and tree growth during the emergence year or the following two years. In contrast, Clay et al. (14, 15) found that oviposition scars were correlated with reduced radial tree growth in the emergence year and the year following. In a follow-up study, Speer et al. (137) found that three of five tree species examined still showed increased growth five years after the emergence. Yang & Karban (162) found that, at low densities, periodical cicada nymphs have little effect on tree growth, while at higher densities, feeding nymphs reduce growth. Koenig & Liebhold (64) examined the relationship between cicadas and oak tree growth at a regional scale. Oaks in counties with cicadas grew approximately 4% less during the emergence year than trees in counties without cicadas, and a 13- or 17-year pattern in tree growth was detected.

Experimental manipulations have failed to confirm the conclusion that feeding cicada nymphs or oviposition damage cause reductions in tree growth or performance. In one study, trees covered with netting (to reduce cicada oviposition) did not show measurable increases in growth or reproduction compared to trees with no nets (15, 43). In another study, Yang & Karban (163) found that additions of cicada nymphs did not significantly reduce the growth of sycamore saplings.

Resource Pulses and Forest Ecosystems

Periodical cicada nymphs and adults feed on root and shoot xylem, respectively, and employ bacterial endosymbionts to synthesize essential amino acids from this relatively nutrient-poor food source (112); thus, during their lifetimes, periodical cicadas convert relatively inaccessible or unavailable resources into forms more readily accessible to other organisms. Many species of *Magicicada* predators increase (leave more offspring) during emergence years, and the resources that cicadas provide enable some predator species to remain common for several years following an emergence (65). Predators consume many cicadas, but since periodical cicadas emerge in satiating densities, many cicadas simply die and fall to the ground and decay. Whatever the way in which cicadas die, the nutrients that they collected over many years and over a large area are deposited onto a relatively small area during a brief period of time (149). Yang (157) found that cicada carcasses following an emergence represent a stored pulse of resources that leads to increases in the biomass of both bacteria and fungi in the soil. Cicada carcasses can also represent important pulses of nutrients, particularly phosphorus, to aquatic habitats that border forests (123). Macroarthropod decomposers also experience increases in the days following the emergence (158). These decomposers cause available nitrogen in the soil to rise approximately 2–3-fold for several months following adult disappearance. Fertilization by cicada carcasses has significant, localized effects on plants. For example, sycamores that were experimentally fertilized by dead adult cicadas grew approximately 10% more than controls in the year following the emergence, and this effect persisted for at least two years (163). However, the net effects are sometimes difficult to characterize; American bellflowers in plots fertilized with dead cicadas grew 61% larger and produced seeds that were 9% larger than controls (157, 161), but fertilized bellflowers were themselves preferred by mammalian herbivores and lost 78% more biomass than controls (160).

Host Plant–Cicada Interactions

Although ecologists have made considerable progress toward understanding plant defenses in general, the defenses employed by trees against cicada feeding are largely unexplored. Before induced resistance (e.g., to insect herbivory or oviposition) became a well-accepted phenomenon, White (151) and White & Lloyd (152) documented that many trees responded to cicada eggs by overgrowing them with callus tissue, smothering them with gums, or infusing them with secondary chemicals. Because cicadas have little ability to move as nymphs, reducing cicada egg survival likely translates into long-lasting benefits to trees. In the years since this early work, there has been little progress toward understanding defenses of trees against cicada nymphs, although elucidating this interaction would surely repay the effort; *Magicicada* spend the vast majority of their lives feeding on trees, and yet we know almost nothing about this process, the hurdles that they must overcome to be successful, or the ways that trees protect themselves against these superabundant herbivores.

Host plants are sources of information as well as food for periodical cicadas and their symbionts. Hosts appear to provide information that adults use to make decisions about where to oviposit (150). Female cicadas choose sunlit branches to place their eggs, positioning their relatively immobile offspring for the next 13 or 17 years (159). Sunlit branches presumably indicate sites with rapid growth, supplying feeding nymphs with better nutrition. Growth conditions and growth rates vary considerably for nymphs of similar age in the same forest or orchard (154). Over the course of 13 or 17 years, conditions change; trees that were excellent hosts for cicada nymphs when they were first selected may become less suitable with time (62). This degradation of reliable information over time may be one factor that limits the duration of cicada life spans.

Cicada nymphs probably use information from their hosts as a means of counting years (2, 84). Nymphs that were fed on trees that had been experimentally induced to go through two seasonal cycles of leaf abscission and leaf production in a single year emerged in 16 years (17 seasonal cycles) (63). Nymphs that were reared for their last nine months under various lab conditions nevertheless emerged at the proper time with the rest of their cohort (41). These results suggest that the cues and clock that nymphs use to time their emergence are set at least nine months before. This suggestion is supported by the observation that *Magicicada* nymph eye color changes from white to red over a similar time frame prior to emergence (8, 91).

Magicicada Bacterial Endosymbionts

All cicadas feed on xylem, a nutrient-poor food source. As in all animals with nutrient-deficient diets, essential amino acids must be supplied by symbionts. Cicadas have two specialized coprimary bacterial endosymbionts (112). *Sulcia* is found in most Auchenorrhyncha (the hemipteran suborder containing cicadas, planthoppers, and relatives) (114, 142). *Sulcia* produces eight essential amino acids. *Sulcia*'s coprimary endosymbiont partner, *Hodgkinia*, is restricted to cicadas and generally synthesizes two amino acids and vitamin B_{12} (112, 113). Genome sequences of *Sulcia* and *Hodgkinia* have been published for cicadas from three cicada subfamilies (13, 112, 143). *Sulcia* is conserved in size and essential amino acid production capabilities and evolves slowly. *Hodgkinia* appears to evolve rapidly and affords evolutionary innovation. It was first discovered by McCutcheon et al. (112, 113) in 2009 from the cicada *Diceroprocta semicincta* (Cicadinae). The second *Hodgkinia* sequenced came from the cicada *Tettigades ulnaria*. It had only a single *Hodgkinia* genome, but its relative *Tettigades undata* possessed two cytologically distinct but codependent lineages that together contributed the necessary amino acid subunits (143). This splitting of one lineage into two had never been seen in any other bacterial endosymbiont. Other Tettigades species were examined and found to possess anywhere from one to eight separate *Hodgkinia* lineages (88). Even more unexpected, the *Hodgkinia* of *Magicicada* (Cicadettinae) was broken into >27 pieces with a total genome size of >1,000 kb, reminiscent of the complexity found in plant mitochondria and suggesting lineage splitting followed by complementary degradation (13).

Campbell et al. (13) proposed that the genome degradation, found in all seven species of *Magicicada Hodgkinia*, might be related to the long life cycle. Their argument was that reduced host-level selection during nymphal stages with, presumably, lower energy demands than adult stages provides a much greater opportunity for *Hodgkinia* splitting events. Among *Magicicada* species, *Hodgkinia* lineage splitting has a long history, with some *Hodgkinia* gene lineages being shared by all seven species and even by some of *Magicicada*'s relatives in Australia (12, 13). Campbell et al. (12) found that *Magicicada Hodgkinia* were much more fragmented than originally calculated and that this extreme fragmentation put an added burden on maternal transmission of endosymbionts, suggesting that the fragmentation was maladaptive (11), as had been previously suspected (143). This burden is believed be an illustration of Muller's Ratchet, where asexual reproduction leads the symbionts down an evolutionary rabbit hole from which there is no escape (4, 111), but emerging evidence suggests that mutation rate itself may also contribute to genome degradation (6, 145). Degradation of *Hodgkinia* is believed to have enabled a takeover of the role of *Hodgkinia* by fungal endosymbionts in the genus *Ophiocordyceps* (110) that evolved multiple times from fungal parasites of cicada nymphs. *Magicicada*, however, is not known to be infected by *Ophiocordyceps*, but it may be a prime candidate for infection in the future given the massive fragmentation of its *Hodgkinia* endosymbionts.

SUMMARY POINTS

1. *Magicicada*'s awe-inspiring life history is unique among insects and appreciated by both scientists and nonscientists.
2. Periodical cicada populations are divided into year classes (broods) that, although remarkably stable in distribution, are dynamic over time and space and experience gene flow via adult emergence four years early or late.
3. *Magicicada* contains four monophyletic lineages; three of these lineages demonstrate nonsynchronic parallel divergence into 13- and 17-year life cycles with a history of gene flow between the 13- and 17-year pairs.
4. Reproductive character displacement in two 13-year *Magicicada* species indicates selection against gene flow between two of the deepest diverging extant lineages.
5. Periodical cicadas are divided into eastern (e), middle (m), and western (w) mitochondrial haplotype lineages; *Magicicada tredecim* exists as a single southern (s) monophyletic lineage and is not involved in this e, m, and w pattern.
6. Nymphal growth is uneven in rate among individuals and decoupled from emergence timing.
7. The genetic machinery for four-year jumps in life-cycle length evolved before the diversification of *Magicicada* and is key to understanding the evolution of life-cycle control in this lineage; these jumps add flexibility to an otherwise rigid life history.
8. Our understanding of the importance of prime numbers for periodical cicadas would benefit from modeling studies incorporating increased biological realism (including four-year-early and four-year-late emergences).
9. Periodical cicadas provide important pulsed resources for forest ecosystems.
10. The fungal parasite *Massospora* changes *Magicicada* behavior and may play a role in controlling population density.
11. Two specialized bacterial endosymbionts provide *Magicicada* with all of their essential amino acids; endosymbiont chromosomal duplication and fragmentation is extreme in *Magicicada* and is not seen outside cicadas. The phylogeographic pattern of the *Magicicada* endosymbiont *Hodgkinia* parallels the e, m, and w pattern revealed by *Magicicada* mitochondria (both are maternally inherited and rapidly evolving).

FUTURE ISSUES

1. How do plants defend against cicadas?
2. Does competition between broods prevent spatial overlap of broods?
3. How is the life-cycle length controlled, and how do periodical cicadas count years? What genes, regulatory sequences, or epigenetic controls are involved?
4. What is the mechanism for plastic four-year jumps resulting in brood shifts, and can permanent life-cycle switches take place by genetic assimilation starting from a four-year jump?
5. How will climate change affect life-cycle evolution and populations of *Magicicada* in the future?
6. How can we incorporate increased biological realism into mathematical models for the evolution of *Magicicada* life cycles?
7. How do endosymbionts and parasites (especially *Massospora*) influence *Magicicada* population density and interactions with predators?
8. What limits cicada population size and survival? Do *Magicicada* exhibit any special adaptations that enhance their survival at low densities?
9. What proportion of periodical cicadas die due to developmental failure during the juvenile stages? Do some laggards never emerge? Do nymphs grow during the winter?

DISCLOSURE STATEMENT

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Supplemental Material >

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Created by Aaron Kane using data from https://cicadas.uconn.edu.

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Errata

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