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AUTHOR(S):

Sota, Teiji

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Life-cycle control of 13- and 17-year periodical cicadas: A hypothesis and its implication in the evolutionary process

Teiji Sota

Department of Zoology, Graduate School of Science, Kyoto University, Kyoto, Japan

Correspondence
Teiji Sota, Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto, 606-8502, Japan.
Email: sota.teiji.4e@kyoto-u.ac.jp

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Abstract

Periodical cicadas of the genus *Magicicada* exhibit a spectacular life-cycle phenomenon, with periodic mass emergence being observed every 13 or 17 years in the eastern United States. It is entirely unclear how their periodical life cycles are controlled. Here, I review previous knowledge and hypotheses about *Magicicada* life cycles and propose an integrated hypothesis of the life-cycle control mechanism, which includes critical body weight for adult metamorphosis, an internal 4-year clock, associated 4-year gate in $4 \times n$ years of age for the timing of the metamorphosis decision, and genetic differences in growth rates between 13- and 17-year cicada nymphs (the former is faster). If the last (fifth) instar nymphs reach critical body weight in any of the 4-year gates (8, 12, 16, and 20 years of age, but not other years), they prepare for adult eclosion in the following year. The proposed hypothesis can explain the synchronized emergence of cicadas with varying growth trajectories in scheduled years (13 or 17 years of age) and the off-schedule emergence of some cicadas in 4 years earlier or later than the scheduled year, owing to their phenotypic plasticity that arises in response to large variations in the realized growth rate. The proposed hypothesis can also explain how evolutionary life-cycle shifts between 13- and 17-year cycles occur through phenotypic plasticity and selection on growth rate during climatic changes. It also facilitates understanding of the evolutionary mechanism of *Maigicicada*, which contains three species groups that are parallelly diverged into 13- and 17-year life cycles.

KEYWORDS

biological clock, developmental plasticity, evolutionary history, genetic differences, parallel evolution

1 | INTRODUCTION

Long (>2 years), periodical, semelparous life cycles of organisms, represented by bamboos (Janzen, 1976; Zheng et al., 2020) and periodical cicadas of the genus *Magicicada*

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(Simon et al., 2022), are remarkable life-history phenomena. In addition to these two representative organisms, two cicadas with 4- and 8-year cycles (Simon et al., 2022), one millipede group with an 8-year cycle (Niijima et al., 2021), two genera of beetles with 3-, 4-, and 5-year periodical life cycles (Heliövaara et al., 1994), and a monocarpic subshrub with a 6-year cycle (Kakishima et al., 2011, 2019) are known. These periodical life cycles are highly specific among living plants and animals but pose a general question regarding how organisms precisely count time durations longer than 2 years to synchronize the timing of reproduction among individuals. The control mechanisms of such life cycles are almost entirely unknown. My review presents a hypothesis of life-cycle control in periodical cicadas of the *Magicicada*, occurring in the eastern United States. These cicadas show mass adult emergence every 13 or 17 years following their long juvenile life as nymphs in the soil. Their semelparous life cycle with long periodicity is regarded as an adaptive strategy to secure reproduction by reducing predation risk (Lloyd & Dybas, 1966a, 1966b) and to survive harsh climatic conditions during glacial periods (Cox & Carlton, 1988; Yoshimura, 1997). Recent molecular phylogenetic studies have revealed the evolutionary history of three extant species groups and seven 13- and 17-year cicada species (Du et al., 2019; Fujisawa et al., 2018; Koyama et al., 2016; Sota et al., 2013).

Several previous studies on *Magicicada* biology have been reviewed by Martin and Simon (1990), Williams and Simon (1995), and Simon et al. (2022). These reviews commonly mention that one of the most important questions remains unresolved: how do *Magicicada* control their life cycles with 13- or 17-year juvenile periods, or how do *Magicicada* nymphs count years? The apparently age-based timing of adult metamorphosis may have evolved from size-based timing determination, which may be common in nonperiodical cicadas (Yoshimura, 1997), but no theory has been proposed concerning the timing mechanism. Periodical cicadas appear to count the passing years based on the seasonally fluctuating xylem constituents (Karban et al., 2000) or soil temperature, but this enables the counting of only one annual cycle. Therefore, additional internal mechanisms likely exist to count the number of annual cycles greater than two. For counting 13 or 17 years, a scientific writer Hayes (2004) noticed that the two life cycles can be broken down as $(3 \times 4) + 1 = 13$ and $(4 \times 4) + 1 = 17$, and proposed the idea of counting with a 4-year sub-cycle, which could be repeated either three or four times, followed by a single additional year. Although he did not develop a life-cycle control hypothesis with a 4-year sub-cycle, this could be a key component of the year-counting mechanism. For the genetic basis of two life cycles, Lloyd et al. (1983) and Cox and Carlton (1991) proposed that the 4-year difference is caused by a single-locus two-allele system dominated by either a 17-year allele (Lloyd et al., 1983) or a 13-year allele (Cox & Carlton, 1991). However, circumstantial evidence that these hypotheses have relied on has been falsified (Marshall, 2001). In addition to the above ideas on year counting and genetic differences between the two life cycles, no comprehensive hypothesis has been proposed for the control mechanism of the 13- and 17-year life cycles.

In this review, I revisit previous knowledge and hypotheses about *Magicicada* life cycles and propose a hypothetical mechanism to explain the well-controlled 13- and 17-year life cycles, with the aim that hypothesis testing will promote the understanding of their life-cycle control mechanisms. Some components of my hypothesis are mentioned in Simon et al. (2022), to which I have contributed. However, the hypothesis in an integrated form has not yet been presented. A testable hypothesis is essential for determining the direction of studies to resolve the question of life-cycle control. The life-cycle control hypothesis presented here should be able to explain how to count two life-cycle lengths with the same mechanism. Furthermore, the mechanism should be able to account for the canalization of the juvenile period to ensure synchronized emergence in the presence of environmental or genetic variation in growth rate. The proposed hypothesis contains largely unresolved aspects of life-cycle control in insects and other organisms, such as the timing of metamorphosis and the role of developmental plasticity.

2 | BIOLOGY AND PREVIOUS HYPOTHESES

2.1 | The *Magicicada* species groups, species, and broods

The genus *Magicicada* comprises three species groups, Decim, Cassini, and Decula, each containing one 17-year species and one or two 13-year cicadas (Figure 1a–c). The Decim group contains the 13-year species *Magicicada tredecim* and the pair of 13- and 17-year species (*Magicicada neotredecim* and *Magicicada septendecim*), which is called the Neosep lineage (Simon et al., 2022). The Cassini group contains a 13-year species *Magicicada tredecassini* and a 17-year species *Magicicada cassini*. Finally, the Decula group contains a 13-year species *Magicicada tredecula* and a 17-year species *Magicicada septendecula*. The paired 13- and 17-year cicadas (species) in each of the Neosep, Cassini, and Decula groups are indistinguishable by external morphology and male songs (except for

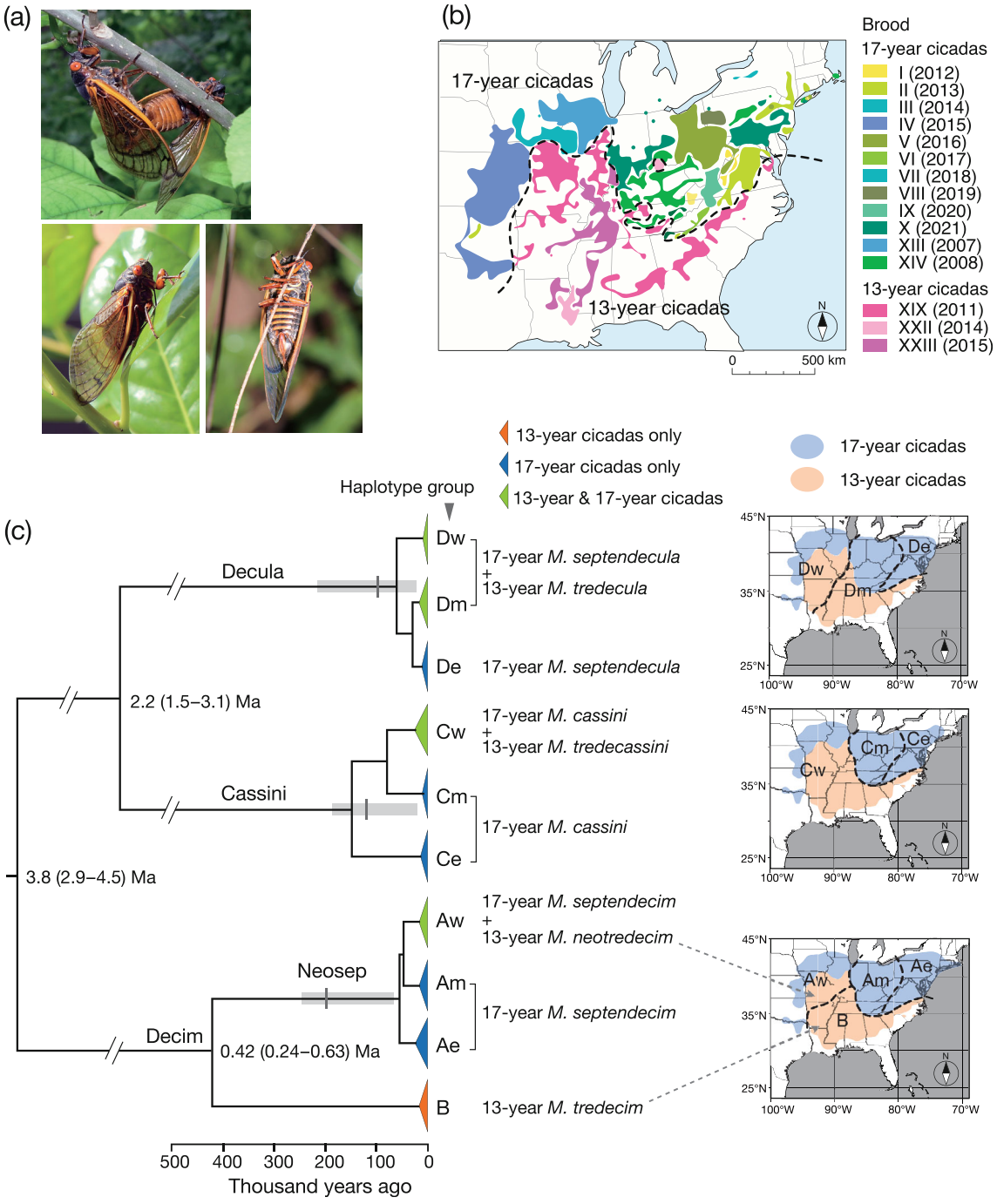

FIGURE 1 (a) Adults of *Magicicada*. Top, *Magicicada tredecim*; bottom-left, *Magicicada tredecassini*; bottom-right, *Magicicada tredecula*. Photographs by Teiji Sota. (b) Distribution of broods with the approximate boundary of 13-year and 17-year broods. Brood numbers in roman numerals are followed by most recent emergence years in parentheses. (c) Mitogenome phylogeny of *Magicicada* with divergence time estimation (left) and distribution of haplotype groups in each species group (right) based on Du et al. (2019). Divergence times of 13- and 17-year broods (species) in each of Neosep, Cassini, and Decula inferred by Fujisawa et al. (2018) based on transcriptome data are indicated by horizontal gray bars (vertical gray bars show 95% CI) [Color figure can be viewed at wileyonlinelibrary.com]

the character-displaced *M. neotredecim* in the Neosep pair; Cooley et al., 2006) and are discriminated only by the length of the juvenile period.

An important but unfamiliar term used in studying *Magicicada* is "brood," which is a group of population of one or more *Magicicada* species simultaneously emerging as adults in specific calendar years at 13- or 17-year intervals. Starting in 1893, Marlatt (1898) defined brood numbers in Roman numerals I to XVII for 17-year cicadas and XVIII to XXX for 13-year cicadas. However, not all of

these broods exist. In 17-year cicadas, 12 of 17 possible broods exist (Broods I–X, XIII, and XIV), whereas there are only three of 13 possible broods in 13-year cicadas (Broods XIX, XXII, and XXIII) (Figure 1b). Brood numbers are useful for specifying consecutive parent-offspring population groups that share emergence years. It must be noted that a brood is not composed of a single species, but three in most cases. The 13-year Brood XIX and XXIII contain four species owing to the fact that the Decim group contains two 13-year species. Importantly, the different broods are allopatric and allochronic. In general, the 17- and 13-year broods occur in the north and south, respectively (Figure 1b); however, they occur close to each other under the same climatic conditions at the boundary zone (Figure 1b). In each 17- or 13-year brood, adult emergence of different broods is completely allochronic, whereas co-emergence occurs every 221 years between the 17- and 13-year broods (thus, not strictly allochronic).

2.2 | Life history of *Magicicada*

Periodical cicadas of the genus *Magicicada* emerge as adults from late-April to early-June, mate and oviposit in twigs of trees during their adult life of approximately 4–6 weeks; nymphs hatch approximately 6–8 weeks after egg deposition, enter the soil, and feed on the root xylem fluid (Williams & Simon, 1995). Nymphs usually live within 60-cm depth, most frequently at 20–45 cm (Marlatt, 1907). It is noteworthy that clear seasonal changes in the soil temperature occur at these depths. The nymphal stage consists of five instars, and the total duration is essentially 13 or 17 years, with some variations at low frequencies (see the next section); thus, nymphs repeatedly overwinter in the non-feeding state. Nymphs have reddish eyes in the first and second instars but white eyes thereafter (Marlatt, 1907), and the eye color changes from white to red in the fifth instar 7–11 months prior to adult eclosion (Bryce & Aspinwall, 1975; Maier, 1980) (Figure 2a). The change in eye color may indicate that the nymph has irreversibly proceeded to the developmental stage toward adult metamorphosis. Eye pigmentation facilitates better vision and allows visual inspection of the aboveground environment for the timing of adult eclosion, which occurs after overwintering.

Since 13- and 17-year cicadas generally occur in the southern and northern parts of eastern United States (Figure 1b), they appear to have adapted to different climatic conditions. However, the difference in life-cycle length is maintained at the boundary of 13- and 17-year broods, and transplant experiments have shown that the life cycle or growth rate is unchanged (Williams & Simon, 1995). Therefore, the difference in life-cycle length likely has a genetic basis.

2.3 | Nymphal growth pattern

Knowledge of nymphal growth and development is essential for constructing the hypothesis of life-cycle control. However, field data on the entire juvenile stage are limited because of the long underground life of nymphs. Marlatt (1907) described the approximate duration of each instar for 13- and 17-year cicadas based on consecutive field samplings over 10–11 years. The duration of each instar in 13-year cicadas of Brood XIX from 1881 to 1891 (10 years) was 1–1.5, 2, 3, and 3–4 years for the first, second, third, and fourth instars, respectively, leaving 3–4 years in the fifth instar until adult emergence. The duration of 17-year cicadas of Brood X from 1885 to 1896 (11 years) was 1, 2, 3–4, and 3–4 years for the first, second, third, and fourth instars, respectively; data for the fifth instar are lacking. Complete data for a cohort of the 17-year cicada *M. septendecim* Brood II in Connecticut throughout the juvenile period (1979–1995) were reported by Maier (1996) (Figure 2b,c). In these data, the median starting age in years of each instar could be calculated as the age at which 50% of larvae reached that instar as follows: 1.0 for the second instar; 4.3 for the third instar; 8.1 for the fourth instar; 12.3 for the fifth instar, respectively. These results imply that the duration of the first through fifth instars is approximately 1, 3, 4, 4, and 5 years, respectively. Maier's (1996) data revealed a large variation in the length of each instar, each observed across several years (Figure 2c). Fragmental data on juvenile age structure compiled by White and Lloyd (1975) for two 13-year and twelve 17-year samples were generally consistent with Marlatt's (1907) and Maier's (1996) data in terms of the mean instar number at different cohort ages (Figure 2b).

Koyama et al. (2015) statistically compared the available data for instar composition of 13- and 17-year cicadas (Maier, 1996; White & Lloyd, 1975) and showed that the 13-year cicada cohort exhibited a more advanced instar composition than that of the 17-year cicadas of the same age, implying that 13-year cicada nymphs developed faster than 17-year cicada nymphs. Koyama et al. (2015) also found that 17-year cicada cohorts of the same age showed more advanced instar compositions in warmer habitats, implying that nymphs have faster growth rates or longer feeding periods in warmer habitats (see also White & Lloyd, 1975). These studies also suggest that genetic differences in developmental characteristics, such as growth rate, are involved in life-cycle differences.

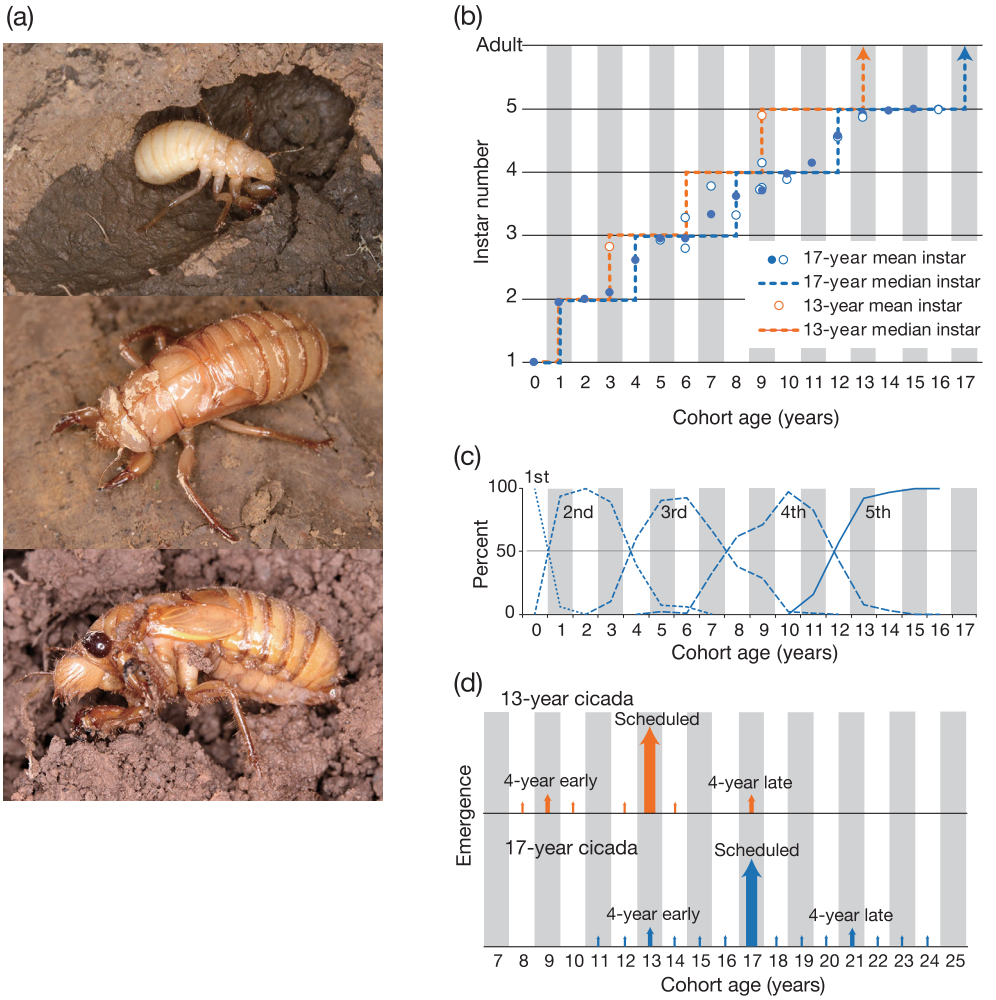

FIGURE 2 (a) *Magicicada* nymphs. Top, third instar of Brood XXII *Magicicada tredecassini* in Ohio; middle, white-eyed fifth instar of Brood XIV *Magicicada cassini* in Ohio; bottom, red-eyed fifth instar of Brood IX in West Virginia. Photographs by Teiji Sota, November 2019. (b) Developmental schedule of *Magicicada* spp. in terms of instar number of nymphs until adult emergence in 13-year (orange) and 17-year (blue) cicadas. Circles represent mean instar number of field-collected samples calculated from White and Lloyd (1975) (open orange and blue circles) and Maier (1996) (closed blue circles). Changes in median instar number are depicted with broken lines for 13-year cicada (orange line), the medians were calculated from White and Lloyd's (1975) data and inferred from Marlatt's (1907) description of instar durations. For 17-year cicada (blue line), the medians were determined from Maier's (1996) data for *Magicicada septendecim*. (c) Instar composition in a cohort of the 17-year cicada *M. septendecim* at Connecticut, 1979–1995. Adapted from Maier (1996). (d) Variation in cohort age at adult emergence inferred from emergence records of various broods based on Marshall (2001) and Marshall et al. (2011, 2017). Mass emergence is usually confined to on-schedule and 4-year early/late emergences. Emergence in other years indicated with thin arrows is not exhaustive especially for 13-year cicadas (D. Marshall, personal communication.) [Color figure can be viewed at wileyonlinelibrary.com]

2.4 | Adult body size and nymphal growth rate

Body size is a principal component of life-history traits that affects fitness. Adult body size of cicadas is a function of the nymphal period and growth rate. Koyama et al. (2015) studied adult size (head width) of all 13- and 17-year species across the geographic range of *Magicicada* and found that body size generally increases with increasing annual mean temperature of habitats within species, showing the converse Bergmann cline. This geographic pattern may be related to faster growth rates or longer feeding periods in warmer habitats, as mentioned in the previous section. Koyama et al. (2015) also found that paired 13- and 17-year cicadas of the same species group or lineage (i.e., Neosep, Cassini, Decula) had similar sizes under the same annual mean temperature condition. This implies that 13- and 17-year cicadas genetically have the same body size to be attained under the same climatic conditions and that 13-year cicada nymphs have

faster growth rates than 17-year cicada nymphs and reach the final size earlier than the 17-year cicadas.

2.5 | Variation in the nymphal period or emergence years of a cohort

Although the nearly perfect synchrony of emergence among individuals within a brood has been established by many historical records, the emergence of a few or more individuals (stragglers) can be seen in different off-schedule years, most frequently 4 years earlier than the scheduled emergence year in 17-year cicadas (Marshall, 2001; Williams & Simon, 1995). However, the frequency and population density of off-schedule emergence at different ages have not been well documented. As an attempt to reconstruct the occurrence of off-schedule emergence, Kritsky (1999) examined 839 historical records of *Magicicada* emergence in Ohio State between 1804 and 1995 and assigned 22 records (2.7%) to 4-year early emergence and seven records (0.9%) to 1-year late emergence of 17-year broods. These figures indicated that the relative frequency of off-schedule to on-schedule emergence was low, at least for a noticeable emergence size. Marshall (2001) and Marshall et al. (2011, 2017) reviewed previous records and conducted additional surveys to understand the overall picture of off-schedule emergence (Figure 2d). Marshall et al. (2017) concluded that off-schedule emergence with chorusing (mass emergence) was found to be only 4 years earlier or later than the scheduled year (Figure 2d). The adult population density of off-schedule emergence in these years appears to be small but could exceed the lowest density of on-schedule emergence, approximately 1 individual per m^2 (Marshall et al., 2011, 2017). A very small numbers of stragglers were found to occur in other years between 6 years earlier and 7 years later than the scheduled emergence year (Figure 2c). These facts imply that the duration of the juvenile period of the cohort (brood) can vary considerably but it typically shows a trimodal variation. Such variation in the juvenile period is thought to be due to genetic variation or developmental plasticity in response to variable environmental conditions (Marshall, 2001; Martin & Simon, 1990).

2.6 | Brood and life-cycle shifts

The presence of stragglers together with the fact that the brood numbers of adjacent broods of the same life cycle often differ by 4 years or 1 year, led to the proposal of a hypothetical brood shift mechanism in 17-year broods by temporary 4- or 1-year jumps (acceleration or deceleration) in the emergence year (Cooley et al., 2018; Lloyd & Dybas, 1966b; Simon et al., 2022). This mechanism was also applied to the three 13-year broods with supporting evidence from the mitochondrial DNA phylogeny (Du et al., 2019). Another hypothesis derived from the jump phenomenon is that a permanent life-cycle shift from the 17- to the 13-year cycle can occur from a temporal 4-year jump (Marshall & Cooley, 2000; Martin & Simon, 1988; Simon et al., 2000). This hypothesis is based on the discovery of a new lineage of 13-year Decim (*M. neotredecim*) that diverged from the 17-year Decim (*M. septendecim*), which postulates that southern *M. septendecim* populations undertook a 4-year jump and joined the adjacent 13-year brood, in such a way that life-cycle mutants (i.e., 13-year cicadas in a 17-year brood) joined a large 13-year brood. Joining larger broods with mixed species would be effective in lowering predation impact (Lloyd & Dybas, 1966b). Marshall and Cooley (2000) called this process "nurse-brood facilitation." The formation of mixed broods can increase the strength of interspecific interference (reproductive) and/or competition among nymphs. However, niche differences between species (e.g., microhabitats) may effectively resolve the maladaptive effects of mixed-species broods. Dybas and Lloyd (1962) found that reproductive isolation between *M. septendecim* and *M. cassini* was nearly perfect in the prezygotic stage based on song and body size differences. Marshall and Cooley (2000) also proposed "life-cycle canalization," in which a temporal life-cycle shift (e.g., 4-year jump) owing to phenotypic plasticity under unusual climatic conditions leads to a permanent life-cycle shift through "canalizing selection" on genes related to life-cycle length. This life-cycle shift mechanism was first proposed by Lloyd and Dybas (1966b) and was compared to genetic assimilation by Waddington (1953).

3 | HYPOTHESIS AND PREDICTIONS

3.1 | Hypothetical mechanism of life-cycle control

The life-cycle control mechanism of *Magicicada* is assumed to be shared among the three species groups (i.e., it evolved in a common ancestor; Sota et al., 2013). It is assumed that the duration of the juvenile period is basically either 13 or 17 years based on genetic differences but there is developmental plasticity that can result in 4-year early or late emergence in each of the 13- and 17-year cicadas. Thus, adult emergence occurs at 9, 13, 17, or 21 years of age, but normally not in the years

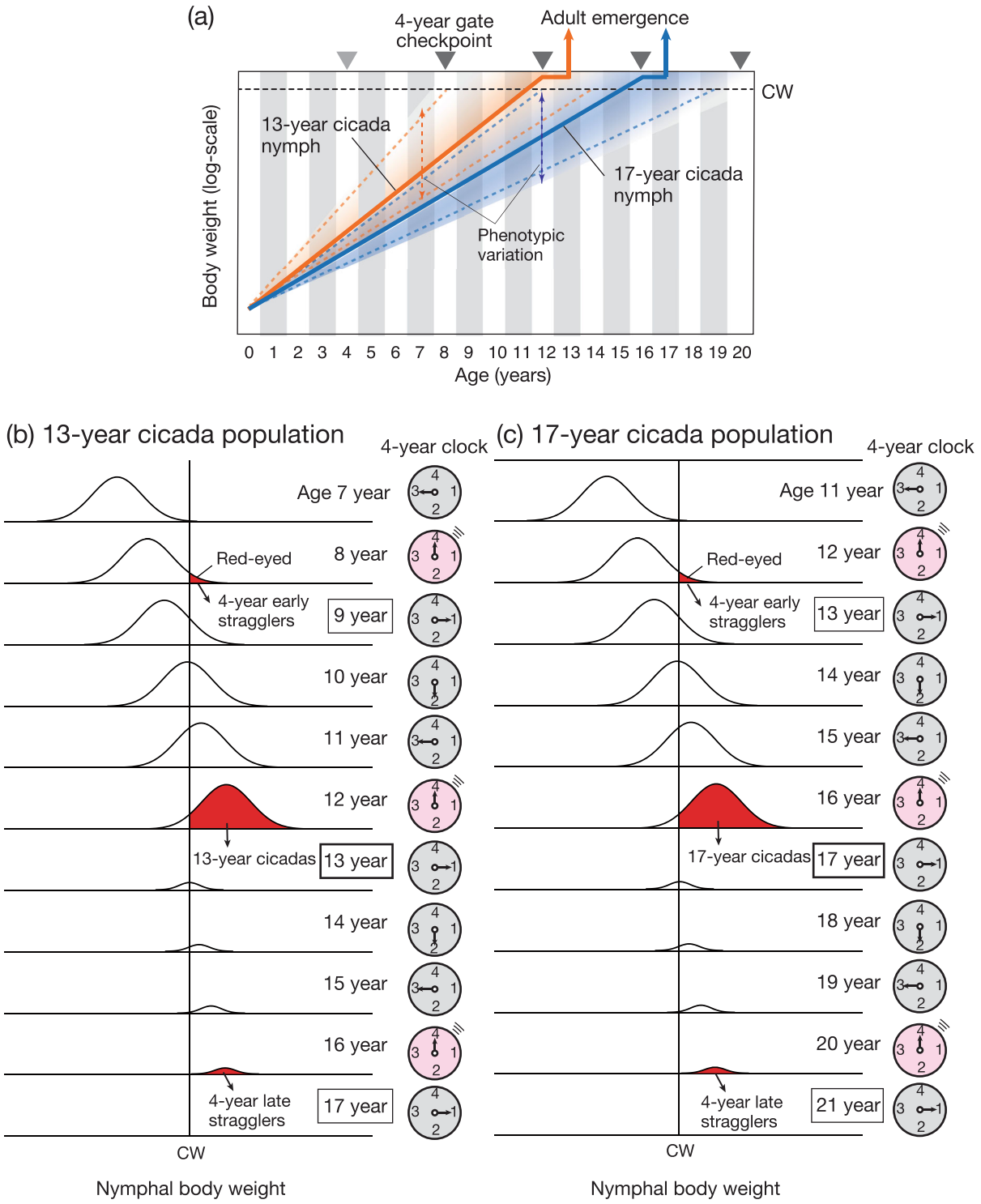

FIGURE 3 Hypothetical mechanism of life-cycle control in *Magicicada*. (a) Growth patterns of 13- and 17-year cicada nymphs. Reverse triangles indicate 4-year gates (check-point years) for critical body weight (CW) at 4-year intervals of age from the hatching; 13-year cicadas have genetically higher growth rate (orange line) than 17-year cicadas (blue line), but phenotypic variation among individuals can be large (double-arrowed vertical broken lines; example growth patterns are shown by broken lines). (b) A schematic representation of the mechanism of the major 13- and 17-year emergence and 4-year early/late emergence (stragglers) in 13-year (b) and 17-year cicadas (c), showing the changes in nymphal body weight distribution with age. Nymphs with body weight exceeding CW in the check-point years (8, 12, 16, and 20 years of age) will have red eyes and emerge in the following year [Color figure can be viewed at wileyonlinelibrary.com]

in-between. In essence, the timing of adult emergence (metamorphosis) is assumed to be determined by the interaction of the internal clock, genetically determined growth rate, and critical body weight, as described in the four steps below.

1. In the final instar of nymphs, there is a critical body weight (CW) for adult metamorphosis (to metamorphose into adults), which is determined genetically and specific to the species group (Figure 3a); CW may depend on sex as females are generally larger than males in the adult stage (Koyama et al., 2015). It is assumed that under the same climatic condition, CW is the same for 13- and 17-year cicadas within the same species group. This assumption is based on the fact that adult sizes did not differ between 13- and 17-year cicadas of the same species group under the same climatic conditions (Koyama et al., 2015). However, CW may differ under different climatic conditions as adult sizes are larger at warmer habitats (Koyama et al., 2015). CW for adult metamorphosis has been proposed in the study of hemipteran and holometabolous insects (Nijhout, 1981; Nijhout et al., 2006) and is defined as the minimal mass at which further growth is not necessary for a normal time course to adult metamorphosis (Davidowitz et al., 2003). Differences in adult body size can be caused by genetic differences in CW as was shown in *Manduca sexta* (Davidowitz et al., 2003) and *Drosophila* species (Hironaka et al., 2019).
2. The growth rate of nymphs is a quantitative genetic trait, which may be defined as the annual rate of logarithmic body weight increase. For simplicity, I assume that the growth rate is unchanged among instars. Under the same climatic condition, the growth rate is faster in the 13-year cicadas than in the 17-year ones (Koyama et al., 2015; White & Lloyd, 1975), such that on average 13-year genotypes reach CW in 12 years and 17-year genotypes do so in 16 years (Figure 3a). However, realized growth rates of individuals in a population may show a variation according to varying environmental conditions (e.g., nutrition and temperature), which may produce substantial variation in the timing of reaching CW (Figure 3a–c).
3. Nymphs have a 4-year clock which can count 4-year intervals and a developmental gate (hereafter 4-year gate) for the decision to metamorphose into adults, which opens at every fourth year of juvenile life (i.e., 4, 8, 12, 16, ..., years of age). The 4-year clock hypothesis is based on the idea of Hayes (2004) and the facts of the difference between 13- and 17-year cycles and the 4-year early/late straggler events. I assume that the 4-year clock is an innate biological clock, like the circannual clock (Miyazaki et al., 2014; Numata et al., 2015) which can be corrected by the annual seasonal cycle of soil temperature or host plant physiological state. Note that the life-cycle length includes a single additional year after $4 \times n$ years (i.e., $12 + 1$, $16 + 1$). In this additional year, the nymphs have their last overwintering period. This may effectively enable synchronized eclosion among nymphs that have reached a metamorphosis-competent state at varying times before the last winter.
4. In a population of 13-year cicadas, the majority of the nymphs usually reach CW between 9 and 12 years of age (variation owing to environmental and/or genetic factors), pass the gate in the 12th year, and emerge as adults at 13 years of age (Figure 3b). Nymphs that have reached CW at 9–11 years old must wait until the 12th year when the gate is open. A small portion of nymphs that have reached CW by 8 years of age pass the gate of the eighth year and emerge as adults at 9 years of age (4-year early stragglers). However, if some nymphs have not reached CW by 12 years of age, they may pass the 16th-year gate and emerge at 17 years of age (4-year late stragglers). Similarly, the majority of the 17-year cicada nymphs reach CW by 16 years and emerge as adults at 17 years of age; however, some individuals may emerge 4 years earlier (13-years old) if they have reached CW by 12 years of age or emerge 4 years later (21-years old) if they did not reach CW by 16 years but did so by 20 years of age instead (Figure 3c).

Thus, the present hypothesis can explain how synchronized emergence at 4-year intervals with two alternative years for the majority can be controlled, and concomitantly, how typical off-schedule emergences (4-year early/late stragglers) occur (Figure 3b, c). It predicts that 4-year early/late stragglers occur when the actual growth rate (affected by nutritional and temperature conditions) is either very fast or slow. These cases of variation in life-cycle length are regarded as phenotypic plasticity of the life cycle.

3.2 | Life-cycle shift via plasticity and selection

The present hypothesis can explain the mechanism of evolutionary shift between the 13- and 17-year life cycles as a replacement for a population with one predominant life cycle (e.g., 13-year) with an allochronic population with the other predominant life cycle (e.g., 17-year; Figure 4). The life-cycle shift may have occurred

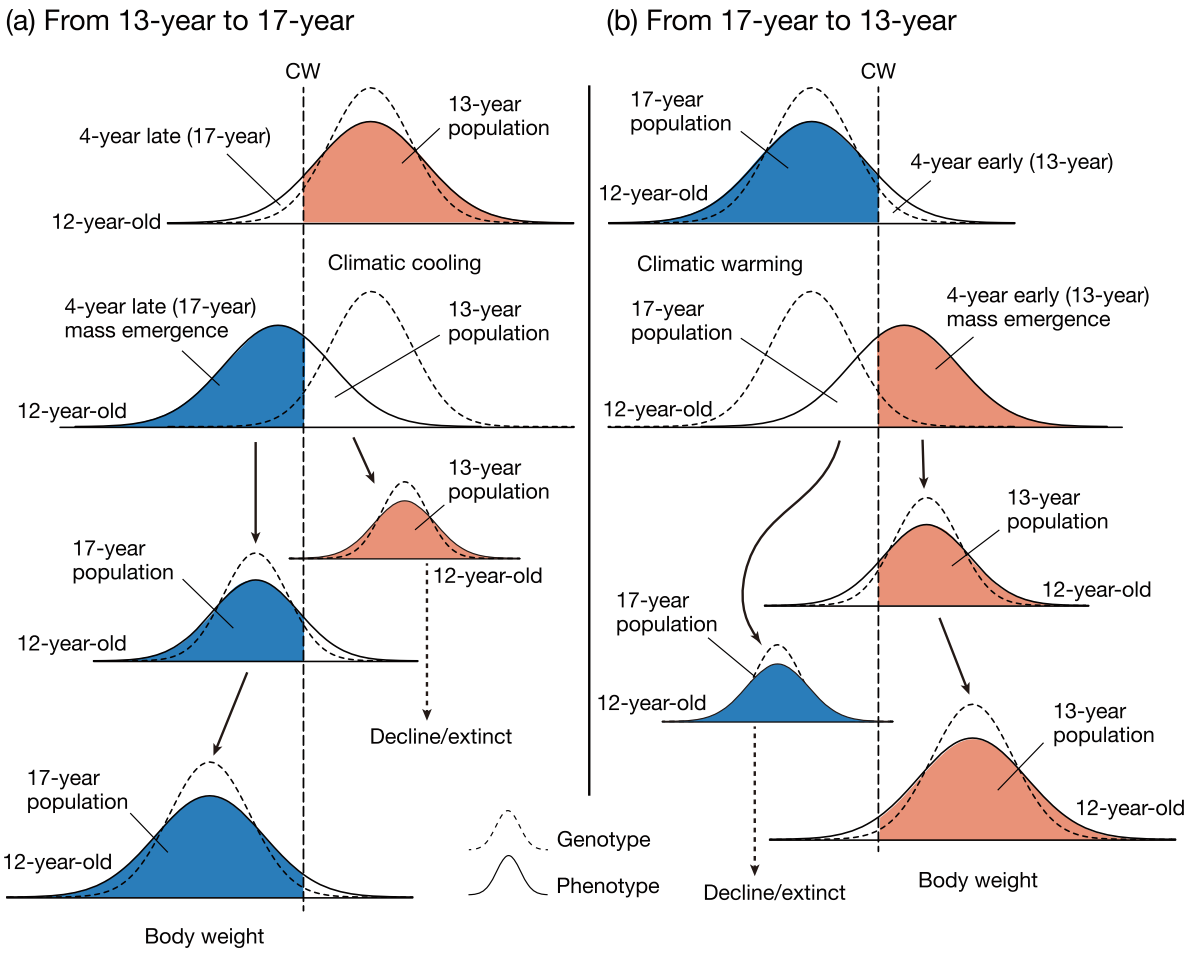

FIGURE 4 Hypothetical life-cycle shifts during climatic cooling (a) and warming (b). Phenotypic and genetic body size distributions of nymphs at 12 years of age (a 4-year gate year) are indicated by solid and broken lines, respectively. CW, critical body weight. (a) Initial 13-year population is replaced with 17-year cicada population during climatic cooling. (b) Initial 17-year population is replaced with 13-year population during climatic warming [Color figure can be viewed at wileyonlinelibrary.com]

repeatedly during a period of climatic change, such as global cooling/warming in the Quaternary, by a temporal shift of the life cycle owing to phenotypic plasticity and selection on the trait responsible for life-cycle difference, the growth rate. I assume that growth rate is a quantitative genetic trait containing some standing genetic variation (Barrett & Schluter, 2008) and also shows a large phenotypic variation in response to varying soil temperature and plant productivity, which would be greatly affected by climatic conditions. Since the threshold response with CW is only effective in the 4-year gate, a discrete change in the emergence year can occur, despite the growth rate being a continuous variable. During a period of climatic cooling, for example, the phenotypic growth rate will be reduced, and 4-year late emergence (17-year) will increase, while normal 13-year emergence will decrease, leaving an expanding 17-year and a shrinking 13-year population (Figure 4a). Here, I assume a selective advantage of slower growth rate under cooler conditions, and selection on growth rate will ultimately lead the population to a predominantly 17-year life cycle. During the life-cycle shift, both life cycles may coexist allochronically in the same area, but the original life cycle will eventually disappear (become extinct) owing to its suboptimality and partly to its competition (among nymphs) with the predominant 17-year population. The life-cycle shift mechanism presented here is essentially identical to that of the "life-cycle canalization" proposed by Marshall and Cooley (2000), which implies that the life-cycle shift under unusual climatic conditions owing to developmental plasticity is genetically fixed through canalizing selection. Note, however, that the authors considered life-cycle shifts during a relatively short-term, temporary climatic anomaly.

The neighboring south-to-north distribution of the 13- and 17-year life cycles with the life-cycle boundary (Figure 1b) is thought to indicate differential adaptation to warmer/cooler climates in these life cycles. The

observation that nymphs develop faster and adult size is larger in warmer habitats within the same life-cycle species (Koyama et al., 2015) implies that local climatic conditions (e.g., temperature) affect realized growth rate and final body weight of nymphs, which can be affected by the growing season length and host plant nutritional conditions that would be affected by the climatic conditions. Since adult body sizes of sibling 13- and 17-year species are similar to each other under the same temperature conditions (Koyama et al., 2015), the primary genetic difference between the life cycles would exist in the growth rate, or more correctly, the developmental rate to attain the same CW. However, there may be a genetic change in CW along the climatic gradient (i.e., larger in southern areas), which may be reflected in the variation in adult body size along the climatic gradient.

3.3 | Hypothesis testing

Hypothesis testing essentially requires showing the existence of CW and 4-year clock and gates for the basic life-cycle control mechanisms, and the existence of genetic differences in growth rate for the control of the alternative life-cycle length. Experimental studies on life-cycle control mechanisms by rearing are difficult because of the long juvenile period and the difficulty in rearing soil-collected nymphs. Practically, digging and checking nymphal growth and development over the years (e.g., 8–16 years old for 13-year cicadas; 11–20 years old for 17-year cicadas) will have to be conducted to test the 4-year gate and CW hypothesis, as well as the developmental plasticity in juvenile period length by showing the periodical occurrence of well-grown, red-eyed fifth instar nymphs that are likely to prepare for adult metamorphosis in the 4-year gates (i.e., 8, 12, and 16 years in 13-year cicadas; 12, 16, and 20 years in 17-year cicadas). The majority of the nymphs will have red eyes in the year preceding the regular emergence year, 12 and 16 years of age for 13- and 17-year cicadas, respectively, and small numbers of red-eyed nymphs (to be stragglers) will appear 4 years early or late in the year preceding regular emergence. Between the 4-year gate years, nymphs will have white eyes, irrespective of body weight. These observations provide circumstantial evidence for a 4-year clock and gate. The presence of CW can be evidenced by the distribution of weight for white- and red-eyed nymphs of the same age, with the latter being larger.

It is important to understand the process of adult metamorphosis in *Magicicada* in terms of gene and hormonal expression that controls metamorphosis. Although the molecular mechanisms underlying metamorphosis in cicadas are unknown, metamorphosis in insects is generally controlled by juvenile hormones (JH) and ecdysteroids (20-hydroxyecdysone, E20), where JH maintains the juvenile state. The disappearance of JH leads to a transition from nymphs to adults in hemimetabolous insects, and E20 facilitates molting to adults (Martín et al., 2021). The metamorphosis process is also controlled by genes in the metamorphosis gene network (MGN), including Krüppel-homolog 1 (*Kr-h1*), ecdysone inducible protein 93F (*E93*), and broad-complex (*Br-C*). In a hemimetabolous insect, adult metamorphosis is specified by the suppression of *Kr-h1* and *Br-C* and increased expression of *E93* (Martín et al., 2021). These general schemes may be used in cicadas. Therefore, it is necessary to study the expression profiles of MGN genes to identify the developmental states of nymphs prior to adult emergence. In *Magicicada*, changes in eye color from white to red occur 7–11 months before eclosion, and the nymphs, overwinter and eclose the following spring. To test the hypothesis of CW and the 4-year gate, the relationship between body weight and MGN gene expression should be compared between white-eyed and red-eyed nymphs that occur in the 4-year gate years (i.e., 12 or 16 years). Since nymphal diapause during overwintering may alter the expression of JH, E20, and MGN genes from those expected during adult metamorphosis (Zhai et al., 2017), studying the gene and hormonal expression of nymphs both before and after overwintering is necessary.

Experimental crossing studies of the genetic background of different nymphal periods of 13- and 17-year cicadas within species groups are also difficult to perform because of the long nymphal periods. Therefore, hypothesis testing for the control of the alternative life-cycle lengths must rely on comparative genomic studies of paired 13- and 17-year species in the same species group. The discovery of genomic regions and genes associated with life-cycle differences is the primary target of the genomic comparison. In addition, we may need to consider the possibility that non-genetic and epigenetic differences are involved in the divergence of the two life cycles. This possibility can be tested by comparing epigenetic states (e.g., DNA methylation) between the genomes of paired 13- and 17-year species.

3.4 | Possible nature of the internal clock and an alternative year-counting method

The 4-year clock is the most difficult component to resolve in my hypothesis. This clock should be an internal one because external cues in nature are unlikely to provide signals at 4-year intervals to *Magicicada* nymphs in various broods with different phases. The internal mechanisms for counting more than 2 years are unknown in living

organisms. The existence of a circannual clock has been demonstrated in some insects, such as the varied carpet beetle *Anthrenus verbasci*, which has an extended larval period of up to several years (Miyazaki et al., 2014; Numata et al., 2015). The 4-year clock, if it exists, may use the annual cycle count at the base. *Magicicada* nymphs may count 1 year by host plant activity (Karban et al., 2000) (or soil temperature directly) or they may have an intrinsic circannual rhythm that is corrected by the annual cycle of soil temperature fluctuation or host plant conditions. The mechanism of the 4-year clock can be epigenetic. For example, some epigenetic states change yearly from 1, 2, 3, and 4 and then return to 1. At State 4, checking for the CW for adult eclosion would work, and if clarified, signals for adult metamorphosis would be released. Epigenetic changes must occur annually and are controlled regularly by the occurrence of the overwintering period. Recent epigenetic studies have revealed that the level of DNA methylation is roughly correlated with age in mammals (Bergsma & Rogaeva, 2020). In bamboos, an endogenous biological clock is thought to be involved in the control of the flowering periodicity (Franklin, 2004); a recent study on age-associated epigenetic changes in a bamboo species observed methylome changes, which were likely controlled by an internal epigenetic clock associated with chronological age (Zhang et al., 2021).

It may be necessary to consider the possibility of life-cycle control without a 4-year clock. In the millipede *Parafontaria laminate armigera*, which exhibits an 8-year periodical life cycle, the larvae molt once a year from the second year of juvenile life, and eclose as adults at the seventh molting (Niijima & Shinohara, 1988). Here, the advance of the juvenile instar and the timing of reproduction are controlled by a prolonged period of chilling during the intervening winter (Fujiyama, 1996), and if the number of molts for adult eclosion is genetically determined, the internal clock may not be required to control the periodicity. In *Magicicada*, instar duration is highly variable (Figure 2b). Nevertheless, considering the case in which they have a genetically determined number of years for each instar may be useful, and the counting error can be corrected when the duration of the instar changes owing to environmental variation. Thus, if year counting can be linked to (hypothetical) fixed molting intervals of 3 or 4 years for 13- and 17-year cicadas, respectively, it may follow: $13 = (1+2)+3+3+3+1 = 3\times4+1$ and $17 = (1+3)+4+4+4+1 = 4\times4+1$, where $1+2$ and $1+3$ are the total durations of the first and second instars. The molting interval is determined by the growth rate, which differs between the 13- and 17-year cicadas. Incorporating 4-year acceleration and deceleration as phenomena related to plasticity in this system is difficult, but incorporating 4-year acceleration in 17-year cicadas and 4-year deceleration in 13-year cicadas as a genetic variation within populations (e.g., fast and slow growth alleles) is possible. Given that the 4-year acceleration of 17-year cicadas is a relatively well-known phenomenon, but other stragglers are not, the above hypothesis cannot be completely ruled out.

3.5 | Parallel divergence of 13- and 17-year life cycles in three species groups

The ultimate goal of our study may be to reconstruct the history of life-cycle divergence and brood formation. One of the most interesting aspects of the evolutionary history of *Magicicada* is the synchronization of life cycles among the three species groups. Each brood of periodical cicadas usually consists of three species from three species groups. In each group, a pair of 13- and 17-year cicadas (species) diverged in parallel, although in the Decim species group, the paired species (Neosep) are sister to another 13-year species *M. tredecim* that diverged earlier. Earlier researchers (Alexander & Moore, 1962) considered that the two life cycles diverged after the species groups diverged. Particularly, Cox and Carlton (1988) and Yoshimura (1997) hypothesized a simultaneous origin of 13- and 17-year life cycles during the glacial period, implying parallel divergence of periodical from nonperiodical life cycles in the three species groups. However, Sota et al. (2013) suggested that the basic mechanism controlling the periodic life cycles may have evolved in the common ancestor of all *Magicicada*, which existed in the Pliocene (i.e., prior to the Pleistocene), because it is unlikely that such complicated life-cycle divergence can evolve independently among the three different lineages. The hypothesis presented here assumes that at least the basic framework of life-cycle control had evolved in the common ancestor of *Magicicada*, and subsequent life-cycle shifts have occurred based on genetic variations in growth rate (or in other traits) after the divergence of species groups. It is likely that the three species groups diverged allopatrically and formed or joined broods of 13- or 17-year life cycles at various times and locations during the process of range expansion, resulting in a large overlap in distribution ranges among the three groups. At present, there is no evidence of a shared life-cycle control mechanism. Therefore, to clarify whether the three species groups have a common life-cycle control mechanism is an important subject of comparative genomic studies.

Based on the current knowledge of *Magicicada* phylogeny and an assumption that lineage divergence reflects life-cycle divergence, the initial divergence of 13- and 17-year cicadas occurred in the Decim group 0.4–0.5 million years ago (Du et al., 2019; Sota et al., 2013); this divergence was

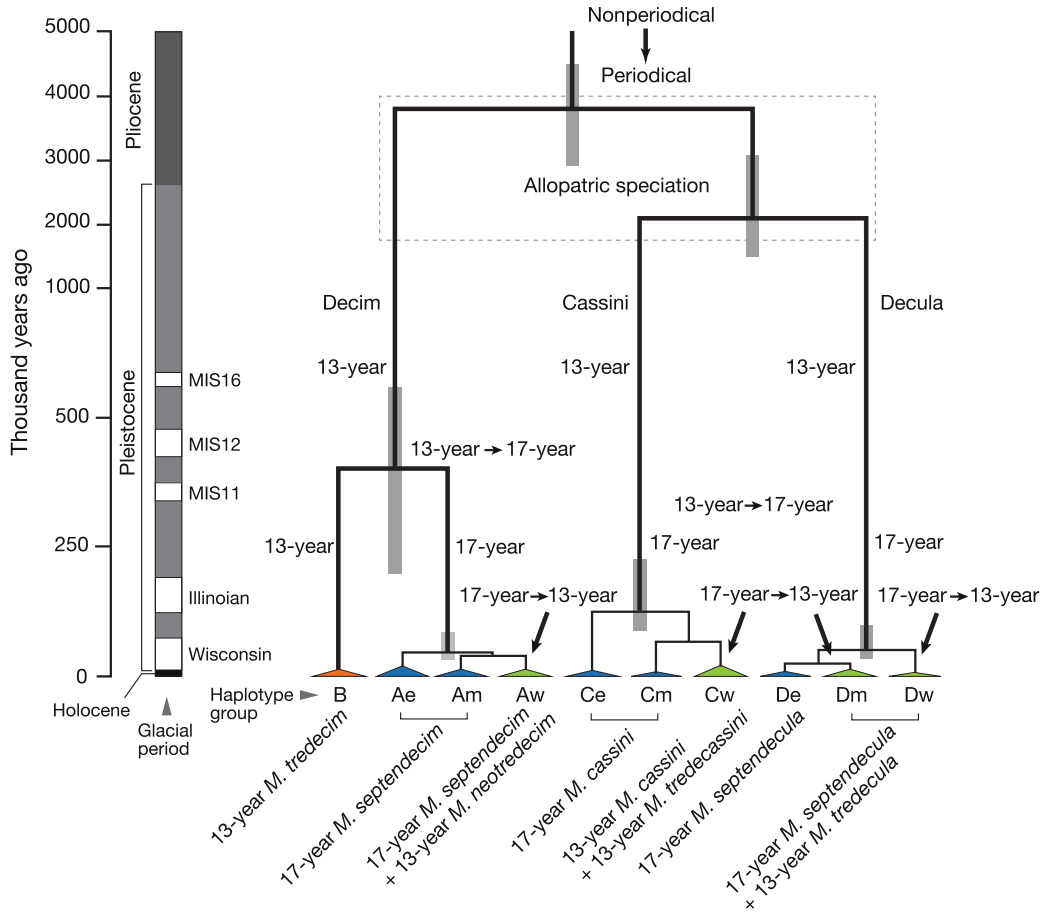

FIGURE 5 A hypothetical history of life-cycle changes in *Magicicada*. The phylogeny is based on the clocked mitogenome tree in Du et al. (2019). Haplotype groups are as shown in Figure 1c. For major nodes, 95% CI of divergence times are indicated by gray bars. Note that the scale of *y*-axis changes from 0–500 kya (1×) to 500–1000 kya (0.5×), and 1000–5000 kya (0.25×), where kya means 1000 years ago. The periods of extensive glaciation are indicated along the *y*-axis according to the "Timeline of glaciation" (Wikipedia, 2022). MIS numbers are the marine isotope stages [Color figure can be viewed at wileyonlinelibrary.com]

likely associated with the onset of extensive glacial cycles in the Pleistocene (Figure 5). Other life-cycle divergence events were more recent, 10,000–26,000 years ago according to mitochondrial DNA data (Du et al., 2019), or 95,000–197,000 years ago from analysis of nuclear DNA data (Fujisawa et al., 2018). The life-cycle evolution may have occurred as follows (Figure 5): at the time of *M. tredecim*-Neosep divergence, all *Magicicada* populations had 13-year cycles, followed by a 17-year population (Neosep lineage) derived from the 13-year population (*M. tredecim*) in the north because of selection for a slower growth rate in cooler climates. Here, I assumed that the fast growth rate is maladaptive under cooler climates with low plant productivity. The 17-year Decim expanded their range, and the Cassini and Decula populations eventually joined the 17-year broods through life-cycle shifts aided by nurse-brood facilitation (Marshall & Cooley, 2000). During the last glacial period, all *Magicicada* populations, except *M. tredecim*, might have had a 17-year life cycle as the divergence time of the 13- and 17-year life cycles was <26,000 years (Figure 1). All of the present 13-year cicadas, except *M. tredecim* (i.e., *M. neotredecim*, *M. tredecassini*, and *M. tredecula*), may have diverged from 17-year cicadas since the last glacial period. The divergence of *M. neotredecim* from *M. septendecim* may have occurred around the boundary of *M. septendecim* and *M. tredecim*, where *M. tredecim* or 13-year cicadas of other species groups occurred as nurse broods (Cooley et al., 2001; Marshall et al., 2003; Marshall & Cooley, 2000; Simon et al., 2000). The reproductive character displacement in male songs between *M. neotredecim* and *M. tredecim* implies the occurrence of reinforcement in reproductive isolation during secondary contact (Marshall & Cooley, 2000). *M. neotredecim* is confined to the mid-western part of *Magicicada*'s range, where the life-cycle boundary of the Cassini group occurs. The Cassini group contained only one haplotype group (Cw) with both life cycles, implying a single life-cycle shift event. However, the Decula group showed life-cycle divergence in two haplotype groups (Dw and Dm), implying repeated life-cycle shifts. The above hypothetical process of

life-cycle divergence can be tested by analyzing the genomic divergence of species and populations in detail. In addition, the process of brood formation can be reconstructed using extensive mitochondrial haplotype data covering local populations of all species in all broods.

4 | CONCLUSIONS

The life-cycle control hypothesis mentioned here includes assumptions for some unknown aspects of the biological clock and developmental control of the insect group. Nevertheless, the hypothesis is explicit concerning the interrelationships between genetics and phenotypic plasticity in life cycles and, as a particular merit, can explain life-cycle variation (occurrence of straggler) owing to environmental variation in growth rate as well as life-cycle shift (evolution) through selection of growth rate, which may occur during climatic changes. Ongoing and future studies on the genome and gene expression will support or reject some of the components of the hypothesis, and I expect that the mystery of *Magicicada* will be resolved in the next decade. In the present review, I have mentioned little about the adaptive significance and selection factors/processes for the 13- and 17-year periodical life cycles, and the role of prime numbers, which are highly controversial and require extensive consideration. However, these issues must be discussed separately.

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CONFLICF OF INTEREST

The author declares no conflict of interest.

ORCID

Teiji Sota https://orcid.org/0000-0002-0400-9147

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