Ecophysiological responses to climate change in cicadas

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Abstract. Cicadas are large hemipteran insects characterized by unique life-history traits, such as extraordinarily long life cycles, a subterranean/terrestrial habitat transition, xylem sap-feeding and melodious sound production. These fascinating features of cicadas have attracted much attention in the research fields of physiology and ecology, resulting in an accumulation of knowledge about the underlying mechanisms and their adaptive significance. Although community-level responses to recent climate change have already been documented for cicada fauna, an understanding of their causal relationships is still at the initial stages. In this review, we summarize current knowledge about environmental adaptations of cicadas to facilitate a deeper understanding of the ecophysiological consequences of climate change. We first outline the diverse responses of cicadas to environmental factors, mainly temperature, and their strategies to cope with naturally fluctuating environments. Then, we discuss the consequence of upcoming climate change by consolidating the current findings. This review highlights the fact that fitness-relevant activities are fine-tuned to a species-specific temperature optimum to achieve habitat segregation among coexisting species, implying that cicada diversity is highly susceptible to climate warming. As a result of their conspicuous large bodies and species-specific calling songs, cicadas are promising candidates for use as bioindicator species to monitor ecological impacts of climate change. We encourage future works that continuously quantify population- and community-level responses to upcoming climate change, as well as unveil mechanistic links between physiological traits and ecological consequences.

Key words. Global warming, life-cycle strategy, phenology, thermal response, urban heat island.

Introduction

Cicadas (Hemiptera: Cicadoidea) are characterized by melodious calling songs, large bodies and unique life histories, and are one of the most familiar insects to humans. Besides being sometimes utilized as foods and medicines, they often appear in cultural activities, such as literary, artistic and folkloric works (Beamer, 1928; Myers, 1929; Kato, 1956; Feng *et al.*, 2018). In particular, their visual appearance and calling songs are commonly associated with a seasonal symbol that evokes summer images. From a biological perspective, cicadas are fascinating as research objects because of their peculiar life-cycle traits, such as extraordinarily long life cycles (Karban, 1986), drastic habitat transition between subterranean and terrestrial phases (Harvey & Thompson, 2006), xylem sap-feeding (Cheung & Marshall, 1973), melodious sound production (Pringle, 1957), evaporative cooling (Sanborn, 2002), and humidity-induced hatching (Moriyama & Numata, 2006). Because of the discriminative acoustic interactions within and between species, cicadas are considered to be a favourable model for studying sympatric speciation (Marshall *et al.*, 2011; Hertach *et al.*, 2016). Cicadas also perform important roles in ecosystem function, including fluxes between belowground

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and aboveground nutrients (Callaham *et al.*, 2000; Yang, 2004, 2008; Aoki *et al.*, 2011). In particular, periodical cicadas of the *Magicicada* spp. have long attracted biologists because of their mysterious prime-numbered life cycles: adults of sympatric species synchronously emerge from the ground only once every 13 or 17 years. Many studies have aimed to reveal behavioural and ecological aspects of these periodical cicadas (Williams & Simon, 1995; Grant, 2005).

Recent ecosystem degradations observed across the globe have been associated with the rapid climate change resulting from anthropogenic activities (Hughes, 2000; Walther *et al.*, 2002). The predicted future progression of climate change, represented by warming, will have a direct influence on ectothermic insects, potentially followed by community- and ecosystem-level changes via biological interactions. However, there are practical difficulties in tracing qualitative and quantitative changes in insect communities over decades. In this context, cicadas are promising candidates for use as biological indices to assess the ecological impact of climate change. As a result of the conspicuous large bodies and species-specific calling songs, compositional changes in cicada fauna can attract considerable attention from not only biologists, but also the general public. Moreover, cicadas leave a cast-off skin (exuvia) of the final-instar nymph on or near the host plants on which they have grown. This trace enables us to measure both the number and the species composition of cicada fauna in a study site. Indeed, recent changes in cicada community structures have been widely publicized and considered as social problems (Cyranoski, 2007; Holden, 2007). Nevertheless, only a few studies have addressed the physiological and ecological mechanisms of recent cicada community changes. The present review aims to summarize current knowledge surrounding environmental adaptations of cicadas and to facilitate a deeper understanding of the ecophysiological consequences of climate change. We first outline the influence of climatic factors, mainly temperature, on cicada behaviour and physiology. Next, we introduce cicadas' peculiar adaptive strategies to cope with naturally fluctuating environments. Then, the known influence of climate change on cicada fauna and its causal mechanisms are addressed. Finally, we attempt to discuss the future consequence of upcoming climate change by consolidating the current findings.

Effects of climatic factors on cicada behaviour and physiology

Abiotic environmental factors serve important roles in determining the distribution and species diversity of cicadas. Among them, temperature appears to be the factor most highly correlated with cicada behaviour and physiology as a result of its inevitable direct influence on metabolic activities in ectothermic insects.

Effects of climatic factors on developmental rate

The nymphal period of cicadas is long, with great diversity (from 2 to 17 years) (Karban, 1986). Cicadas feed solely on plant xylem fluid, which contains extremely dilute concentrations of nutrients such as amino acids and minerals, throughout their life cycle (Cheung & Marshall, 1973; Lloyd & White, 1987). This is assumed to be a fundamental reason for the slow development of cicadas, although other adaptive strategies of cicadas favour a prolonged development for synchronizing the period of adult emergence and for attaining larger body sizes (White & Lloyd, 1975; Karban, 1986, 1997; Saulich, 2010). With the exception of periodical cicadas that have fixed 13- or 17-year life cycles, nymphal periods of cicadas usually vary over several years within a single species, probably depending on nutritional and temperature conditions of feeding nests (Karban, 1986). Because of the limited accessibility of underground insects and the difficulty in mass rearing on experimental scales, temperature effects on nymphal development have not been definitely determined. However, underground assessment of instar compositions and analyses of their correlation with climate conditions have revealed an overall association between temperature and nymphal growth rates. An interspecies comparison across a geographical range demonstrated that nymphal growth tends to proceed more rapidly in species living in warmer regions (Karban, 1986). Even within a single species, warmer habitats have been shown to increase the nymphal growth rate (White & Lloyd, 1975). A higher temperature may enhance cicada growth rates indirectly via increasing plant activity, as well as directly by increasing the metabolic rate. Nymphal growth rates can also be enhanced on host plants rich in nutritional quality, such as plants receiving high amounts of sunlight (Yang, 2006; Karban, 2014) and fertilization (Ito & Nagamine, 1981; Callaham *et al.*, 2002).

In periodical cicadas, increasing their growth rate in warmer climates may allow them to attain larger adult body size during the fixed developmental period (Koyama *et al.*, 2015). A larger size is likely to be more profitable for adults because of competitive advantages in singing males and higher fecundity in females (Karban, 1986, 1997). Using a rearing experiment with artificially modulated temperature cycles, Karban *et al.* (2000) demonstrated that nymphs of periodical cicadas accurately maintain the 17-year cycle by counting the number of seasonal oscillations rather than by monitoring the passage of real time or thermal accumulation.

In the year of adult emergence, the final (fifth)-instar nymphs move close to the soil surface by making a tunnel to wait for the appropriate emergence time (Beamer, 1928; Maier, 1980; Williams & Simon, 1995). Heath (1968) demonstrated that a soil temperature above a certain threshold stimulates the emergence of periodical cicadas. Experimental soil heating during the emergence period also verified that warmer conditions result in earlier emergence of *Neotibicen dealbatus* (Smith *et al.*, 2006). In addition, developmental modelling revealed that temperature during the growth period also influences to the cicada emergence date. Sato & Sato (2015) calculated the emergence date from the 12-year collection records of two Japanese cicadas, *Cryptotympana facialis* and *Graptopsaltria nigrofuscata*, and found that thermal accumulation during late spring is the most decisive for predicting emergence date. In many species, the time of emergence of males precedes that of females (Mohri *et al.*, 1962; White *et al.*, 1979; Sato & Sato, 2015). This phenomenon is mathematically explained as an
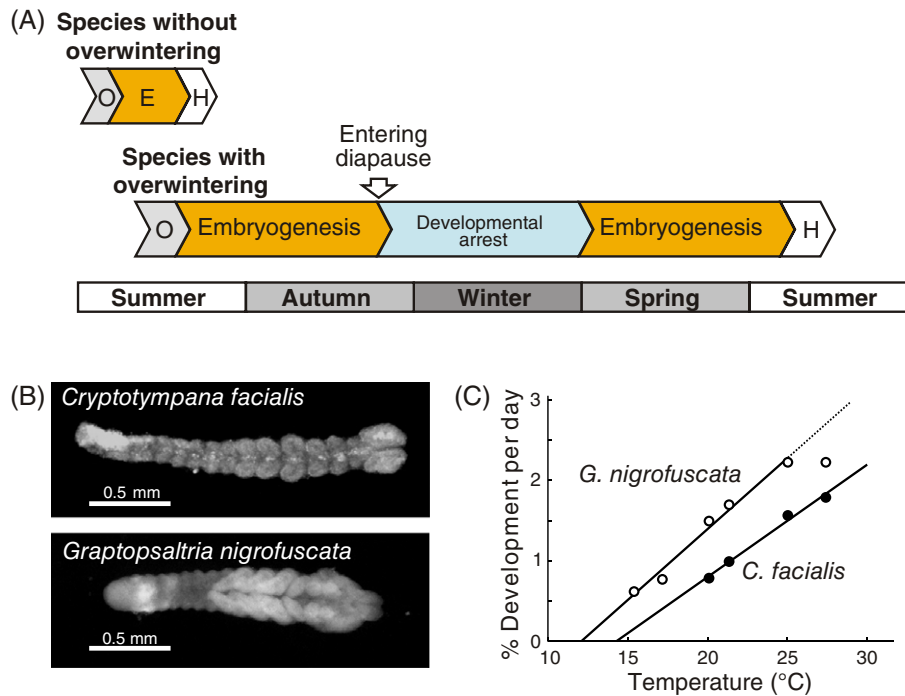
Fig. 1. Temperature regulation of embryonic development in temperate cicadas. (A) Schematic illustration of developmental courses for species with or without overwintering at the egg stage. In species with overwintering, temperature-dependent embryogenesis is arrested by entering diapause in a particular developmental stage. O, oviposition; E, embryogenesis; H, hatching. (B) The stages of embryonic diapause in two Japanese cicadas. (C) A relationship between temperature and developmental rates of the two cicadas. (B) and (C) are reproduced from Moriyama & Numata (2008) with permission from Elsevier. [Colour figure can be viewed at wileyonlinelibrary.com].

adaptive strategy that maximizes mating success between males assumed to have multiple-copulation and females assumed to have single-copulation (Saisho, 2010). Cicadas living in tropical regions where the temperature does not oscillate seasonally also show seasonal emergence patterns (Wolda, 1989). However, there are no consistent correlations of their emergence with other climatic factors, and the regulatory mechanism remains unknown.

The relationship between temperature and development rate has been shown more precisely for embryonic development than for nymphal development. Cicadas lay their eggs into live or dead tissues of host plants depending on the species (Beamer, 1928; Myers, 1929; White & Lloyd, 1981; Moriyama *et al.*, 2016). Eggs of some species hatch after several weeks of development, and their developmental period is shortened at higher ambient temperature (Azuma, 1976; Williams & Simon, 1995; Strauss & Lakes-Harlan, 2006) (Fig. 1A). Eggs of some temperate species hatch in the summer of the next year after overwintering, and their egg periods are prolonged up to 10–12 months (Beamer, 1928; Kato, 1956) (Fig. 1A). The regulatory mechanisms of the long embryonic development were studied in detail in two Japanese cicadas, *C. facialis* and *G. nigrofuscata* (Moriyama & Numata, 2008). In these species, embryogenesis stops at a particular developmental stage (Fig. 1B). This programmed developmental arrest (i.e. diapause) is effectively terminated by exposure in winter to low temperature, as observed in winter diapause of many other

species (Danks, 1987). Thereafter, post-diapause embryonic development is initiated when the ambient temperature exceeds the lower developmental threshold in the next spring, and proceeds as a function of temperature (Fig. 1C). Notably, it was found that the long egg periods of these cicadas are a result of their extraordinarily slow developmental rate among insect eggs (Honěk, 1996), rather than to prolonged diapause. By contrast to nymphal development, embryonic development is a process free from nutritional constraint, implying that cicadas possess an inherent system for keeping low developmental rates, which can be speculated to involve enzymes optimized for slow metabolism.

Effects of climatic factors on adult behaviour

Temperature also has a substantial influence on adult behaviours, such as flight, oviposition and calling. In ectothermic insects, appropriate behavioural performance is generally possible in a restricted body temperature range between lower and upper lethal temperature limits (Chown & Nicolson, 2004) (Fig. 2). Intensive studies on the thermal biology of adult cicadas have been performed across the globe, and the accumulated knowledge has been summarized in detail (Heath *et al.*, 1971; Sanborn, 2002; Sanborn *et al.*, 2017). These previous studies have rigorously collected the records of the temperature responses of hundreds of cicada species living in North
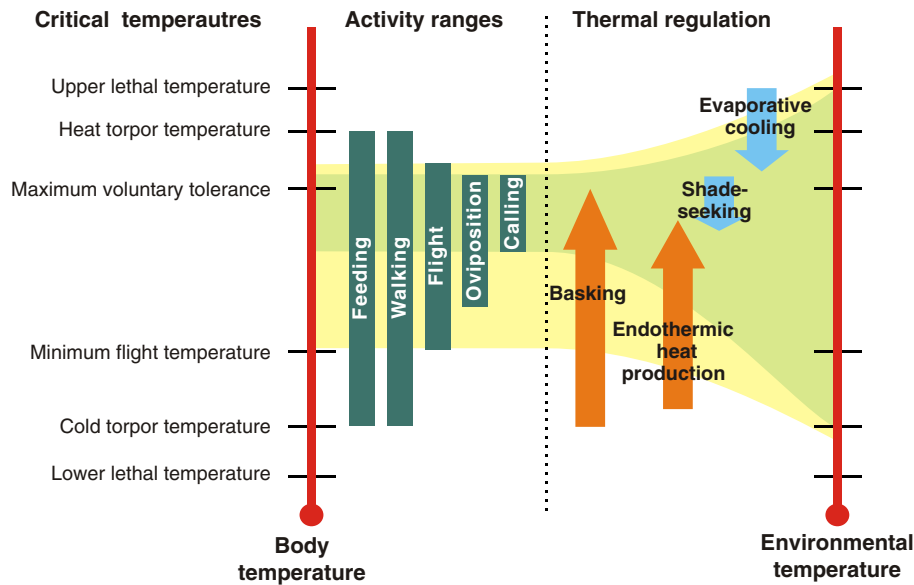
Fig. 2. A schematic illustration of thermal physiology in adult cicadas. Each activity is performed in a limited range of the body temperature between the lethal limit temperatures (green bars). Cicadas can regulate their body temperature in both upward (orange arrows) and downward directions (light blue arrows) by employing behavioural and physiological mechanisms. These mechanisms allow them to maintain their body temperature in the relatively narrow range and to perform suitable activities over a broader range of environmental temperature (right versus left temperature gauges). Image adapeted from Heath *et al.* (1971), Sanborn (2002) and Chown & Nicolson (2004). [Colour figure can be viewed at wileyonlinelibrary.com].

America (Sanborn *et al.*, 2017), Australia (Sanborn *et al.*, 2004a), South America (Sanborn *et al.*, 1995a, 2004b, 2011a), Africa (Sanborn *et al.*, 2003a) and Europe (Sanborn *et al.*, 2011b). The records mainly include (i) minimum flight temperature, above which cicadas are able to perform flight activity; (ii) maximum voluntary tolerance temperature, at which cicadas attempt to escape from a heat source or are motivated to shift to shade-seeking behaviour (see below for details); and (iii) heat torpor temperature, which induces a behavioural failure and thus indicates an upper limit for ecologically relevant activities (Fig. 2). The minimum flight temperature appears to be related to morphological parameters of the flight apparatus, rather than adaptation to the habitat climate (Sanborn, 2002). In the periodical cicada *Magicicada cassini*, at temperatures below their minimum flight temperature (20.7–20.9 °C) (Heath, 1967; Sanborn & Heath, 2009) adults withstand predators by remaining stationary or escape by dropping down (Langley *et al.*, 2010). Above this lower thermal limit, a higher temperature causes a higher proportion of cicadas to escape by flying away.

Calling is the behaviour most sensitive to body temperature change and is performed only in a narrow temperature range (Fig. 2). Known temperature ranges for calling vary from 2.2 to 11.2 °C depending on the species (Sanborn *et al.*, 2011c). Sound properties, such as frequency, pulse rate and sound intensity, are crucial for mate attraction (Doolan & Mac Nally, 1981; Doolan & Young, 1989; Sueur *et al.*, 2006; Fonseca & Correia, 2007) and species discrimination (Marshall & Cooley, 2000; Fonseca & Revez, 2002; Sueur, 2002; Sanborn *et al.*, 2002a; Sueur & Aubin, 2003). Thus, the calling sound should be tuned correctly. Sound production of cicadas is achieved by a highly sophisticated system requiring coordination of the

nerves, muscles, tymbal and amplification/resonance apparatus (Pringle, 1957; Young & Bennet-Clark, 1995). Nerve and muscle activities are sensitive to temperature, causing a temperature-dependent change in sound properties of calling songs (Sanborn, 2001). For example, it is reported that sound intensity increases at elevated body temperature in *Neotibicen winnemanna* and three *Tibicina* species (Sanborn, 1997; Sueur & Sanborn, 2003). Temporal parameters of a sound, such as the duration and interval of pulsed sound elements, can be influenced by temperature (Fonseca & Revez, 2002). On the other hand, the frequency is considered to be determined by the structural properties of the sound-producing apparatus (Bennet-Clark & Young, 1992) and thus is relatively robust against temperature change (Marshall & Cooley, 2000; Villet *et al.*, 2003; Sanborn *et al.*, 2011c). The relationship between temperature and calling songs is sometimes more complicated. In the bladder cicada *Cystosoma saundersii*, the tymbal muscle is warmed up as the singing progresses, leading to more rapid and stronger muscle responses and, consequently, causing a sound pattern shift (Josephson & Young, 1979). Song types can be changed from warm-up buzzes to slow songs to fast songs with increasing body temperature in *N. winnemanna*, in which warming of the tymbal muscle is considered to be necessary for fast song production (Sanborn, 1997, 2001). However, the calling songs of cicadas are influenced by multiple factors, and the temperature responses for sound construction are not always consistent among the species (Sanborn & Maté, 2000; Fonseca & Revez, 2002; Sanborn *et al.*, 2002b, 2011c).

Oviposition behaviour, a parameter directly associated with fitness, is also a temperature-sensitive process. Many cicadas lay eggs into twigs or bark of trees, whereas some species lay eggs

in stems of herbaceous plants. Before oviposition, females need to grip the substrate tightly and make a hole in the relatively hard wood tissues by using a spear-shaped ovipositor (Myers, 1929; Moriyama *et al.*, 2016). Thus, egg nest production is likely to be possible in a body temperature range optimal for muscular performance (Hastings & Toolson, 1991). A comparative study between *Cacama valvata* and *Hadoa bifidus* demonstrated that the reproductive output is greatly influenced by temperature, and species-specific performance curves convincingly reflect these species' geographical distributions (Toolson, 1998).

Ecophysiological adaptations to naturally fluctuating environments

As noted above, temperature has a crucial influence on the physiological processes of cicadas. There is ample evidence that the thermal responses of cicadas are adjusted to diverse habitat environments. In addition, cicadas are known to possess behavioural and physiological abilities with respect to regulating their body temperature against a naturally fluctuating temperature.

Adjusting thermal responses

Comparative analyses of thermal response records from hundreds of cicada species revealed that the heat torpor temperature and the maximum voluntary tolerance appear to be adjusted to the temperature range actually experienced by a given species in the adult period (Sanborn, 2002; Sanborn *et al.*, 2011d, 2017). Such a species-specific configuration of thermal responses may play roles not only in determining their geographical distribution patterns, but also in forming sympatric segregation patterns based on microhabitat structure (Hastings & Toolson, 1991; Sanborn *et al.*, 2003a, 2004a, b), emergence phenology (Sanborn *et al.*, 2017), and time of daily activity (Sanborn, 2000; Sanborn *et al.*, 2002a).

Behavioural regulation of body temperature

The behavioural regulation that most cicadas employ is basking in the sun (Sanborn, 2002). This utilization of solar radiation is a cost-effective way of obtaining heat energy. In some situations, basking adults can attain a body temperature 10 °C higher than the ambient temperature (Heath *et al.*, 1972; Sanborn, 2000). The warming up by basking is often required for reproductive activities such as male calling (Heath, 1967) and oviposition (Yang, 2006), for which optimal body temperature is often considerably higher than ambient temperature (Hastings & Toolson, 1991) (Fig. 2).

After attaining a desirable body temperature, cicadas change their orientation relative to the sun or switch to shade-seeking behaviour to avoid overheating (Sanborn, 2002). In *Magicicada cassini*, the amount of solar radiation received is controlled by holding the wings in the open or closed position (Heath, 1967). In addition, body surface colour is an important feature to regulate the efficiency of heat gain (Clusella-Trullas *et al.*, 2007). The desert-inhabiting cicadas *Cacama valvata* and *Okanagades gracilis* hold their ventral side, which is covered with white wax-like materials, toward the sun to reflect solar radiation when the body temperature exceeds an optimal range (Heath *et al.*, 1972; Sanborn *et al.*, 1992).

Physiological regulation of body temperature

Cicadas are principally ectothermic animals that primarily rely on external heat sources of ambient temperature and solar radiation load. However, some cicadas can use endogenously produced heat for body-temperature regulation. These endothermic cicadas are known to be able to elevate their body temperature up to a level comparable with that of solar basking ectothermic species (Sanborn *et al.*, 1995a, b, 2004c; Sanborn, 2000). Heat energy is generated by activation of flight muscles without flying, comparable with the shivering observed in true endothermic animals (Bartholomew & Barnhart, 1984; Sanborn *et al.*, 1995b, Sanborn, 2000). Several South African platypleurine cicadas generate heat by telescoping pulsation of the abdomen (Villet *et al.*, 2003; Sanborn *et al.*, 2003b, 2004c). Singing activity can be another source of heat (Josephson & Young, 1979; Mac Nally & Young, 1981). For example, in an endothermic species, *Neotibicen winnemanna*, buzzing and slow song production elevate body temperature, permitting performance of the full song (Sanborn, 1997). However, the warming-up effect of the tymbal muscle activity is negligible in some species (Fonseca & Revez, 2002). Endogenous heat production consumes considerable resources and is energetically expensive (Bartholomew & Barnhart, 1984; Sanborn *et al.*, 1995a, b). However, it enables cicadas to utilize the period that is unavailable for sympatric ectothermic competitors or to escape from sudden attacks by endothermic predators.

Some cicadas living in hot regions employ an interesting thermoregulatory mechanism. At a high ambient temperature above the optimal activity range, they decrease their body temperature by enhancing water evaporation from the body surface, such as by sweating in mammals (Toolson, 1987; Hadley *et al.*, 1991; Sanborn *et al.*, 1992). They bear many pores on the dorsal exoskeleton of the thorax and abdomen, from which water is extruded to evaporate. Thoracic temperature can be maintained approximately 5 °C below the ambient temperature during evaporative cooling, protecting insects from high-temperature otherwise lethal conditions (Sanborn, 2002). Some cicadas living in mild and humid climates also possess similar pore-like structures (Toolson & Toolson, 1991). Their cooling ability, however, is quite limited, and thus these apparatuses are considered to be a trace of the ancient function because of their tropical origin. Generally, in insects, such evaporative cooling is not favoured for body temperature regulation because of the limited water reserves in small insect bodies (Chown & Nicolson, 2004). Cicadas are xylem sap feeders, which extract nutrition from a large amount of dilute food source, and thus have access to an excess of water. This feature may facilitate the evolution of evaporative cooling mechanisms among cicadas living in a hot climate.

Adaptation to precipitation

Besides temperature, precipitation has a great influence on cicada fitness, especially in important life-cycle events, including adult eclosion and hatching. Heavy rain during adult eclosion is likely to cause a fatal defect to fragile expanding adults. It is commonly observed that, just before emergence, final-instar nymphs wait in a subterranean tunnel until the weather conditions become favourable (Alexander & Moore, 1962; Williams & Simon, 1995).

The most challenging period in the life cycle of cicadas comes at the beginning phase of the nymphal stage (Ito & Nagamine, 1981; Karban, 1997). Newly hatched nymphs have a difficult task to burrow into the soil before they are hunted by enemies such as ants and to search out a suitable rootlet for the subsequent nymphal development (Karban, 1984; Moriyama & Numata, 2006). Mortality in this critical period can be as high as 98% in the periodical cicadas *Magicicada* spp. (Karban, 1997) and a sugarcane pest cicada, *Mogannia minuta* (Ito & Nagamine, 1981). In some species, including *C. facialis*, egg hatching has been shown to be triggered by external moisture (Beamer, 1928; Moriyama & Numata, 2006, 2011). This mechanism allows nymphs to hatch on rainy days, when they successfully burrow into the wet, soft soil; otherwise, nymphs are faced with a high risk of predation and desiccation on the hard-to-penetrate dry soil (Moriyama & Numata, 2006).

Impact of recent climate change on cicada fauna

Broad impacts on insect communities by recent climate change, mainly represented by global warming, have been documented (Hughes, 2000; Walther *et al.*, 2002). The most widely accepted biological responses to climate change include poleward shifts of distribution ranges (Parmesan *et al.*, 1999; Hickling *et al.*, 2006), phenological shifts of biological events (Parmesan & Yohe, 2003; Root *et al.*, 2003), extirpation of local populations (Hughes, 2000) and outbreaks of pest insects (Breshears *et al.*, 2005). The physiological mechanisms underlying these ecological changes appear to be diverse at the taxon or community levels. Therefore, studies of individual features of insect life-cycle strategies are required. Until now, only a limited number of studies have addressed these issues in cicadas.

Observed responses to recent climate change

In Japan, the calling songs of cicadas are traditionally recognized as a feature of summer. The Japan Meteorological Agency has collected long-term records of the first singing date for several cicada species. Statistical models have demonstrated that recent warming caused an advance of the emergence date of six Japanese cicada species at the rate of 3.13–4.65 days for every 1 °C elevation in temperature, whereas precipitation does not have a significant relationship with emergence date (Ellwood *et al.*, 2012). This warming-driven phenological shift is likely the result of an acceleration of nymphal development, as predicted by Sato & Sato (2015).

A climatic influence on cicada fauna has become apparent in relation to urbanization. In highly urbanized areas, air temperature is further elevated by the urban heat island effect in addition to global warming. This local acceleration of the warming effect can provide a forecast of biological responses to future global warming, even though the urban heat island effect is not perfectly homologous to global warming caused by greenhouse gases. Two ubiquitous cicadas in the Korean Peninsula, *Cryptotympana atrata* and *Hyalessa maculaticollis* (Hyalessa *fuscata*), are known to form colonies of higher density in urban areas than in peripheral rural areas in Seoul (Kim *et al.*, 2014; Nguyen *et al.*, 2018). Nguyen *et al.* (2018) found that the higher density is most strongly correlated with ambient temperature among various environmental factors. It was speculated that higher urban temperature supports the larger population by increasing fecundity and decreasing winter nymphal mortality, although the causal relationship remains to be tested. In North America, the adult body size of the periodical cicadas living in the northern part of the distribution range is predicted to be relatively small as a result of the slow growth rate in the cooler climate (Koyama *et al.*, 2015). However, cicadas residing in urban sites have a larger body size even in the northern regions (Beasley *et al.*, 2018).

Ecophysiological evidence: an example in Osaka

A drastic species composition change in cicada fauna has appeared in the southwestern part of Japan, remarkably in urbanized regions. The most prominent case of community degradation has been observed in Osaka, where the diversity of cicadas was lost as a result of domination by a single native cicada, *C. facialis* (Fig. 3). The extensive infestation of *C. facialis* in residential areas brought about new social problems. First, these cicadas start to make loud and noisy songs at sunrise. The sound intensity of singing males exceeds 90 db (Cyranoski, 2007; Numata & Shiyake, 2007). Second, some adult females try to lay eggs mistakenly into optical fibre cables instead of twigs. This strange behaviour resulted in more than 1000 fibre network breakages per year (Holden, 2007). Consequently, a new type of optical fibre cable resistant to *C. facialis* was developed and used to replace the existing cables (Itou *et al.*, 2010).

Then, using ecophysiological approaches, we addressed causal mechanisms underlying this cicada community degradation in Osaka. The infestation of *C. facialis* is considered to have taken place during the late 20th Century (Numata & Shiyake, 2007). In this period, by a combination of global warming and the urban heat island effect, the air temperature increased by 0.29 °C per decade in Osaka. Because the geographical distribution range of *C. facialis* is located in more southern regions compared with other sympatric cicada species, climate warming was assumed to be a primary cause of *C. facialis* infestation. We first tested the most intuitive hypothesis that the warming directly improved overwintering survival of warm-adapted *C. facialis* by mitigating winter cold. Cold tolerance of overwintering eggs of *C. facialis* was investigated together with that of the formerly most prevalent species, *G. nigrofuscata* (Moriyama & Numata, 2009). Although they also experience winter during

Fig. 3. A representative photograph depicting the recent domination of cicada fauna by *Cryptotympana facialis* in Osaka. In urban sites, the population of *C. facialis* (white arrows) drastically increased during the late 20th Century, whereas the other native cicadas, including the formerly most prevalent species, *Graptopsaltria nigrofuscata* (grey arrow), were overwhelmed. [Colour figure can be viewed at wileyonlinelibrary.com].

coincides with that of either the early-summer or autumn rainy season depending on the species but not with the low-rainfall period in mid-summer (Moriyama & Numata, 2011). The synchrony of potential hatching time windows with rainy seasons is reasonable because all of these species hatch in response to rain (Moriyama & Numata, 2006, 2010, 2011). Experimental shifts of potential hatching time windows of *C. facialis* confirmed a strong influence of synchrony with rainy seasons on their fitness. The hatching rates dropped to approximately 10% in the mid-summer dry season, whereas they were approximately 70% in the rainy season (Moriyama & Numata, 2011). Estimation of the hatching time in the past clearly illustrated the process of how warming improved the synchrony of hatching time and rainy season in *C. facialis* (Fig. 4). These findings suggested that a phenological shift as a result of climate warming may support stable population growth prerequisite for the consequent infestation of *C. facialis*. Consistent with our findings, the current distribution pattern of *C. facialis* is well predicted by a computational model that takes into account the probability of synchrony between hatching time and rainy season precipitation (Saito *et al.*, 2016).

Besides the essential effect of temperature increase, several other factors have been proposed to cooperatively contribute to the drastic cicada community change in Osaka. For example, habitat fragmentation in urban areas confers a different predation risk between *C. facialis* and *G. nigrofuscata*, which have different escaping behaviours (Takakura & Yamazaki, 2007). Endo & Osawa (2018) highlighted the possibility that acoustic interference from *C. facialis* has a negative effect on a sympatric *G. nigrofuscata* population. From a habitat survey across an urban–forest gradient in Osaka, it was shown that soil hardness is the most relevant habitat factor to the species composition, and that urban sites with greater soil hardness tend to be more dominated by *C. facialis* with decreasing cicada diversity (Moriyama & Numata, 2015). This is consistent with the finding that first-instar nymphs of *C. facialis* show outstanding performance in burrowing among the native cicada species, indicating that soil compaction as a result of urbanization may act preferentially toward *C. facialis* (Moriyama & Numata, 2015).

the nymphal stages, underground nymphs are unlikely to be subjected to severe cold as a result of the thermal insulation of soil (Hoshikawa *et al.*, 1988). We measured tolerance to three types of cold: short-term (24 h) cold tolerance to sub-zero temperatures, long-term (up to 30 days) exposure to moderate cold and naturally fluctuating winter cold. The results of all these experiments suggested that eggs of *C. facialis* possess an adequate capacity for tolerating any low temperatures recorded in Osaka, although we found that eggs of *C. facialis* are less able to withstand extremely low temperature compared with *G. nigrofuscata* (Moriyama & Numata, 2009).

Next, we focused on the hatching phenology of cicadas because hatching time is predicted to be shifted by warming via accelerated embryonic development, as described above (Moriyama & Numata, 2008). From the assessment of the hatching time of five cicada species living in Osaka, we found that, in the current temperature regime of Osaka, their hatching time

Cicada responses to predicted future climate change

As noted above, body size increase, phenological advancement, population density change, species composition change and diversity loss have been recognized as perceivable responses of cicada communities to the climate change that has already taken place in cicada communities. The Intergovernmental Panel on Climate Change predicts that further temperature increases and other accompanying effects will be inevitable during the 21st Century (IPCC, 2014). Here, we attempt to present potential influences of future climate change on cicada fauna based on the current knowledge.

First, there have been attempts to predict the future distribution change by exploiting climate envelope models, which could be improved by considering temperature responses based on important life-history traits, such as egg production (Toolson,
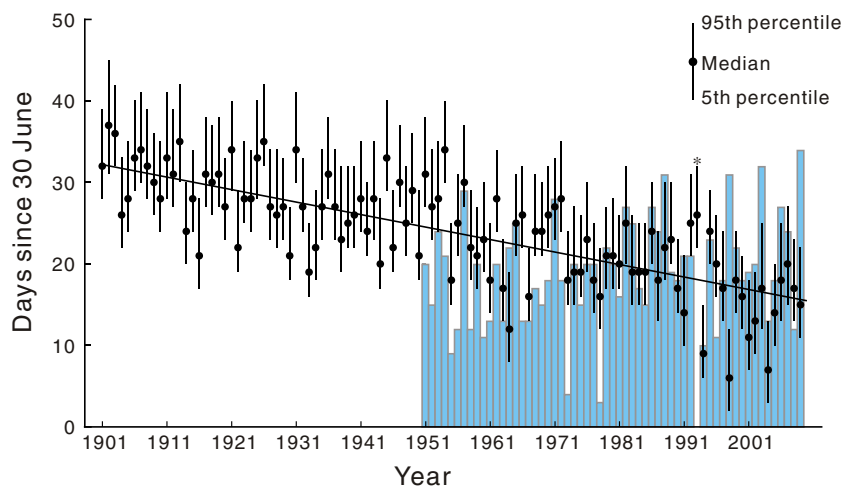
Fig. 4. Warming-driven phenological shift in hatching time improves synchronization with the rainy season in *Cryptotympana facialis*. The potential hatching time (black circles and lines) was estimated using meteorological records and a day-degree-based temperature response curve for embryonic development of this species. The hatching time is drawn together with the range of the rainy season (blue bars). The records of rainy season before 1950 and in 1993 (marked by an asterisk) were not available. It is shown that the warming-driven phonological shift improved synchrony between the hatching time and the rainy season in the 1980s and thereafter (Moriyama & Numata, 2011). [Colour figure can be viewed at wileyonlinelibrary.com].

1998) and hatching synchrony (Saito *et al.*, 2016). Both the model built for 17-year *Magicicada* species in North America (Cooley *et al.*, 2013) and the model built for *C. facialis* in Japan (Saito *et al.*, 2016) agreed that temperature is the most reliable predictor of the current distribution range. Although the climate envelope models predict that warming may potentially cause a poleward shift of their distribution ranges, it was emphasized that habitat expansion may progress less than expected as a result of increasing climate extremes and limited dispersal abilities of cicadas (Karban, 1981; Numata & Shiyake, 2007; Cooley *et al.*, 2013; Saito *et al.*, 2016).

Climate change can have opposite influences on sympatric species as a result of the different adaptive strategies employed by individual species and also because inter-specific interactions. For example, male calling activity is allowed within a highly limited temperature range that is different for different species (Sanborn *et al.*, 2011c). This elaborate tuning of this reproductive activity has been shown to be required not only for mate attraction of conspecific females (Doolan & Mac Nally, 1981; Fonseca & Correia, 2007), but also for segregation among sympatric species by appropriate exhibition of a species-specific song character or by use of a different time of day (Marshall & Cooley, 2000; Fonseca & Revez, 2002; Sueur, 2002; Sanborn *et al.*, 2002a). Sympatric species also appear to segregate microhabitat use finely by setting a species-specific optimum for temperature tolerance (Sanborn, 2002; Sanborn *et al.*, 2017). Rapid warming will disrupt these balances of sympatric speciation, and this may cause diversity loss. As observed in Osaka (Moriyama & Numata, 2011, 2015), a population increase of a particular species because of climate change may impose aberrant interspecific competition pressures such as sound interference (Endo & Osawa, 2018) and subterranean nymphal competition (Karban, 1984; Lehmann-Ziebarth & Heideman, 2005) on sympatric species.

Warming can influence symbiotic interactions between microbes and cicadas. Plant sap-feeding hemipteran insects usually harbour particular microbes essential for growth and reproduction of the host insects (Moran *et al.*, 2005). Cicadas are known to have symbiotic bacteria and fungi, which are considered to supply nutrients in which xylem fluid is deficient, such as essential amino acids and vitamins (McCutcheon *et al.*, 2009a, b; Christensen & Fogel, 2011; Matsuura *et al.*, 2018). However, these symbiotic relationships have been shown to be vulnerable to high temperature caused by climate warming in some hemipteran insects (Prado *et al.*, 2010; Kikuchi *et al.*, 2016), as known in the famous example of coral bleaching (Baird *et al.*, 2009; Ainsworth *et al.*, 2016). In cicadas, warming-driven symbiotic degradation may be a potential cause of a collapse of southern boundary populations.

Besides warming, precipitation is an indispensable factor, especially for the establishment of nymphal growth (Beamer, 1928; Moriyama & Numata, 2006, 2011). At least in some cicadas, synchrony between hatching time and rainy season appears to be critical for a stable population increase (Moriyama & Numata, 2011). Increasing heterogeneity or uncertainty in future precipitation patterns (IPCC, 2014) may disrupt established synchrony between hatching and rainy season. Moreover, an increasing trend of heavy precipitation can increase a catastrophic risk to nymphs by flooding of their underground nests.

Conclusions and perspectives

The studies introduced in this review highlight the fact that behavioural and physiological activities of cicadas are fine-tuned to a particular temperature optimum as a species-specific life-cycle strategy, and that this attunement forms the foundation of maintaining cicada diversity. Although the influence of climate change on cicada fauna is

becoming apparent, causal relationships between them have been revealed only in limited cases. Future studies will need to carry out continuous assessments that indicate population- and community-level responses to upcoming climate change, and to unveil mechanistic links between physiological traits and ecological consequences.

There is already some evidence of genetic adaptation of insects to recent climate change (Hoffmann, 2017; Garnas, 2018). Until now, such adaptation has not been reported in cicadas, although there are some suggestions of adaptation to urban sites by larger body size (Beasley *et al.*, 2018; Nguyen *et al.*, 2018) and higher song frequency (Shieh *et al.*, 2012). Considering the long generation time of cicadas, rapid evolution is less likely compared with that in short-lived insects. Taken together with cicadas' limited dispersal ability and delicate temperature sensitivity, this implies that cicadas are highly susceptible to climate change. As a result of their conspicuous nature, cicadas are a promising bioindicator insect for environmental change, and the change in their calls has already been perceivable by the public in some cities. Cicadas' call songs will be a potential alarm for ecosystem degradation as a result of climate change.

Acknowledgements

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