



## Research

# Documenting Single-Generation Range Shifts of Periodical Cicada Brood VI (Hemiptera: Cicadidae: *Magicicada* spp.)

John R. Cooley,<sup>1,3,✉</sup> David C. Marshall,<sup>2</sup> and Chris Simon<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, The University of Connecticut–Hartford, Hartford, CT 06103, USA, <sup>2</sup>Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, CT 06269, USA, and <sup>3</sup>Corresponding author, e-mail: [cicada@uconn.edu](mailto:cicada@uconn.edu)

Subject Editor: Katherine Parys

Received 2 December 2020; Editorial decision 17 February 2021

## Abstract

Historically, most North American periodical cicada (Hemiptera: Cicadidae: *Magicicada* spp. Davis 1925) distribution records have been mapped at county-level resolution. In recent decades, *Magicicada* brood distributions and especially edges have been mapped at a higher resolution, aided by the use of GIS technology after 2000. Brood VI of the 17-yr cicadas emerged in 2000 and 2017 and is the first for which detailed mapping has been completed in consecutive generations. Overlaying the records from the two generations suggests that in some places, Brood VI expanded its range slightly between 2000 and 2017, although the measured changes are close to the lower limit of detectability given the methods used. Even so, no simple alternative to range expansion easily accounts for these observations. We also bolster Alexander and Moore's assertion that *M. cassini* does not occur in Brood VI.

**Key words:** range shift, historical range map, climate change, historical record, periodical cicada

Species range shifts are an active area of research, fueled by the urgency of understanding how species might respond to projected climate change (Menendez 2007). Quantifying range shifts, however, is difficult because of the challenge of using point data to infer species ranges (Yalcin and Leroux 2017) and the inherent biases of methods that infer change by comparing historical records (including museum specimens) and contemporary range maps (e.g., Parmesan 1996). The periodical cicadas (Hemiptera: *Magicicada* Davis 1925) of eastern North America are potentially useful bioindicators, since they are key components of eastern temperate deciduous forest biomes and have been mapped more thoroughly and for longer periods than most North American species (Cooley et al. 2013b). Periodical cicadas sidestep some of the pitfalls of inferring distributions and their shifts because they have been recently surveyed in extremely fine detail, so conclusions about their range shifts can be made on the basis of direct observation rather than on the basis of estimated ranges (Table 1).

*Magicicada* have life cycles of 13 or 17 yr and mass, periodical emergences termed ‘broods’ each of which represents a year-class and is designated by a Roman numeral reflecting its life cycle and

emergence order. The 15 extant broods fit together somewhat like puzzle pieces (Marlatt 1902; Fig. 1). Although periodical cicada emergences have been mapped in great detail, attempts to make generalizations about brood ranges are problematic. For example, Stannard (1975) delineated ranges for periodical cicada broods in Illinois, but his inferred ranges were based on few data points and have not stood up to more detailed examination (Cooley et al. 2013a). Given that periodical cicada broods are known to have complex, interdigitating ranges, unless the underlying data are extremely fine grained, the assumptions involved in connecting data points to construct range maps could easily have overwhelming influence on any conclusions.

Although periodical cicada brood ranges are difficult to characterize, it is clear that they must have changed substantially over time. Many contemporary populations or even entire broods of periodical cicadas exist far north of the last glacial boundary, so periodical cicadas must have a history of confinement in and expansion from restricted glacial refugia (Sota et al. 2013, Fujisawa et al. 2018, Du et al. 2019). However, attempts to infer change by comparing historical and contemporary records have met with limited success.

Although different sets of published maps show different ranges, these mismatches can be as much due to methodological differences as to actual range shifts. For example, [Marlatt's \(1923\)](#) maps often suggest broader ranges than do [Simon's \(1988\)](#) maps of the same broods ([Fig. 2](#)), but that should not be taken as an unqualified indication that all brood ranges are shrinking; rather, the criteria for delineating brood boundaries in the two sets of maps are not the same (see [Supp Mater \[online online\]](#)).

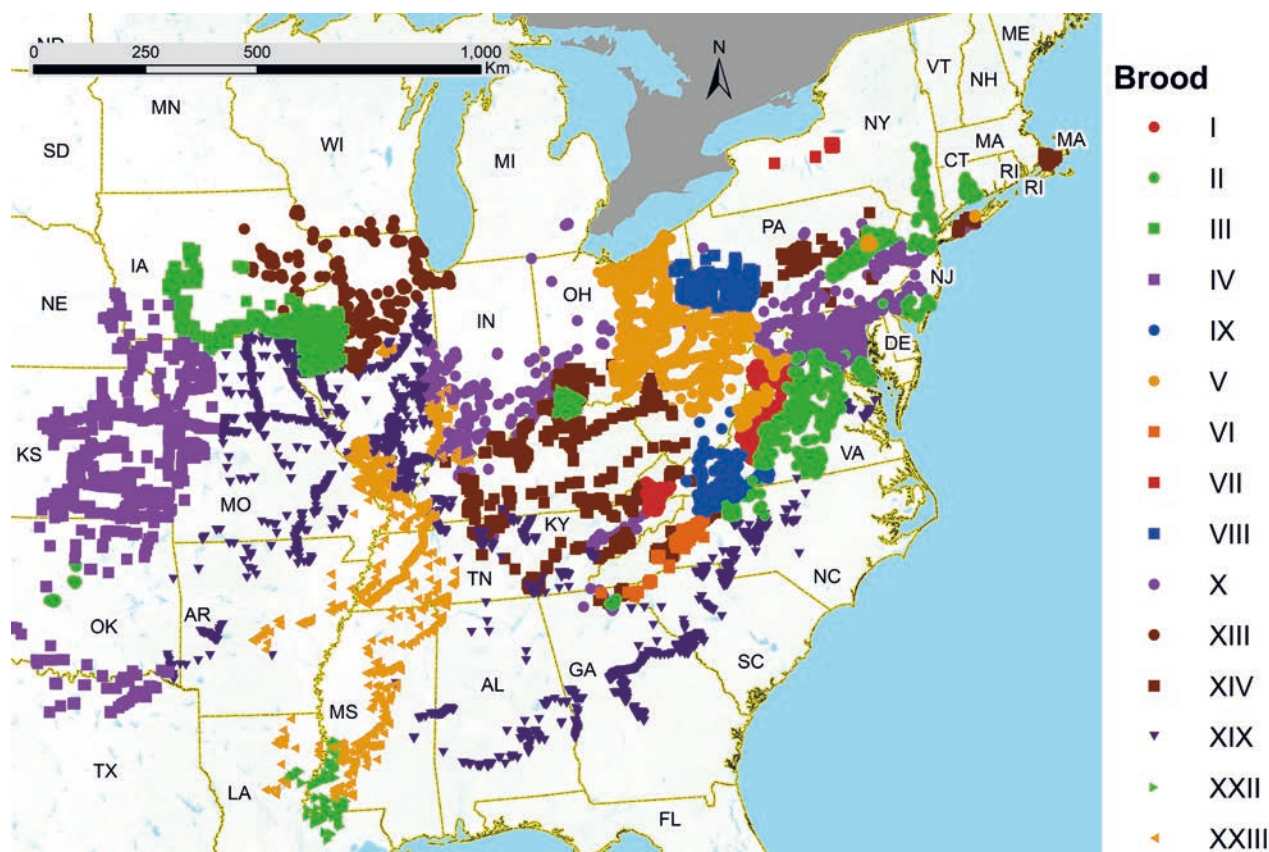
As part of our long-term project to map periodical cicada emergences, we made detailed maps of Brood VI in 2000 and 2017. Historical estimates of this brood's range vary widely. [Marlatt \(1923\)](#) stated that Brood VI was an 'unimportant scattering brood', with populations spread over eastern North America, from Georgia to Wisconsin and considerably overlapping other broods, though dense

populations of Brood VI were reported only in mountainous areas of North Carolina, southwestern South Carolina, and northeastern Georgia ([Marlatt 1898; Fig. 2](#)). [Maier \(1985\)](#) noted that many scattered eastern reports of Brood VI were likely attributable to misidentification or off-cycle emergences as hypothesized by [Lloyd and Dybas \(1966\)](#) and [Lloyd and White \(1976\)](#). [Marshall \(2001\)](#) extended this observation to scattered reports across the general range of periodical cicadas. Broods V, X, and II could each produce off-cycle stragglers in Brood VI emergence years via 1-yr delays, 4-yr early emergences, or 4-yr late emergences, respectively ([Lloyd and Dybas 1966](#), [Lloyd and White 1976](#), [Simon and Lloyd 1982](#), [Maier 1985](#), [Marshall 2001](#), [Marshall et al. 2011](#), [Cooley et al. 2018](#)), accounting for some of the confusion surrounding Brood VI. [Simon's \(1988\)](#) revised map of Brood VI confined it to a 'core' mountainous region in North Carolina, South Carolina, and Georgia, with all other populations doubtful ([Fig. 2](#)).

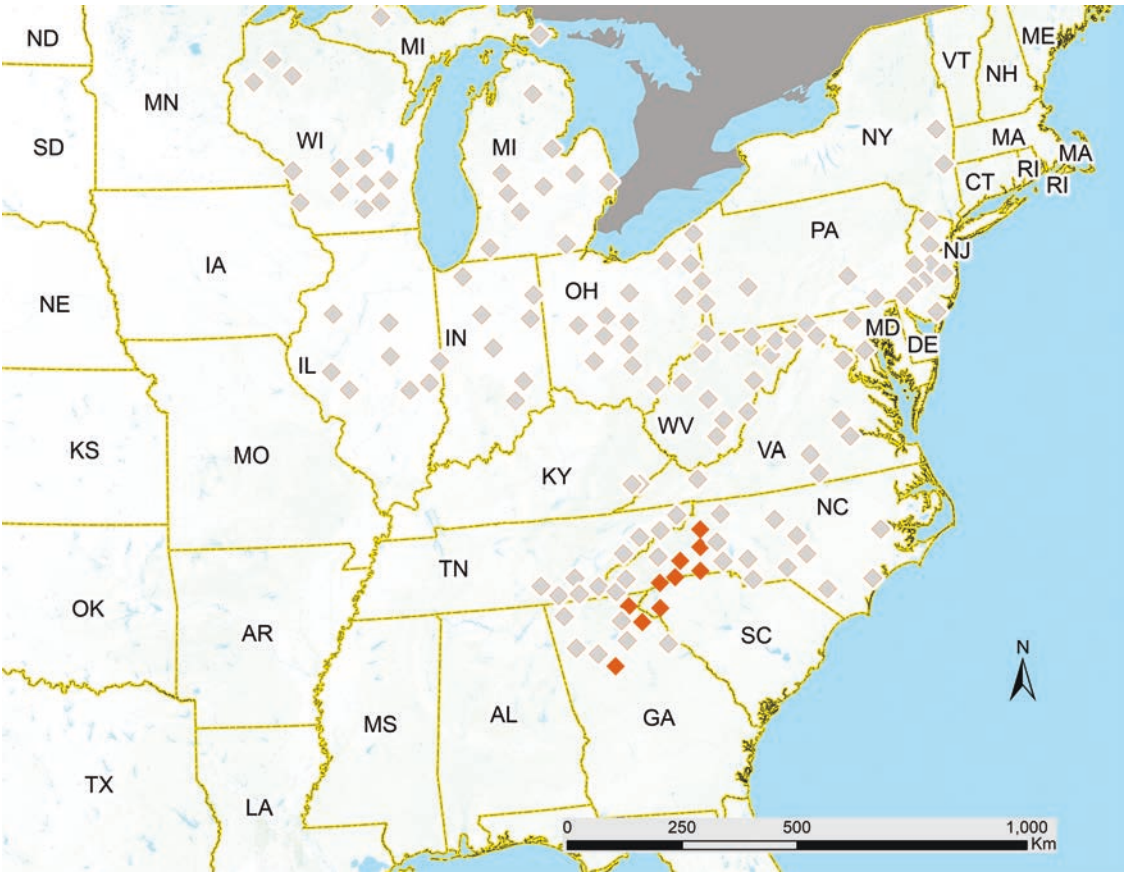
Although we did not make our 2000 and 2017 maps of Brood VI with the intent of detecting range changes, nevertheless, they provide an opportunity to examine the cross-generational stability of a brood's range while sidestepping some of the issues that have hampered past efforts. Our efforts also provide an opportunity to investigate another unusual aspect of this brood: although most 17-yr broods contain all three 17-yr species (*M. septendecim* (Linnaeus 1758), *M. cassini* (Fisher 1852) and *M. septendecula* Alexander and Moore 1962), a lack of museum specimens led [Alexander and Moore \(1962\)](#) to speculate that Brood VI does not contain *M. cassini* even though -cassini cicadas are found in neighboring 13- and 17-yr broods (ICZN 33.3.1 provides direct instructions upon how to act in cases of prevailing usage. Although '*cassini*' is the original spelling, usage of the '*cassini*' spelling appears to be more prevalent,

**Table 1.** Contemporary georeferenced brood maps

| Brood           | Publication                                                                       |
|-----------------|-----------------------------------------------------------------------------------|
| I               | <a href="#">Cooley (2015)</a>                                                     |
| II              | <a href="#">Cooley et al. (2015)</a>                                              |
| III             | <a href="#">Cooley et al. (2013a)</a>                                             |
| V               | <a href="#">Cooley et al. (2018)</a>                                              |
| VII             | <a href="#">Cooley et al. (2004)</a>                                              |
| X               | <a href="#">Cooley et al. (2009)</a>                                              |
| XIII            | <a href="#">Cooley et al. (2016)</a>                                              |
| XIV             | <a href="#">Cooley et al. (2011)</a>                                              |
| XIX (partial)   | <a href="#">Marshall and Cooley (2000)</a> , <a href="#">Cooley et al. (2001)</a> |
| XXII (partial)  | <a href="#">Kritsky et al. (2017)</a>                                             |
| XXIII (partial) | <a href="#">Cooley et al. (2006)</a>                                              |



**Fig. 1.** Verified records of all periodical cicada broods, based on published and unpublished georeferenced maps ([Table 1](#)).



**Fig. 2.** Brood VI county map redrawn from Simon (Simon 1988). Filled symbols represent counties with well-supported records; gray symbols represent counties reported in Marlatt (Marlatt 1923) for which there are unclear records or that have become extinct.

especially in the past 50 yr, so we adopt the ‘*cassini*’ spelling in this article, acknowledging that the original spelling is ‘*cassinii*’). Though no published project to date has deliberately searched for *M. cassini* in Brood VI, establishing its absence, as we have here, is key baseline information should the species be found at some later date.

Materials and Methods

2000 Records

Between 10 May and 23 May 2000, we collected ‘verified’ records by driving within the approximate published range of Brood VI (Simon 1988) looking for active periodical cicadas, noting species present and using criteria described in Cooley et al. (2013a) to classify our observations of full choruses, lighter choruses, single or scattered individuals, and absence of cicadas (Table 2). We did not take records if we were unsure about whether or not cicadas were present. Density information is essential for distinguishing ordinary emergences from possible ‘straggler’ or off-cycle emergences. Periodical cicadas depend on high population density and predator-swamping (White and Lloyd 1979; Lloyd and White 1980; Karban 1982a,b; Williams et al. 1993; Williams and Simon 1995; Marshall 2001), so records of single or scattered individuals are unlikely to represent sustaining populations. Lacking GPS technology in 2000, we marked presence and absence records on 1:150,000 paper maps (DeLorme 2012), placing our marks relative to the detailed information on road orientation, intersections, and other printed landmarks offered in this map series. In situations where cicada choruses were

**Table 2.** Density ratings by record type

| Record type               | Rating | 2000 count | 2017 count |
|---------------------------|--------|------------|------------|
| No cicadas present        | 0      | 260        | 877        |
| Cicadas heard in distance | 1      | 5          | 34         |
| Single cicada             | 2      | 1          | 16         |
| Scattered cicadas         | 3      | 5          | 280        |
| Light chorus              | 4      | 6          | 371        |
| Full chorus               | 5      | 147        | 932        |
| Total                     |        | 424        | 2,510      |

not immediately adjacent to roads, we designated their locations using guidance from the maps’ topography and forest cover features. While driving within the range of the brood and within appropriate habitat (deciduous forest), we recorded positive locations on the map at approximately 1-km or smaller intervals. We attempted to identify the edges of the emergence by collecting both positive and negative records, locating the edges of the brood with multiple flanking presence and absence records whenever possible. We digitized the maps in ArcGIS 10.5 (ESRI 2009) by transferring locations on the paper maps to locations on maps composed of US Census 2000 TIGER Line Data County-Level All Roads, Linear Hydrography, and Area Hydrography Shapefiles (US Census Bureau). Through trial and error, we estimate that this method has a resolution on the order of 200 m or better. We conducted all mapping activities under appropriate conditions for periodical cicada activity; weather in April and

**Table 3.** Summary of data points collected 2000–2017, with expected numbers of positive 2017 observations in each category based on the 2000 data

| Record type          | Records collected in 2000/<br>as percentage of positive records | Records Collected in 2017/<br>as percentage of positive records | Expected number of 2017 positives in each category based on 2000 data |
|----------------------|-----------------------------------------------------------------|-----------------------------------------------------------------|-----------------------------------------------------------------------|
| Negative (absence)   | 261                                                             | 880                                                             |                                                                       |
| One or a few cicadas | 6/3.77                                                          | 295/18.1                                                        | 61.5                                                                  |
| Light chorus         | 11/6.91                                                         | 404/24.79                                                       | 112.8                                                                 |
| Full chorus          | 142/89.31                                                       | 931/57.12                                                       | 1,455.7                                                               |
| Total positive       | 159                                                             | 1,630                                                           |                                                                       |

The actual number of each category of positive records in 2017 differed significantly from the predicted number ( $\chi^2 = 1,825.61$ , 2 df,  $P < 0.001$ ). If the 'light chorus' and 'full chorus' categories are combined, the 'one or a few cicadas' category is still overrepresented in the 2017 data ( $\chi^2 = 921.091$ , 1 df,  $P < 0.001$ ).

May 2000 was generally warm and sunny. Data from the year 2000 are summarized in Table 3.

### 2017 Records

During the next emergence of Brood VI, in the period spanning 29 April–12 June 2017, we and our collaborators collected data with handheld GPS units or custom GPS dataloggers that had a minimum resolution of approximately 10 m. When possible, we took records at roughly 150-m intervals, and sometimes as often as every 30–40 m (i.e., much more often than in the 2000 study). To the best of our abilities, and given limits imposed by time and weather, in 2017 we revisited data points taken in 2000 within a few calendar days of our earlier records, to minimize effects of emergence timing, which can vary across generations depending on spring conditions. In 2017, we also inspected counties in Wisconsin noted in Marlatt (1923) as having Brood VI; weather had prevented us from doing a thorough search of Wisconsin in 2000. In 2017, we used crowdsourced records from our website ([www.cicadas.uconn.edu](http://www.cicadas.uconn.edu)) to direct some of our mapping efforts (the website did not exist in 2000). Although individual crowdsourced records are not necessarily reliable, in aggregate they can help target search efforts and reveal previously unknown populations (Cooley 2015, Cooley et al. 2015). Data from 2017 are summarized in Table 3.

Estimating brood boundary changes by comparing our datasets is not straightforward, and we wanted to develop a method of estimating change that was conservative and that avoided the known biases in our data. Our data collection methods in 2000 and 2017 were not identical; our 2017 data set contains far more data points collected using GPS dataloggers, which we first used starting with Brood XIII in 2007 (Cooley et al. 2016). In 2017, our work was also guided by records we collected via a crowdsourcing website that did not exist in 2000; although we did not include any of these records in our final data set, we did use them to guide our mapping efforts. Our 2000 and 2017 data

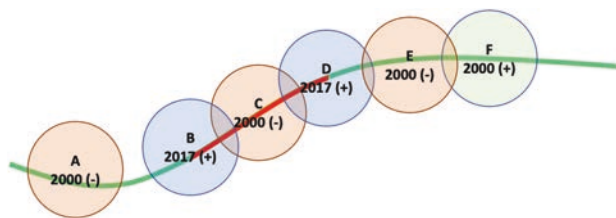
sets are not repeated visits to the same points; instead, they are repeated visits to local areas, in which points collected in 2000 and 2017 rarely fall on the exact same locations.

Perhaps most importantly, the arrangement of our data points along passable roads limits our ability to estimate brood boundaries. In some regions, such as parts of the Midwest, roads are arbitrarily arranged on a grid with roughly 1-mile spacing; these dense road networks make range-map construction relatively straightforward, with some reassurance that the arbitrarily arranged roads cross the actual brood boundaries in ways that roughly approximate unbiased sampling. In other regions, such as the Appalachians, roads generally follow ridges or valleys and form only sparse networks if they are interconnected at all. Since these landscapes are topographically complex on an extremely small scale, maps made using such feature-based road networks may be biased in ways that are not evident or easily quantifiable. For this reason, most standard methods of estimating distributions, either by drawing envelopes around our data points or by rasterizing or kriging our data set, are not good options, since they would make unwarranted assumptions about areas that we could not sample. Consequently, we developed two novel methods of estimating boundary changes that rely only minimally on inferences about presence or absence in unsampled areas.

In spite of the limitations of our data, some patterns bear explanation, such as instances in which the reported densities are not the same in both sampling years, or situations in which absence records from one year are closely associated with presence records from the other year. We used two methods focused on these patterns to quantify changes (if any) in brood distribution between 2000 and 2017. First, instead of an arbitrary, fixed raster grid, we built 'floating' raster-like neighborhoods placed only in locations where there were sufficient data from both 2000 and 2017. Based on Strang's (2013) estimate of a 52 ha minimum patch size for stable periodical cicada populations, we assumed that each positive record represented at the very least a minimum-sized viable patch. Accordingly, we constructed neighborhoods of 400 m radius around each record collected in 2000 and 2017 using the ArcGIS 10.5 'Buffer' tool (ESRI 2009); a 400-m-radius circle has an area of approximately 52 ha. For each such neighborhood, we assigned the reported density as the highest of any record from the same year found in that neighborhood. Then, we examined the records from the other sampling year that also fell in the 400-m neighborhood and found the record with the highest density. By comparing these records, we inferred whether the density decreased, stayed the same, or increased between 2000 and 2017. These inferences do not rely on any single record and are made only in locations where cicadas were present in both survey years.

We also estimated brood boundary changes by looking for situations in which negative records from one year (2000 or 2017) were flanked in close proximity by positive records from the other year. First, we rarefied the negative records by eliminating all negative records for which a positive record collected in the same year fell within a 400 m radius. We then used the ArcGIS 'Buffer' tool to construct a 400-m buffer around the remaining negative records and merged any overlapping buffers. Then, we searched for instances in which the buffered negative records from one year were overlapped by 400-m buffered positive records from the other year. In this manner, we constructed linear features connecting alternating sequences of negative records from one year with positive records from the other year (Fig. 3). This method is extremely conservative, since it prevents construction of features in areas where sampling was sparse. Because

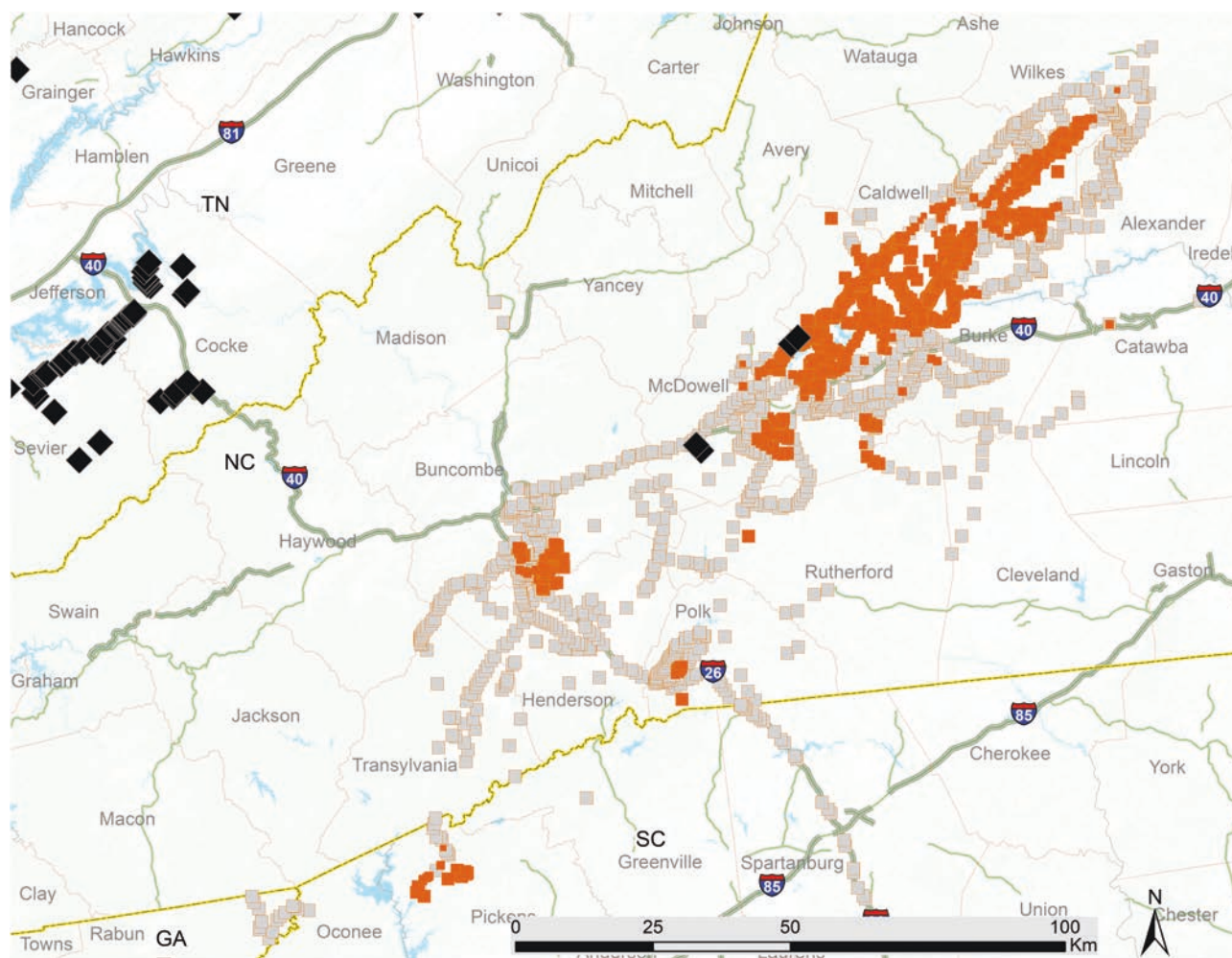
the sampling densities in 2017 were much greater than the densities in 2000, we a priori expect more examples of negative records taken in 2000 flanked by positive records taken in 2017, simply as a function of greater sampling effort in 2017. For that reason, counts of such instances are of no value; however, the lengths of these features are estimates of the minimum extent to which the range changed.



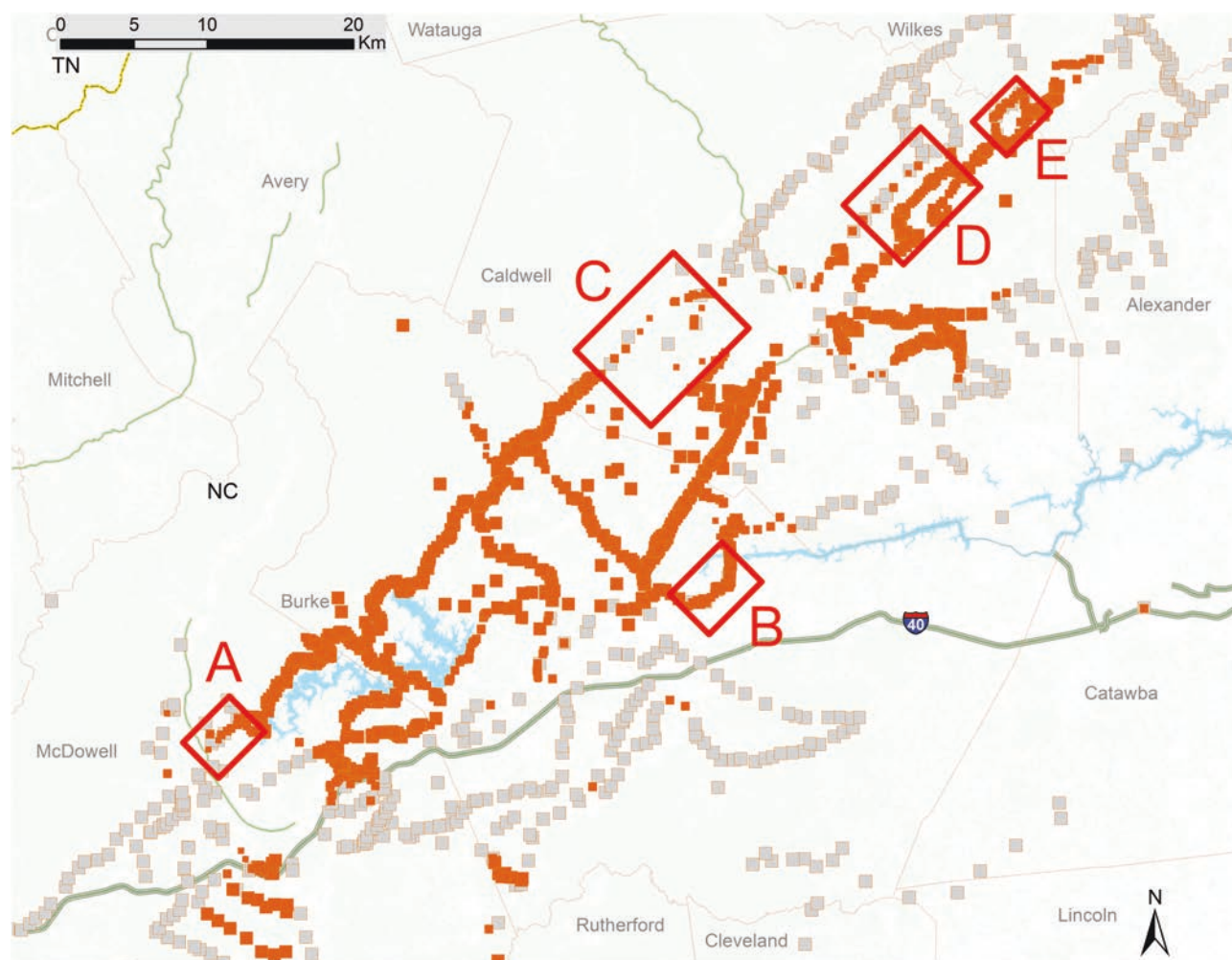
**Fig. 3.** Illustration of 'Linear Feature' method. Hypothetical sequence of records (A, B, C, D, E, and F) taken along the light grey (green in online version) road. Each has been buffered with a 400-m buffer. Records B, C, and D are connected to form a linear feature (shown in dark grey (red in online version)). Record A is not included, since its buffer does not overlap Record B. Record E is not included, because its buffer is overlapped by a positive record from the same year.

## Results

We found that Brood VI has a distribution similar to that shown in [Simon \(1988\)](#), extending roughly from Tiger, Georgia to Moravian Falls, North Carolina, with a gap separating populations in northeast Georgia from those in South Carolina and a larger gap separating these populations from the 'main body' of the brood in North Carolina ([Figs. 4 and 5](#)). Within each major segment of the brood, periodical cicadas were more or less continuously distributed within forested areas with no absences in appropriate habitat. We also found that the brood lacks *M. cassini* and contains only *M. septendecim* and *M. septendecula*; the latter sometimes forming dense, loud, apparently single-species choruses of continuous sound. The main body of Brood VI in North Carolina is not currently in contact with Brood II ([Cooley et al. 2015](#)) or Brood X ([Cooley et al. 2009](#)); our unpublished data from Broods IX and XIX also provide no evidence of contact with Brood VI. We did find extensive contact or slight overlap between North Carolina portions of Broods VI and XIV. Weather prevented us from searching for Brood VI in Wisconsin in 2000. In 2017, we only briefly searched Wisconsin counties recorded by [Marlatt \(1923\)](#) as having Brood VI periodical cicadas (an area roughly bounded by Dodgeville on the west, Janesville on the south, and the Wisconsin Dells on the north). We found no evidence of them in this region, although our search



**Fig. 4.** Verified Brood VI locality records (square symbols). Filled symbols are positive (presence) records; gray symbols are negative (absence) records. Diamond symbols are verified *M. cassini* records from neighboring broods.



**Fig. 5.** Main body of Brood VI. Verified Brood VI records (square symbols). Filled symbols are positive (presence) records; gray symbols are negative (absence) records. Rectangles indicate extent of areas shown in Figs. 6A–E.

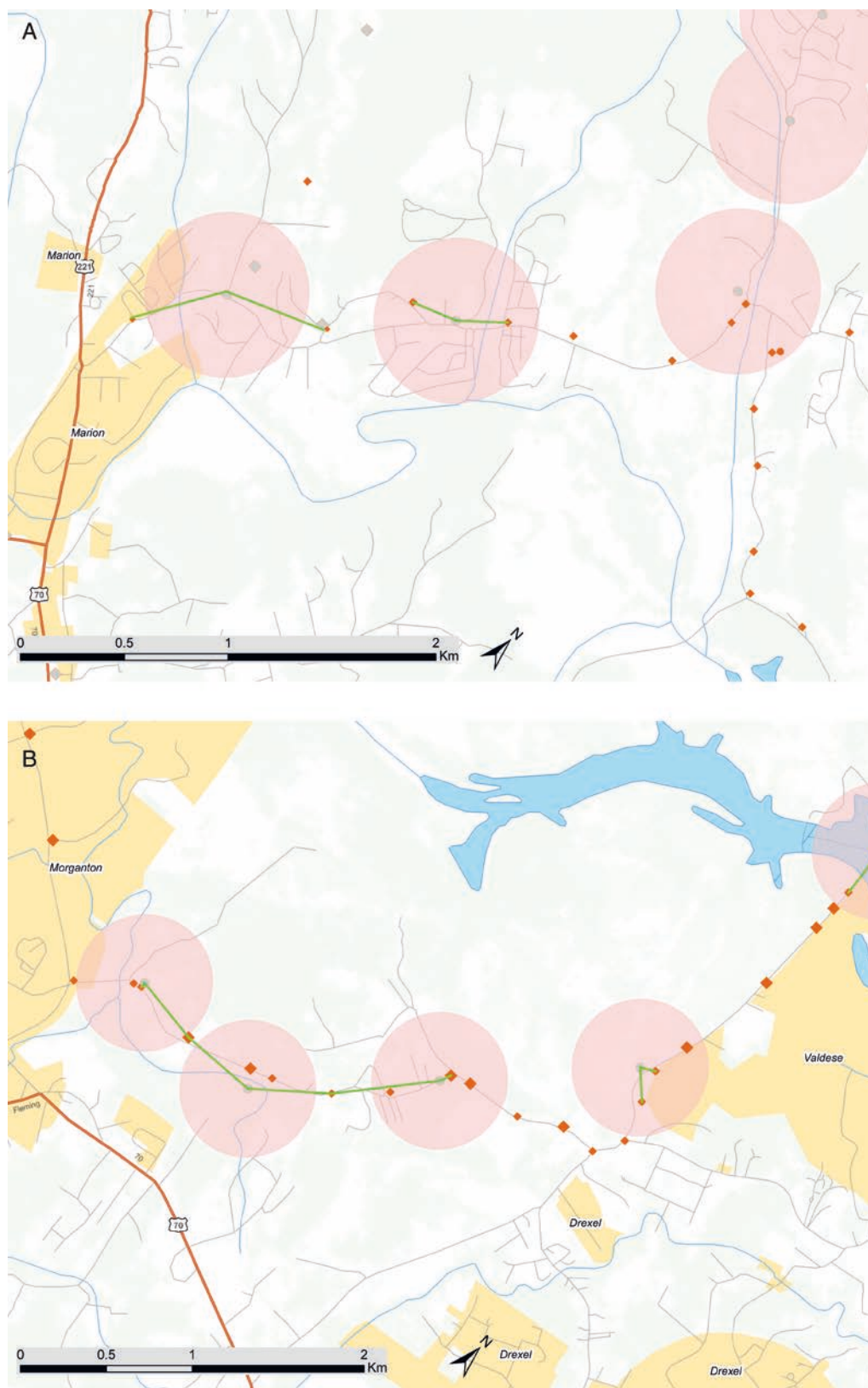
should not be considered exhaustive, and the status of Brood VI in Wisconsin remains uncertain.

Although the recorded distributions of Brood VI in 2000 and 2017 were similar, records from 2017 extended slightly farther from the core of the main body of Brood VI in most directions. Many of our records for each sampling year did not have records from the other year falling within their 400-m-radius neighborhood. For most of the records that could be paired, the density was unchanged between 2000 and 2017. Among records where the density changed between 2000 and 2017, the density was most likely to increase (Fig. 6A–D, Table 4). For 31 linear extension features measured to estimate expansion of the brood's range, all involved 2000 absence records in close proximity to 2017 presence records. The average length of these features was 0.546 km, up to a maximum of 3.47 km (Fig. 6A–D and Table 4). Most of these features are extremely short and do not extend beyond the 400-m-radius neighborhood of the negative records at their core, suggesting that they represent isolated patches in which cicadas were present in 2017 and not 2000. Two of these features were longer (Fig. 6D and E), suggesting locations where cicadas expanded their range over a more substantial area.

Our neighborhood analysis identified some locations in which cicada densities appear to have changed, especially around the periphery of the brood. Some of the 2017 peripheral records were recorded as light choruses, with an occasional record of single or

scattered individuals beyond (Fig. 6A–D). Some of the peripheral locations where only single or scattered cicadas were found in 2000 had light choruses in 2017; similarly, some of the peripheral locations that had light choruses in 2000 had full choruses in 2017. We found no examples of locations in which periodical cicadas were present in 2000 but absent in 2017, although we found one instance in which a location was marked as having strong choruses in 2000 but only light choruses in 2017. We found no *M. cassini* in any Brood VI population in Georgia, South Carolina, or North Carolina; however, this species is found in the adjacent Broods II, X, and XIV, including small portions of XIV that overlap Brood VI (Fig. 4).

Between 29 April and 25 June 2017, the website [www.magicicada.org](http://www.magicicada.org) received 9,077 crowdsourced reports of periodical cicadas whose locations could be resolved. Of these records, the majority were in the Washington, DC metropolitan area, within the range of Brood X and likely reflecting significant 4-yr early emergences of that brood (Supp Fig. 1 [online only]). We found that 246 of the crowdsourced records were within the known range of Brood VI as updated by Simon (1988), and some revealed areas that we had missed sampling in 2000. During this period, we received two reports from WI: one, from Marathon County, does not seem to be credible, since it is located far north of any other verified records in any other brood, and the other report, from Dane County, is in a county that Marlatt mapped as having Brood VI. Although our



**Fig. 6.** (A–E) Detail maps of Fig. 5. Range shift of Brood VI 2000–2017. 2000 Brood VI records (circles) and 2017 Brood VI records (squares). Filled symbols are positive (presence) records; gray symbols are negative (absence) records. Presence records are scaled by estimated density; largest symbols represent full choruses, whereas smallest symbols represent single individuals. The 400-m neighborhoods surrounding 2000 Brood VI negative records are shown (shaded circles) as are linear features (lines connecting records). See text for details.



Fig. 6. Continued.



Fig. 6. Continued.

**Table 4.** Comparison of records in ‘neighborhood’ of 400 m radius around each data point

|      | Total | Higher density 2000 | No change | Higher density 2017 | No comparable record |
|------|-------|---------------------|-----------|---------------------|----------------------|
| 2000 | 424   | 10                  | 143       | 37                  | 234                  |
| 2017 | 2,495 | 33                  | 447       | 98                  | 1,917                |

current methods of collecting crowdsourced records allow photo and/or sound verification, we did not collect such information in 2017, so this record must be considered plausible but unconfirmed. We received no reports of 2017 emergences in Connecticut, where Maier (1985) found a population of Brood II stragglers on a Brood VI schedule.

## Discussion

Brood VI consists of at least two and possibly three disconnected parts. Among all periodical cicada broods, some disjuncts appear to be relicts of once-larger distributions (Facon et al. 2006, Kritsky et al. 2017), whereas other disjuncts are best explained as having independent origins, formed by temporal shifts from a neighboring brood on a different schedule (Simon and Lloyd 1982; Cooley 2015; Cooley et al. 2015, 2018). The northeast GA populations of Brood VI are part of a complex of small, isolated populations of other 17-yr broods (II, X, and XIV; Cooley et al. 2009, 2011, 2015) reminiscent of those on Long Island (Simon and Lloyd 1982). It remains unknown whether the isolated GA populations of Brood VI are relicts of a once-larger distribution, whether they were formed contemporaneously with the main body of Brood VI but are disjunct because

the events leading to their formation were spatially heterogeneous in nature, or whether, like the Long Island broods, these southern disjuncts formed independently, but synchronic with the main body of a brood with which they share no recent common history.

We found no *M. cassini* in Brood VI, confirming Alexander and Moore’s statement that this species is absent in this brood (Alexander and Moore 1962). This absence is interesting because the three morphologically distinct forms (-decim, -cassini, -decula) typically co-occur except in some peripheral sections of the *Magicicada* distribution (only -decim in Brood VII; Cooley et al. 2004, Gilbert and Klass 2006) and along the northern edge of Broods X (Cooley et al. 2009) and XIII (Cooley et al. 2016), and only -cassini in the far southwest (unpublished data, Brood IV). In contrast to these peripheral populations, Brood VI is centrally located and surrounded by or slightly overlapping other broods in which *M. cassini* is present; in the most extreme example, where Broods VI and XIV slightly overlap in McDowell County, NC, in 2008 we found scattered and lightly chorusing Brood XIV *M. cassini* within 75 m of full Brood VI emergences that lacked *M. cassini*. Whether *M. cassini* was once in Brood VI but has since been lost or whether this species has never been in Brood VI remains unknown. Even though *M. cassini* is found in Broods IX and XIV nearby, the 3-yr offset separating Broods VI and IX and the 8-yr offset between Broods VI and XIV may make it difficult for *M. cassini* temporally to colonize into Brood VI by straggling, since straggling intervals of other than  $\pm 1$ ,  $\pm 4$  yr seem relatively uncommon (Kritsky 1987, Marshall et al. 2017).

We received many crowdsourced reports of periodical cicadas emerging in the Washington–Baltimore and Cincinnati metropolitan areas, which are not in the range of Brood VI as traditionally understood. These populations, which emerged in 2017 (and in prior Brood VI emergence years), seem best understood as 4-yr early ‘straggler’ emergences of Brood X, since they fall within the known range

of this brood (see Kritsky 1987) for further discussion of ‘Brood VI’ records in southern Ohio and Indiana. Although cicadas of any one brood show remarkable fidelity to their emergence schedule, the formation of the broods and the divergence of these cicadas into two life cycles (13 vs 17 yr) must have involved at least temporary life cycle switching (Simon and Lloyd 1982; Kritsky 1988; Marshall et al. 2011, 2017; Cooley et al. 2018), so straggler emergences are not unheard of, though they are generally not thought to be extensive or involve emergences of sufficient density to create choruses as were heard in the DC-Baltimore and Cincinnati metro areas in 2017. A full understanding of these emergences awaits the 2021 emergence of Brood X (see [Supp Mater \[online only\]](#)).

Our data include records of Brood VI in NC, SC, and GA, extending slightly farther outward from the main body of the brood in 2017 compared with 2000, suggesting that Brood VI cicadas emerged over a slightly larger area in 2017. However, since past efforts to understand range shifts in these species have been complicated by the difficulty of distinguishing actual shifts from data artifacts, it is worth considering the ways in our data could be biased. First and foremost, practical considerations prevented us from collecting records according to a repeated sampling design. Our data were not collected in a manner specifically designed to reveal range changes but are instead two maps of the same phenomenon created using slightly different techniques. In 2000, we dedicated some of our time to mapping the brood, but we also took records while traveling to a field site where we were conducting behavioral experiments; in transit to the site, we traveled on routes multiple times over periods of days and weeks, taking records along the way. In 2017, we did not make many repeated passes through given areas; with the benefit of our previous records as well as crowdsourced records, we could plan our mapping efficiently so that we passed through some areas only once. Thus, although our 2000 records tend to depict some chorus intensities as they were over several days, our 2017 records tend to be a more focused snapshot of chorus activity. Such differences in our 2000 and 2017 sampling schemes could have led to underestimates of the extent of the 2017 emergence in areas that were visited only once, and this bias would have a tendency to show the brood’s range shrinking between 2000 and 2017.

Weather-mediated differences in emergence timing in different years could also bias our data by causing a declining chorus to be scored as weak in one generation and strong in another, simply due to differences in emergence phenology. The weather in 2000 and 2017 was not exactly the same; for instance, annual average temperature in Asheville NC near the main body of Brood VI was 11.7°C in 2000 and 15.9°C in 2017 (National Weather Service 2020). On the other hand, May 2000 was slightly warmer than May 2017 across the range of Brood VI (average monthly temperatures at Asheville 19°C in 2000 vs 18.2°C in 2017; National Weather Service 2020). We cannot confirm or exclude the possibility that weather-related phenological differences between 2000 and 2017 contributed to the patterns we found.

The possibility that our data include unquantifiable biases is somewhat mitigated by our intentionally conservative methodological design. Our ‘neighborhood’ method mitigates potential biases by favoring records of higher density and reducing the reliance of our conclusions on any single record. The linear feature method is necessarily inexact, but its biases are conservative—due to the density of sampling and the large number of negative records, all linear features are relatively short, and because estimates are made only for locations where sampling was conducted in both 2000 and 2017, areas that were not well-sampled in either year are not included and do not influence our results. Our conclusions are also based on patterns

across the main range of Brood VI, insulating them from the effects of local anomalies.

The simplest explanation for the patterns in our data set is that Brood VI expanded its range slightly over one generation from 2000 to 2017. These likely changes are small—on the order of one or a few kilometers, and they suggest that brood boundaries are more dynamic, at least on extremely small scales, than previously appreciated. Some of the patterns in our data suggest the manner in which broods might expand their ranges. Records in the ‘one or a few’ and ‘light chorus’ categories were considerably more common in the 2017 data set than in the 2000 data set (Table 3), which is consistent with a brood dispersing and expanding over a larger area. Although the distinction between light and strong choruses can be strongly affected by weather conditions or emergence phenology, if we combine both light and strong chorus categories, then the ‘one or a few’ category is still overrepresented relative to choruses in the 2017 data set. Some variation in local densities has been reported for other broods; for example, Karban (2014) found that local population densities of Brood II differed considerably over the course of three generations. A recurrent pattern in our dataset is that records around the periphery of the brood (in either sampling year) include a number of low-density records (single or scattered individuals) that could represent adults that had dispersed away from main chorusing centers, facilitated by a relatively continuous forest cover (Cook and Holt 2006) and reflecting patterns noted in Karban (1981) and Strang (2013). If so, then cases in which we found that a low-density population record from 2000 was replaced by a higher-density population record in 2017 could represent successful reproduction by dispersing cicadas; the high fecundity of female periodical cicadas (up to 600 eggs; Marlatt 1923) makes rapid increases in population density possible under the right conditions.

Although the magnitudes of the apparent range shifts we identified might seem slight, nothing substantially more is required to explain the current extent of the periodical cicada distribution. Indeed, moving at a rate of only 2 km per generation, periodical cicadas could cover a distance of 500 km in only 250 generations, or 4,250 yr, ample time to leave glacial refugia and fill expanding forest biomes in postglacial North America. Indeed, it may well be that the cicadas’ own dispersal and colonization abilities were less limiting than the rate of deciduous forest expansion. On the other hand, given cicadas’ ability to spread, it is difficult to reconcile a change of even 0.5 km over one periodical cicada generation with the strong pattern of parapatry found today across the *Magicalcadas* broods, since just a few thousand years of even slight expansion of adjacent broods would create deep overlaps. Broods clearly have the potential to expand and overlap each other, so some other process must maintain brood parapatry. Perhaps periodical cicadas can expand relatively easily into new territory, even if it is already occupied by a different periodical cicada brood (e.g., Lloyd and Dybas 1966, Lloyd et al. 1983), and parapatry is maintained because local brood coexistence may be unstable and only temporary (Lloyd and White 1976). Possibly, the seeming present-day stability of periodical cicada broods is a dynamic equilibrium, in which brood boundaries ebb and flow, tracking conditions as local populations prosper or wane, such that conditions at any one time are simply snapshots of a system that is more in flux than previously assumed.

## Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

Stragglers

'Stragglers' or off-cycle cicadas, are relatively common, at least in low densities, with 4-yr shifts most common and 1-yr shifts less so, other shifts even rarer. But there are also notable examples of mass off-cycle emergences in 17-yr cicadas. Dybas (1969) reported periodical cicada emergences but no chorusing or egg-laying in the suburbs of Chicago in 1969, 4 yr prior to the emergence of Brood XIII; 4-yr early emergences with moderate chorusing were reported in similar locations in 2003 and 2020, again, 4 yr prior to Brood XIII emergences (Cooley et al. 2016). In 2017, as we mapped the expected Brood VI emergence, we received reports of substantial numbers of Brood X stragglers emerging 4 yr early. Accordingly, we mapped these unexpected emergences in order to compare them to emergences expected in 2021 (Supp Fig. 1 [online only]).

Back to the Future

Simon (1988) updated the maps of periodical cicada brood distributions created by Marlatt in the late 1800s and early 1900s (Marlatt 1923). Updating information came from numerous publications since Marlatt, her personal field observations, Cooperative Extension records, and USDA Animal and Plant Health Inspection Service files. All maps report records by county only. Comparing the Simon (1988) map of Brood VI represented by filled symbols (Fig. 2) to the Marlatt map (represented by filled and empty symbols; Fig. 2) to the 2017 map (Supp Fig. 1 [online only]) gives the impression of a decline and resurgence of 'Brood VI' records over time. However, we suggest that the areas of Marlatt's (1923) Brood VI map falling outside of the Simon (1988) map represent 4-yr early Brood X stragglers, and that apparent changes in abundance between Marlatt's map (Marlatt 1923) and our 2017 crowdsourced data reflect technological changes in data collection methodology, changes in Brood X abundance, changes in the frequency of straggling from Brood X, or some combination of the above. In 2017, we mapped in detail an area west of Washington DC from the Potomac River south to Reston, VA. Some choruses were as loud as typical emergences and the duration of the emergence in the DC area was typical of periodical cicadas. Additional detailed observations of stragglers were observed in the Cincinnati metropolitan area. These observations will be the subject of a future paper.

Fig. S1. Crowdsourced records collected in 2017.

## Acknowledgments

Elias Bonaros, Steve Chiswell, Gerry Bunker, Diler Haji, Gene Kritsky, Dan Mozgai, Karen Slon, Teiji Sota, and Jin Yoshimura helped with data collection. Will Cooley assisted with data interpretation. The National Geographic Society CRE-sponsored project 'Making Modern Maps of *Magicicada* Emergences' provided funding for this project. This work is partially supported by the National Science Foundation under grant nos. NSF DEB 04-22386, DEB-09-55849, DEB 16-55891 to Chris Simon and J. Cooley (and others) and grants from the University of Connecticut, Vice President's Research Excellence Program. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

## References Cited

- Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species. (Homoptera: Cicadidae, *Magicicada*). Miscellaneous Publication 121. University of Michigan Museum of Zoology, Ann Arbor, MI. pp. 1–59.
- Cook, W. M., and R. D. Holt. 2006. Influence of multiple factors on insect colonization of heterogeneous landscapes: a review and case study with periodical cicadas (Homoptera: Cicadidae). *Ann. Entomol. Soc. Am.* 99: 809–820.
- Cooley, J. R. 2015. The distribution of periodical cicada (*Magicicada*) Brood I in 2012, with previously unreported disjunct populations (Hemiptera: Cicadidae). *Am. Entomol.* 61: 52–57.
- Cooley, J. R., C. Simon, D. C. Marshall, K. Slon, and C. Ehrhardt. 2001. Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Hemiptera: *Magicicada* spp.): genetic, morphological, and behavioural evidence. *Mol. Ecol.* 10: 661–671.
- Cooley, J. R., D. C. Marshall, and C. Simon. 2004. The historical contraction of periodical cicada Brood VII (Hemiptera: Cicadidae: *Magicicada*). *J. N. Y. Entomol. Soc.* 112: 198–204.
- Cooley, J. R., D. C. Marshall, K. B. Hill, and C. Simon. 2006. Reconstructing asymmetrical reproductive character displacement in a periodical cicada contact zone. *J. Evol. Biol.* 19: 855–868.
- Cooley, J. R., G. Kritsky, J. D. Zyla, M. J. Edwards, C. Simon, D. C. Marshall, K. B. R. Hill, and R. Krauss. 2009. The distribution of periodical cicada Brood X. *Am. Entomol.* 55: 106–112.
- Cooley, J. R., G. Kritsky, M. D. Edwards, J. D. Zyla, D. C. Marshall, K. B. R. Hill, G. J. Bunker, M. L. Neckermann, and C. Simon. 2011. Periodical cicadas (*Magicicada* spp.): the distribution of Broods XIV in 2008 and 'XV' in 2009. *Am. Entomol.* 57: 144–151.
- Cooley, J. R., D. C. Marshall, A. F. Richards, R. D. Alexander, M. D. Irwin, J. R. Coelho, and C. Simon. 2013a. The distribution of periodical cicada Brood III in 1997, with special emphasis on Illinois (Hemiptera: *Magicicada* spp.). *Am. Entomol.* 59: 9–14.
- Cooley, J. R., M. L. Neckermann, G. J. Bunker, D. C. Marshall, and C. Simon. 2013b. At the limits: habitat suitability modeling of Northern 17-year periodical cicada extinctions (Hemiptera: *Magicicada* spp.). *Glob. Ecol. Biogeogr.* 22: 410–421.
- Cooley, J. R., C. Simon, C. Maier, D. C. Marshall, J. Yoshimura, S. M. Chiswell, M. D. Edwards, C. W. Holliday, R. Grantham, J. D. Zyla, et al. 2015. The distribution of periodical cicada (*Magicicada*) Brood II in 2013: disjunct emergences suggest complex origins. *Am. Entomol.* 61: 245–251.
- Cooley, J. R., G. Kritsky, D. C. Marshall, K. B. R. Hill, G. J. Bunker, M. L. Neckermann, J. Yoshimura, J. E. Cooley, and C. Simon. 2016. A GIS-based map of periodical cicada Brood XIII in 2007, with notes on adjacent populations of Broods III and X (Hemiptera: *Magicicada* spp.). *Am. Entomol.* 62: 241–246.
- Cooley, J. R., N. Arguedas, E. Bonaros, G. J. Bunker, S. M. Chiswell, A. DeGiovine, M. D. Edwards, D. Hassanieh, D. Haji, J. Knox, et al. 2018. The periodical cicada four-year acceleration hypothesis revisited: evidence for life cycle decelerations and an updated map for Brood V (Hemiptera: *Magicicada* spp.). *PeerJ* 6: e5282.
- DeLorme. 2012. North Carolina atlas and gazetteer. DeLorme, Yarmouth, ME.
- Du, Z., H. Hasegawa, J. R. Cooley, C. Simon, J. Yoshimura, W. Cai, T. Sota, and H. Li. 2019. Mitochondrial genomics reveals shared phylogeographic patterns and demographic history among three periodical cicada species groups. *Mol. Biol. Evol.* 36: 1187–1200.
- Dybas, H. S. 1969. The 17-year cicada: a four year mistake? *Bull. Field Mus. Nat. Hist.* 40: 10–12.
- ESRI. 2009. ArcGIS 9.3. ESRI, Redlands, CA.
- Facon, B., B. J. Genton, J. Shykoff, P. Jarne, A. Estoup, and P. David. 2006. A general eco-evolutionary framework for understanding bioinvasions. *Trends Ecol. Evol.* 21: 130–135.
- Fujisawa, T., T. Koyama, S. Kakishima, J. R. Cooley, C. Simon, J. Yoshimura, and T. Sota. 2018. Triplicate parallel life cycle divergence despite gene flow in periodical cicadas. *Commun. Biol.* 1: 26.
- Gilbert, C., and C. Klass. 2006. Decrease in geographic range of the Finger Lakes Brood (Brood VII) of the periodical cicada (Hemiptera: Cicadidae: *Magicicada* spp.). *J. N. Y. Entomol. Soc.* 114: 78–85.
- Karban, R. 1981. Flight and dispersal of periodical cicadas. *Oecologia* 49: 385–390.
- Karban, R. 1982a. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology* 63: 321–328.
- Karban, R. 1982b. Population ecology of periodical cicadas. Ph.D. dissertation, University of Pennsylvania, Philadelphia, PA.
- Karban, R. 2014. Transient habitats limit development time for periodical cicadas. *Ecology* 95: 3–8.
- Kritsky, G. 1987. An historical analysis of periodical cicadas in Indiana (Homoptera: Cicadidae). *Proc. Indiana Acad. Sci.* 97: 295–322.
- Kritsky, G. 1988. The 1987 emergence of the Periodical Cicada (Homoptera: Cicadidae: *Magicicada* spp.: Brood X) in Ohio. *Ohio J. Sci.* 88: 168–170.
- Kritsky, G., R. Troutman, D. Mozgai, C. Simon, S. M. Chiswell, S. Kakishima, T. Sota, J. Yoshimura, and J. R. Cooley. 2017. Evolution and geographic extent of a surprising Northern disjunct population of 13-year Cicada Brood XXII (Hemiptera: Cicadidae, *Magicicada*). *Am. Entomol.* 63: E15–E20.

- Lloyd, M., and H. S. Dybas. 1966. The periodical cicada problem. II. Evolution. *Evolution* 20: 466–505.
- Lloyd, M., and J. A. White. 1976. Sympatry of periodical cicada broods and the hypothetical four-year acceleration. *Evolution* 30: 786–801.
- Lloyd, M., and J. White. 1980. On reconciling patchy microspatial distributions with competition models. *Am. Nat.* 115: 29–44.
- Lloyd, M., G. Kritsky, and C. Simon. 1983. A simple Mendelian model for 13- and 17-year life cycles of periodical cicadas, with historical evidence of hybridization between them. *Evolution* 37: 1162–1180.
- Maier, C. T. 1985. Brood VI of 17-year periodical cicadas, *Magicicada* spp. (Hemiptera: Homoptera: Cicadidae): new evidence from Connecticut (USA), the hypothetical 4-year deceleration, and the status of the brood. *J. N. Y. Entomol. Soc.* 93: 1019–1026.
- Marlatt, C. L. 1898. A consideration of the validity of the old records bearing on the distribution of the broods of the periodical cicada, with particular reference to the occurrence of Broods VI and XXIII in 1898. *USDA Bureau Entomol. Bull.* 18: 59–78.
- Marlatt, C. L. 1902. New nomenclature for the broods of the periodical cicada. In U. S. D. O. A. (ed). *United States Division of Entomology*, Washington, DC.
- Marlatt, C. L. 1923. The periodical cicada. *USDA Bureau Entomol. Bull.* 71: 1–183.
- Marshall, D. C. 2001. Periodical cicada (Homoptera: Cicadidae) life-cycle variations, the historical emergence record, and the geographic stability of brood distributions. *Ann. Entomol. Soc. Am.* 94: 386–399.
- Marshall, D. C., and J. R. Cooley. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of new species, 13-year *Magicicada neotredecem*. *Evolution* 54: 1313–1325.
- Marshall, D. C., J. R. Cooley, and K. B. R. Hill. 2011. Developmental plasticity in *Magicicada*: thirteen year cicadas emerging in seventeen and twenty-one years (Hemiptera: Cicadidae). *Ann. Entomol. Soc. Am.* 104: 443–450.
- Marshall, D. C., K. B. R. Hill, and J. R. Cooley. 2017. Multimodal life cycle variation in 13- and 17-year periodical cicadas (*Magicicada* spp.). *J. Kansas Entomol. Soc.* 90: 211–226.
- Menendez, R. 2007. How are insects responding to global warming? *Tijdschr. Entomol.* 150: 355–365.
- National Weather Service. 2020. Monthly average temperatures Asheville area 1857 – present. (<https://www.weather.gov/media/gsp/Climate/AVL/newAVLmonthlyTobs.pdf>) (accessed 1 January 2021).
- Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765–766.
- Simon, C. 1988. Evolution of 13- and 17-year periodical cicadas. *Bull. Entomol. Soc. Am.* 34: 163–176.
- Simon, C., and M. Lloyd. 1982. Disjunct synchronic populations of 17-year periodical cicadas: relicts or evidence of polyphyly? *J. N. Y. Entomol. Soc.* 90: 275–301.
- Sota, T., S. Yamamoto, J. R. Cooley, K. B. R. Hill, C. Simon, and J. Yoshimura. 2013. Different histories of divergence into 13- and 17-year life cycles among three periodical cicada lineages. *Proc. Natl. Acad. Sci. USA* 110: 6919–6924.
- Stannard, L. J. 1975. The distribution of periodical cicadas in Illinois. II. *Nat. Hist. Surv. Biol. Notes* 91: 3–12.
- Strang, C. A. 2013. Geography and history of periodical cicadas (Hemiptera: Cicadidae) in DuPage County, Illinois. *Great Lakes Entomol.* 46: 193–203.
- White, J., and M. Lloyd. 1979. 17-Year cicadas emerging after 18 years: a new brood? *Evolution* 33: 1193–1199.
- Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annu. Rev. Entomol.* 40: 269–295.
- Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-yr periodical cicadas (Cicadidae: *Magicicada*): phenology, mortality, and predator satiation. *Ecology* 74: 1143–1152.
- Yalcin, S., and S. J. Leroux. 2017. Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Glob. Ecol. Biogeogr.* 26: 609–624.