The periodical cicada four-year acceleration hypothesis revisited and the polyphyletic nature of Brood V, including an updated crowd-source enhanced map (Hemiptera: Cicadidae: *Magicicada*)

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The periodical cicadas of North America (*Magicicada* spp.) are well-known for their long life cycles of 13 and 17 years and their mass synchronized emergences. Although periodical cicada life cycles are relatively strict, the biogeographic patterns of periodical cicada broods, or year-classes, indicate that they must undergo some degree of life cycle switching. We present a new map of periodical cicada Brood V, which emerged in 2017, and demonstrate that it consists of at least four distinct parts that span an area in the United States stretching from Ohio to Long Island. We discuss mtDNA haplotype variation in this brood in relation to other periodical cicada broods, noting that different parts of this brood appear to have different origins. We use this information to refine a hypothesis for the formation of periodical cicada broods by 1- and 4-year life cycle jumps.

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Abstract

The periodical cicadas of North America (*Magicicada* spp.) are well-known for their long life cycles of 13 and 17 years and their mass synchronized emergences. Although periodical cicada life cycles are relatively strict, the biogeographic patterns of periodical cicada broods, or year-classes, indicate that they must undergo some degree of life cycle switching. We present a new map of periodical cicada Brood V, which emerged in 2017, and demonstrate that it consists of at least four distinct parts that span an area in the United States stretching from Ohio to Long Island. We discuss mtDNA haplotype variation in this brood in relation to other periodical cicada broods, noting that different parts of this brood appear to have different origins. We use this information to refine a hypothesis for the formation of periodical cicada broods by 1- and 4-year life cycle jumps.

Introduction

North American periodical cicada (*Magicicada*) adults emerge synchronously, predictably, and in overwhelming numbers; their black bodies, orange wing veins, striking red eyes, and loud acoustical choruses are unmistakable. Although early European settlers in North America mistook these insects for migratory locusts (Kritsky 2004), their sudden appearances and equally sudden disappearances are not caused by movement, but by long life cycles (13- or 17- years) spent mostly underground with only a brief aboveground adult phase. Perhaps one of the strangest aspects of *Magicicada* is the existence of broods, which are multispecies assemblages in which all members, regardless of species, emerge synchronously on the same schedule. Across the eastern and central United States, the broods form a patchwork pattern

of interlocking year classes that are generally parapatric, temporally offset, and resemble puzzle pieces. Such spatial relationships suggest the existence of some kind of competitive interactions that limit brood overlaps, such as underground competition among nymphs and/or aboveground competition among adults (Bulmer 1977; Lehmann-Zeibarth et al. 2005). These spatial patterns also suggest some mechanism for brood formation by which broods give rise to each other and thus have parent-child relationships (Marlatt 1902). While *Magicicada* are well-known for their fixed life cycles, two kinds of life cycle shifts have been demonstrated; permanent life cycle shifts (e.g., cicada populations change cycles and stay on their new cycle; Martin and Simon 1988; Martin and Simon 1990; Marshall and Cooley 2000; Simon et al. 2000; Cooley et al. 2001), and temporary life-cycle shifts (e.g., cicada populations adopt the alternate cycle but return to their original cycle; Simon and Lloyd 1982; Kritsky 1988; Marshall et al. 2011; Marshall et al. 2018). While both kinds of life-cycle shifts were hypothesized by Lloyd and Dybas (1966), temporary life-cycle switching is thought to be responsible for brood formation within life-cycles (Marlatt 1902; Lloyd and Dybas 1966; Lloyd and White 1976; Simon and Lloyd 1982).

Given the spatial and temporal relationships of the 17-year broods, Lloyd and Dybas (1966) developed a general “4-year acceleration” hypothesis by which most broods could be derived by simple one- or four-year temporary life cycle advancements (or “accelerations”) from an ancestral parent brood on the same schedule as Brood XIV (Fig 1; see also Lloyd and White 1976; Simon 1983). The discovery of persistent disjunct “miniature” brood isolates on Long Island, New York and elsewhere (Simon and Lloyd 1982; Cooley 2015; Cooley et al. 2015) and genetic evidence that many broods have complex, multiple origins (Martin and Simon

1988; Martin and Simon 1990; Simon et al. 2000; Cooley et al. 2001; Sota et al. 2013) suggest that the process modeled by this hypothesis, in which populations become temporally isolated and form new broods or join existing ones, may be more common than previously thought and apply to more than just the known disjunct populations. Here we test whether the main body of Brood V has a single origin, or whether it reflects multiple episodes of brood formation.

Seventeen-year periodical cicada Brood V, whose range includes a variety of different climate and habitat types, emerged in 1931, 1948, 1965, 1982, 1999, and 2016. Brood V contains all three named 17-year cicada species (*M. septendecim, M. cassini,* and *M. septendecula*) and has a reported range whose various parts are in close proximity to or in contact with Broods I, VIII, IX, X, and XIV (Marlatt 1923; Simon and Lloyd 1982; Simon 1988). Brood V is close to the boundary between eastern and middle periodical cicada haplotypes as defined by Sota et al. (2013), but sampling in that paper did not encompass the full range of Brood V. In this paper, we genotype samples of Brood V and neighboring Brood I in Virginia and West Virginia, collate historical records, and create a new georeferenced map of Brood V's 2016 emergence. Our genetic, geographic, and historical data suggest that like Broods IX and X (Sota et al. 2013), Brood V is composed of at least four subpopulations with separate evolutionary origins and that the main range of Brood V is not of a single origin but rather consists of fused eastern and western populations. We propose hypotheses for the formation of these subpopulations and review the temporal and geographic relationships of other broods in contact with Brood V. We suggest that Lloyd and Dybas's (1966) "4-year acceleration" hypothesis be expanded to consider decelerations (or temporary life cycle retardations), which

92 are sometimes more geographically parsimonious. We also document changes in the
93 distribution of Brood V in parts of its range.

94 Methods

95 *Verified Records*

96 In May and June 2016, we collected records of the Brood V emergence across its range
97 by searching for active choruses on days with appropriate weather conditions. We used mobile
98 GPS dataloggers to collect information about the density of cicadas and the species present
99 (more details of the methods can be found in Cooley et al. 2013; Cooley et al. 2016). In
100 northeast Ohio, particularly Cuyahoga, Medina and Lake counties, and in eastern Suffolk County
101 (Long Island) New York, data were collected by trained surveyors with handheld GPS devices
102 visiting preselected locations on multiple days throughout the emergence. Distributional
103 information was organized and mapped using ArcGIS 10.5 (ESRI 2009). Cuyahoga and Medina
104 county Ohio data were deposited in a database managed by Cleveland Metroparks. All data
105 were also included in the periodical cicada database found at www.magicicada.org.

106 *Crowdsourced Records*

107 The website www.magicicada.org collected unverified ("crowdsourced") periodical
108 cicada sightings from the general public in May 2016. We used these records to inform our
109 decisions about areas to map in detail. Individual crowdsourced records are not necessarily
110 reliable; thus, we weighted crowdsourced records by assigning higher confidence to records
111 that were clustered or that were in close proximity to verified records as described in Cooley et
112 al. (2015). After we had stopped collecting data from the general public, we received an

unusual number of reports from Carbon County, Pennsylvania, via the website cicadamania.com, which we then investigated.

Overlaps

Because roads are sparse in the parts of Virginia where Brood V contacts Brood I, direct measurements of overlaps are impractical. Instead, we made conservative estimates of overlaps by constructing linear features in Arc GIS 10.5 that linked verified presence observations of Brood I with verified presence records of Brood V. To do so we looked for instances in which series of verified records of one brood are clearly within territory occupied by the other brood; for example, if we collected 11 records along a route occupied by Broods I and V in the order (V_1 V_2 V_3 I_4 V_5 I_6 V_7 I_8 I_9 I_{10} I_{11}), then we constructed a single linear feature connecting (I_4 V_5 I_6 V_7). We extracted the lengths of all linear features as conservative estimates of overlap. We did not use records of single individuals as endpoints of these features.

Historical Data

Historical data from Brood V can be found in Marlatt (1923), Simon (1988), Kritsky et al. (1999; for Ohio only), and Simon and Lloyd (1982; for Long Island only). Additional historical records were gleaned from *Magicicada* published literature, museum specimens in the University of Michigan Museum of Zoology (UMMZ) and from unpublished field notes and records in the www.magicicada.org database. To verify the historical presence of the newly discovered disjunct population in Carbon County, Pennsylvania, we gathered data from archived copies of newspapers in the Carbon County area for the Brood V emergence years 1883, 1897, 1931, 1948 and 1965 and 1999. We searched for the terms “cicada” or “locust” (an

archaic term for cicadas used in North America; (Kritsky 2001, 2004) in the months of January through August in three newspaper archives: Library of Congress's Chronicling America Historic American Newspapers, the Pennsylvania Historical Newspapers, and Newspapers.com.

Genetic Data

We amplified and sequenced a 525-bp portion of mitochondrial cytochrome oxidase subunit I (COI) for 64 *M. septendecim* specimens collected in 2016 from Brood V, and in 2012 from Brood I using methods described in Sota et al. (2013). Haplotypes were compared to previously reported mitochondrial haplotypes of *M. septendecim* from Broods I and V (Sota et al. 2013) to determine haplotype groups. We used TCS version 1.21 to construct a haplotype network (Clement et al. 2000). Details of specimens and accession numbers of the reference haplotype sequences are given in Table 1. Methods are identical to those in Sota et al. (2013).

Results

Brood V consists of four distinct parts: 1) A large body of the brood extending from the Ohio Valley to Lake Erie; 2) A separate, southeastern portion associated with the Shenandoah Valley and in close contact with Brood I; 3) a small disjunct population of *M. septendecim* in Carbon County, Pennsylvania, associated with the Lehigh River in and around the town of Jim Thorpe; and 4) A previously known disjunct population of *M. septendecim* on eastern Long Island containing only *M. septendecim* (Figs. 2- 5). We found that Brood V in Virginia is largely parapatric with Brood I; for the five Virginia locations where we found measurable overlap, estimated overlaps were limited to 0.51±0.45 km, with the largest overlap less than 1.3km (Fig. 6).

Crowdsourced Records

In this study, we evaluated 1361 crowdsourced data points, most of which were within the range of Brood V, but some of which were from as far away as California (well outside the range of *Magicicada*). Crowdsourced records suggest that we did not miss any significant populations (Figs. 2-4). The existence of the Carbon County, Pennsylvania population was initially revealed to us by records provided by the general public.

Genetic Data

We obtained COI sequences for 64 *M. septendecim* from 17 populations in Ohio, West Virginia, and Virginia (Table 1). All haplotypes are variants of mitochondrial lineage *A*, which is restricted to *M. septendecim* and *M. neotredecim* (Martin and Simon 1988; Martin and Simon 1990; Marshall and Cooley 2000; Simon et al. 2000; Cooley et al. 2001; Sota et al. 2013). Midwestern portions of Brood V contain only the Midwest haplotype, *Am*. Eastern populations of Brood V possess the Eastern haplotype, *Ae*. Brood V populations in mountainous areas along the Virginia-West Virginia border contain both haplotypes *Ae* and *Am* in the same forest patches in multiple locations (Fig. 7). Disjunct populations of Brood V on Long Island were entirely *Ae*. Populations from Jim Thorpe, Pennsylvania were not genotyped.

Historical records and population status

Changes in brood ranges and abundance in Ohio

The recession of Brood V boundaries in Ohio has been discussed for over a century. Webster mapped the 1897 emergence, noting that in Erie County, periodical cicadas could be found in an area that was “little more than a peninsula-like extension, and will probably not

appear again." Gossard (1916) surveyed the next emergence in Erie County and documented that the brood persisted for another generation. Forsythe (1976) checked the distribution in 1965 and found cicadas just south of the Erie County line. The brood did emerge in 2016 just north of the county line, suggesting that there may have been doubt about the line when mapping the 1965 and later emergences.

The recession of the southwestern Ohio limits of Brood V, noted by Kritsky et al. (1999), continued with the 2016 emergence. The emergences in Ross, Pike, and Scioto counties were scattered, with only light chorusing observed in the eastern portion of the counties compared to strong choruses reported in 1897. Forsythe (1976) noted that such light emergences suggest that "relatively small, isolated locations may be more persistent than originally supposed."

Carbon County Pennsylvania disjunct population

Even though the Carbon County Pennsylvania disjunct of Brood V (Fig. 5) has not been reported in the scientific literature until now, it has been documented in museum collections and local newspaper reports. We found 12 *M. septendecim* in the UMMZ collected 6/23/1982 by J. A. Lankalis in Mauch Chunk (Prior to 1953, Jim Thorpe was named Mauch Chunk, and the name has persisted because it is also the name of a nearby ridge). The UMMZ collection also contains four *M. septendecim* collected 5/13/1982 in Lehigh Gorge. Jim Thorpe is the gateway to the Lehigh Gorge.

The earliest news report of periodical cicadas on the same schedule as Brood V in Carbon County Pennsylvania is from 1880; in March of that year, the *Carbon Advocate*, of Leighton, predicted that periodical cicadas would appear that summer "in accordance with long

established customs;" the same paper later reported on May 29 that a substantial emergence had occurred. In June 1897, the *Allentown Morning Call* noted the emergence of periodical cicadas in Schuylkill County, which is immediately to the southwest of Carbon County. While we did not find any periodical cicadas in Schuylkill County in 2016, we did not search the county exhaustively, and we did find periodical cicadas in Carbon County within 7km of the Carbon/Schuylkill County line. In June 1931, the same newspaper reported periodical cicadas in Leighton and Mauch Chunk. The *Allentown Morning Call* also reported periodical cicadas in June 1948 and June 1965, with specific mentions of Mauch Chunk and Carbon County. In sum, these newspaper reports seem largely credible, since they describe cicadas in approximately the correct locations in Brood V emergence years; thus, these records support the existence of this disjunct at least as far back as 1880. Complete details of Pennsylvania Brood V historical records are included in the Supplemental Information (Data S1).

Long Island disjunct populations

Brood XIV is the main brood on Long Island and only small pockets of Broods I, V, and IX exist in a restricted area of northeastern Long Island (Simon and Lloyd 1982). The Long Island disjunct of Brood V (Fig. 4) was first recorded in 1914 by WT Davis (Simon and Lloyd 1982). Like the Long Island disjuncts of Broods I, IX and X (Simon et al. 1981; Simon and Lloyd 1982; Cooley et al. 2009, C. Simon field notes), these populations of Brood V appear to be declining and may go extinct in the near future. For example, Long Island Brood X has declined precipitously since 1970; an article in Newsday (Nelson 2004) documented only small numbers of Brood X individuals emerging on Long Island in 2004 in areas that had large emergences in 1987 (C. Simon field notes) and 1970, including protected areas such as Connetquot State Park.

Similarly, detailed qualitative records of Brood V in Wildwood State Park, Wading River, Long Island in 1982 and 1999, (C. Simon field notes, *Magicicada* database) and our survey in 2016, and anecdotal reports from residents of Calverton suggest a steep decline in *Magicicada* density both in protected and developed areas of north eastern Long Island. No records of Brood XI on Long Island exist beyond those recorded by W.T. Davis in the early 1900's and reported in Simon and Lloyd (1982).

Discussion

Crowdsourcing as a biological tool

Crowdsourcing has been a key component of periodical cicada mapping ever since C. L. Marlatt constructed maps by enhancing older datasets with reports from state entomologists, agricultural experiment station bulletins, weather service observers, post offices, and entomological enthusiasts (Marlatt 1898). Our crowdsourced periodical cicada records continue the tradition of citizen science successfully contributing to this effort. The emergence and evolution of citizen science as a subdiscipline of ecology and conservation biology, along with its challenges and opportunities have been reviewed by Silvertown (2009) and Pocock et al. (2017b). Recently, citizen science has emerged as a tool for evaluating species responses to forest management plans (Mair and Ruete 2016; Mair et al. 2017), mapping the arrival and spread of invasive species (Pocock et al. 2017a), pollinator monitoring (Roy et al. 2016), and tracking monarch butterfly populations (Schultz et al. 2017). The citizen science approach is particularly powerful in the context of periodical cicada research due to the large range of potential habitat, the short duration of adult emergences, and the limited number of "expert"

mappers. Notably, the Carbon County Pennsylvania Brood V disjunct was originally brought to our attention on the basis of citizen science reports; given the small size of this population, it is unlikely that we would have found it otherwise. We expect that citizen science efforts will continue to play an important role in monitoring whether the reported ranges of periodical cicada broods remain stable or undergo changes in the future.

Brood V has multiple origins

Although some morphometric studies suggested that broods are single-origin monophyletic assemblages (Simon 1983), Marlatt (1902) acknowledged the possibility of broods having multiple origins, noting that, "In the case of a widely-scattered brood ...it is quite possible that certain swarms originated from a later-appearing brood by retardation of individuals, and other swarms from an earlier brood by acceleration in time of appearance of individuals...but with the broods presenting a compact range a singleness of origin is evident" (Marlatt 1902). Marlatt considered Brood V to have a "compact range." He was unaware of the small disjunct populations of Brood V in Carbon County Pennsylvania and on Long Island, which by his reasoning, would be best explained as independently derived from a different brood.

Genetic data also indicate that the different parts of Brood V have unique histories, extending the findings of Sota et al. (2013) that Broods VI, IX, X, and XIV have multiple origins. Brood V *M. septendecim* from Midwestern localities belong to a central US mtDNA clade (*Am*) shared with all other Midwestern *M. septendecim* brood populations, while Brood V *M. septendecim* from eastern portions of the range belong to an eastern mtDNA clade (*Ae*), shared

261 with all other eastern *M. septendecim* brood populations (Sota et al. 2013). In the middle of
262 the main body of Brood V, in the Shenandoah Valley of Virginia and surrounding areas
263 extending into West Virginia, there is a boundary between haplotypes *Ae* and *Am*. In this
264 region, Brood V overlaps Brood I, which also contains both haplotypes *Ae* and *Am*, as does
265 Brood IX (Table 1, Fig. 7; Sota et al. 2013). The spatial, temporal, and genetic relationships of
266 Broods I, V, and IX suggest that they are derived from each other by four-year jumps (discussed
267 below), and because Brood V has the westernmost extent of these broods, it may have been a
268 conduit for Midwestern haplotype *Am* to enter eastern populations of Broods I and IX. Further
269 exploration of this hypothesis awaits detailed mapping of Brood IX in 2020 and more fine-scale
270 genetic data for both mtDNA and nuclear genomes.

271 ***Four-year jumps***

272 *Magicicada* stragglers, or off-cycle cicadas, are a well-documented phenomenon that
273 has complicated efforts to map broods (Marshall 2001). If stragglers emerge in sufficient
274 numbers to satiate predators, then they may establish populations on a new schedule. Early
275 emergences, or accelerations (written as "-4"), have been suggested to result from crowding or
276 better than average environmental conditions (e.g., longer growing seasons) that allow a
277 fraction of the population to complete development ahead of schedule (Williams and Simon
278 1995). Unexpectedly late emergences, or decelerations (written as "+4"), may be caused by
279 worse than average environmental conditions that prevent a fraction of the population from
280 completing development in the expected time (see Karban et al. 2000; also Lloyd and Dybas
281 1966; Lloyd and White 1976). The spatial association of brood pairs (Alexander and Moore
282 1962) offset by one year (I/II, III/IV, IX/X, XXII/XXIII) and by four years (XIV/I/V/IX, II/VI/X/XIV,

283 XIX/XXIII) suggests that both one- and four- year jumps are important for shaping *Magicicada*
284 spatiotemporal patterns (Lloyd and Dybas 1966). Among the possible jumps that have been
285 documented (Cooley et al. 2011; Marshall et al. 2011; Cooley et al. 2016), four-year jumps
286 appear particularly common; Marshall *et al*. (2018) used repeated censuses to demonstrate
287 that individual cicadas are more likely to accelerate by four years than by one year.
288 Furthermore, no straggler emergences dense enough to form choruses have been documented
289 with 1-year offsets from their broods, while straggler choruses with 4-year offsets are common
290 (see below). Whether 4-year jumps are favored by some unknown selective advantage, or
291 whether they are a reflection of the developmental processes underlying periodical cicada life
292 cycles remains unknown.

293 Four-year accelerations are well-documented in *Magicicada*. We hypothesize that
294 accelerations occur during warmer times when growing seasons are lengthened and cicadas
295 can complete development quickly. Dybas and Lloyd (1969) found choruses of periodical
296 cicadas in the Chicago metropolitan area in 1969, four years before the emergence of Brood
297 XIII, the only brood in the area; such choruses were also found in 2003 (Cooley et al. 2016).
298 Broods that are offset by 4 years, such as Broods I, V, IX and XIV could be related to each other
299 by the brood derivation scheme Lloyd and Dybas (1966) based on their "4-year acceleration"
300 hypothesis, although as originally published there was no parent-child relationship between
301 Broods I and XIV (Fig 1). Simon and Lloyd (1982) modified this scheme to include a derivation of
302 Brood I from V and XIV from I via accelerations (Fig. 8a, b) to accommodate the Long Island
303 broods (see also Simon et al. 1981).

Four-year decelerations have likely also played a role in *Magicicada* evolution. We hypothesize that decelerations occur during colder times when growing seasons are shortened and an extra four years are needed for cicadas to complete development. A large chorusing population of Brood IV emerged four-years late north of Omaha, Nebraska in 2002, where no other cicada broods are found (reported in Marshall et al. 2011). Similarly, Maier (1985) described reported Brood VI populations in the Hudson River Valley as possible four-year decelerations from resident Brood II populations and also suggested that the miniature broods on Long Island may have arisen from decelerations without offering an explanation for the phenomenon. Aside from such straggling, some brood relationships appear best explainable by four-year delays; a disjunct of Brood I in northeastern Tennessee, 300 km southwest of the main range of the brood (Cooley 2015), is partially surrounded by Brood XIV and may have been derived by a four-year deceleration from it (Fig 9). On Long Island, a population synchronous with Brood I appeared repeatedly in exactly the same woods and oviposited in exactly the same trees as Brood XIV that appeared four years earlier (Simon et al. 1981). Thirteen-year cicadas also undergo decelerations; Marshall *et al*. (2011) explained the unexpected emergence of light choruses within the territories of 13-year broods as 4-year late cicadas. Finally, Lloyd and Dybas (1966) suggested that a 4-year deceleration was responsible for the initial formation of 17-year cicadas from 13-year ancestors.

The eastern section of the main range of Brood V

While the Ohio Valley portion of Brood V occupies a heterogeneous region, the gap between the Shenandoah and Ohio Valley portions of the brood coincides with a shift between two major watersheds; the Shenandoah portion of Brood V lies in the James River drainage

adjacent to Brood I, while the Ohio Valley portion occupies the Ohio River drainage adjacent to present day Brood VIII (Figs. 3, 6). Drainage changes may be important in shaping the boundaries of other periodical cicada broods (Cooley et al. 2013; Cooley et al. 2016), and the divide between watersheds may explain the gap between the two major portions of Brood V, the eastern portion in the James River watershed being derived from Brood I by a 4-year deceleration, and the western portion in the Ohio River watershed derived from Brood IX (the supposed precursor of Brood VIII in the Lloyd and Dybas 1966 scheme) by a 4-year acceleration. These hypotheses can be tested by new data from complete mtDNA genomes and endosymbiont genomes currently under investigation.

The Long Island disjuncts

While some schemes for the derivation of Long Island disjunct "miniature broods" from ancestral Brood XIV populations involve both 1- and 4-year changes (Fig. 8b), a scheme involving only four-year changes (Fig. 8d) provides a simpler explanation. Four-year jumps alone can explain the Long Island broods via the following deceleration series: [XIV]+4 →[I]+4 →[V]+4 →[IX]. The small Long Island disjunct population of Brood X could then have been derived from a single four-year acceleration from Brood XIV during warmer times [XIV]-4→ [X]. These insights suggest that the four-year acceleration hypothesis should be updated and renamed the "four-year jump hypothesis" to accommodate both life cycle accelerations and decelerations (Fig. 8d).

The eastern PA Brood V disjunct and the four-year jump model

346 While a four-year jump model can account for the timing and geography of the Long
347 Island broods, the Carbon County Pennsylvania population of Brood V is not easily accounted
348 for by single one- and/or four- year-life-cycle jumps from surrounding populations of Brood II or
349 nearby populations of Brood XIV. Instead, at least two one- and/or four- year changes are
350 required to derive Brood V from either of these potential parents. In one scenario, the
351 ancestors of Carbon County Brood V were Brood XIV cicadas, which underwent one 4-year
352 deceleration (delay) to join the Brood I schedule, followed by another 4-year deceleration to
353 adopt their current Brood V schedule [XIV]+4→[I]+4→[V]. In the second scenario, the
354 ancestors of this Brood V population were Brood II cicadas that underwent a 1-year
355 acceleration to join the Brood I schedule followed by a 4-year deceleration to become Brood V
356 [II]-1→[I]+4→ [V]. Alternatively, the ancestors could have been Brood II cicadas that
357 underwent a 4-year deceleration (joining the Brood VI schedule) followed by a 1-year
358 acceleration [II]+4→[VI]-1→ [V]. These scenarios, involving either a Brood XIV or a Brood II
359 ancestor, each require at least one four-year deceleration. Of these scenarios, a Brood II
360 ancestor seems more plausible because a) no populations of Brood XIV are currently found
361 nearby (Cooley et al. 2011), and b) present-day Carbon County Brood V populations are
362 encircled by Brood II (Cooley et al. 2015). However, all of these hypotheses are diminished by
363 the complete absence of any cicadas on a Brood I or Brood VI cycle in or near Carbon County
364 (Cooley 2015); thus, each scenario requires that the shift away from the intermediate stage of
365 either scenario be so complete that it left behind no local populations on the intermediate
366 schedule. A similar problem of multiple shifts leaving no intermediates arises in explaining the

origin of populations of Brood II in eastern Oklahoma, found occupying a gap within Brood IV (Cooley et al. 2015).

Concluding Remarks

In one sense, the brood concept is a bookkeeping tool; periodical cicada broods are numbered sequentially with an arbitrary start date of 1893 (Marlatt 1902). In another sense, the brood concept seems to reflect at least some biological reality. To persist, broods rely on sufficient density and geographic spread to effect predator satiation (White and Lloyd 1979; Lloyd and White 1980; Karban 1982a, b; Williams and Simon 1995); this reliance on high densities selects for temporal and spatial cohesiveness because small numbers of potential founders are unlikely to persist for long. Yet such cohesiveness is not absolute, or broods would not give rise to other broods. Our study adds to the accumulating evidence that year classes that were previously thought to have single evolutionary origins are, in a sense, polyphyletic, with multiple origins. In turn, the increasingly evident polyphyly of many broods suggests that periodical cicada life cycles are more plastic than previously thought (Marshall et al. 2003; Marshall et al. 2011; Marshall et al. 2018) and that there may be a heretofore underappreciated tension between life cycle plasticity and selection for strict brood cohesiveness. Even so, successful life cycle switching appears infrequent enough that the broods' spatiotemporal patterning seems interpretable in light of past climate and landscape changes given sufficient integrative data.

Acknowledgements

David Rothenberg and Dan Gilrein, Cornell Cooperative Extension Entomologist Suffolk Co. NY, assisted with field work, as did David Marshall, who also assisted with manuscript preparation. Full records, many with species information, are available at www.magicicada.org. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the NSF or the University of Connecticut.

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Table 1(on next page)

Mitochondrial haplotypes of select Brood V and Brood I *M. septendecim* specimens.

See Fig. 7 for mapped locations of specimens.

1

Brood	Year	Location	State	County	Latitude	Longitude	No. of samples	Sample code (haplotype group: haplotype accession)	Haplotype group
I	1978	A	NY	Suffolk	40.903	-72.862	3	en0001 (Ae: AB740808) en0002 (Ae: AB740809) en0005 (Ae: AB740810)	Ae
I	2012	B	VA	Shenandoah	38.6861	-78.7338	4	V68B	Ae
I	2012	C	WV	Pendleton	38.515	-79.1404	4	en1027 (Am); en1028 (Am); en1029 (Am: AB740828); en1030 (Ae: AB740808)	Ae, Am
I	2012	D	WV	Pendleton	38.5121	-79.2557	4	en1023,1024,1026 (Am: AB740828); en1025 (Am: AB74026)	Am
I	2012	E	VA	Rockingham	38.3853	-79.0246	3	en1013-1015 (Ae: AB740808)	Ae
I	2012	F	WV	Pendleton	38.3041	-79.1918	4	en0913,0914,0916 (Ae: AB740808); en0915 (Ae)	Ae
I	2012	G	VA	Augusta	38.2152	-79.1232	4	en1016-1019 (Ae: AB740808)	Ae
I	2012	H	VA	Augusta	38.1614	-79.1741	3	en1020-1022 (Ae: AB740808)	Ae
I	2012	I	VA	Rockbridge	37.84432	-79.59543	4	12.VA.RKB	Ae
I	2012	J	VA	Botetourt	37.5555	-79.6355	4	V57	Ae
V	1999	K	OH	Ross	39.317	-82.777	3	en0011 (Am: AB740826) en0012 (Am: AB740827) en0013 (Am: AB740828)	Am
V	2016	L	VA	Shenandoah	38.87299	-78.63828	4	en0961-0964 (Ae: AB740808)	Ae
V	2016	M	VA	Augusta	38.21769	-79.21769	4	en1001-1004 (Ae: AB740808)	Ae
V	2016	N	VA	Augusta	38.1839	-79.21317	4	en0957-0960 (Ae: AB740808)	Ae
V	2016	O	VA	Bath	38.0921	-79.78225	4	en1009-1012 (Am: AB740828)	Am
V	2016	P	VA	Bath	37.95093	-79.86982	4	en1005,1007 (Am: AB740828); en1006 (Ae: AB740808); en1008 (Am)	Ae, Am
V	2016	Q	VA	Alleghany	37.85146	-79.80739	4	en0997-0999 (Am: AB740828); en1000 (Ae: AB740808)	Ae, Am

2

3

Figure 1

The original Lloyd and Dybas “4-year acceleration” scheme (Lloyd and Dybas 1966b).

Broods in parentheses were considered of uncertain existence.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

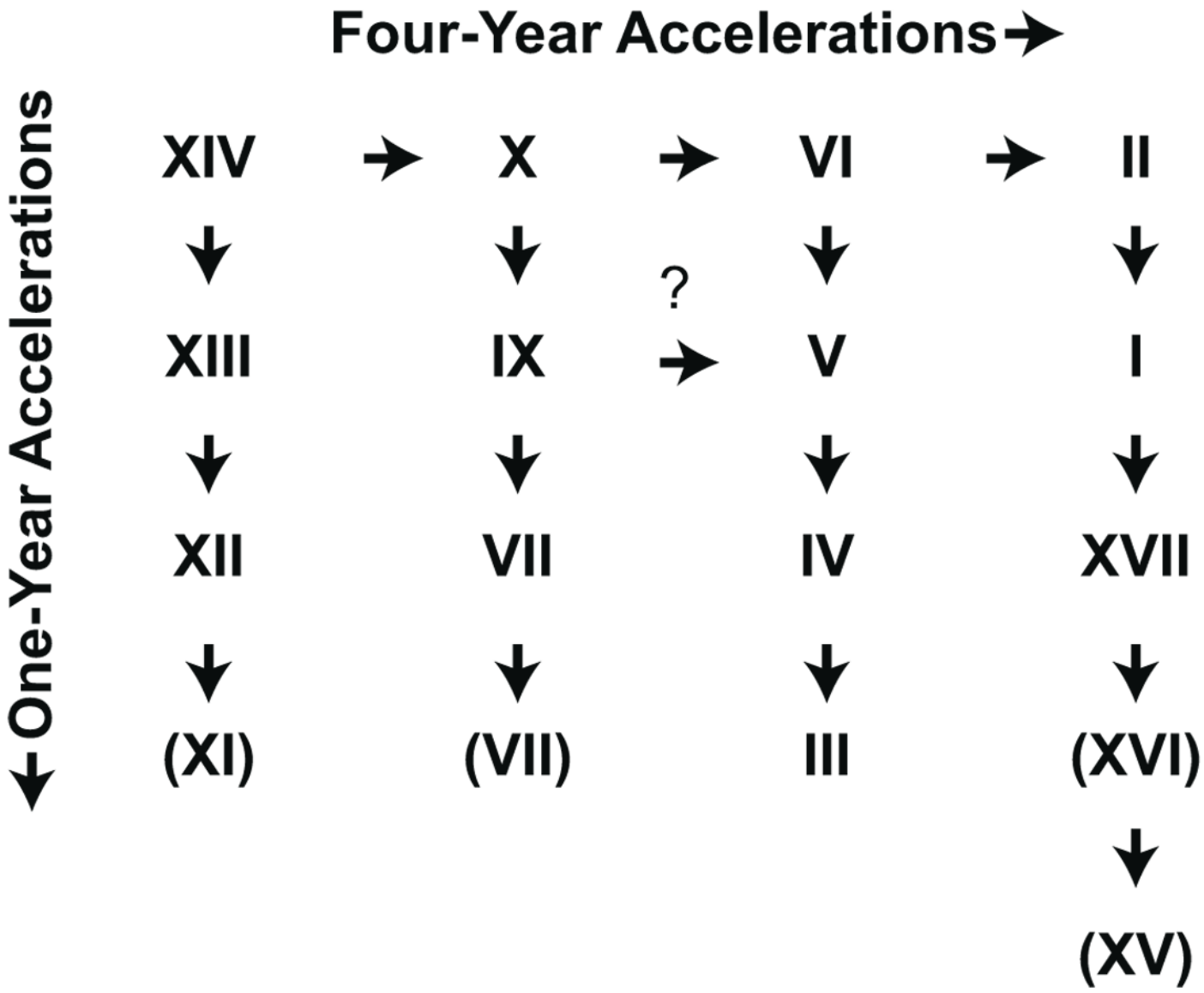


Figure 2

Overview of 17-year periodical cicada Brood V records from 2016

Orange circles are positive records, while gray circles are 2016 negative (absence) records. Symbol size reflects weights applied to reflect confidence (See text). Smaller symbols are crowdsourced records with low confidence; larger symbols have higher confidence (note that in Southern VA crowdsourced records in the range of Brood II were checked by the authors a week or more after the reports; we found no evidence of cicadas and their absence is indicated by grey dots).

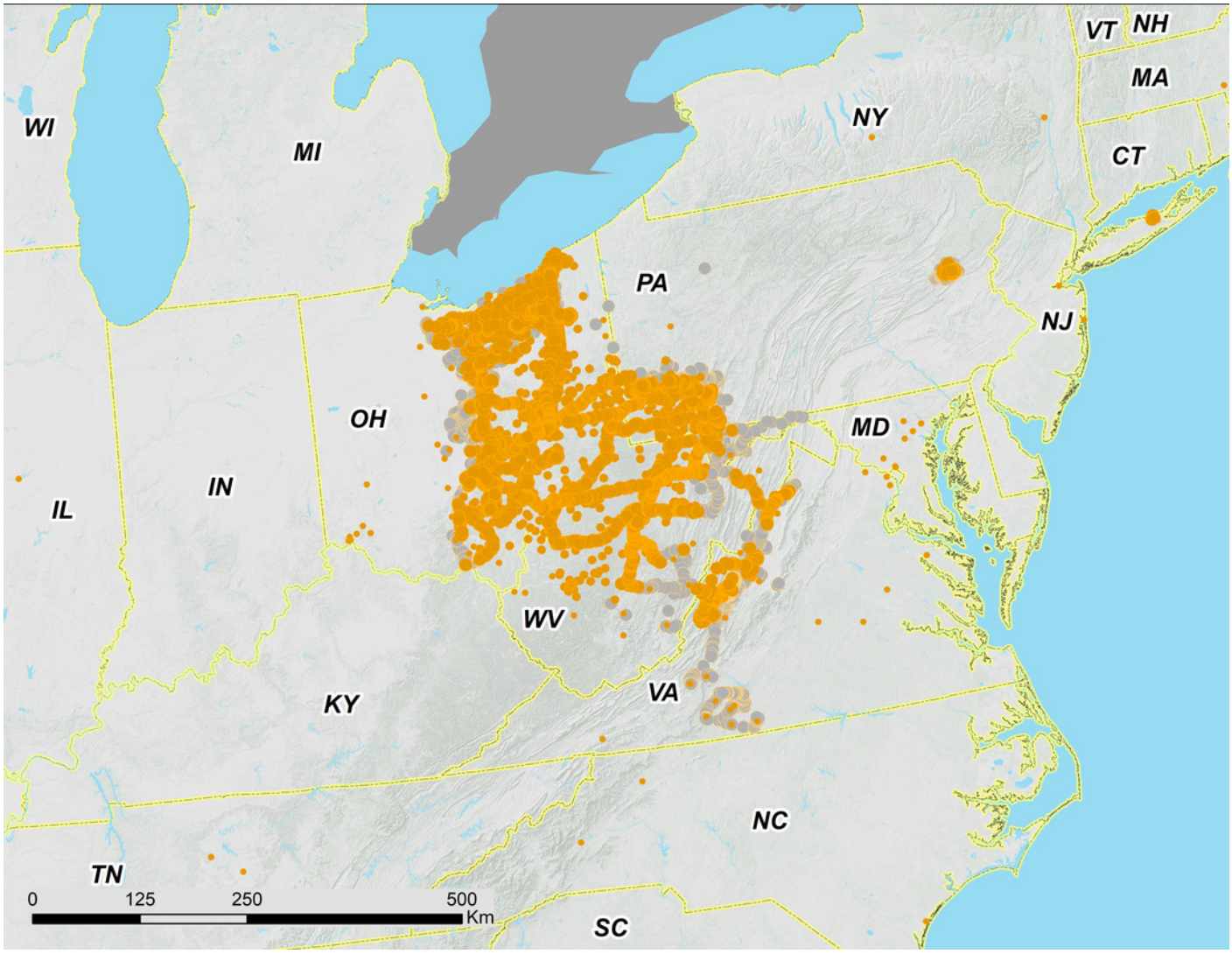


Figure 3

Ohio Valley and Virginia portions of 17-year periodical cicada Brood V.

Orange symbols are verified positive records, gray symbols are verified 2016 negative records. Circles are presence records from 2016, squares from 1999, and crosses from 1982. Symbol size reflects weights applied to reflect confidence (See text). Smaller symbols are crowdsourced records with low confidence; larger symbols have higher confidence.

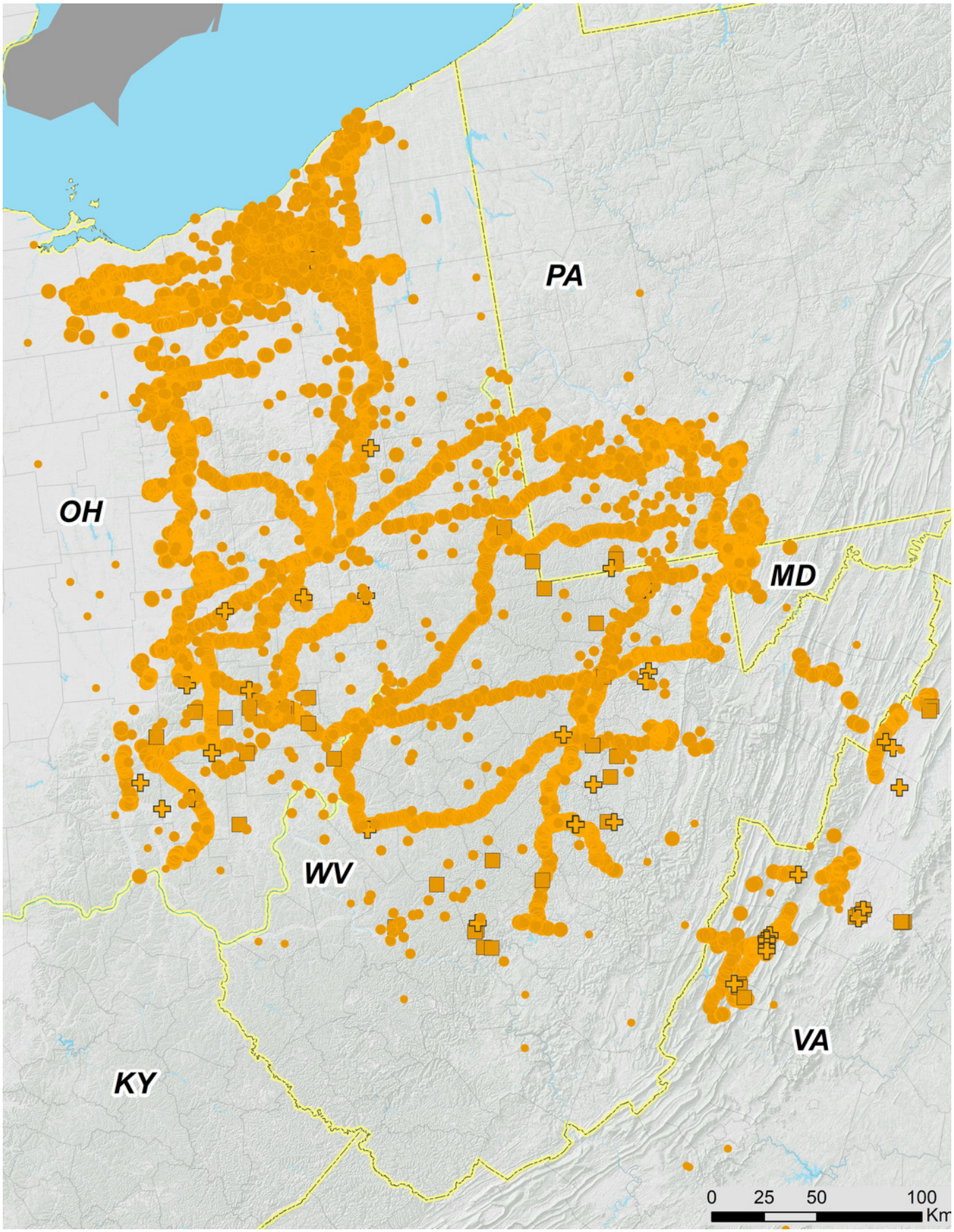

PA
OH
MD
WV
VA
KY
0
25
50
100
Km

Figure 4

Long Island portion of 17-year periodical cicada Brood V.

Orange symbols are verified positive records, gray symbols are verified negative records. Circles are records from 2016, squares from 1999, and crosses from 1982. State Parks are shown in green; Calverton National Cemetery is shown in light green.

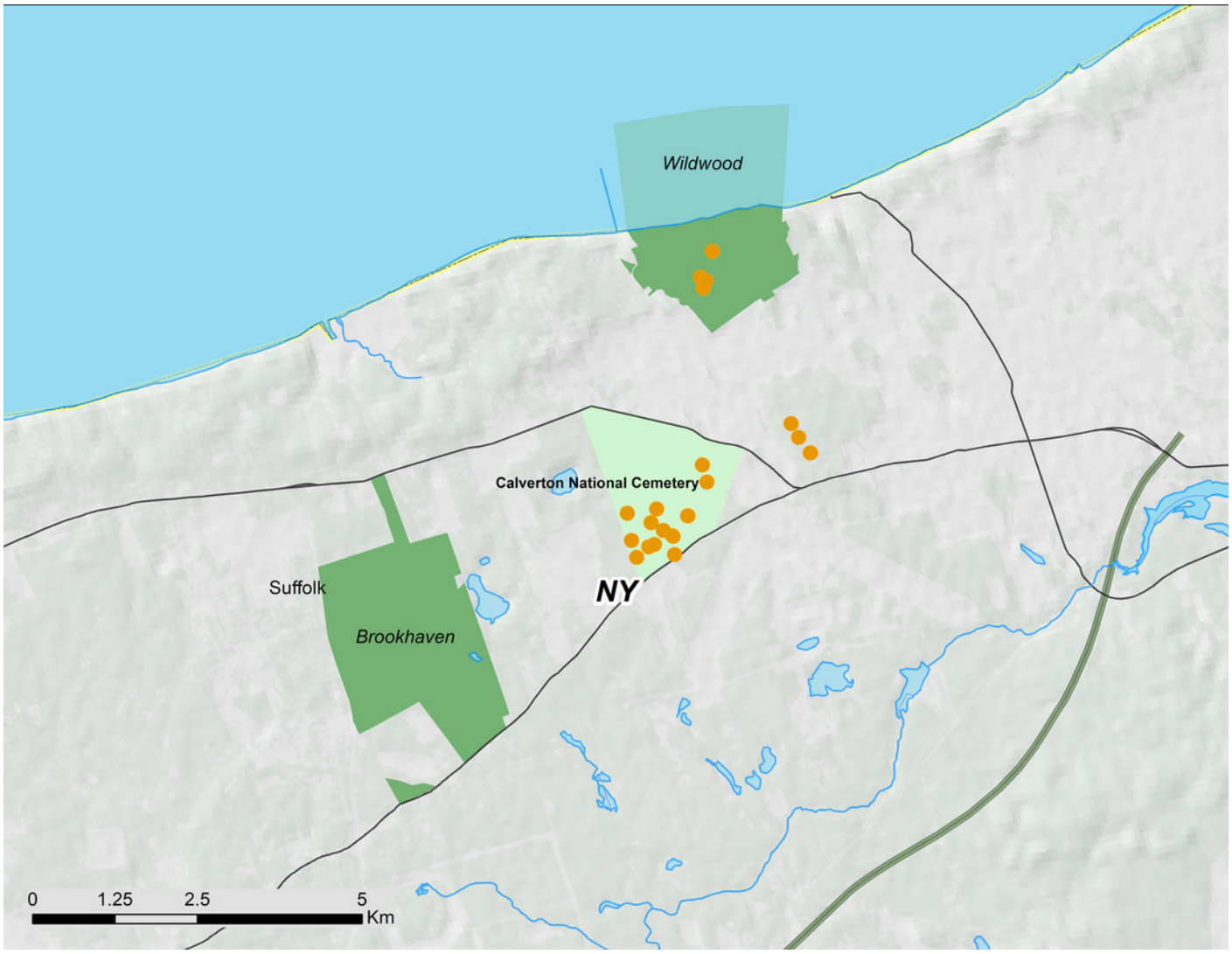


Figure 5

Carbon County, PA portion of 17-year periodical cicada Brood V as mapped in 2016.

Orange symbols are verified positive records, gray symbols are verified negative records. Brood II presence records shown in red and reprinted from Cooley et al. (2015).

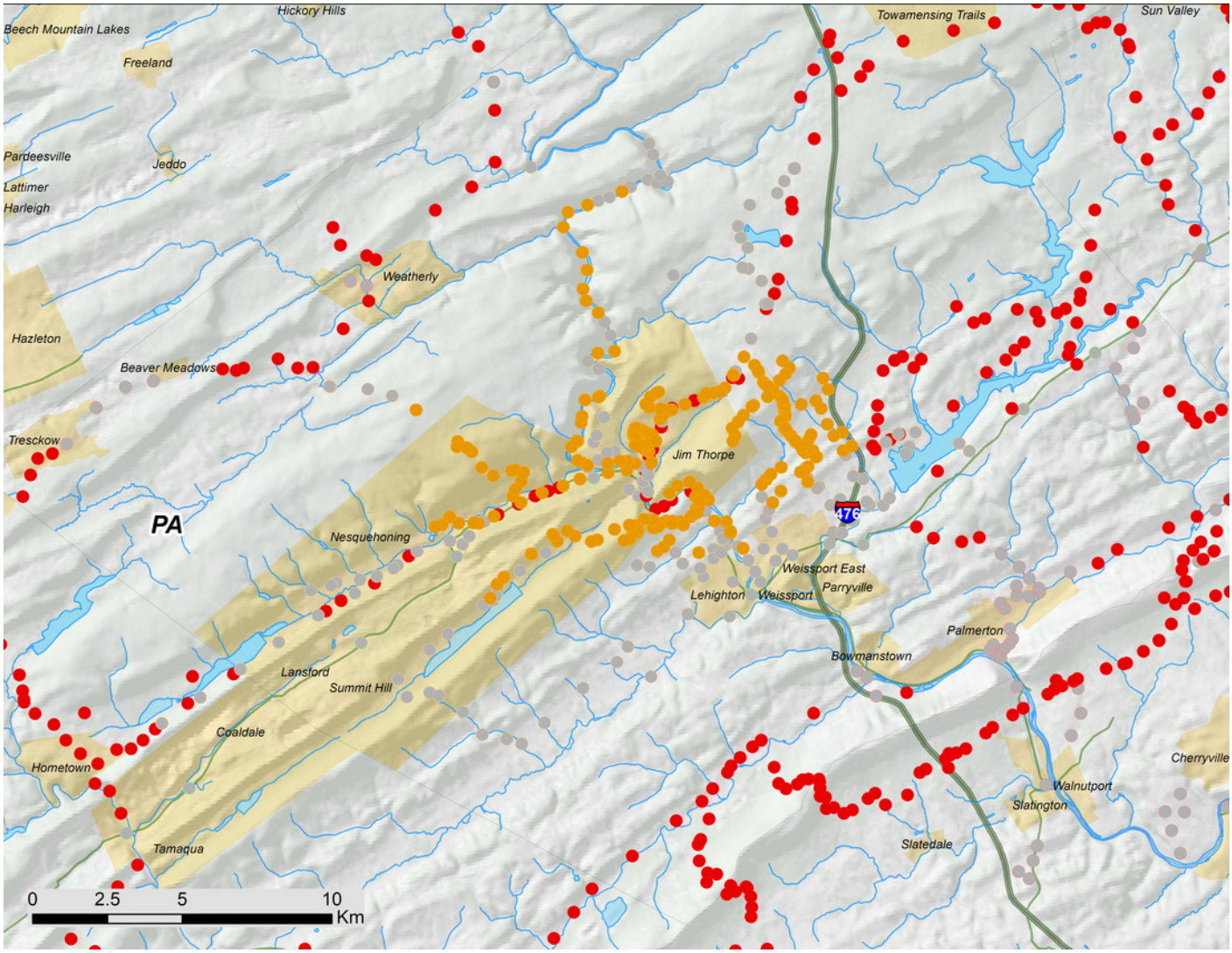


Figure 6

Associations of 17-year periodical cicada Broods.

Periodical cicada Broods V (orange symbols), I (purple symbols; Cooley 2015), II (red symbols Cooley et al. 2015), IX (pink symbols) and X (blue symbols; Cooley et al. 2009).

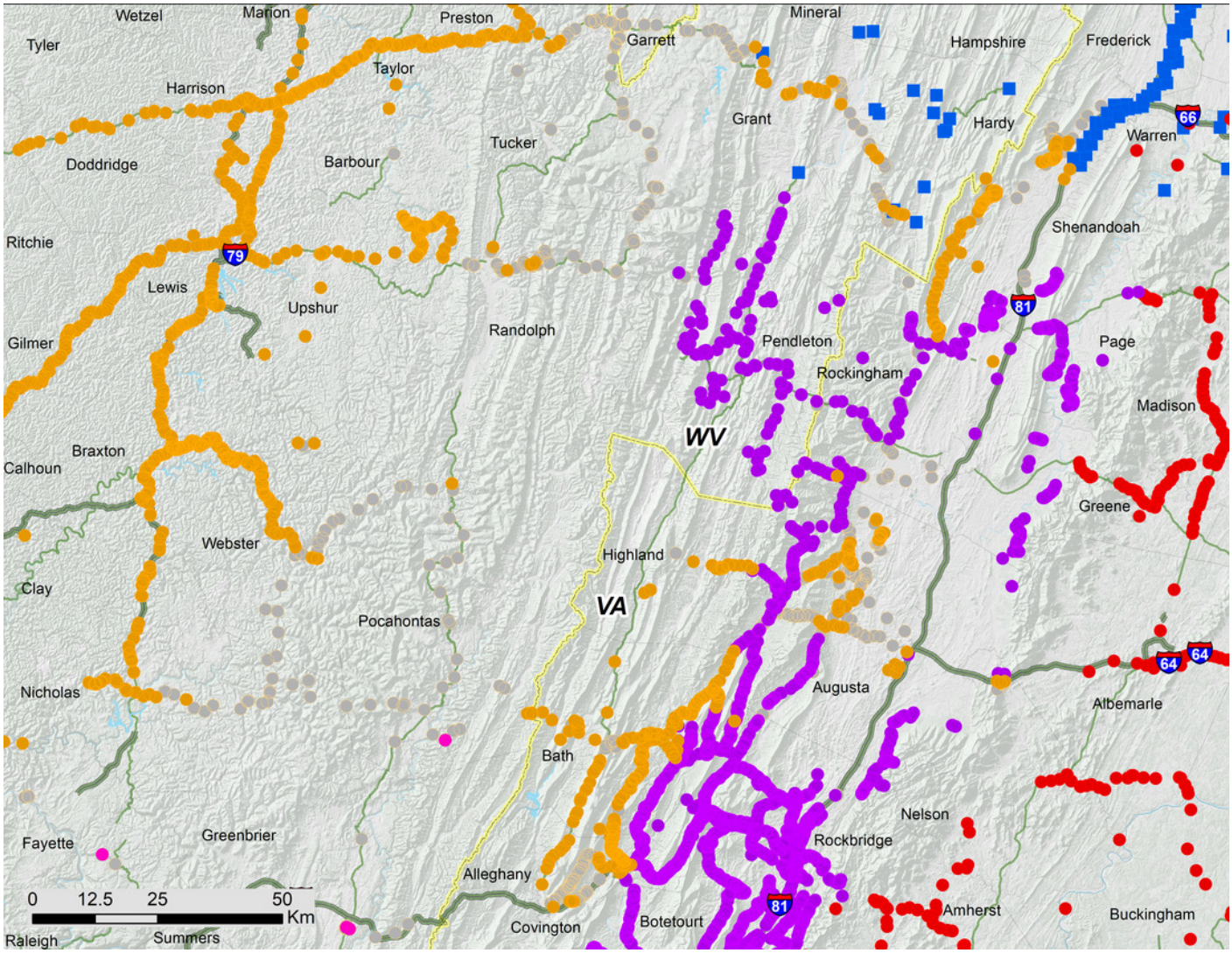


Figure 7

Periodical cicada mtDNA haplotypes in Broods I and V.

Haplotype *Ae* (triangles) and *Am* (circles) are found in 17-year periodical cicada Broods V (orange symbols) and I (purple symbols) following terminology of Sota et al. (2013). Genetic data from Table 1; haplotype network constructed using TCS version 1.21 (Clement et al. 2000)

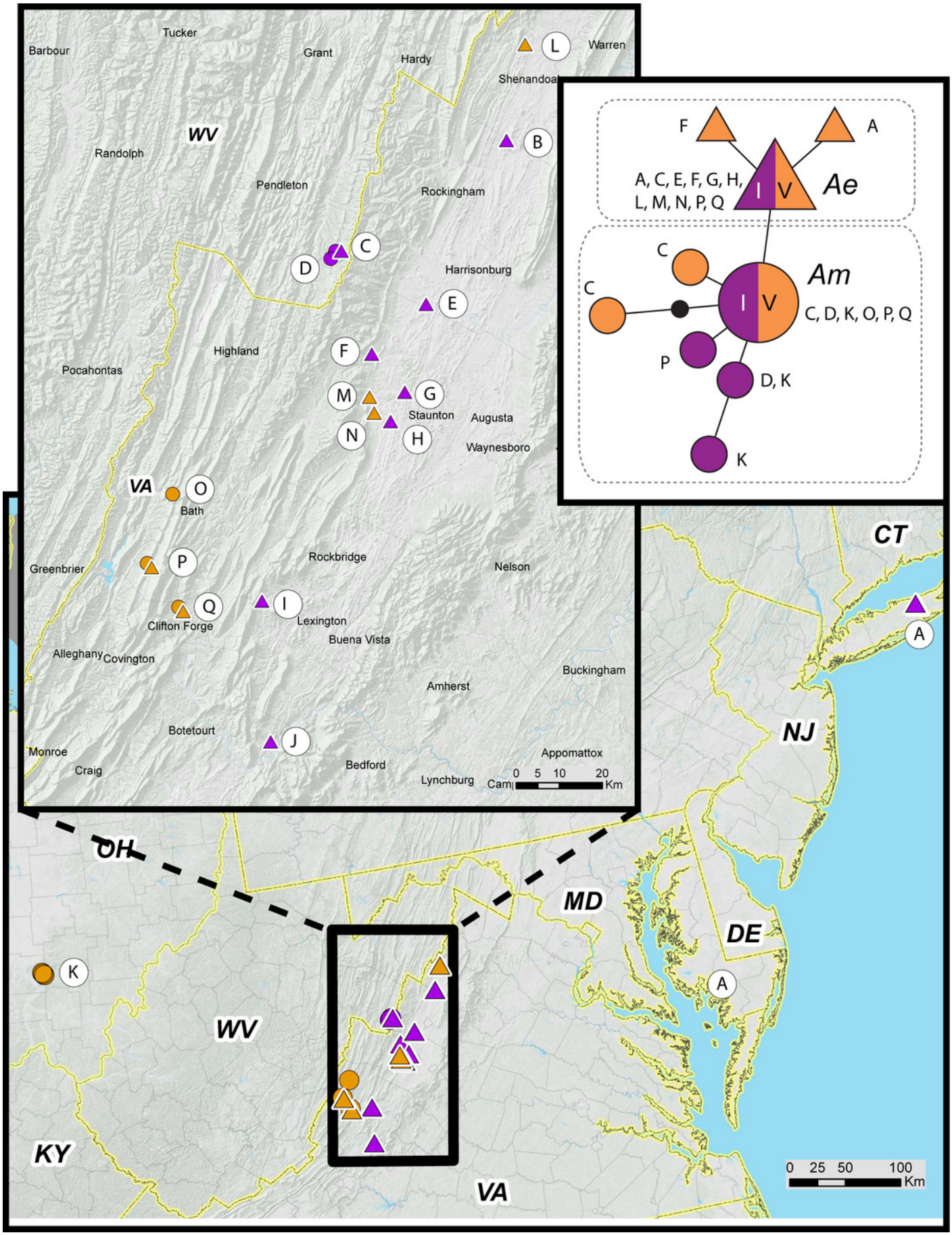

Tucker
Barbour
Grant
Hardy
Warren
Shenandoah
WV
Randolph
Pendleton
Rockingham
Harrisonburg
Highland
Pocahontas
Staunton
Augusta
Waynesboro
VA
Bath
Greenbrier
Rockbridge
Nelson
Clifton Forge
Lexington
Buena Vista
Alleghany
Covington
Buckingham
Amherst
Botetourt
Monroe
Craig
Bedford
Lynchburg
Appomattox
0 5 10 20
Km
F
A
A, C, E, F, G, H,
L, M, N, P, Q
I V
Ae
C
C
I V
Am
C, D, K, O, P, Q
P
D, K
K
CT
NJ
DE
MD
OH
WV
KY
VA
0 25 50 100
Km

Figure 8

Hypotheses for periodical cicada brood formation based on the original Lloyd and Dybas (1966b) “4-year acceleration” hypothesis.

A) The Simon and Lloyd (1982) modified brood derivation scheme. Solid single arrows indicate that the two broods have contiguous or closely associated geographic ranges, dashed arrows that they do not. Triple arrows indicate that the broods’ ranges are closely associated in three different parts of the country suggesting the possibility of polyphyletic origins (repeated migration between overlapping broods over generations). Broods in parentheses are of doubtful existence consisting of very few records; no arrows lead from them. Broods in square brackets could be derived as shown but there is no need to do so since a simpler derivation exists. We added the parentheses to Brood XV and subtracted them from XI; B) Possible scenario for the formation of disjunct LI broods by four-year accelerations superimposed on the Lloyd and Dybas scheme. Grey broods do not occur on LI. Brood XIV is the most widespread and abundant LI brood. Disjunct LI broods are marked with primes. Doubtful and extinct broods have been removed. C) Scenario for the formation of disjunct LI broods by three four-year decelerations and one on-year acceleration. D) Our new four-year jump model for deriving all 17-year periodical cicada broods from a postulated Brood XIV ancestor, by a combination of 4-year and 1-year accelerations, modified from Lloyd and Dybas (1966) and Simon and Lloyd (1982). Broods for which there are no or doubtful historical records are excluded. Double-headed arrows have been added to show both accelerations and decelerations. Triple arrows indicate the possibility of continuous migration through time between geographically overlapping populations over generations. Black arrows indicate jumps that are hypothesized to occur with high probability, grey arrows indicate jumps that are hypothesized to be rare or that do not occur today but may have occurred in the past. Dashed arrows indicate doubtful processes due to lack of geographic proximity. Broods in parentheses are probably not self-perpetuating at present but may have been in

the past. Broods in square brackets are extinct. Under this scheme, one-year decelerations are unlikely and are not shown.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

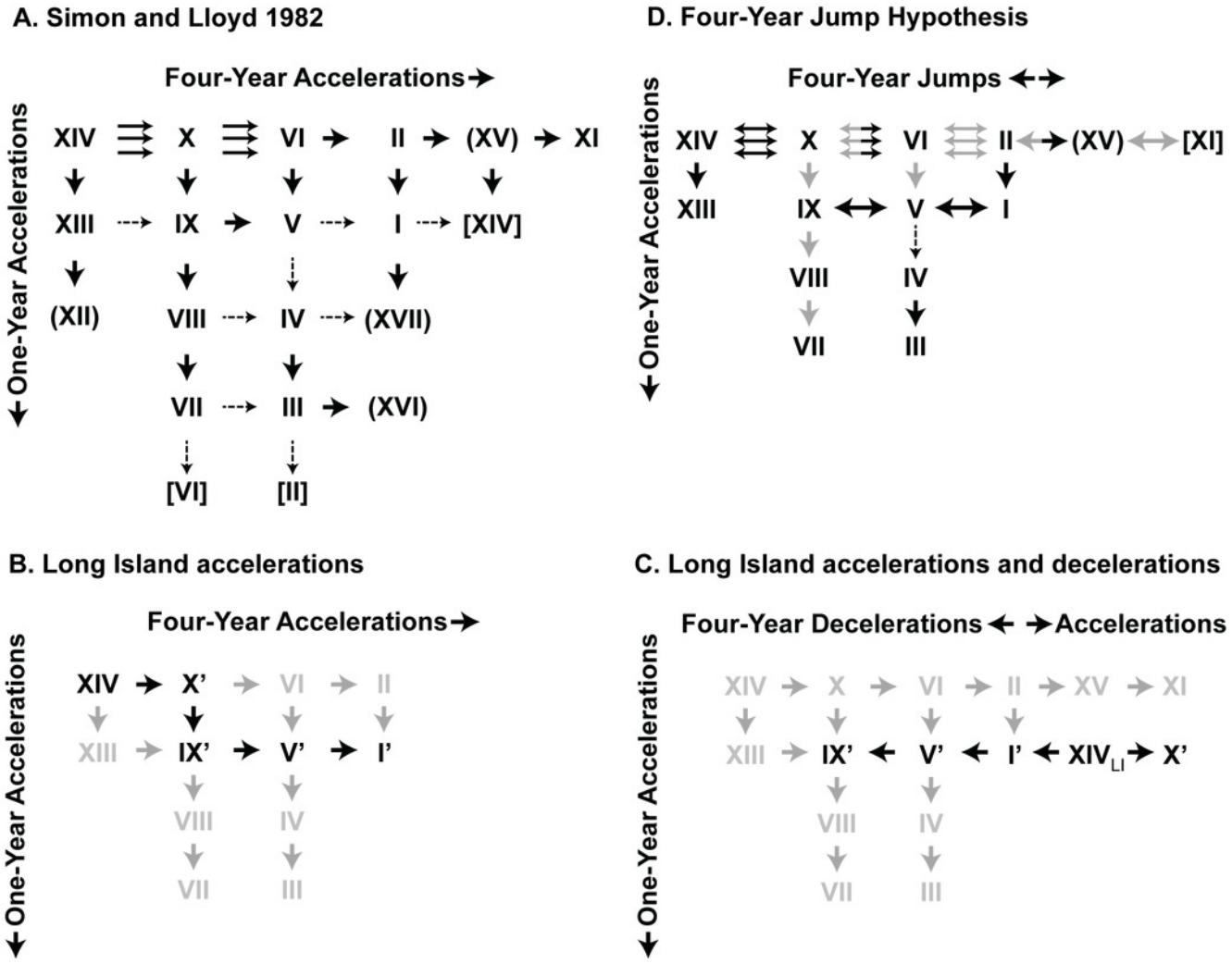
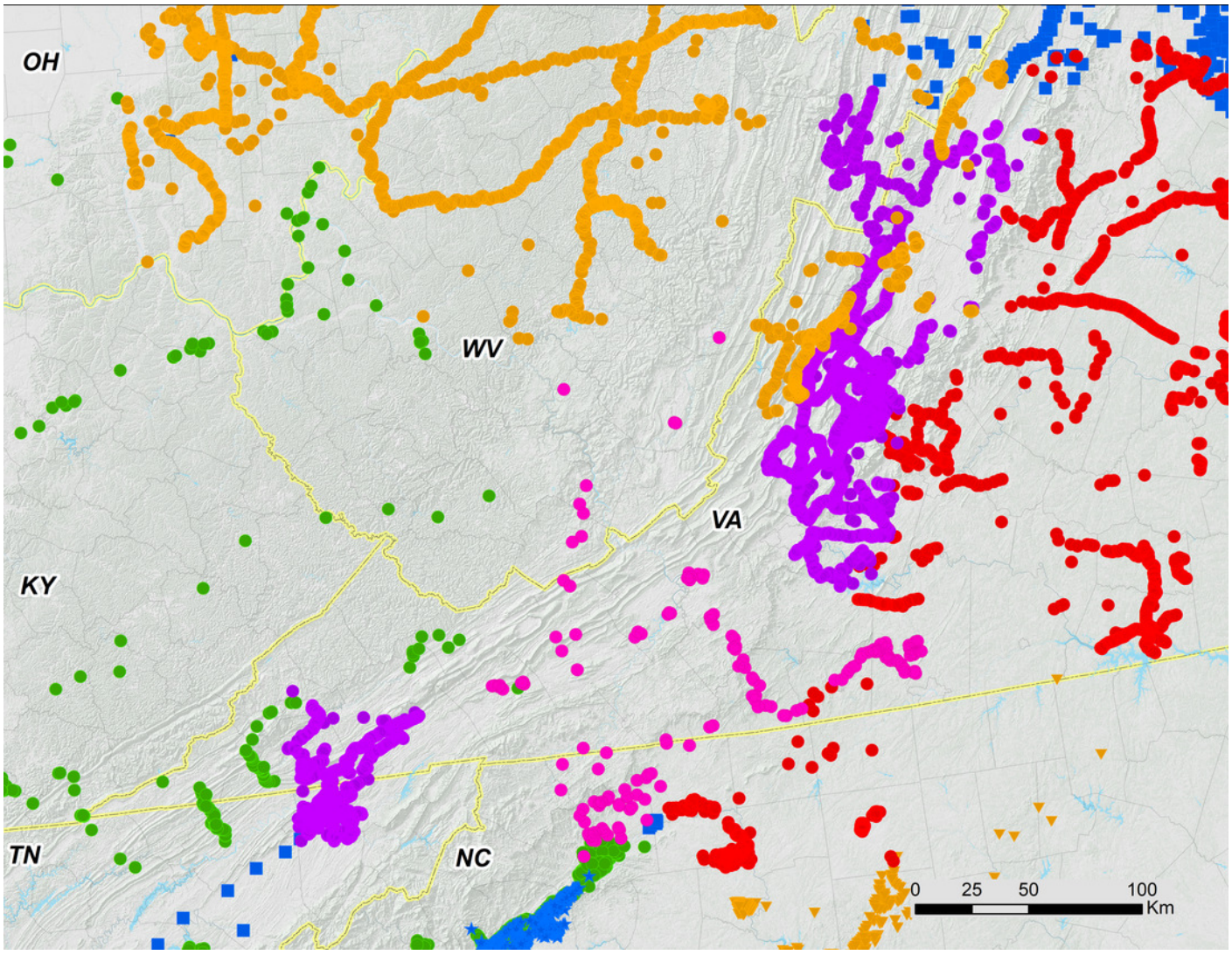


Figure 9

Periodical cicada Brood I disjunct populations in relation to other broods.

Brood I (purple) in the Shenandoah Valley of Virginia with a disjunct population of 200 km southwest in northeast TN that is partly surrounded by Brood XIV (green). Broods II (red), V (orange), VI (blue stars), IX (pink) and X (blue) also shown. Other broods omitted for clarity. Redrawn from (Cooley et al. 2009; Cooley et al. 2011; Cooley 2015; Cooley et al. 2015; Cooley et al. In Prep.).