

Article

## Biogeography of the Cicadas (Hemiptera: Cicadidae) of North America, North of Mexico

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**Abstract:** We describe and illustrate the biogeography of the cicadas inhabiting continental North America, north of Mexico. Species distributions were determined through our collecting efforts as well as label data from more than 110 institutional collections. The status of subspecies is discussed with respect to their distributions. As we have shown over limited geographic areas, the distribution of individual species is related to the habitat in which they are found. We discuss the biogeography of the genera with respect to their phylogenetic relationships. California is the state with the greatest alpha diversity (89 species, 46.6% of taxa) and unique species (35 species, 18.3% of taxa). Texas, Arizona, Colorado and Utah are the states with the next greatest alpha diversity with Texas, Arizona and Utah being next for unique species diversity. Maine, New Hampshire and Rhode Island are the states with the least amount of cicada diversity. Diversity is greatest in states and areas where there is a diversity of plant communities and habitats within these communities. Mountainous terrain also coincides with increases in diversity. Several regions of the focus area require additional collection efforts to fill in the distributions of several species.

**Keywords:** cicada; distribution; *Diceroprocta*; *Tibicen*; *Okanagana*; *Okanagodes*; *Cacama*; *Magiccicada*; *Platypedia*; *Cicadetta*

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## 1. Introduction

Cicadas are large, generally conspicuous insects in their environments. The calling songs of the males are thought of as a sign of summer and cicadas are part of the popular culture in multiple regions of the world. Even though the presence of cicadas is generally easy to ascertain and they are popular with amateur entomologists, there is still much to be determined with respect to the diversity and distributions of cicada species in the world. For example, over the past decade we and our colleagues have expanded our knowledge of the ranges of cicada species throughout the New World while simultaneously increasing our understanding of the known cicada diversity in individual countries by as much as 500% [1–25] including the first records of cicadas in El Salvador [1]. The uncertainty in the composition of the New World cicada fauna included, until recently, North America, north of Mexico where 17 species were removed from the fauna in the first comprehensive study of the region [26].

The diversity of the cicadas of North America, north of Mexico recently has been determined [26]. The biogeography of individual species has been investigated as part of studies on the biology of specific taxa [19,23,24,27–32] but a complete review of the biogeography of the North American cicadas has not been produced. The distributions of cicadas for a limited number of states have been published but more recent analyses have added to the often dated and incomplete cicada diversity within those states [21,33–50].

This study is the summary of our field research and the data obtained from the labels of cicada specimens stored in more than 110 institutional collections. We illustrate the distribution of each species currently known to inhabit North America, north of Mexico. We attempt to associate the distributions with phytogeographic regions if possible and host plants if the data exist since cicadas are often limited in their distribution by the phytogeographic region they inhabit [18,21,27,29–31,49,51–57]. We have also elevated subspecies to species rank in part based on geographic separations [27,29,30]. These data will provide an historical perspective on the distribution of cicadas from the region so changes due to human activity can be monitored and species that might be considered for conservation efforts can be identified.

## 2. Results and Discussion

The cicada fauna of North America, north of Mexico currently consists of 170 species and 21 subspecies [26]. The taxa are distributed among 16 genera, eight tribes, and three subfamilies within the family Cicadidae. The taxonomy and a list of the species currently known to inhabit North America, north of Mexico are summarized in Table 1. The table also contains a summary of the states and/or provinces for which we have records for each species as illustrated in the figures. The genera are discussed following the higher taxonomy listed in Table 1.

**Table 1.** Diversity and distribution of the cicadas of North America, north of Mexico. All species are members of the family Cicadidae. State and provincial abbreviations follow the postal code system for the USA and Canada.

Subfamily	Tribe	Genus	Species	Distribution
Cicadinae	Cryptotympanini	<i>Cacama</i>	<i>C. californica</i> Davis	CA, NV
			<i>C. collinaplaga</i> Sanborn & Heath	TX
			<i>C. crepitans</i> (Van Duzee)	CA
			<i>C. moorei</i> Sanborn & Heath	AZ, NV
			<i>C. valvata</i> (Uhler)	AZ, CA, CO, KS, NV, NM, OK, TX, UT
			<i>C. variegata</i> Davis	TX
		<i>Diceroprocta</i>	<i>D. apache</i> (Davis)	AZ, CA, CO, NV, UT
			<i>D. arizona</i> (Davis)	AZ
			<i>D. aurantiaca</i> Davis	NM, TX
			<i>D. averyi</i> Davis	TX
			<i>D. azteca</i> (Kirkaldy)	KS, OK, TX
			<i>D. bequaerti</i> (Davis)	AL, AR, LA, MS, OK, TX
			<i>D. bibbyi</i> Davis	TX
			<i>D. biconica</i> (Walker)	FL
			<i>D. canescens</i> Davis	TX
			<i>D. cinctifera cinctifera</i> (Uhler)	NM, TX
			<i>D. cinctifera limpia</i> Davis	TX
			<i>D. cinctifera viridicosta</i> Davis	TX
			<i>D. delicata</i> (Osborn)	LA, TX
			<i>D. eugraphica</i> (Davis)	AZ, CO, KS, NM, OK, TX
			<i>D. knighti</i> (Davis)	AZ
			<i>D. lata</i> Davis	TX
			<i>D. marevagans</i> Davis	TX
			<i>D. olympusa</i> (Walker)	AL, FL, GA, MS, NC, SC
			<i>D. semicincta</i> (Davis)	AZ, NM

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Diceroprocta</i>	<i>D. swalei swalei</i> (Distant)	AZ
			<i>D. swalei davisii</i> Davis	AZ
			<i>D. texana</i> (Davis)	TX, NM
			<i>D. viridifascia</i> (Walker)	AL, FL, GA, LA, MS, NC, SC, VA
			<i>D. vitripennis</i> (Say)	AL, AR, IL, IN, KS, KY, LA, MI, MS, MO, NE, OK, TN, TX, WI
		<i>Tibicen</i> (eastern species)	<i>T. auriferus</i> (Say)	AR, KS, MO, NE, NM, OK, TX
			<i>T. canicularis</i> (Harris)	AR, CT, DC, IL, IN, IA, KS, ME, MB, MD, MA, MI, MN, MO, NE, NB, NH, NJ, NY, NC, ND, NS, OH, ON, PA, PE, QC, RI, SC, SD, TN, VT, VA, WV, WI
			<i>T. davisii davisii</i> (Smith & Grossbeck)	AL, DE, DC, FL, GA, LA, MD, MA, MS, NJ, NY, NC, PA, SC, TN, TX, VA, WV
			<i>T. davisii hardeni</i> Davis	AR, MS
			<i>T. latifasciatus</i> (Davis)	MD, NJ, NC, VA
			<i>T. linnei</i> (Smith & Grossbeck)	AL, AR, CT, DE, DC, FL, GA, IL, IN, IA, KS, KY, LA, ME, MD, MA, MI, MN, MS, MO, NE, NJ, NY, NC, OH, ON, PA, SC, TN, VT, VA, WV, WI
			<i>T. lyricen lyricen</i> (Degeer)	AL, AR, CT, DE, DC, FL, GA, IL, IN, IA, KS, KY, LA, MD, MA, MI, MS, MO, NE, NH, NJ, NY, NC, OH, OK, ON, PA, RI, SC, TN, TX, VA, WV, WI
			<i>T. lyricen engelhardti</i> (Davis)	AL, CT, DE, DC, FL, GA, IN, KY, MD, MA, MS, NJ, NY, NC, OH, PA, RI, SC, TN, VA, WV

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Tibicen</i>	<i>T. lyricen virescens</i> Davis	FL, GA, NC, SC
			<i>T. pruinosus pruinosus</i> (Say)	AL, AR, CO, FL, GA, IL, IN, IA, KS, KY, LA, MA, MD, MI, MN, MS, MO, NE, NJ, NY, NC, OH, OK, PA, SC, SD, TN, TX, VA, WV, WI
			<i>T. pruinosus fulvus</i> Beamer	KS, OK
			<i>T. robinsonianus</i> Davis	AL, AR, DC, FL, GA, IN, KS, MD, MS, MO, NC, OH, PA, TN, TX, VA
			<i>T. similaris</i> (Smith & Grossbeck)	AL, FL, GA, LA, MS, NC, SC
			<i>T. superbus</i> (Fitch)	AR, KS, LA, MO, NM, OK, TX
			<i>T. tibicen tibicen</i> (Linnaeus)	AL, AR, CT, DE, DC, FL, GA, IL, IN, IA, KS, KY, LA, MD, MA, MI, MS, MO, NE, NJ, NY, NC, OH, OK, PA, RI, SC, SD, TN, TX, VT, VA, WV, WI
			<i>T. tibicen australis</i> (Davis)	AL, FL, GA, MS, NC, SC, TN, VA
			<i>T. winnemanna</i> (Davis)	AL, AR, DE, DC, GA, IN, KY, LA, MD, MS, NC, OH, OK, PA, SC, TN, TX, VA, WV
		<i>Tibicen</i> (western species)	<i>T. bifidus</i> (Davis)	AZ, CO, KS, NM, OK, TX, UT
			<i>T. chiricahua</i> Davis	AZ, NM
			<i>T. chisosensis</i> Davis	TX
			<i>T. duryi</i> Davis	AZ, CO, NM, OK, TX, UT
			<i>T. inauditus</i> Davis	AZ, CO, NM, OK, TX
			<i>T. longiperculus</i> Davis	AZ
			<i>T. parallelus</i> Davis	AZ
			<i>T. simplex</i> Davis	AZ
			<i>T. texanus</i> Metcalf	NM, OK, TX
			<i>T. townsendii</i> (Uhler)	AZ, NM, TX

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Tibicen</i> (large species)	<i>T. auletes</i> (Germar)	AL, AR, CT, DE, DC, FL, GA, IL, IN, IA, KS, KY, LA, MD, MA, MI, MS, MO, NE, NJ, NY, NC, OH, OK, PA, SC, TN, TX, VA, WV, WI
			<i>T. cultriformis</i> (Davis)	AZ, NM
			<i>T. dealbatus</i> (Davis)	CO, IA, KS, MT, NE, NM, ND, OK, SD, TX, WY
			<i>T. dorsatus</i> (Say)	AR, CO, ID, IL, IA, KS, MO, MT, NE, NM, OK, SD, TX, WY
			<i>T. figuratus</i> (Walker)	AL, AR, FL, GA, LA, MS, NC, SC, TN, TX, VA
			<i>T. pronotalis pronotalis</i> Davis	IA, MO, NE, ND, OK, SD
			<i>T. pronotalis walkeri</i> Metcalf	AL, AR, FL, GA, IL, IN, IA, KS, KY, LA, MD, MI, MN, MS, MO, NE, NC, ND, OH, OK, SD, TN, TX, VA, WV, WI, WY
			<i>T. resh</i> (Haldeman)	AR, KS, LA, MS, NE, OK, SC, TN, TX
			<i>T. resonans</i> (Walker)	AL, FL, GA, LA, MS, NC, SC, TN, TX, VA
			<i>T. tremulus</i> Cole	CO, KS, NE, OK, TX
		<i>Cornuplura</i>	<i>C. nigroalbata</i> Davis	AZ
	Fidicinini	<i>Beameria</i>	<i>B. ansercollis</i> Sanborn & Heath	UT
			<i>B. venosa</i> (Uhler)	AZ, AR, CO, IA, KS, MO, NE, NM, OK, TX, UT
			<i>B. wheeleri</i> Davis	AZ, NM
		<i>Pacarina</i>	<i>P. puella</i> Davis	AZ, LA, OK, TX
			<i>P. shoemakeri</i> Sanborn & Heath	AZ, CO, NM, TX
	Hyantiini	<i>Quesada</i>	<i>Q. gigas</i> (Olivier)	TX
	Cicadini	<i>Neocicada</i>	<i>N. chisos</i> (Davis)	TX
			<i>N. hieroglyphica hieroglyphica</i> (Say)	AL, AR, DE, FL, GA, IL, IN, KS, KY, LA, MD, MS, MO, NJ, NY, NC, OH, OK, SC, TN, TX, VA
			<i>N. hieroglyphica johannis</i> (Walker)	AL, FL, GA, NC, SC

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
Cicadettinae	Taphurini	<i>Magicicada</i>	<i>M. cassinii</i> (Fisher)	GA, IA, IL, IN, KS, KY, MD, MO, NC, NE, NJ, NY, OH, OK, PA, TN, TX, VA, WI, WV
			<i>M. neotredicim</i> Marshall & Cooley	AR, IA, IL, IN, KY, MO, TN
			<i>M. septendecim</i> (Linnaeus)	CT, DC, DE, GA, IA, IL, IN, KS, KY, MA, MD, MI, MO, NC, NE, NJ, NY, OH, PA, RI, SC, TN, VA, WI, WV
			<i>M. septendecula</i> Alexander & Moore	GA, IA, IL, IN, KS, KY, MO, NC, NJ, NY, OH, PA, TN, VA, WV
			<i>M. tredecassini</i> Alexander & Moore	AL, AR, GA, IA, IL, IN, KY, MD, MO, MS, NC, OK, SC, TN, VA
			<i>M. tredecim</i> (Walsh & Riley)	AL, AR, GA, IL, IN, KY, LA, MD, MO, MS, NC, OK, SC, TN, VA
			<i>M. tredecula</i> Alexander & Moore	AL, AR, GA, IA, IL, IN, KY, LA, MO, MS, NC, OK, SC, TN, VA
	Cicadettini	<i>Cicadetta</i>	<i>C. calliope calliope</i> (Walker)	AL, AR, CO, FL, GA, IL, IN, IA, KS, KY, LA, MD, MS, MO, NE, NC, OH, OK, SC, SD, TN, TX, VA
			<i>C. calliope floridensis</i> (Davis)	AL, FL, GA
			<i>C. cameroni</i> (Davis)	TX
			<i>C. kansa</i> (Davis)	CO, KS, LA, NE, NM, OK, TX
			<i>C. texana</i> (Davis)	TX
Tibicininae	Platypediini	<i>Platypedia</i>	<i>P. affinis</i> Davis	UT
			<i>P. aperta</i> Davis	CA
			<i>P. areolata</i> (Uhler)	BC, CA, ID, MT, NV, OR, UT, WA, WY
			<i>P. balli</i> Davis	AZ

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Platypedia</i>	<i>P. barbata</i> Davis	CA
			<i>P. bernardinoensis</i> Davis	AZ, CA, CO, NM
			<i>P. falcata</i> Davis	AZ, CA, OR, TX, WA
			<i>P. intermedia</i> Van Duzee	CA, NV
			<i>P. laticapitata</i> Davis	CA
			<i>P. mariposa</i> Davis	CA
			<i>P. middlekauffi</i> Simon	CA
			<i>P. minor</i> Uhler	CA, OR
			<i>P. mohavensis mohavensis</i> Davis	AZ, CA, CO, NV, NM, UT
			<i>P. mohavensis rufescens</i> Davis	AZ, CA, CO, NV, NM, UT
			<i>P. putnami putnami</i> (Uhler)	AZ, BC, CA, CO, ID, MT, NE, NV, NM, OR, SD, UT, WA, WY
			<i>P. putnami keddiensis</i> Davis	CA
			<i>P. putnami lutea</i> Davis	AZ, CA, CO, ID, MT, NV, NM, OR, SD, UT, WA, WY
			<i>P. putnami occidentalis</i> Davis	CA
			<i>P. rufipes</i> Davis	CA
			<i>P. scotti</i> Davis	CA
			<i>P. similis</i> Davis	CA, OR
			<i>P. sylvesteri</i> Simons	CA
			<i>P. tomentosa</i> Davis	CA
			<i>P. usingeri</i> Simons	CA
			<i>P. vanduzeei</i> Davis	CA
		<i>Neoplatypedia</i>	<i>N. ampliata</i> (Van Duzee)	CA, OR
			<i>N. constricta</i> Davis	AZ, CA, CO, ID, NV, NM OR, UT
	Tibicinini	<i>Clidophleps</i>	<i>C. beameri</i> Davis	CA
			<i>C. blaisdelli</i> (Uhler)	AZ, CA



Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Clidophleps</i>	<i>C. distanti distanti</i> (Van Duzee)	CA, NV
			<i>C. distanti truncata</i> (Van Duzee)	CA
			<i>C. rotundifrons</i> (Davis)	AZ, CA
			<i>C. tenuis</i> Davis	CA, NV
			<i>C. vagans</i> Davis	AZ, CA, NV
			<i>C. wrighti</i> Davis	CA
		<i>Okanagana</i>	<i>O. annulata</i> Davis	CA, CO
			<i>O. arboraria</i> Wymore	CA
			<i>O. arctostaphylae</i> Van Duzee	CA
			<i>O. aurora</i> Davis	CA, NV
			<i>O. balli</i> Davis	IL, IA, KS, MN, NE, ND, SD, WI
			<i>O. bella</i> Davis	AB, AZ, BC, CA, CO, ID, MT, NV, NM, OR, SD, UT, WA, WY
			<i>O. canadensis</i> (Provancher)	AB, BC, CA, CO, ID, ME, MB, MI, MN, MT, NB, NH, NY, NT, OH, ON, OR, PA, QC, SK, SD, UT, VT, WI
			<i>O. canescens</i> Van Duzee	CA, WA
			<i>O. catalina</i> Davis	CA
			<i>O. cruentifera</i> (Uhler)	CA, ID, NV, OR, UT, WY
			<i>O. ferrugomaculata</i> Davis	CA, CO, ID, OR, WA
			<i>O. formosa</i> Davis	NV, UT
			<i>O. fratercula</i> Davis	AB, BC, CA, CO, ID, MT, NV, OR, WA, WY
			<i>O. fumipennis</i> Davis	AZ, CO, NM, UT
			<i>O. georgi</i> Heath & Sanborn	AZ
			<i>O. gibbera</i> Davis	CA, CO, ID, MT, NV, NM, OR, UT, WA
			<i>O. hesperia</i> (Uhler)	AZ, CA, CO, KS, MT, NE NV, NM, OK, SD, TX, UT, WY

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Okanagana</i>	<i>O. hirsuta</i> Davis	CA
			<i>O. lurida</i> Davis	BC, ID, OR, WA
			<i>O. luteobasalis</i> Davis	AB, BC, CA, CO, ID, MB, MT, NV, ND, OR, UT, WA, WY
			<i>O. magnifica</i> Davis	AZ, CA, CO, NV, NM, OR, UT, WY
			<i>O. mariposa mariposa</i> Davis	AZ, CA, NM, OR, UT
			<i>O. mariposa oregonensis</i> Davis	OR
			<i>O. napa</i> Davis	CA, ID, WA
			<i>O. nigriviridis</i> Davis	CA
			<i>O. nigrodorsata</i> Davis	CA, NV, WA
			<i>O. noveboracensis</i> (Emmons)	NY, ON
			<i>O. occidentalis</i> (Walker)	AZ, BC, AB, CA, CO, ID, MT, NV, NM, OR, UT, WA
			<i>O. opacipennis</i> Davis	CA
			<i>O. oregona</i> Davis	CA, ID, MT, OR, WA
			<i>O. orithyia</i> Bliven	CA
			<i>O. ornata</i> Van Duzee	BC, CA, ID, NV, OR
			<i>O. pallidula</i> Davis	CA, NV, OR
			<i>O. pernix</i> Bliven	CA
			<i>O. rhadine</i> Bliven	CA
			<i>O. rimosa rimosa</i> (Say)	AB, BC, CA, CT, ID, IL, IN, IA, ME, MB, MD, MA, MI, MN, MT, NV, NB, NH, NJ, NY, ND, OH, ON, OR, PA, QC, SD, UT, VT, VA, WA, WI, WY
			<i>O. rimosa ohioensis</i> Davis	OH
			<i>O. rubrovenosa</i> Davis	AZ, CA, OR, UT
			<i>O. salicicola</i> Bliven	CA
			<i>O. salicicola</i> Bliven	CA
			<i>O. schaefferi</i> Davis	AZ, CO, NV, NM, UT

Table 1. Cont.

Subfamily	Tribe	Genus	Species	Distribution
		<i>Okanagana</i>	<i>O. sequoiae</i> Bliven	CA
			<i>O. simulata</i> Davis	CA, OR
			<i>O. sperata</i> Van Duzee	CA, NV
			<i>O. striatipes</i> (Haldeman)	AZ, CA, CO, ID, KS, MT, NE, NV, NM, OR, SD, UT, WY
			<i>O. sugdeni</i> Davis	UT
			<i>O. synodica synodica</i> (Say)	AB, AZ, CA, CO, IA, KS, MO, MT, NE, NM, ND, OR, SD, TX, UT, WY
			<i>O. synodica nigra</i> Davis	AZ, NM, UT
			<i>O. tanneri</i> Davis	AZ, CO, UT
			<i>O. triangulata</i> Davis	CA, NV
			<i>O. tristis tristis</i> Van Duzee	AZ, CA, NV, OR, WA
			<i>O. tristis rubrobasalis</i> Davis	CA, NV
			<i>O. uncinata</i> Van Duzee	CA
			<i>O. utahensis</i> Davis	AZ, BC, CA, CO, ID, MT, NV, NM, OR, UT, WA
			<i>O. vanduzeei</i> Distant	BC, CA, ID, NV, OR, UT, WA
			<i>O. vandykei</i> Van Duzee	CA, OR
			<i>O. venusta</i> Davis	CA
			<i>O. villosa</i> Davis	CA
			<i>O. viridis</i> Davis	AR, LA, MS, TX
			<i>O. vocalis</i> Bliven	CA
			<i>O. wymorei</i> Davis	CA
			<i>O. yakimaensis</i> Davis	WA
		<i>Okanagodes</i>	<i>O. gracilis gracilis</i> Davis	AZ, CA, NV, UT
			<i>O. gracilis viridis</i> Davis	AZ, CA
			<i>O. terlingua</i> Davis	TX
		<i>Tibicinoides</i>	<i>T. cupreosparsa</i> (Uhler)	CA
			<i>T. mercedita</i> (Davis)	CA
			<i>T. minuta</i> (Davis)	CA

The North America species are all representatives of the family Cicadidae [26]. The extant Tettigarctidae are only found in Australia. The species are split into the three subfamilies that comprise the Cicadidae. Half of the genera are found in the Cicadinae which is also the most diverse subfamily worldwide. The Cicadettinae are represented by two genera in North America but are found in greater diversity in Australia, Asia, Europe and Africa. The Tibicininae has its greatest diversity in the New World with additional representatives found in Europe, Africa and Asia. Tribal affiliations of the North American genera illustrate phylogenetic relationships to other regions of the world. The Cryptotympanini (including the genera *Cacama*, *Diceroprocta*, *Tibicen* and *Cornuplura* from North America, north of Mexico) extends across Australia, Asia, Madagascar, Europe, North America, Central America and South America. The Fidicinini (including the genera *Beameria* and *Pacarina* from North America, north of Mexico) contains taxa that are primarily found in South and Central America. The Hyantiini (including the genus *Quesada* from North America, north of Mexico) extends across South and Central America extending into North America but has more diversity in South America. The Cicadini (including the genus *Neocicada* from North America, north of Mexico) is primarily composed of Asian species with some genera extending into Europe and North Africa and Central America. The Taphurini (including the genus *Magiccicada* from North America, north of Mexico) includes primarily species from South and Central America, Australia, Asia and Africa. The Cicadettini (including the genus *Cicadetta* from North America, north of Mexico) is found in Europe, Africa, Asia, and is very diverse in Australia with only a single questionable species from South America. The Platypediini (including the genera *Platypedia* and *Neoplatypedia* from North America, north of Mexico) is primarily found in North America, north of Mexico. The Tibicinini (including the genera *Clidophleps*, *Okanagana*, *Okanagodes* and *Tibicinoides* from North America, north of Mexico) has its greatest species diversity in North America, north of Mexico but also contains species inhabiting Europe, North Africa and Asia.

The species distributions are presented in the figures not only to illustrate their ranges but also to provide additional information with respect to their taxonomic or phylogenetic relationships. Subspecies are placed on the same map in order to illustrate the distribution of each subspecies providing the opportunity to differentiate their ranges. Species that were originally described as varieties were elevated to subspecies rank with the publication of the last edition of the *Code* [58]. By placing the subspecies for a taxon on the same map, we hope to facilitate the separation of true species from subspecies as has occurred in several cicada species [10,27,29,30,59–63]. We have used distributional patterns to show geographic isolation along with morphological, acoustical and physiological data to elevate cicada subspecies to species rank in the past [10,27,29,30]. Species that form a complex of related species are also illustrated on a single map when possible. All remaining species are grouped together based on the ability to demonstrate the distributions of the collected species without interference. What we call host plants are plants that we have observed cicadas using as food and/or oviposition sites.

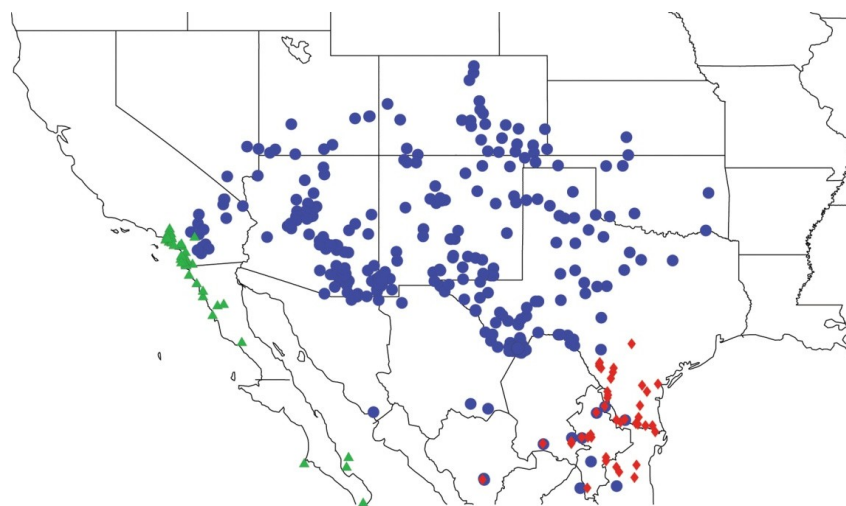
### 2.1. Biogeography of the *Cacama* Species

Half of the species of the genus *Cacama* are found in North America, north of Mexico [24]. All but one of the recently described species are represented in Mexico with the range of the genus

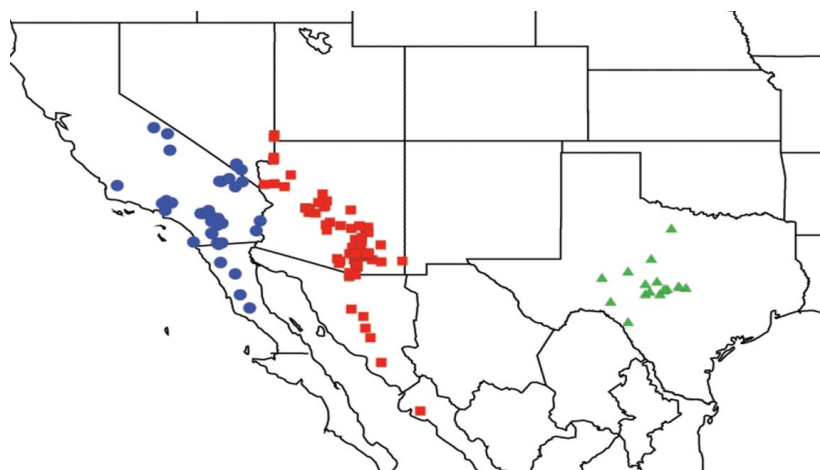
extending into Central America [6,8,24,26]. The species of *Cacama* are associated with *Opuntia* Miller [24,36,49,56,64–69] and are often called “cactus dodgers” based on their habits of flying from cactus pad to cactus pad as they perch for a calling bout. *Cacama crepitans* has also been associated with California sage (*Artemisia californica* Lessing) [69].

*Cacama valvata* is the most widespread member of the genus in North America, north of Mexico found in nine states (Figure 1). In contrast, *C. crepitans* (Figure 1), *C. variegata* (Figure 1), and *C. collinaplaga* (Figure 2) are found in a single state with *C. collinaplaga* being the only species not extending into Mexico. *Cacama californica* and *C. moorei* are each found in two states and Mexico (Figure 2).

**Figure 1.** Distribution of *Cacama crepitans* (green triangles), *C. valvata* (blue circles) and *C. variegata* (red diamonds).



**Figure 2.** Distribution of *Cacama californica* (blue circles), *C. moorei* (red squares) and *C. collinaplaga* (green triangles).



*Cacama collinaplaga* is found in the Hill Country of central Texas [24] in the desert grasslands phytogeographic region [70]. *Cacama moorei* is restricted to the Sonoran Desert [24]. *Cacama crepitans* is found in the California upland forests and woodlands showing a strong affiliation with the Peninsular and Baja Range [71]. *Cacama variegata* is found in the southern portions of the

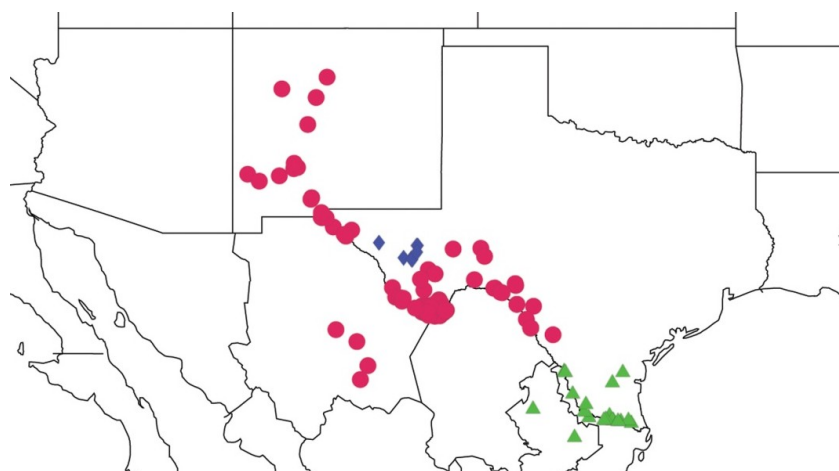
southeastern coastal plain vegetation [72] and desert grasslands [70]. *Cacama californica* is found in several phytogeographic regions with specimens collected with the California upland forests and woodlands as well as portions of the Sonoran and Mojave deserts [71]. *Cacama valvata* has the greatest distribution being found in several plant communities. It has been collected in desert grasslands [70], Great Basin, Chihuahuan, Mojave and Sonoran deserts [56,73], chaparral [74,75], and intermountain deserts [76]. The success of *Opuntia* colonizing various habitats appears to have facilitated the spread of the species into a wide variety of environments.

## 2.2. Biogeography of the *Diceroprocta* species

There are 21 species and three subspecies of the genus *Diceroprocta* in North America, north of Mexico [26]. The genus appears to have originated in Mexico as this is where the genus exhibits its greatest diversity [8]. The genus is most closely related to *Tibicen* with many of the species being assigned to or originally described as part of the genus *Tibicen* [26]. The species of *Diceroprocta* can be separated into two groups, those whose males have rounded opercula and are primarily found in the central and eastern United States and those whose males have pointed opercula and are found in the southern and western United States and the Florida Keys.

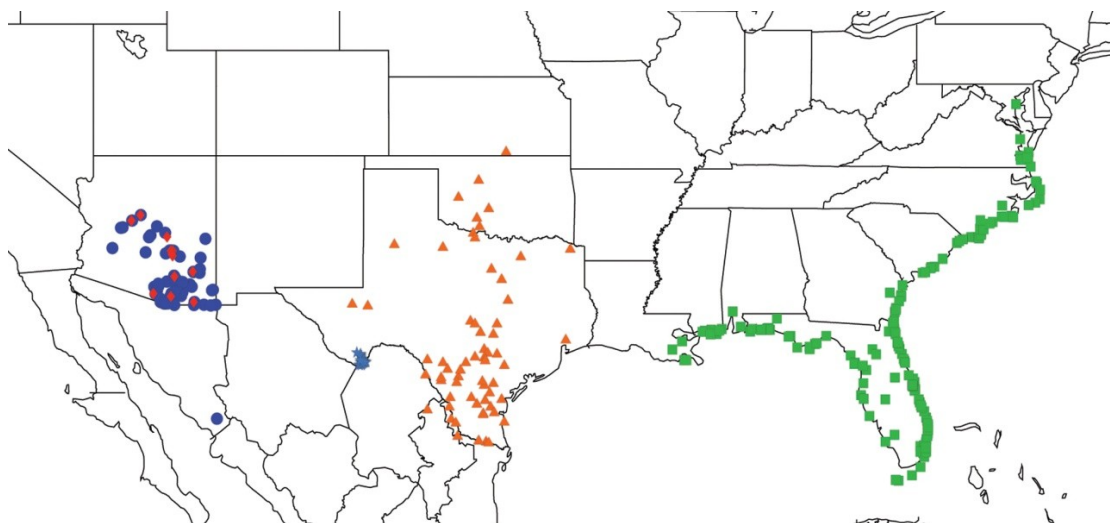
The *D. cinctifera* species complex is associated with riparian habitats of the Rio Grande River system (Figure 3) with *Prosopis* L. being a primary host [77]. It has also been associated with cottonwoods (*Populus* spp.) [66]. *Diceroprocta cinctifera limpia* is found in the Limpa creek tributary system [77,78] whereas *D. cinctifera cinctifera* and *D. cinctifera viridicosta* are found on the Rio Grande proper with *D. cinctifera viridicosta* found on the southern and eastern portion of the river system [77]. Both *D. cinctifera viridicosta* [8] and *D. cinctifera cinctifera* [14] have had their ranges extended into Mexico. *Diceroprocta cinctifera cinctifera* has been associated with mesquite (*Prosopis grandulosa* Torrey) and desert willow (*Chilopsis linearis* (Cav.) Sweet) [56] and we have collected specimens calling from *Acacia* spp., creosote bush (*Larrea tridentate* (D.C.) Coville), ocotillo (*Fouquieria splendens* Engelman) and Fremont cottonwood (*Populus fremontii* Watson). We found *D. cinctifera limpia* calling in cottonwood (*Populus* spp.), *Acacia* spp. and both *D. cinctifera limpia* and *D. cinctifera viridicosta* from mesquite (*Prosopis* spp.).

**Figure 3.** Distribution of *Diceroprocta cinctifera cinctifera* (red circles), *D. cinctifera limpia* (blue diamonds), and *D. cinctifera viridicosta* (green triangles).



The other current subspecies pair of the genus is *D. swalei swalei* and *D. swalei castanea* (Figure 4). Both subspecies are primarily found in Arizona with the known range of *D. swalei swalei* recently being extended into Mexico [8]. Both subspecies are found in the Mexican Highlands Section of the Basin and Range Province [73]. We found the nominotypical subspecies calling from *Acacia* spp. and mesquite (*Prosopis* spp.) and it has also been associated with ocotillo (*Fouquieria splendens*), *Baccharus* spp. and catclaw (*Acacia greggii* Gray). The significant overlap of the subspecies and nominotypical subspecies suggests the subspecies is a color variation and further analyses should be performed to determine the status of subspecies. The known range of *D. canescens* (Figure 4) is more limited being found in the drainage plain of Tornillo Creek and south of the Chisos Mountains in Texas. We found the species associated with *Larrea tridentata* and *Prosopis grandulosa* [56]. *Diceroprocta azteca* expands from Mexico across Texas and Oklahoma and has recently been found in Kansas [79]. It inhabits several habitats but is primarily associated with desert grasslands [70]. We found it calling from mesquite (*Prosopis* spp.) and grasses and it has been associated with various trees, weeds, and bushes [80]. *Diceroprocta viridifascia* (Figure 4) is restricted to primarily coastal environments (Figure 4) but can be found inland along sandy ridges [21]. It has been reported from the Southern Coastal Plains and Southern Florida Coastal Plain ecoregions [81] within Florida [21]. The species has been associated with grasses [82,83], sea oats (*Uniola* spp.) [37,84] as well as oaks (*Quercus* spp.) and other small trees [21]. We found it most often in sand pine (*Pinus clausa* (Chapm. Ex Engelm.) Sargent) and scrub live oak (*Quercus germinata* Small).

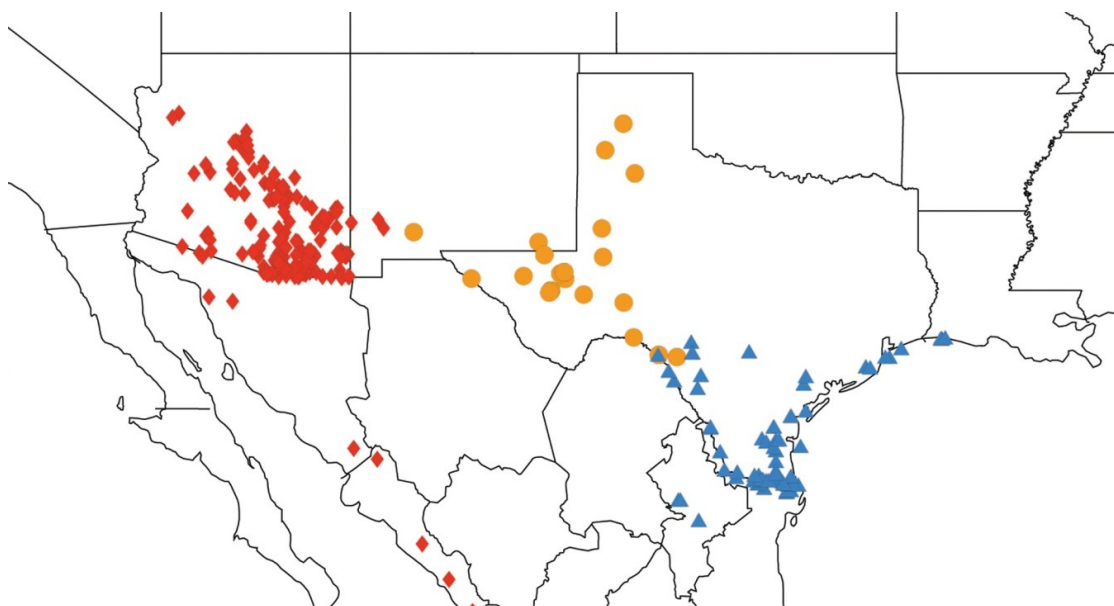
**Figure 4.** Distribution of *Diceroprocta swalei swalei* (blue circles), *D. swalei castanea* (red diamonds), *D. canescens* (light blue stars), *D. azteca* (orange triangles) and *D. viridifascia* (green squares).



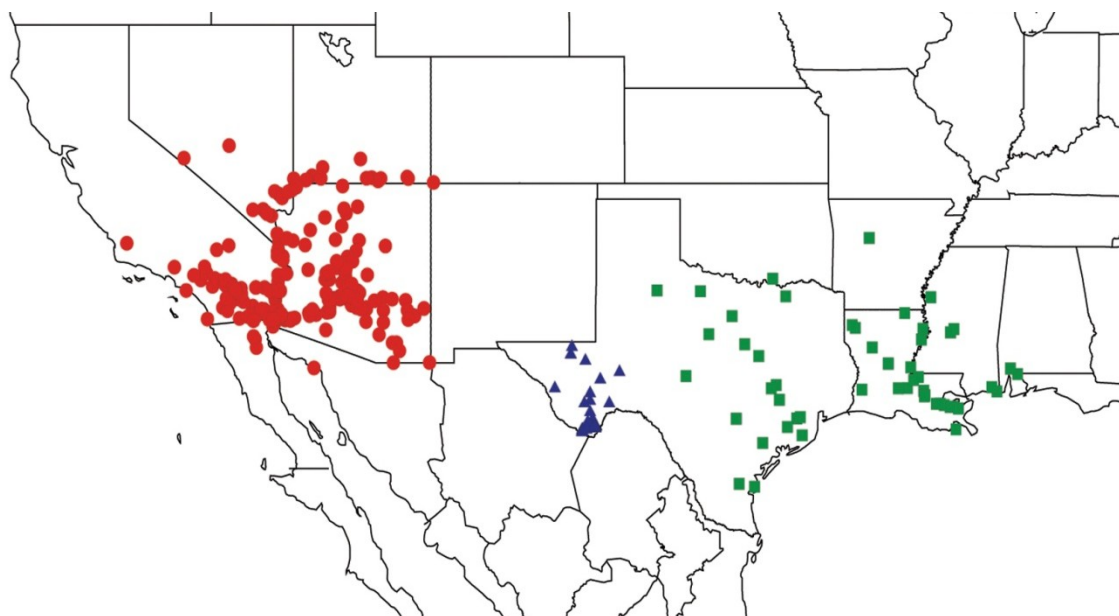
*Diceroprocta aurantiaca* was originally described as a variety of *D. delicata* [85]. It was elevated to species status in part by the different range of the species from *D. delicata* [27]. *Diceroprocta aurantiaca* is found in the desert grasslands and Chihuahuan Desert (Figure 5) [27,70,73]. We found the species associated with *Acacia* spp. and creosote bush (*Larrea tridentata*). In contrast, *D. delicata* inhabits southeastern coastal plain vegetation (Figure 5) [21,72] and is associated with *Iva frutescens* L. [86]. We collected the species from a variety of plants including mesquite (*Prosopis* spp.), scrubby plants

and grasses. *Dicerprocta semicineta* is restricted to the Sonoran Desert (Figure 5) [73] being found primarily in the Mexican Highland Section of the Basin and Range Province. It has significant overlap with *D. apache* (Figure 6) but is generally found in more elevated environments. We found *D. semicineta* calling from mesquite (*Prosopis* spp.), catclaw (*Acacia greggii*), Emory oak (*Quercus emoryi* Torrey), desert willow (*Chilopsis linearis*), Utah juniper (*Juniperus osteosperma* (Torr.) Little) and creosote bush (*Larrea tridentata*) but has also been associated with ocotillo (*Fouquieria splendens*) [87].

**Figure 5.** Distribution of *Dicerprocta aurantiaca* (gold circles), *D. delicata* (blue triangles) and *D. semicineta* (red diamonds).



**Figure 6.** Distribution of *Dicerprocta apache* (red circles), *D. bibbyi* (blue triangles) and *D. bequaerti* (green squares).

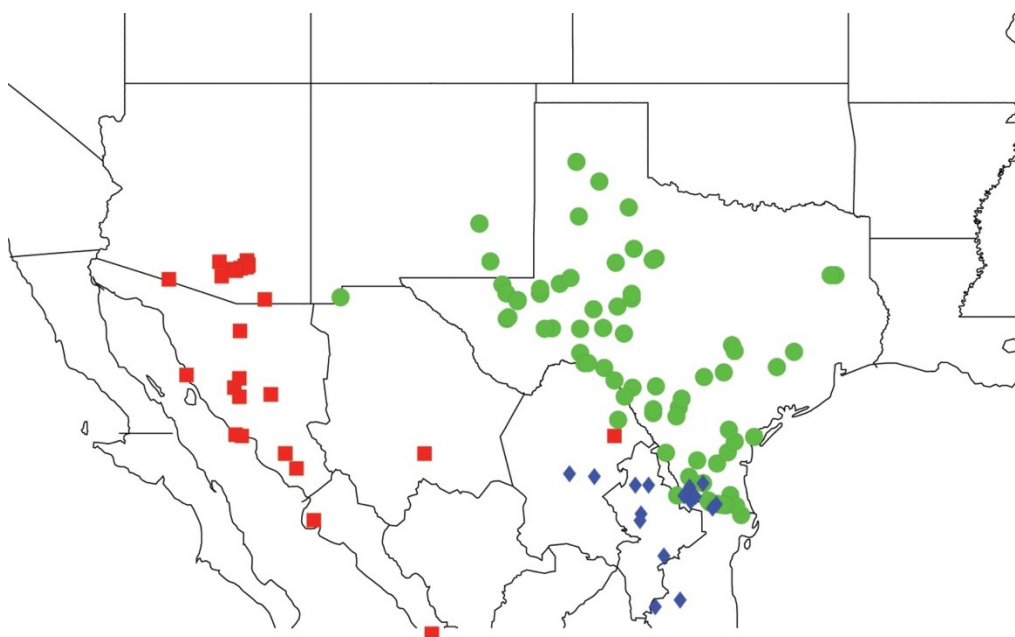




*Diceroprocta apache* is found in the Sonoran desert (Figure 6) [52,88] in riparian habitats e.g., [89–91] following river systems into Nevada and Utah from Arizona and California. It has been associated with Fremont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii* Ball) [89,91], introduced tamarix (*Tamarix chinensis* Loureiro), *Baccharis* spp., *Acacia* spp., velvet mesquite (*Prosopis velutina*) [91], undetermined mesquite (*Prosopis* spp.) [67,92], and palo verde (*Cercidium* spp.) [66,91,93]. *Diceroprocta bibbyi* (Figure 6) is found in creosote flats (*Larrea tridentata*) [56] of western Texas. It was recently described from Mexico [14] and appears to have a more extensive distribution in the Chihuahuan Desert [73]. *Diceroprocta bequaerti* (Figure 6) is found primarily in the southwestern region of the eastern deciduous forests [94] but extends into the grasslands [70] of the southern central United States. We found it associated with willow (*Salix* spp.) and grasses but it has also been reported in poplars (*Populus deltoids* W. Bartram ex Humphrey Marshall), weeds (*Dysphania ambrosioides* (L.) Mosyakin & Clemants) [95], and black mangroves (*Avicennia germinans* (L.) L.) [80].

*Diceroprocta lata* was originally described as a variety of *D. texana* [96]. It was recently reported from the United States and elevated to species status in part by the different range of the species from *D. texana* [29]. *Diceroprocta texana* is associated with *Larrea tridentata* and *Prosopis glandulosa* [29] in the Chihuahua desert [73] and desert grasslands [70] phytogeographic regions. *Diceroprocta lata* is also found in *Prosopis glandulosa* [29] in desert grasslands [70] but on the edges of the Chihuahuan Desert [73]. *Diceroprocta knighti* is restricted to the Sonoran Desert (Figure 7) [73] being found primarily in the Mexican Highland Section of the Basin and Range Province. We found it associated with creosote bush (*Larrea tridentata*), palo verde (*Cercidium* spp.), mesquite (*Prosopis* spp.), and ocotillo (*Fouquieria splendens*).

**Figure 7.** Distribution of *Diceroprocta lata* (blue diamonds), *D. texana* (green circles) and *D. knighti* (red squares).

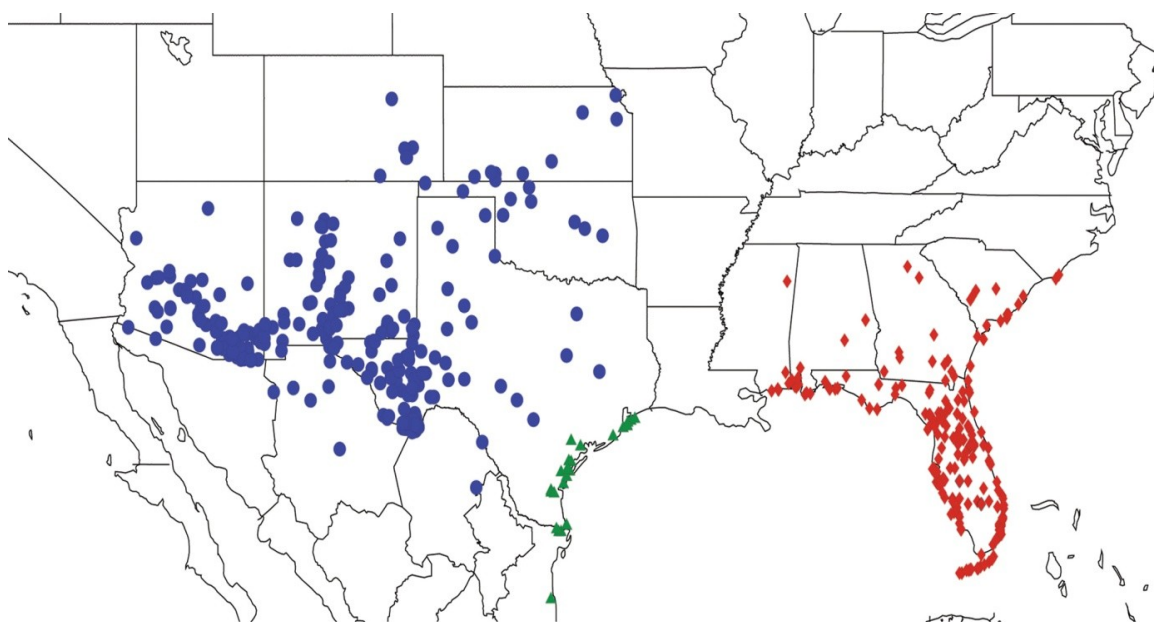


*Diceroprocta eugraphica* has an extensive distribution (Figure 8) across several phytogeographic regions including grasslands [70], intermountain deserts, and the Chihuahuan and Sonoran

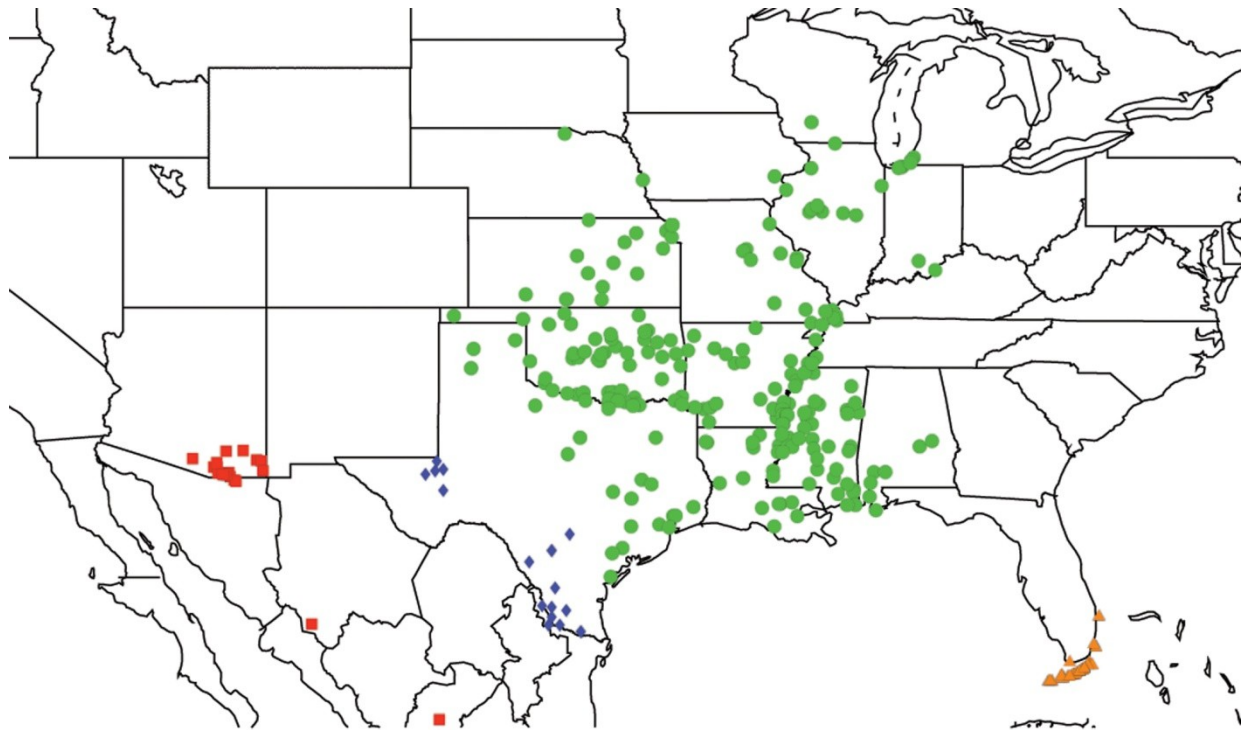
deserts [73]. The species has been reported from creosote flats (*Larrea tridentata*) [56] and Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson)-Pinyon (*Pinus edulis* Engelman)-Juniper (*Juniperus* spp.) woodlands [49] as well as mesquite (*Prosopis* spp.) [80] and we found it associated with four-wing saltbush (*Atriplex canescens* (Pursh)Nuttall), sand sage (*Artemisia filifolia* Torrey), and *Acacia* spp. in some habitats. The known range of *D. eugraphica* was recently extended into Mexico [6]. *Diceroprocta marevagans* is found in coastal environments (Figure 8) of the southeastern coastal plain vegetation [72]. We found it calling from grasses and it has been associated with *Amaranthus* spp. [41,92]. *Diceroprocta olympusa* has the most extensive distribution of any cicada in Florida and is found in all Florida ecoregions except the Everglades [21]. The distribution extends with much less frequency to Mississippi and North Carolina (Figure 8). It often calls from trees but uses grasses as a host plant [21,97].

*Diceroprocta arizona* is another species restricted to the Sonoran Desert (Figure 9) [73] being found primarily in the Mexican Highland Section of the Basin and Range Province. We found it associated with gray oak (*Quercus grisea* Liebmann). *Diceroprocta averyi* has two separate populations in desert grasslands [70]. *Diceroprocta vitripennis* expands further north than any other species of *Diceroprocta* with specimens being collected as far north as Michigan and Wisconsin (Figure 9). It is found in grassland habitats [70] as well as the western portion of the eastern deciduous forest phytogeographic region [94]. We collected the species in willow (*Salix* spp.) and grasses and it has also been reported to use cottonwoods (*Populus* spp.) [98]. *Diceroprocta biconica* has one of the more limited distributions of cicadas in the United States (Figure 9) but is also known from Cuba [10]. It is restricted to the Southern Florida Coastal Plain ecoregion [81], and is found only in the Florida Keys associated with black mangrove (*Avicennia germinans*) [21,53], but has also been observed and collected using multiple ornamental tree species [21]. It shows greater morphological similarities to species of *Diceroprocta* in Cuba and the Bahamas than to the other species of *Diceroprocta* in Florida [2,10,21].

**Figure 8.** Distribution of *Diceroprocta eugraphica* (blue circles), *D. marevagans* (green triangles) and *D. olympusa* (red diamonds).



**Figure 9.** Distribution of *Dicerprocta arizona* (red squares), *D. averyi* (blue diamonds), *D. vitripennis* (green circles) and *D. biconica* (orange triangles).



### 2.3. Biogeography of the Tibicen species

The current status of the genus *Tibicen* is being debated. Boulard [99–103] has argued for the suppression of the genus in favor of *Lyristes* Horvath. The last proposal to suppress the genus was submitted to the International Commission of Zoological Nomenclature was by Melville and Sims [104]. Further comments were made from several scientists [105–107], but no ruling of the commission has occurred. We retain the use of the genus *Tibicen* since Latrielle [108] specifically mentioned *Cicada plebeia* (sic) as the only example of the genus and thus unambiguously designated a type species under Article 12.2.5 [58] regardless of the ambiguities that may have occurred since that designation [99,101–107].

The genus *Tibicen* is found in the Nearctic, Palearctic, Oriental, and Neotropical biogeographical regions with the greatest diversity in the Nearctic region [26]. There are 31 species and six subspecies currently in the genus *Tibicen* in North America, north of Mexico [26]. These species can be split into three groups based on size and the shape of the abdomen [26,60] with preliminary molecular data supporting the three groups [109].

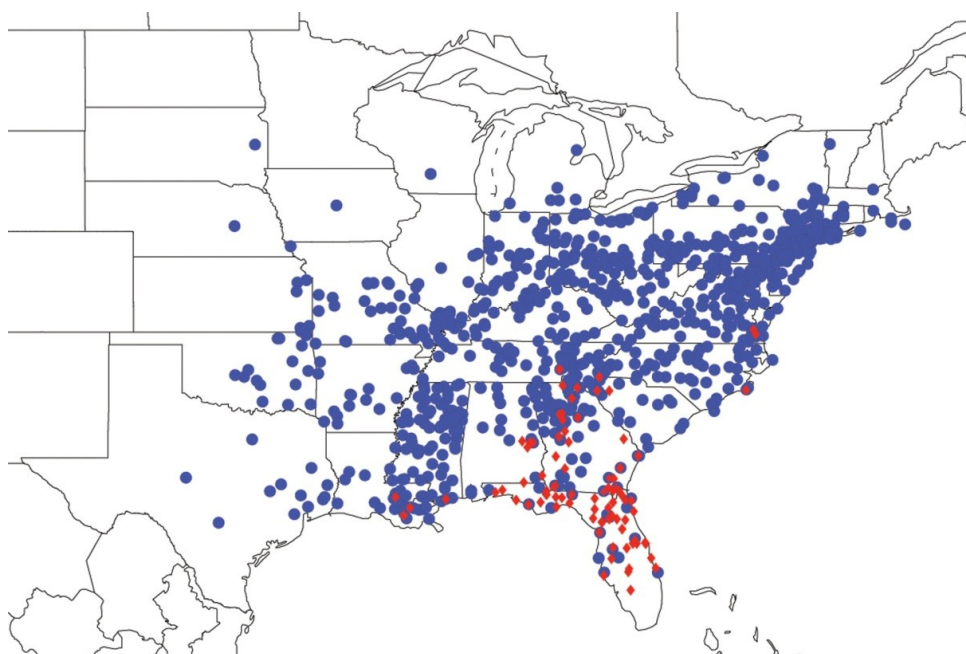
#### 2.3.1. Biogeography of the Eastern *Tibicen* species

Davis [60] characterized the eastern *Tibicen* species as large, usually green and black cicadas. These animals appear to be more closely related morphologically to members of the genus in the Oriental region. They inhabit areas in the eastern half of the United States and southern Canada east of the 100th meridian [26]. There are 12 species and five subspecies within this group.

The name *T. tibicen* was shown to be a senior synonym of a common cicada known as *T. chloromerus* [110]. The species is known as the swamp cicada as it is the only eastern *Tibicen* species to be found in low vegetation in swampy or marshy habitats as well as being found in upland meadows and overgrown fields [111]. The nominotypical subspecies expands across much of the eastern United States (Figure 10) with the subspecies *T. tibicen australis* being found primarily in Florida and Georgia (Figure 10). *Tibicen tibicen tibicen* and *T. tibicen australis* are found in forested environments of the Southern Coastal Plains and Southeastern Plains ecoregions [81] within Florida but was surprisingly absent from the Everglades [21]. The nominotypical subspecies has been observed to oviposit in golden rod (*Solidago* spp.), sumac (*Rhus* spp.), asters (*Aster* spp.), and willow shrubs (*Salix* spp.) with females also observed ovipositing in dead twigs [38,40,43,98]. The significant overlap between the subspecies suggests further analysis is required to determine their status.

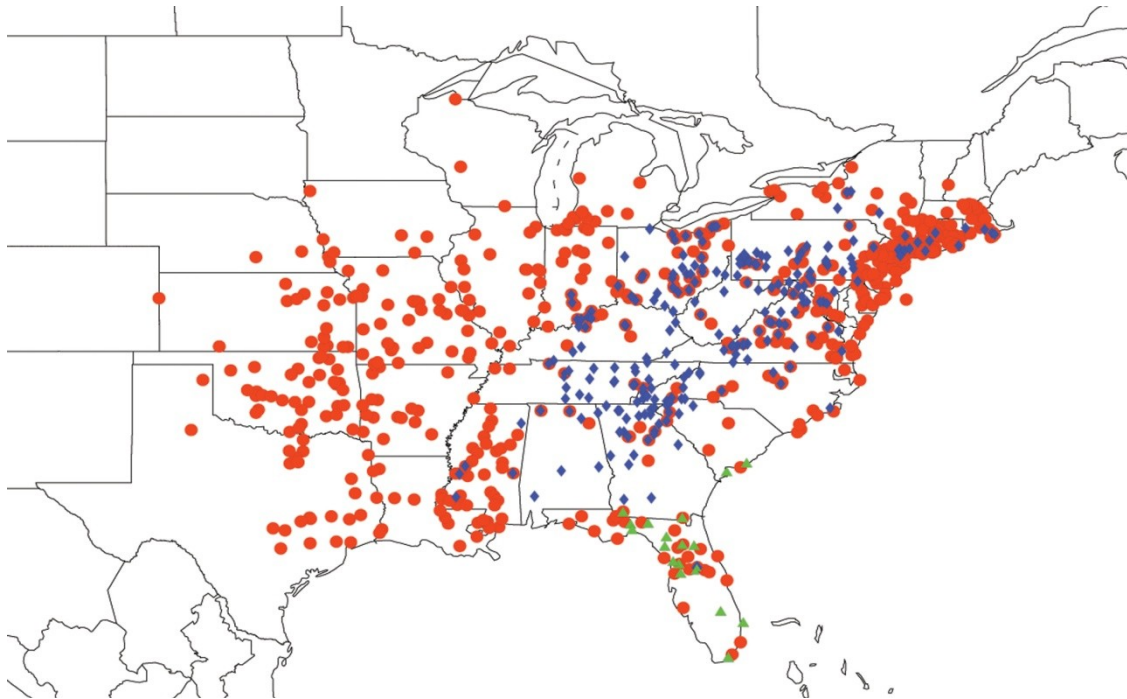
The species *T. lyricen* currently has three described subspecies [26]. All are found in the eastern deciduous forest ecosystems [94]. The nominotypical subspecies has the greatest range (Figure 11) with *T. lyricen engelhardti* being surrounded by the nominotypical subspecies along the Appalachian Mountains and areas west of the mountains and *T. lyricen virescens* (Figure 11) found in southeastern states with greatest concentration of collection localities in Florida (Figure 11). *Tibicen lyricen lyricen* and *T. lyricen virescens* are found in all Florida ecoregions with representatives collected in the Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plain ecoregion [81] within Florida [21]. The nominotypical subspecies has been associated with oaks (*Quercus* spp.), forests that contain maple (*Acer* spp.) and beeches (*Fagus grandifolia* Ehrhart) [45], persimmon (*Diospyros virginiana* L.) [38,112], oaks and peach (*Prunus persica* (L.) Stokes) [112]. The significant overlap in the nominotypical subspecies and *T. lyricen virescens* suggests further work should be performed to determine the status of the subspecies.

**Figure 10.** Distribution of *Tibicen tibicen tibicen* (blue circles) and *T. tibicen australis* (red diamonds).





**Figure 11.** Distribution of *Tibicen lyricen lyricen* (orange circles), *T. lyricen engelhardti* (blue diamonds) and *T. lyricen virescens* (green triangles).

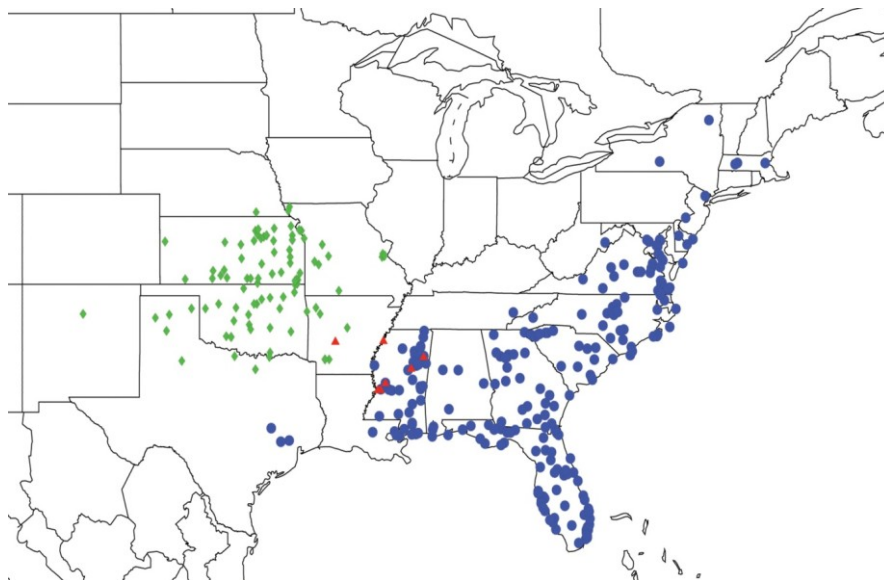


*Tibicen davisii* is another species that also has two subspecies. The distribution of the nominotypical subspecies is across much of the southeast extending north into New England and west into Texas (Figure 12). The subspecies *T. davisii hardeni* is restricted to Mississippi and one collection site in Arkansas (Figure 12). Further analyses should be performed to determine the status of the subspecies. *Tibicen davisii davisii* is found in all Florida ecoregions except the Everglades and insular regions with representatives collected in the Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plain ecoregion [81] within the state of Florida [21]. We have found it a variety of trees including mahogany (*Swietenia mahagoni* (L.) Jacquin) and it has been reported from pine forests (*Pinus* spp.) [38]. *Tibicen auriferus* is found in the grasslands of the central plains (Figure 12). We have collected it from grasses, shrubs and small trees in various localities. It has been associated with grassy areas with shrubs including the prairie grass *Panicum virgatum* L., wood grass (*Sorghastrum nutans* (L.) Nash) and sumac (*Rhus glabra* L.).

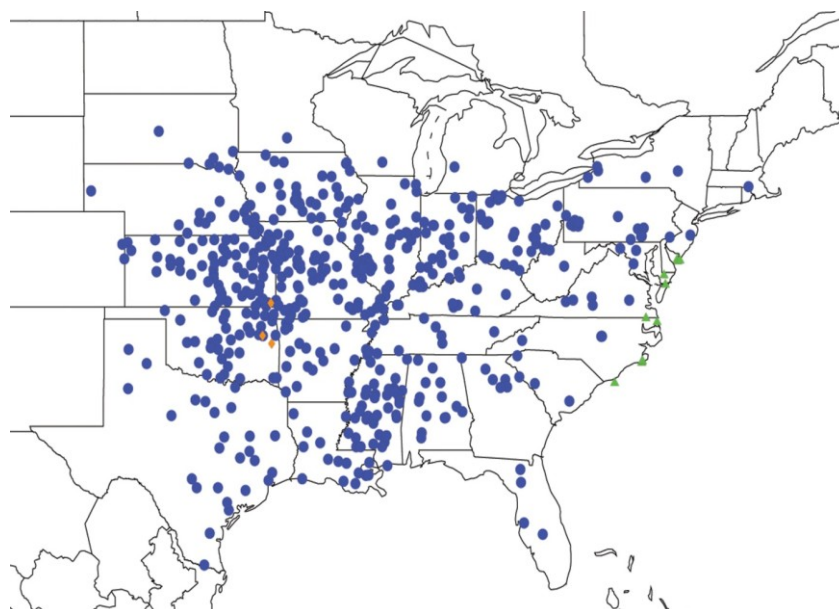
The final species of *Tibicen* in North America, north of Mexico to have subspecies is *Tibicen pruinosus*. The nominotypical subspecies expands across most of the eastern United States in both deciduous forests [94] and grassland [70] ecosystems (Figure 13). The specimen in western Nebraska extends the known range westward beyond what was a recent western expansion of the known range [113]. The species is always associated with trees in the grassland environments, often being found in riparian habitats and is found in high concentration in the towns of the Great Plains regions where trees are common [114]. On a more local scale, *T. pruinosus pruinosus* is found in the forested interior of the Southern Coastal Plains and Southeastern Plains ecoregions [81] within Florida [21]. The species is associated with hardwood environments and has been observed ovipositing in ash (*Fraxinus americana* L.), walnut (*Juglans nigra* L.), elm (*Ulmus* spp.), maple (*Acer* spp.), and sumac (*Rhus* spp.) [98,115]. We also found the species in hackberry (*Celtis occidentalis* L.) and willows

(*Salix* spp.). The subspecies *T. pruinosa fulva* is localized to the southeastern corner of Kansas and eastern Oklahoma (Figure 13) and may represent a local color variation. It is also associated with hardwood environments and has been associated with oak (*Quercus* spp.), walnut (*Juglans nigra*), elm (*Ulmus* spp.), maple (*Acer* spp.), and sumac (*Rhus* spp.) [112,116]. *Tibicen latifasciatus* has been variously classified as a species or subspecies of *T. pruinosa* [26]. *Tibicen latifasciatus* is found in coastal environments in the mid-Atlantic region (Figure 13). The geographic separation from *T. pruinosa* supports the species status for *T. latifasciatus* through geographic isolation. *Tibicen latifasciatus* has been associated with cedar (probably *Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenburg), pines (*Pinus* spp.), oaks (*Quercus* spp.) and hollies (*Ilex opaca* Aiton) [40].

**Figure 12.** Distribution of *Tibicen davisi davisi* (blue circles), *T. davisi hardeni* (red triangles) and *T. auriferus* (green diamonds).

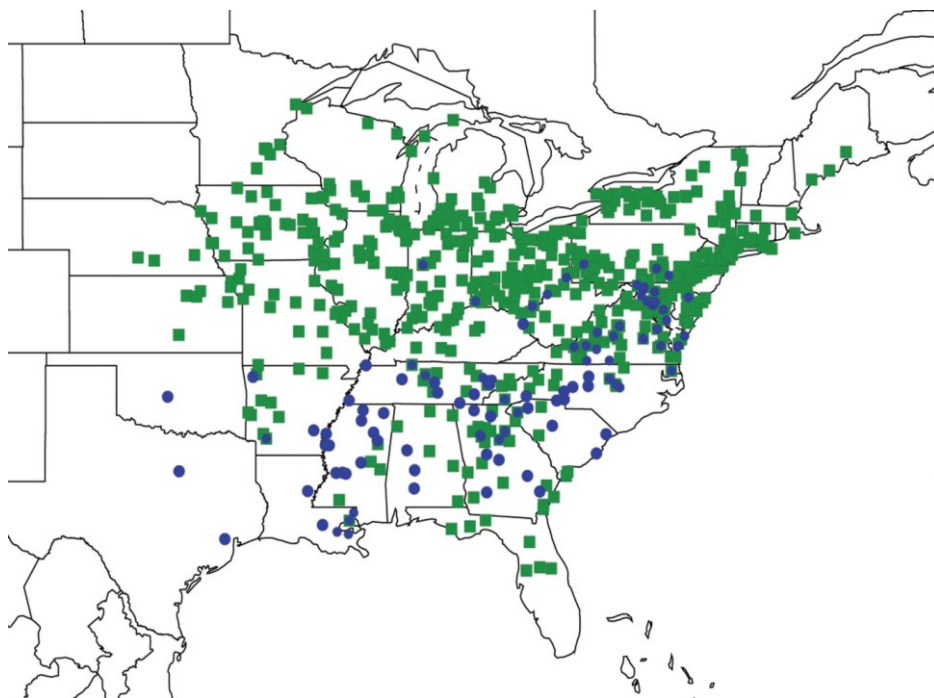


**Figure 13.** Distribution of *Tibicen pruinosa pruinosa* (blue circles), *T. pruinosa fulva* (orange diamonds) and *T. latifasciatus* (green triangles).



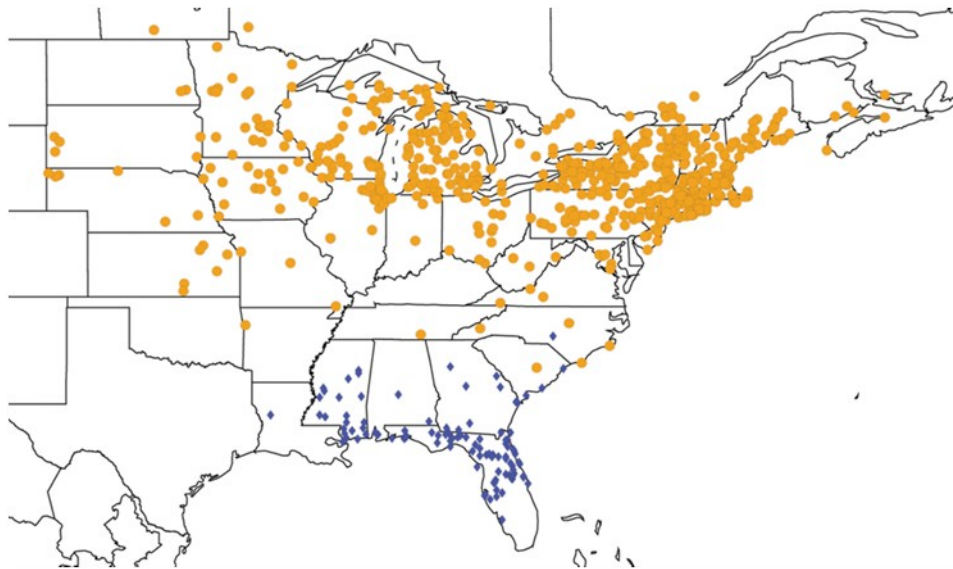
*Tibicen winnemanna* is another species that has been classified as a variety of *T. pruinosus* [26]. It is generally found in areas of the southeast and south (Figure 14) within the eastern deciduous forests [94] where *T. pruinosus pruinosus* is absent (Figure 13) although there is some overlap. We have seen the species using several species of hardwoods as hosts including maple (*Acer* spp.), oak (*Quercus* spp.) and sycamore (*Platanus occidentalis* L.). *Tibicen linnei* is one of the more common species being found in both eastern deciduous forests [94] and grassland [70] ecosystems. Similar to *T. pruinosus pruinosus*, the species is found in trees within the grassland environments. On a more local scale, *T. linnei* is found in forested environments of the Southern Coastal Plains ecoregion [81] within Florida [21]. The species has been associated with slippery elm (*Ulmus rubra* Muhlenberg) [117], maple (*Acer* spp.) [118] and other trees [21,40,45,46,98] but has been reported to avoid pines (*Pinus* spp.) [40].

**Figure 14.** Distribution of *Tibicen winnemanna* (blue circles) and *T. linnei* (green squares).



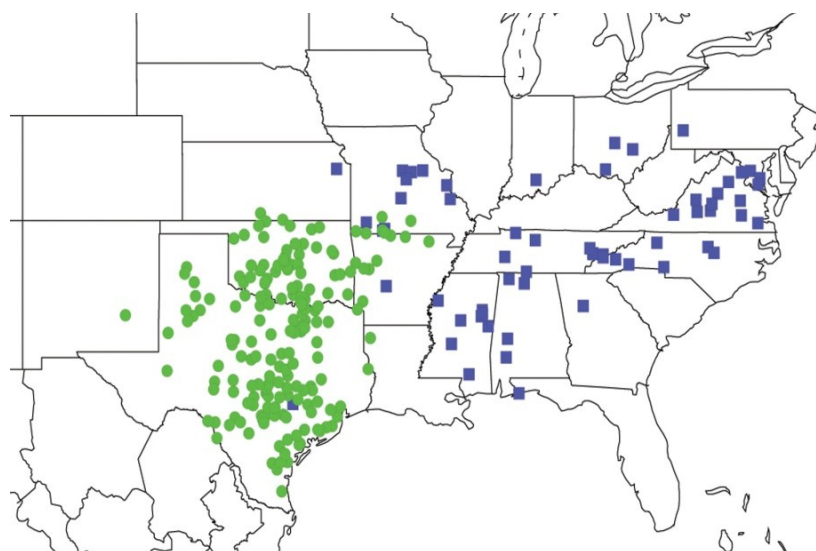
The species *Tibicen canicularis* is named for the dog days of summer and has a wide distribution across the northern United States and southern Canada (Figure 15). Like *Tibicen linnei* and *T. pruinosus pruinosus* it is a common species being found in both eastern deciduous forests [94] and grassland [70] ecosystems. We have seen *T. canicularis* use multiple species of hardwoods as hosts including oaks (*Quercus* spp.) and elm (*Ulmus* spp.). No specific tree species seems to be identifiable as a host and they have been reported to use various trees [119] including oak (*Quercus* spp.) [38] and pine (*Pinus* spp.) forests [40]. *Tibicen similaris* is found in the vegetation of the southeastern coastal plain [72]. On a more local scale, *T. similaris* is found in forested environments of the Southern Coastal Plains and Southeastern Plains ecoregions [81] within Florida [21]. We found it calling from multiple large deciduous trees and it has been associated with turkey oak (*Quercus laevis* Walter) [34].

**Figure 15.** Distribution of *Tibicen canicularis* (gold circles) and *T. similis* (blue diamonds).



*Tibicen robinsonianus* is found across the central region of the eastern deciduous forests [94] (Figure 16). The habits of singing high in trees exhibited by a species with low population densities may explain the spacing seen in the distribution. *Tibicen robinsonianus* inhabits the Southeastern Plains ecoregion [21] and, on a more local scale, the Gulf Coast Flatwoods division of the Southern Coastal Plains ecoregion [81] within Florida. The species has been associated with oaks (*Quercus* spp.), locusts (*Robinia* spp.), and cedar (probably *Juniperus virginiana* L.) [38,78,87,120]. We found them associated with oaks and various other deciduous trees. The final eastern *Tibicen* species, *T. superbis*, is found in trees within grassland environments primarily in eastern Texas and Oklahoma but spreads into neighboring states. We found it in a variety of trees, both native and ornamentals [28] including elm (*Ulmus* spp.), oak (*Quercus* spp.), juniper (*Juniperus* spp.) and mesquite (*Prosopis* spp.).

**Figure 16.** Distribution of *Tibicen robinsonianus* (blue squares) and *T. superbis* (green circles).



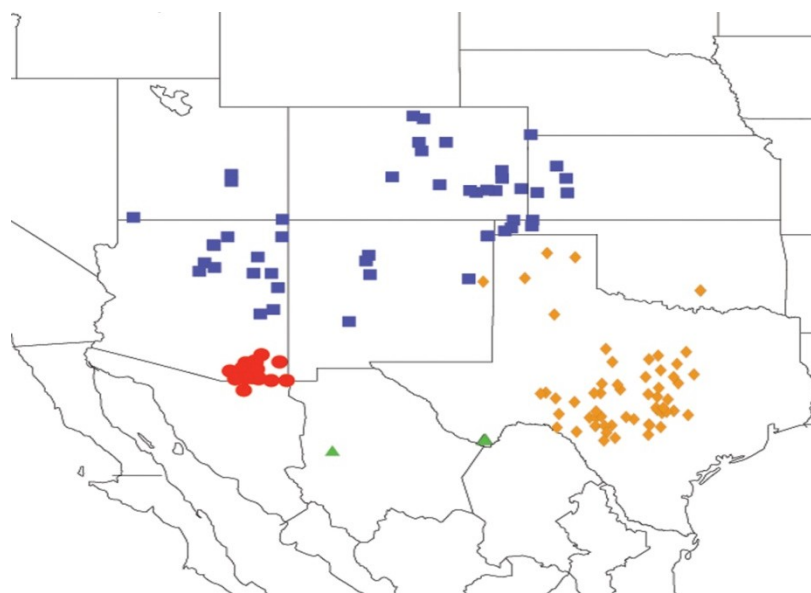


### 2.3.2. Biogeography of the Western *Tibicen* Species

The western *Tibicen* species differ from the other two groups of the genus in that the sides of the abdomen are conspicuously parallel to each other instead of gently tapering. Their coloration is also generally black with orange or reddish markings. Davis [60] suggested that this group more closely resembled *Tibicen plebejus* and thus is more closely related to Palearctic members of the genus. These animals inhabit areas in the southwestern United States [26]. There are 10 species within this group.

*Tibicen bifidus* is found in desert grasslands [30,70] and intermountain deserts [76] (Figure 17). It has been associated with yucca (no species given) [98], sage (*Artemisia* L.) [66,98], fineleaf hymenopappus (*Hymenopappus filifolius* Hooker) [121], *Atriplex* L., willows (*Salicaceae*) [49], *Acacia* Miller and *Juniperus* L. [30]. We also found it associated with Mexican Mormon tea (*Ephedra trifurcata* Torrey ex S. Watson). *Tibicen simplex* was originally described as a variety of *T. bifidus* [96] but was elevated to species status in part based on the distribution of the species [30]. *Tibicen simplex* is also found in desert grasslands [30,70] but in the Mexican Highland Section of the Basin and Range Province of the Sonoran Desert [73] (Figure 17). *Tibicen simplex* is associated with soaptree yucca (*Yucca elata* Engelmann) and females were observed to oviposit in Mexican Mormon tea (*Ephedra trifurca*) [30]. *Tibicen texanus* is found in trees within the grassland habitats [70] (Figure 17). It has been associated with junipers (*Juniperus* spp.) and oaks (*Quercus* spp.) [78]. We collected the species in these trees as well as mesquite (*Prosopis* spp.). *Tibicen chisosensis* is found only in the high Chisos Mountains of Texas at elevations above 1980 m (6000 ft) in Mexican piñon pine (*Pinus cembroides* Zuccarini) [56] but would also call from piñon pine (*Pinus edulis*) and Texas madrone (*Arbutus xalapensis* Kunth). It would have the most restricted range of any species in North America, north of Mexico except that the known range of the species was recently extended into Mexico [8].

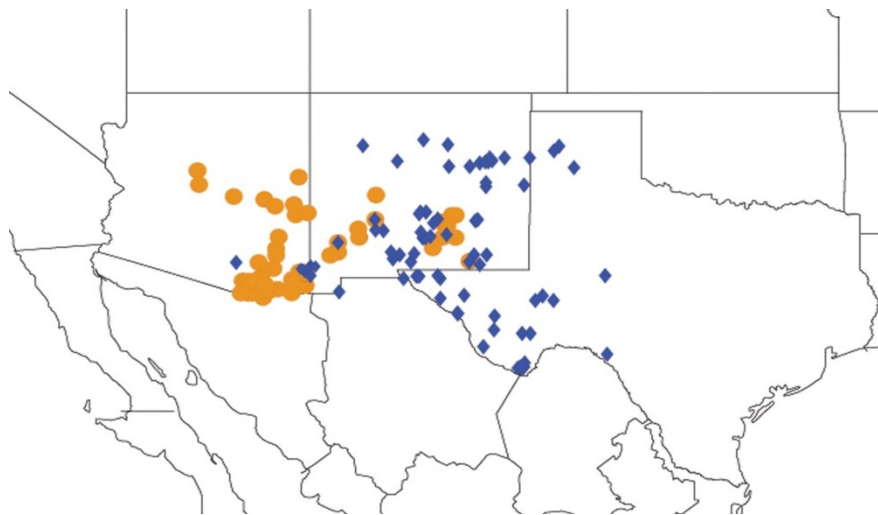
**Figure 17.** Distribution of *Tibicen bifidus* (blue squares), *T. simplex* (red circles), *T. texanus* (orange diamonds) and *T. chisosensis* (green triangles).



*Tibicen chiricahua* is found in the Mexican Highland Section of the Basin and Range Province of the Sonoran Desert [73] and intermountain woodlands [76] (Figure 18). The known range of

*T. chiricahua* was recently extended into Mexico [8]. It has been associated with pines (*Pinus* spp.), juniper (*Juniperus* spp.) and grasses [87] and we found it in mountain mahogany (*Cercocarpus* spp.) and one seed juniper (*Juniperus monosperma* (Engelmann) Sargent). *Tibicen townsendii* is found in desert grasslands [70], intermountain deserts [76], and the Chihuahuan Desert [73]. *Tibicen townsendii* was reported from lower desert mountain vegetation associated with soaptree yucca (*Yucca elata*) in the Chisos Mountains of Texas [56].

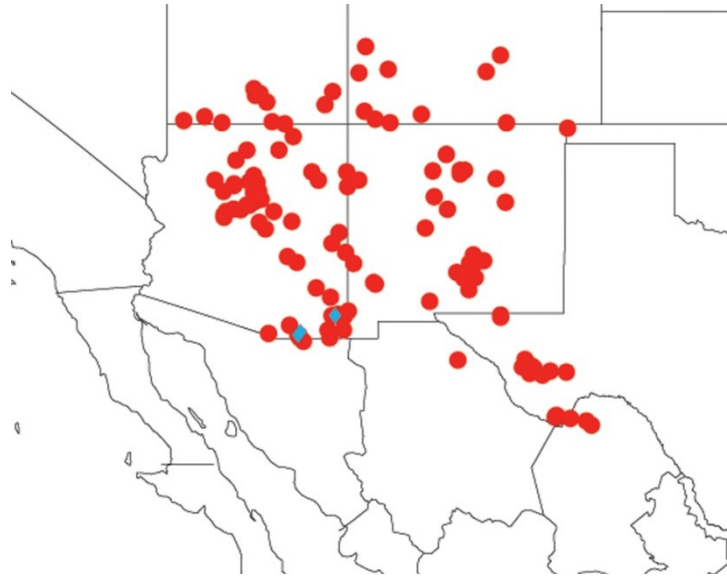
**Figure 18.** Distribution of *Tibicen chiricahua* (gold circles) and *T. townsendii* (blue diamonds).



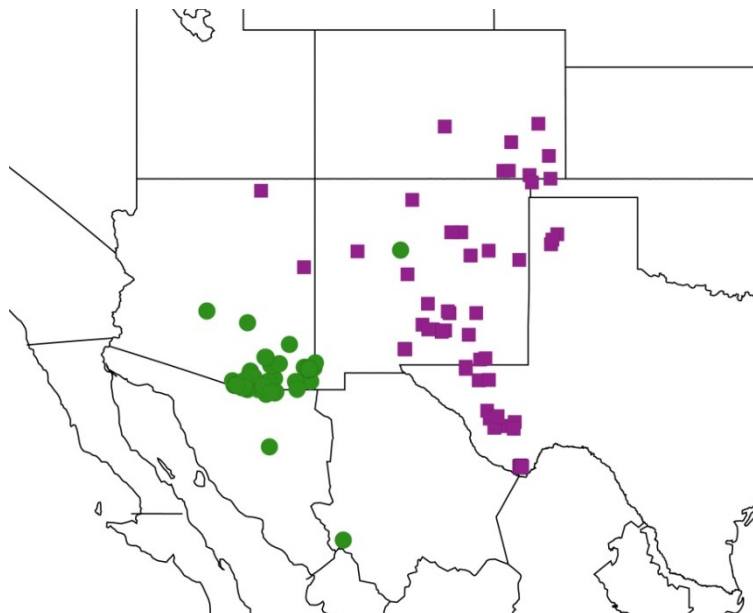
*Tibicen duryi* occurs across much of the southwest in a variety of habitats. It has been recorded from chaparral [74,75], Chihuahuan Desert, Mexican Highland Section of the Sonoran Desert [73], and intermountain woodlands [76]. The species is only found with piñon pine (*Pinus edulis*) [49,67,122] or Mexican piñon pine (*Pinus cembroides*) [56]. *Tibicen longioperculus* is found in the Mexican Highland Section of the Basin and Range Province of the Sonoran Desert [73] (Figure 19). It has been collected only in two locations in southern Arizona. We collected it only in the area of Sunnyside Canyon where alligator juniper (*Juniperus deppeana* Steudel) is found even though there are other species of juniper in other parts of the canyon.

*Tibicen parallelus* is found in the Mexican Highland Section of the Basin and Range Province of the Sonoran Desert [73] (Figure 20) with the known range of *T. parallelus* recently being extended into Mexico [6]. The extra limital point on the map at Albuquerque, New Mexico is the type locality for the species. It may be that the individual who sent the specimens to Davis was from Albuquerque and this mistakenly became the type locality even though this location is distant from the remaining collection sites. We found the species associated with oaks (*Quercus* spp.) as has been reported previously [87] but also collected specimens from alligator juniper (*Juniperus deppeana*). *Tibicen inauditus* is found in trees in desert grasslands [70], intermountain deserts [76], and the Chihuahuan Desert [73]. It has been associated with skunk bush (*Rhus trilobata* Nuttall), soapweed (*Yucca glauca* Nuttall), bear grass (*Xerophyllum tenax* (Pursh) Nuttall) [80], oak (*Quercus* spp.) in various habitats [56,78,123]. We also collected specimens in mesquite (*Prosopis* spp.), juniper (*Juniperus* spp.) and mountain mahogany (*Cercocarpus* spp.).

**Figure 19.** Distribution of *Tibicen duryi* (red circles) and *T. longioperculus* (blue diamonds).



**Figure 20.** Distribution of *Tibicen parallelus* (green circles) and *T. inauditus* (purple squares).



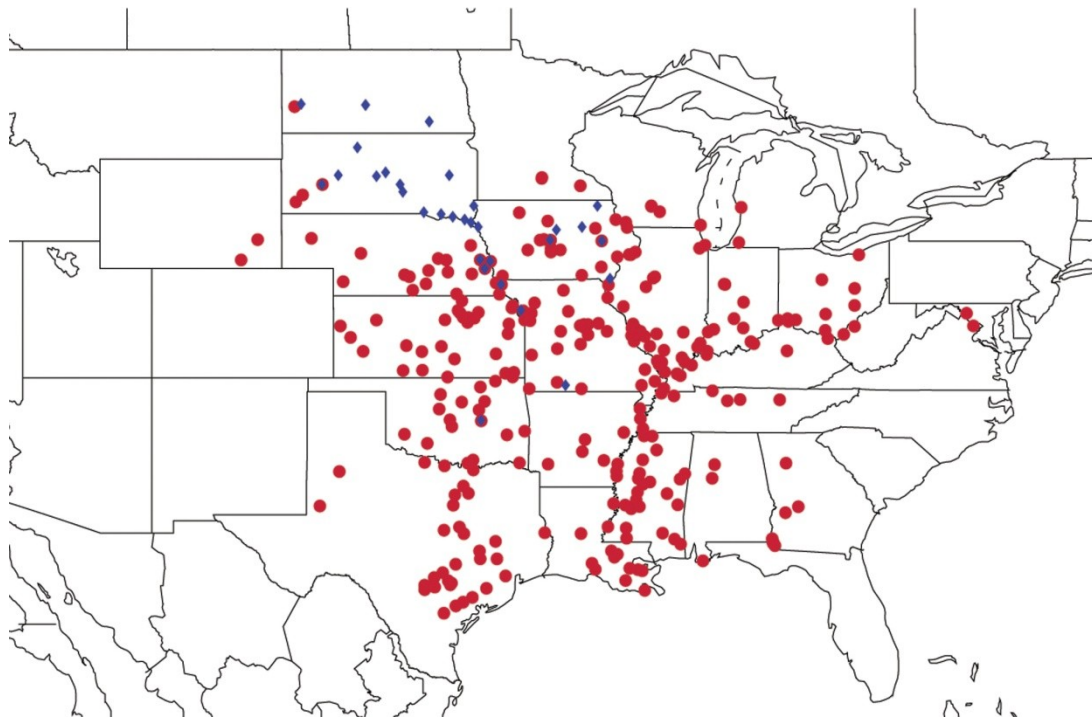
### 2.3.3. Biogeography of the large *Tibicen* species

The large *Tibicen* species are the largest of the genus. The mesonotum is generally decorated with two pipe shaped marks that are similar to the Hebrew letter resh [60]. These species inhabit areas in most of the United States except the states of the Pacific coast, northwestern Rocky Mountains and Northeast. There are nine species and two subspecies within this group.

The final subspecies within the genus *Tibicen* is found in this group. The nomenclature has been confused [26] but was recently analyzed and reorganized based on the *Code* [50]. *Tibicen pronotalis pronotalis* is found in the northern Great Plains (Figure 21). We found the nominotypical subspecies

associated with various isolated trees and riparian habitats including willows (*Salix* spp.). *Tibicen pronotalis walkeri* is found in the grassland habitats [70] and eastern deciduous forests [94] west of the Appalachians (Figure 21). We found this subspecies singing in tall trees, including cottonwoods (*Populus* spp.), and in riparian habitats. It has been reported to be associated with willow (*Salix* spp.), cottonwoods (*Populus* spp.), birch (*Betula* spp.) and maple (*Acer* spp.) [98,112].

**Figure 21.** Distribution of *Tibicen pronotalis pronotalis* (blue diamonds) and *T. pronotalis walkeri* (red circles).

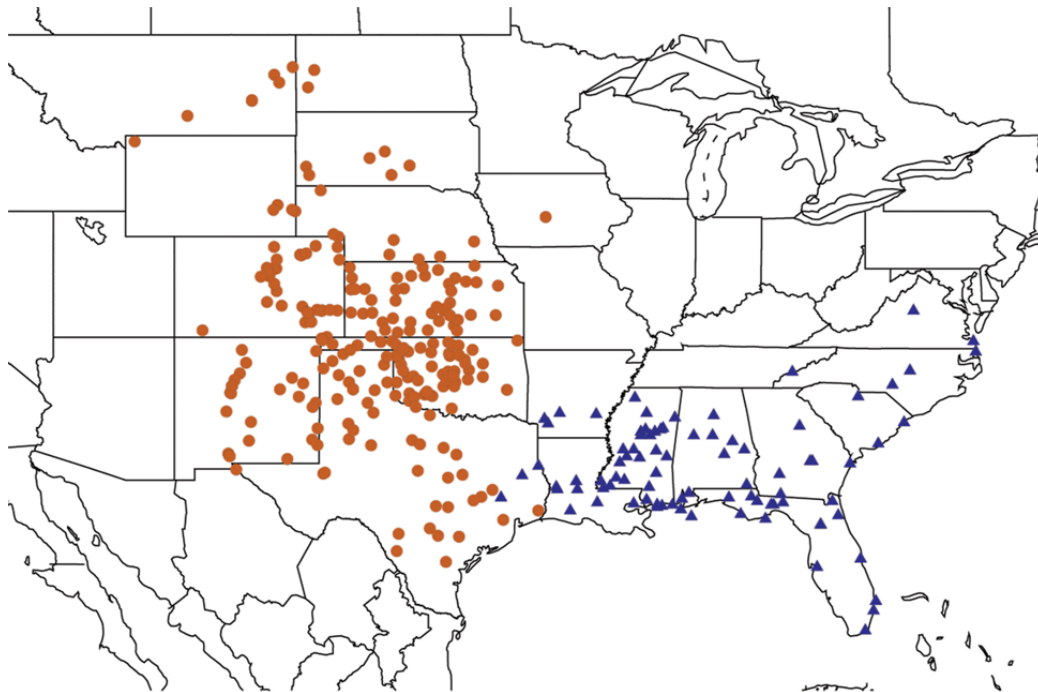


*Tibicen dealbatus* occurs across the grasslands ecosystem [70] across the central United States (Figure 22). The species is always associated with trees in the grassland environments often being found in riparian habitats [49,124]. We found it associated with willow (*Salix* spp.) and cottonwoods (*Populus* spp.) as previously reported [98,124] but also with ornamentals and nut trees in orchards. It has also been reported in high concentrations in introduced salt cedar (*Tamarix ramosissima* Ledebour) [49]. *Tibicen figuratus* is found in the vegetation of the southeastern coastal plain [72]. At a more local scale, *T. figuratus* is found in forested environments of the Southern Coastal Plains and Southeastern Plains ecoregions with representatives collected in the Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plain ecoregion [81] within Florida [21].

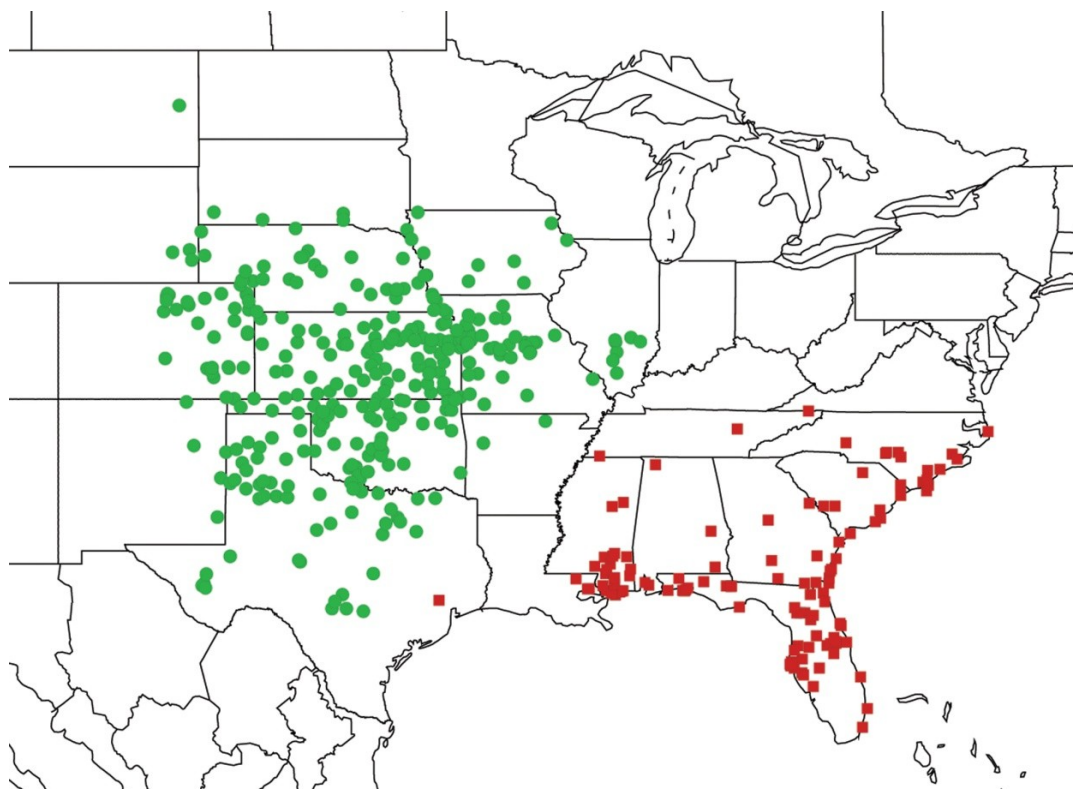
*Tibicen dorsatus* extends across the grasslands [70] ecosystem of the central United States (Figure 23). The species is usually associated with shrubs in the grassland environments. We found it associated with sage (*Artemisia* spp.), squawbush sumac (*Rhus trilobata*) and various shrubs with the occasional hardwood used as a calling perch. It has also been associated with four-wing saltbush (*Atriplex canescens*), and rabbitbrush (*Ericameria nauseosa* (Pallas ex. Pursh) G.L. Nesom & Baird) [49], cottonwoods (*Populus* spp.) [125], willows (*Salix* spp.), elms (*Ulmus* spp.) [112], bluestem grass (*Andropogon* spp.) [126], sumac (*Rhus* spp.) and goldenrod (*Solidago* spp.) [43]. *Tibicen resonans* is found in the vegetation of the southeastern coastal plain [72]. On a more local

scale, *T. resonans* is found in forested environments in all Florida ecoregions except the Everglades with representatives collected in the Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plain ecoregion [81] within Florida [21]. We collected specimens from longleaf pine (*Pinus palustris* Miller) and slash pine (*Pinus elliottii* Engelman) in the panhandle of Florida.

**Figure 22.** Distribution of *Tibicen dealbatus* (orange circles) and *T. figuratus* (blue triangles).



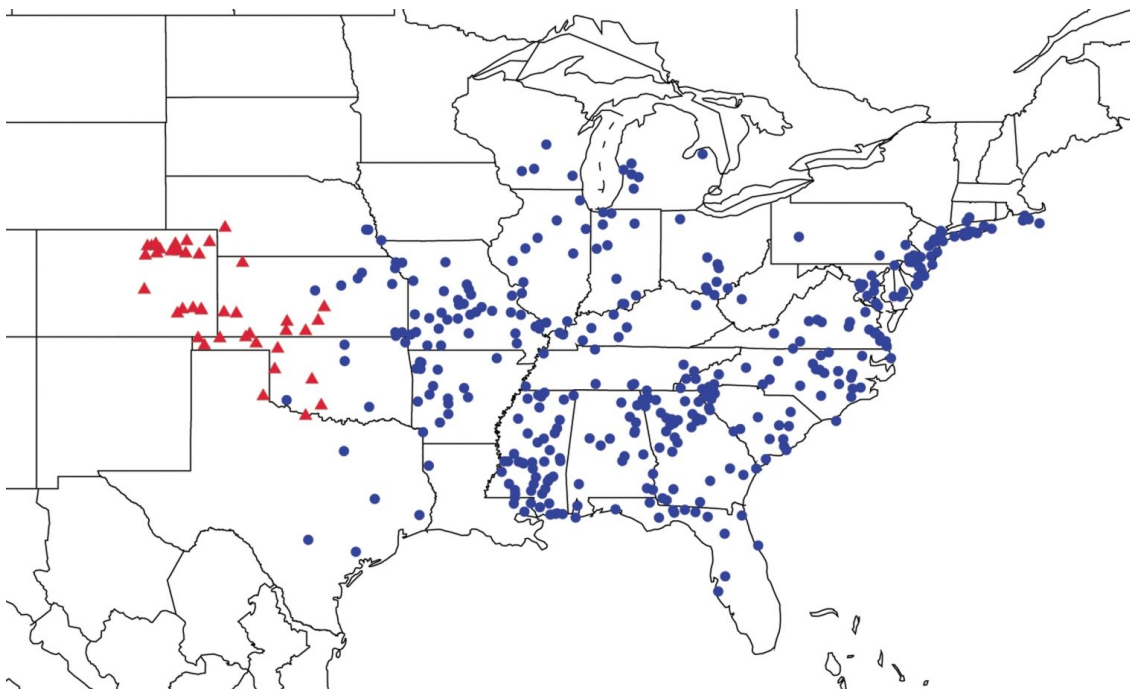
**Figure 23.** Distribution of *Tibicen dorsatus* (green circles) and *T. resonans* (red squares).





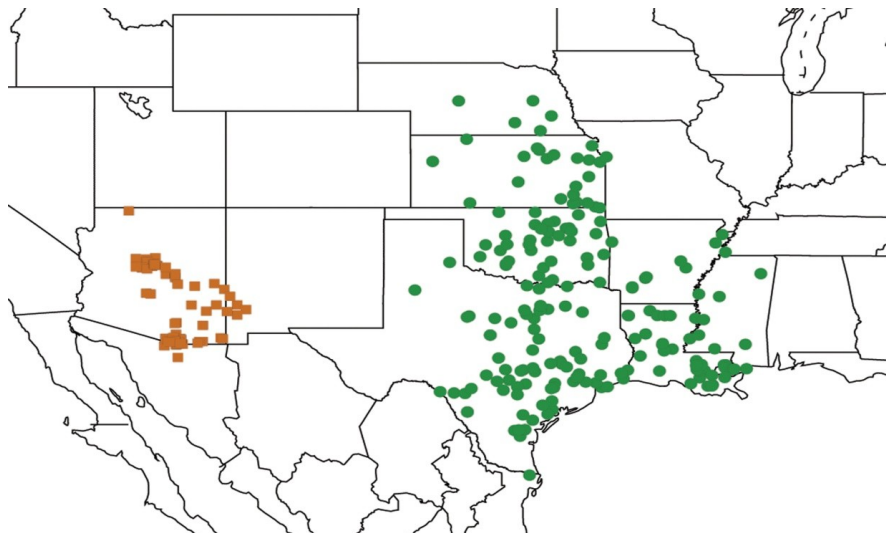
*Tibicen auletes* has the most eastern distribution of the large *Tibicen* species (Figure 24) being found over most of the eastern deciduous forest ecosystem [94]. Within Florida [21], it has been reported from the Southern Coastal Plains and Southeastern Plains ecoregions [81]. The species has been associated with oaks in general (*Quercus* spp.), post oak (*Quercus stellata* Wangenheim), black oak (*Quercus velutina* Lambert), white oak (*Quercus alba* L.), and willows (*Salix* spp.), and other hardwood habitats [38,46,98,112,126]. *Tibicen tremulus* is found in the Great Plains [70]. We found it associated with sage (*Artemisia* spp.).

**Figure 24.** Distribution of *Tibicen auletes* (blue circles) and *T. tremulus* (red triangles).



*Tibicen cultriformis* is found in the Mexican Highland Section of the Basin and Range Province of the Sonoran Desert [73] (Figure 25) with its range recently being extended into Mexico [8]. We found *T. cultriformis* in riparian habitats congregating in cottonwood (*Populus* spp.) and willow (*Salix* spp.) [127]. It also has been associated with black willow (*Salix nigra* Marshall), ash (*Fraxinus* spp.), sycamore (*Platanus wrightii*) and walnut (*Juglans major*) [78]. *Tibicen resh* is found in the grassland habitats [70] and western regions of the eastern deciduous forests [94] (Figure 25). It overlaps the extremes of the ranges of and fills the gap between the generally more western *T. dorsatus* and *T. dealbatus* and generally the more eastern *T. auletes* (see Figures 22–25). We found the species singing in trees, including white ash (*Fraxinus americana*) and willows (*Salix* spp.), and in riparian habitats. *Tibicen resh* has been associated with oaks (*Quercus* spp.) in general [128] and blackjack oak (*Quercus marilandica* Muenchhausen) [112] specifically. A specimen of *Tibicen resh* from South Carolina was verified during this work. However, it is separated from the other specimens by several hundred km and may have been mislabeled.

**Figure 25.** Distribution of *cultriformis* (orange squares) and *T. resh* (green circles).

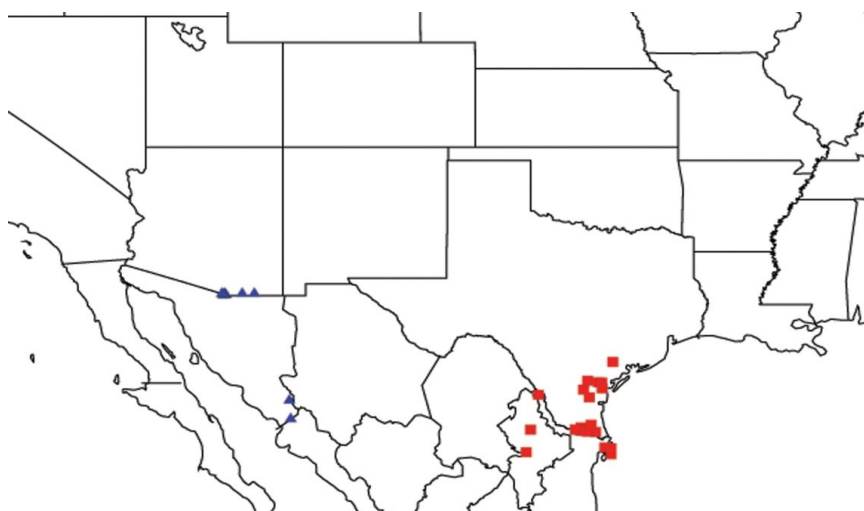


#### 2.4. Biogeography of the *Cornuplura* species

The genus *Cornuplura* is primarily distributed through Mexico [8,26,31]. Davis [129] placed the genus between *Diceroprocta* and *Tibicen*. The species are larger than but most similar to the western *Tibicen* species [26]. *Cornuplura* species are distributed in central and southern Mexico with the known range of one species extending into the region of interest for this work [8,31].

A single species, *C. nigroalbata*, inhabits North America, north of Mexico. The species was originally described from southern Arizona [129] but the known range has been extended to southern Sonora, Mexico [8]. The distribution of the species has its northern limit in the southern portion of Arizona (Figure 26) and is known only from Santa Cruz and Cochise counties [31]. The species is associated with Emory oak (*Quercus emoryi*) and Mexican blue oak (*Quercus oblongifolia* Torrey) [31] in the oak-juniper woodland [130] within the Mexican Highlands Desert Section of the Basin and Range floristic province of North America [73].

**Figure 26.** Distribution of *Cornuplura nigroalbata* (blue triangles) and *Quesada gigas* (red squares).

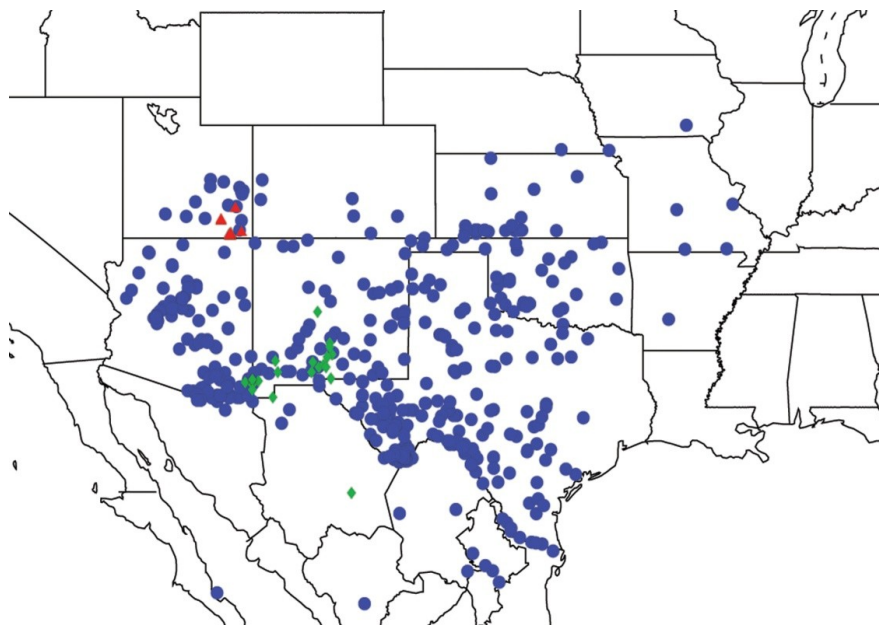


### 2.5. Biogeography of the *Beameria* species

The genus *Beameria* was erected for two species of grass dwelling cicadas of the central and western United States [26] with a third species being described recently [23]. The genus is primarily found in North America, north of Mexico but two of the three species have been reported from Mexico [6,8]. The genus represents the northernmost limit of the genera within the tribe Fidicinini that extends southward through Central and South America to Argentina [4,5,7–9,13–15,17,20,22,131,132].

All species of *Beameria* are associated with grasses [23,36,56,80]. *Beameria venosa* has the greatest distribution being found throughout much of 11 states and Mexico (Figure 27). This species can be found in intermountain deserts [76], Chihuahuan Desert [56,73], chapparal [74,75], and grasslands [70]. *Beameria ansercollis* is known from San Juan County, Utah (Figure 27) in the intermountain desert and steppe habitat [76] where we found it associated with *Atriplex* spp. and Indian rice grass (*Achnatherum hymenoides* Ricker ex Piper). *Beameria wheeleri* is found in the Sonoran Desert [73] of southern New Mexico, southeastern Arizona and northern Mexico (Figure 27). Only *B. wheeleri* can be associated with a definitive host plant. The distribution of *B. wheeleri* is dependent on the presence of grasses of the genus *Sporobolus* R. Brown. Two species of grass with which we found *B. wheeleri* to be associated were *S. wrightii* Munro ex Scribner and *S. airoides* (Torrey)Torrey.

**Figure 27.** Distribution of *Beameria venosa* (blue circles), *B. wheeleri* (green diamonds) and *B. ansercollis* (red triangles).



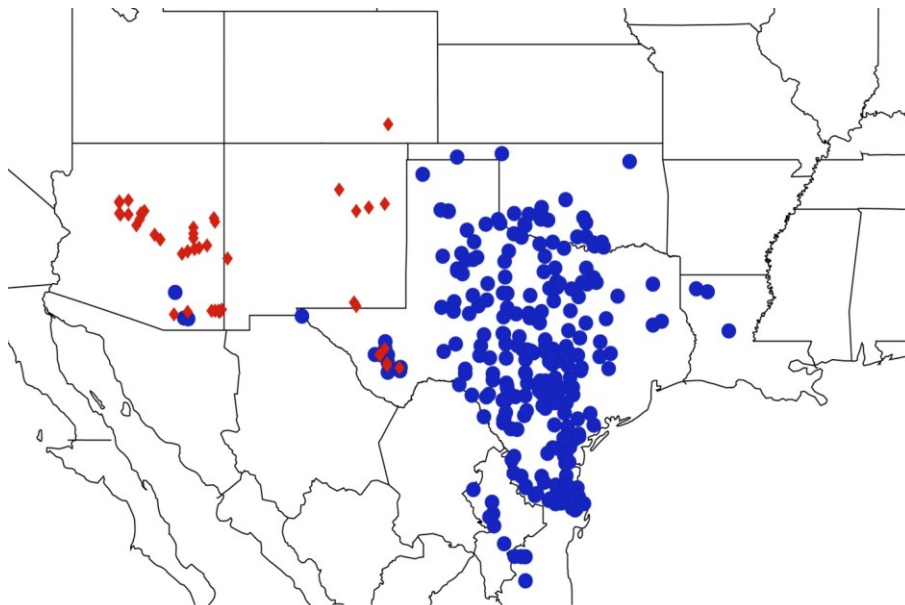
### 2.6. Biogeography of the *Pacarina* Species

The genus *Pacarina* is found primarily in Central America and Mexico [5,8,14,32] and is related to genera that inhabit Central and South America. Two species of the genus inhabit North America, north of Mexico [26,32]. References to *Pacarina championi* (Distant) in the literature from the region are considered erroneous [32].



The two species of *Pacarina* in North America, north of Mexico were first distinguished based on host plants differences [32,133]. We found *P. puella* associated with mesquite (*Prosopis* spp.) and it has been recorded from Arizona, Louisiana, Oklahoma and Texas extending into Central America [5,8,14,32] (Figure 28). We also found the species calling extensively from *Acacia* spp. *Pacarina shoemakeri* is associated with juniper (*Juniperus* spp.) and has been recorded from Arizona, Colorado, New Mexico and Texas in chaparral [49,74,75], intermountain woodlands [76] and elevated regions of the Chihuahuan desert [73]. It is likely that the species will also be found in Mexico. We found *P. shoemakeri* in *Juniperus ashei* Buchholz in Arizona.

**Figure 28.** Distribution of *Pacarina puella* (blue circles) and *P. shoemakeri* (red diamonds).



### 2.7. Biogeography of the Quesada Species

The genus *Quesada* has an extensive distribution within the New World. Although only two species occur in the genus, the distribution extends from central Argentina to Texas [26,129]. It is the only representative of the tribe Hyantiini in North America, north of Mexico. The remaining genera of the tribe are found in Central and South America [17,134].

*Quesada gigas* is the only species of the genus *Quesada* found in North America, north of Mexico. The species may exhibit the greatest latitudinal gradient of any cicada. It has been collected from central Texas (Figure 26) to central Argentina [22,26,129,135]. It appears to have a generalist approach to host plants that facilitates its use of multiple plant communities [22]. For example, in a single park in Brazil, the species was found to use 17 different families as host plants [136]. In Argentina we found *Q. gigas* in the tropical cloud forests of the Yunga and tropical rainforests of the Paranense floristic provinces as well as the temperate Chaco and Espinal floristic provinces [22]. The species disappears in Argentina when potential host trees disappear from the floristic provinces. It is also an endothermic species [135]. The endothermy may permit *Q. gigas* to colonize a greater variety of habitats. The species is associated with the vegetation of the southeastern coastal plain in

Texas [72]. The northern limit of the distribution extends to the grasslands in central Texas [70], similar to that of Argentina.

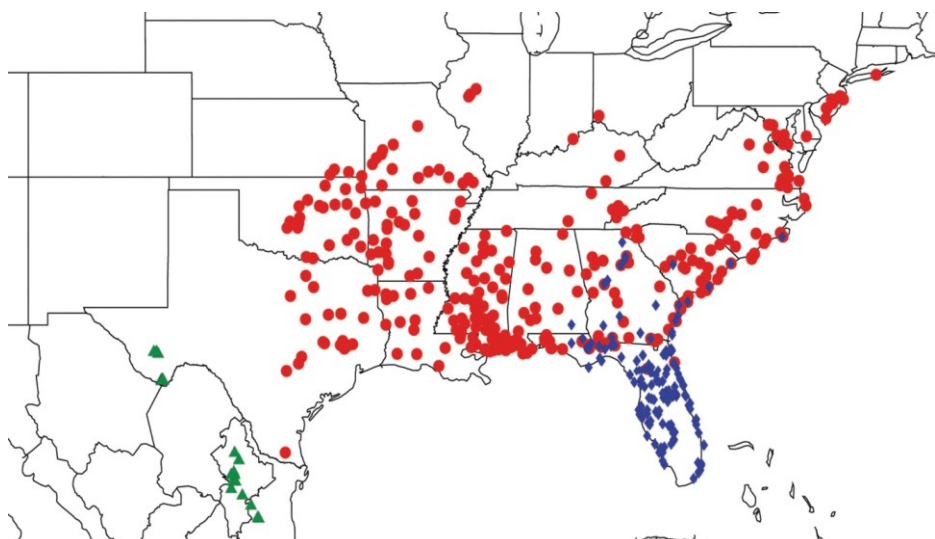
### 2.8. Biogeography of the *Neocicada* Species

The genus *Neocicada* has its greatest diversity in Mexico and Central America [19]. It was reassigned to the subtribe Leptopsaltriina based on molecular evidence [137]. The other genera of this subtribe are distributed in Asia and India so further work appears to be necessary to determine its phylogenetic relationships. Two species and one subspecies inhabit North America, north of Mexico [19,26].

All species of *Neocicada* inhabiting North America, north of Mexico are associated with oaks (*Quercus* spp.) [19,43,56,78,82,87,98]. The general coloration patterns of the species make them difficult to see on oaks. *Neocicada hieroglyphica hieroglyphica* and *N. hieroglyphica johannis* inhabit much of the eastern United States with *N. hieroglyphica johannis* restricted to the southeastern United States (Figure 29). They inhabit the eastern deciduous forests [94] and vegetation of the southeastern coastal plains [72] and we found both subspecies associated with live oak (*Quercus virginiana* Miller) in Florida and the nominotypical subspecies in post oak (*Quercus stellata*) and black oak (*Quercus velutina*) with additional records from blackjack oak (*Quercus marilandica*) [98]. The nominotypical subspecies has been collected in all Florida ecoregions [81], *N. hieroglyphica johannis* is found in the Tallahassee Hills/Volusia Limesink of the Southeastern Plain ecoregion, and both subspecies are found in the Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plain in southern Florida [21]. Further analysis of songs and morphology should be performed to determine the status of the subspecies since there is significant overlap in Alabama, Florida, Georgia, and the Carolinas [21].

*Neocicada chisos* has its northern range limit in southwestern Texas with the majority of its distribution in Mexico [19,56] (Figure 29). It is restricted to mountains in Texas extending to lower elevation Chihuahuan Desert areas of Mexico [19,56,73] and is often found in oaks (*Quercus gravesii* Sudworth and *Q. graciliformis* Muller) in riparian habitats [56] but we also found the species calling from Texas madrone (*Arbutus* spp.).

**Figure 29.** Distribution of *Neocicada hieroglyphica hieroglyphica* (red circles), *N. hieroglyphica johannis* (blue diamonds) and *N. chisos* (green triangles).



### 2.9. Biogeography of the *Magicicada* Species

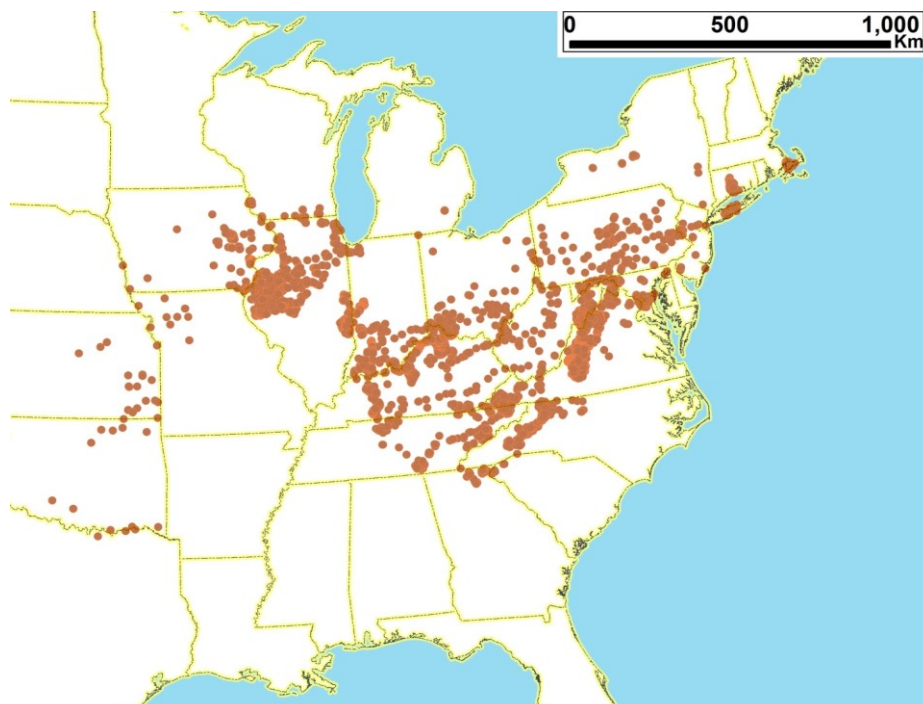
The species of the genus *Magicicada* are also known as periodical cicadas due to the long, predictable life cycle they exhibit. The genus was moved into the Cicadettinae and Taphurini from the Tibicinini of the Tibicininae by Moulds [138]. The seven species are restricted to North America, north of Mexico [26]. Davis [87] compared the genus to *Tibicina* Kolenati but a more detailed analysis placed the genus in the Taphurini [138].

The analysis of the distribution of the *Magicicada* species began with the formation of the year classes or broods by Marlatt [139]. The original brood maps have since been refined [140–142] with more detailed analyses currently being performed e.g., [143–148].

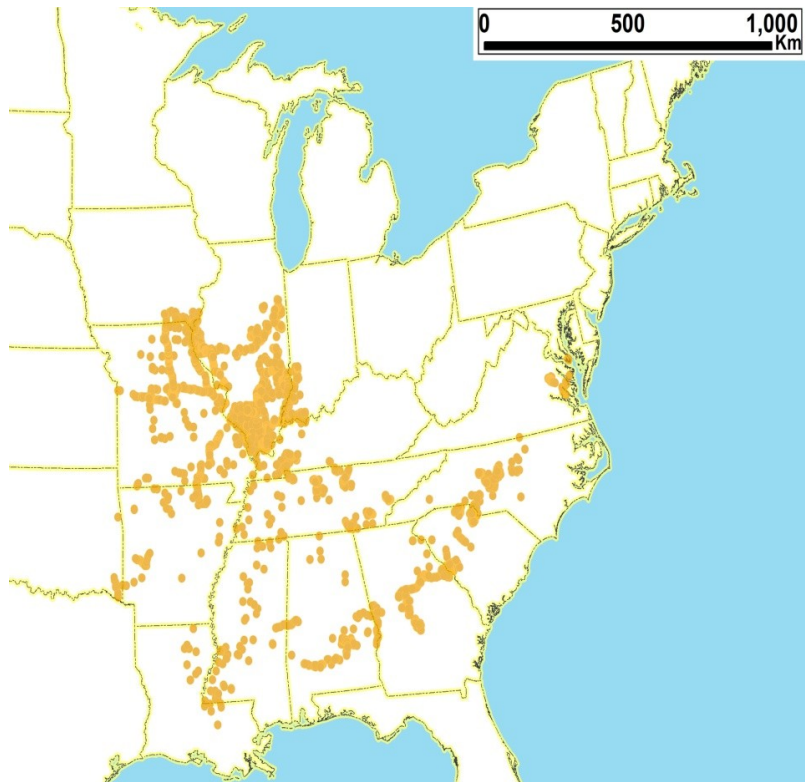
The *Magicicada* species maps presented here (Figures 30–32) were produced and kindly provided by John Cooley. The maps represent collection records from the database of specimens collected by him and or one of his colleagues that are members of the periodical cicada research group. Unverified historical records are not included as these can be incorrect as shown in the significant modifications of the original brood maps produced by Marlatt [139]. Literature records are included in the distribution listed in Table 1.

All species are primarily found in the eastern deciduous forests [94] but extend into the forested areas of eastern tall grass prairie habitats [70] (Figures 30–32). The database used to construct these maps is incomplete for the *-cassinii* and *-decula* species with points representing collection locations of J. Cooley or his co-workers in the *Magicicada* mapping project and do not include potentially incorrect historical or literature records (J. Cooley, personal communication).

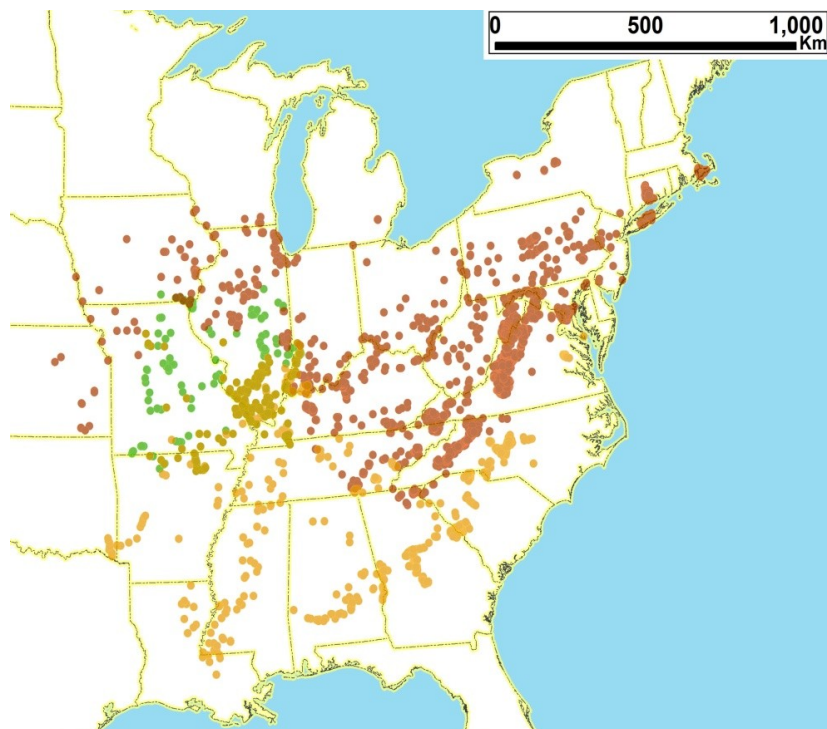
**Figure 30.** Distribution of the 17-year *Magicicada* species (brown circles). All species are represented collectively with each location being a single or multiple species. The distribution of individual species follows the patterns outlined in the text.



**Figure 31.** Distribution of the 13-year *Magicicada* species (gold circles). All species are represented collectively with each location being a single or multiple species. The distribution of individual species follows the patterns outlined in the text.



**Figure 32.** Distribution of *Magicicada septendecim* (brown circles), *M. tredecim* (gold circles) and *M. neotredecim* (green circles).





There is some differentiation in the densities of the individual species across the generic range illustrated in Figures 30 and 31. The northernmost populations are almost entirely *M. septendecim*, the southwestern populations are primarily *M. cassinii* and *M. tredecassini* with the greatest density of *M. septendecula* and *M. tredecula* in the southeast (J. Cooley, personal communication).

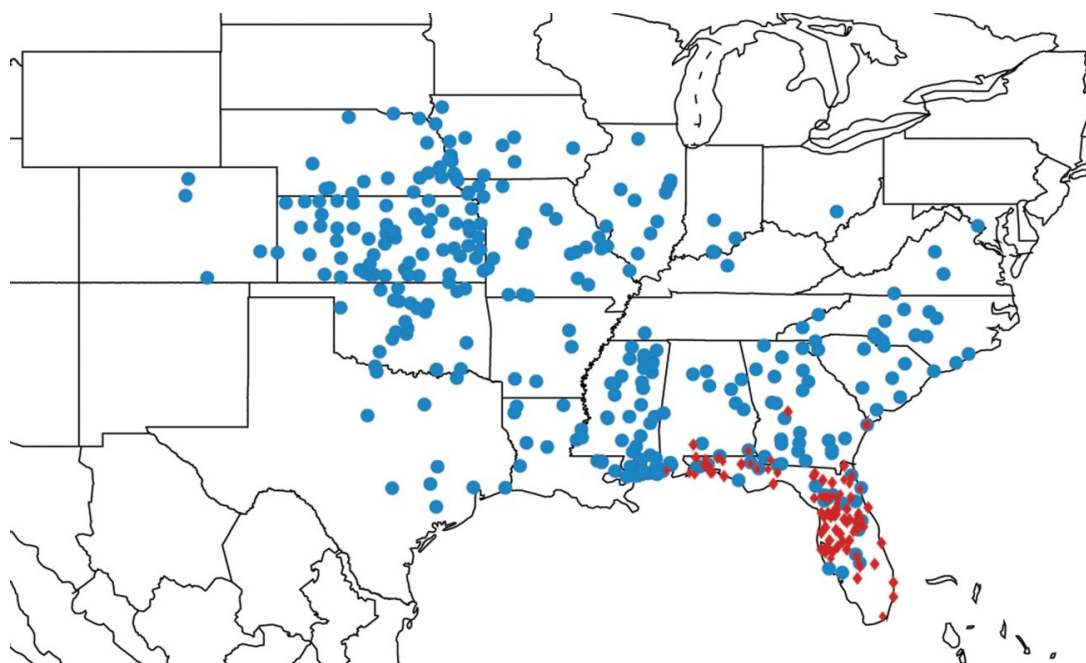
The species use different portions of their habitats [149,150] and have been shown to use a significant number of trees as host plants e.g., [151–154] primarily ovipositing in deciduous trees.

### 2.10. Biogeography of the *Cicadetta* Species

The status of the Cicadettini has long been confused (e.g., [155]) and the tribe continues to be significantly reorganized (e.g., [156]). The four species North American species have been placed in either *Melampsalta* and *Cicadetta* but are now considered to be members of *Cicadetta* [26]. The genus is widespread with members found in the Nearctic, Palaeartic, Oriental and Ethiopian biogeographic regions [26].

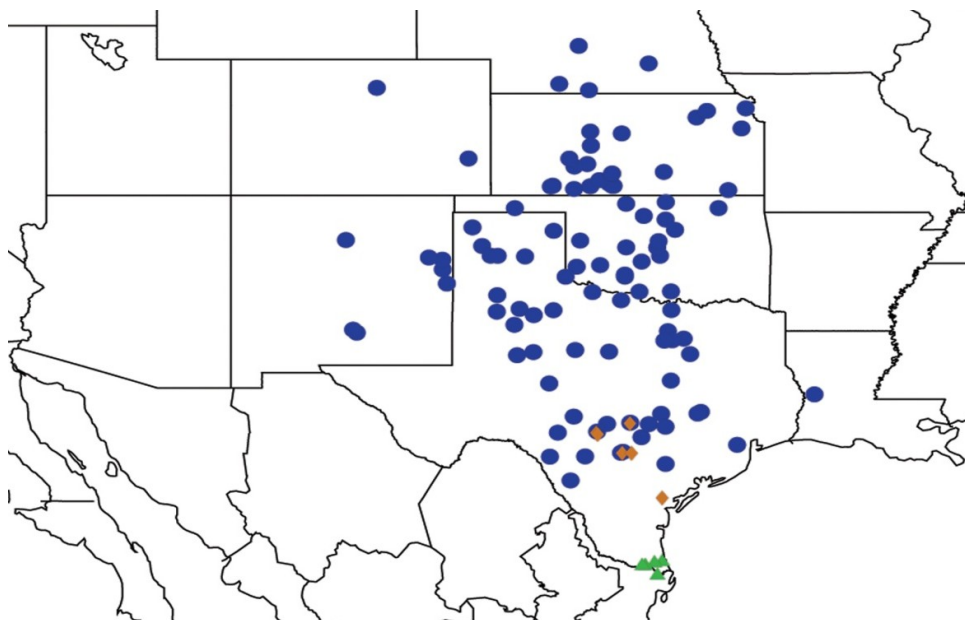
The nominotypical subspecies *C. calliope calliope* is the most widespread in North America (Figure 33) extending from the mid-Atlantic states to the Rocky Mountains. It is found in grasses and weeds and has been associated with meadow environments on grasses and weeds [98] and *Stipa spartea* Trinius-*Andropogon scoparius* (Michaux)Nash habitats [157]. The subspecies *C. calliope floridensis* was erected for Florida specimens that were completely green without black markings [21]. We have also recorded the subspecies from southern Alabama and Georgia (Figure 33). Both subspecies have been associated with the Southeastern Plains, Southern Coastal Plains and Miami Ridge/Atlantic Coastal Strip of the Southern Florida Coastal Plains ecoregions [81] in Florida [21]. The significant overlap of the subspecies suggests the validity of the subspecies needs to be investigated further.

**Figure 33.** Distribution of *Cicadetta calliope calliope* (blue circles) and *C. calliope floridensis* (red diamonds).



The remaining species of *Cicadetta* in North America are found in the grasslands [70] of the central United States (Figure 34). *Cicadetta kansa* has the most extensive distribution of these species being found from Nebraska to Texas and the distribution is coincident with the shortgrass prairie, mixed grass prairie and desert grassland ecotypes [70]. *Cicadetta texana* is found in the southern portion of the mixed grass prairie [70]. *Cicadetta cameroni* has the most limited known range being found only in southern Texas (Figure 34). It currently inhabits vegetation in agriculturally disturbed regions of the vegetation of the southeastern coastal plain [72].

**Figure 34.** Distribution of *Cicadetta kansa* (blue circles), *C. texana* (orange diamonds) and *C. cameroni* (green triangles).



### 2.11. Biogeography of the Platypedia Species

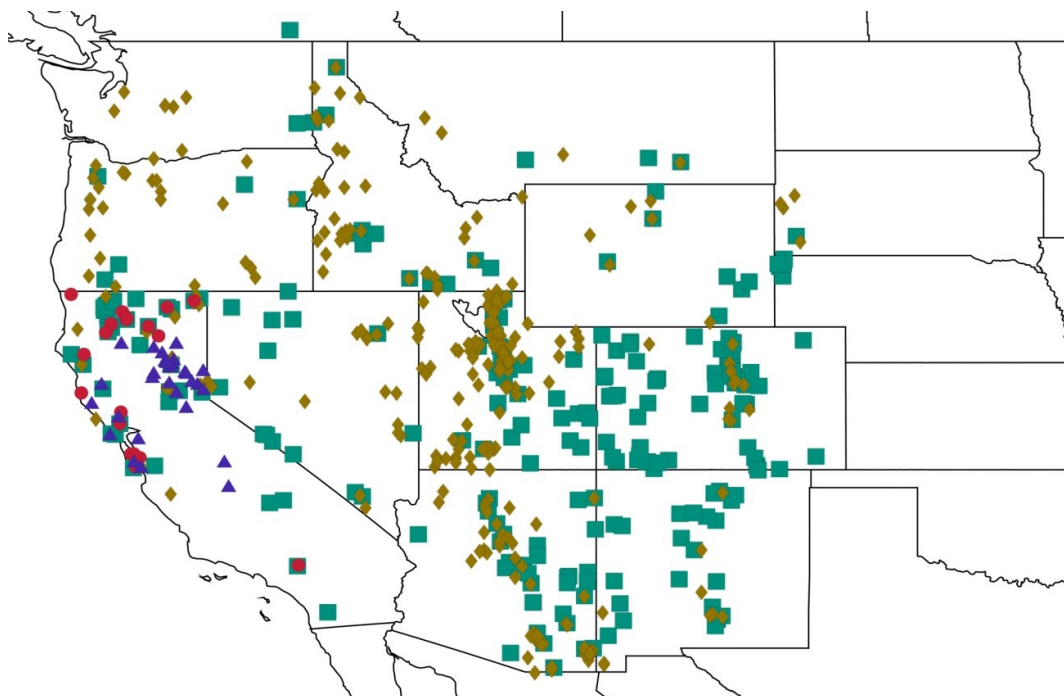
The species of the Platypediini were moved into the Tibicininae from their own family based on an extensive cladistic analysis [138]. The species of the Platypediini differ from the other genera of North American cicadas in that they lack timbal organs and communicate through crepitation (e.g., [158,159]).

There are 21 species and four subspecies of *Platypedia* in North America, north of Mexico [26]. A single species is found only in Mexico with the remaining species of the genus found in the western United States and Canada [26].

Three of the four subspecies of *Platypedia* are subspecies of *P. putnami*. The nominotypical subspecies and *P. putnami lutea* are found over much of the western United States (Figure 35) and have been collected in forested areas of the western portion of the central grassland [70], Rocky Mountain forests [160], Mexican Highlands of the Sonoran Desert [73], intermountain woodlands [76], California forest [71], chaparral [74,75], and Pacific coastal/Cascadian forests [161] ecosystems. *Platypedia putnami putnami* has been associated with skunkbrush (*Rhus trilobata*), wild plum (*Prunus Americana* Marshall), green ash (*Fraxinus pennsylvanica* Marshall), American elm (*Ulmus Americana* L.) and silver maple (*Acer saccharinum* L.) in shrublands [49], aspen (*Populus tremaloides* Michaux) [162], scrub oak (*Quercus turbinella* Greene) [66], mountain mahogany (*Cercocarpus* spp.) [158], various

trees, shrubs and deciduous fruit trees in California [69] and we found it in New Mexico locust (*Robinia neomexicana* Gray). *Platypedia putnami lutea* has been associated with pointleaf manzanita (*Arctostaphylos pungens* Kunth) and silverleaf oak (*Quercus hypoleucoides* Camus) [163] as well as piñon pine (*Pinus edulis*) [164] and greasewood (*Sarcobatus* spp.) [165]. *Platypedia putnami occidentalis* and *P. putnami keddiensis* are found in northern and central California (Figure 35). The single record for *P. putnami occidentalis* in southern California may be a misidentified *P. putnami putnami* which was collected in the same location. *Platypedia putnami occidentalis* and *P. putnami keddiensis* are associated with California forest [71], chaparral [74], and Pacific coastal/Cascadian forests [161] ecosystems.

**Figure 35.** Distribution of *Platypedia putnami putnami* (green squares), *P. putnami lutea* (gold diamonds), *P. putnami occidentalis* (red circles) and *P. putnami keddiensis* (purple triangles).

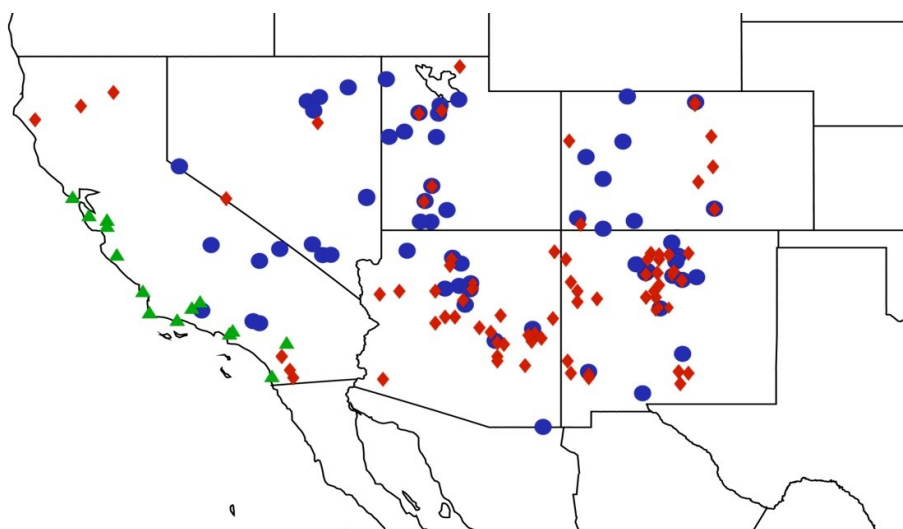


*Platypedia mohavensis mohavensis* and *P. mohavensis rufescens* are found over much of the western United States (Figure 36) and have been collected in Rocky Mountain forests [160], Mexican Highlands of the Sonoran Desert [73], intermountain woodlands [76], California forest [71], and chaparral [74,75] ecosystems. The nominotypical subspecies has been associated with scrub pine (*Pinus* spp.), juniper (*Juniperus* spp.) [158], Russian thistle (*Echinops exaltatus* Schrader) [61], serviceberry (*Amelanchier* spp.) and to a lesser extent rabbitbrush (*Ericameria nauseosa*) [49]. The subspecies *P. mohavensis rufescens* has been associated with scrub pine (*Pinus* spp.), junipers (*Juniperus* spp.), black locust (*Robinia pseudoacacia* L.) and oaks (*Quercus* spp.) [78]. We found it associated with one-seed juniper (*Juniperus monosperma*) and Utah juniper (*Juniperus osteosperma*). *Platypedia barbata* is found in primarily coastal regions of California in what are chaparral [74], and California forest [161] ecosystems.

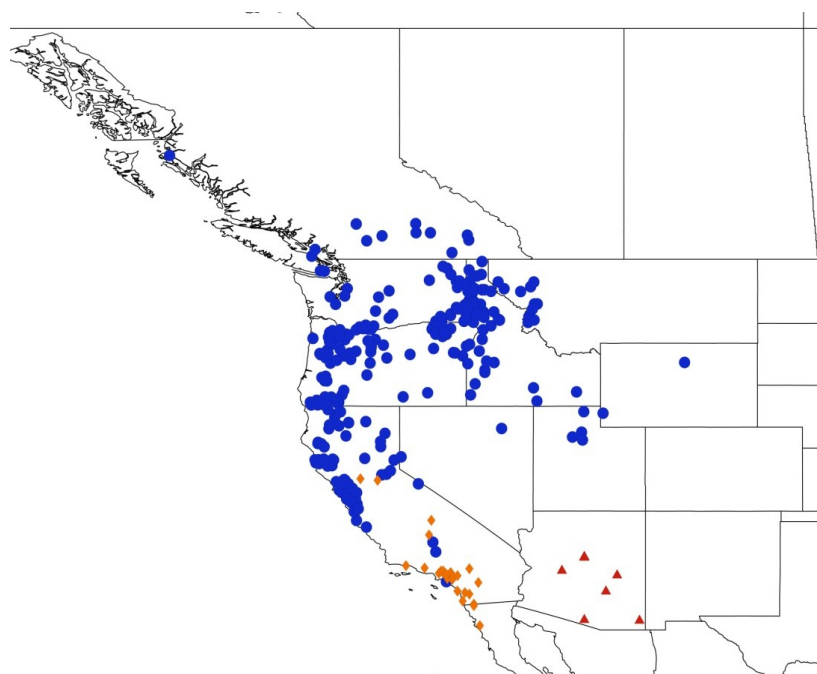
*Platypedia areolata* extends over much of the northwestern United States and southern British Columbia with one specimen having been collected almost at the southern Alaska border along the coast

of British Columbia (Figure 37). It is found in several ecosystems including the Pacific coastal/Cascadian forests [161], intermountain forests [76], Rocky Mountain forests [160] and California forests [71] and chaparral [74]. It has been reported with alder (*Alnus* spp.), sumac (*Rhus* spp.), balsam trees (*Populus* spp.) and manzanita (*Arctostaphylos* spp.) [158,166] and to oviposit in many deciduous fruit and olive (*Olea europaea* L.) trees [44,69]. *Platypedia aperta* is found in southern California and was recently described from Mexico [7]. It is associated with the California chaparral and woodlands [74]. *Platypedia balli* is found in chaparral [74,75] in Arizona (Figure 37). We found it associated with Arizona white oak (*Quercus arizonica* L.) and scrub oak (*Quercus turbinella*).

**Figure 36.** Distribution of *Platypedia mohavensis mohavensis* (blue circles), *P. mohavensis rufescens* (red diamonds) and *P. barbata* (green triangles).



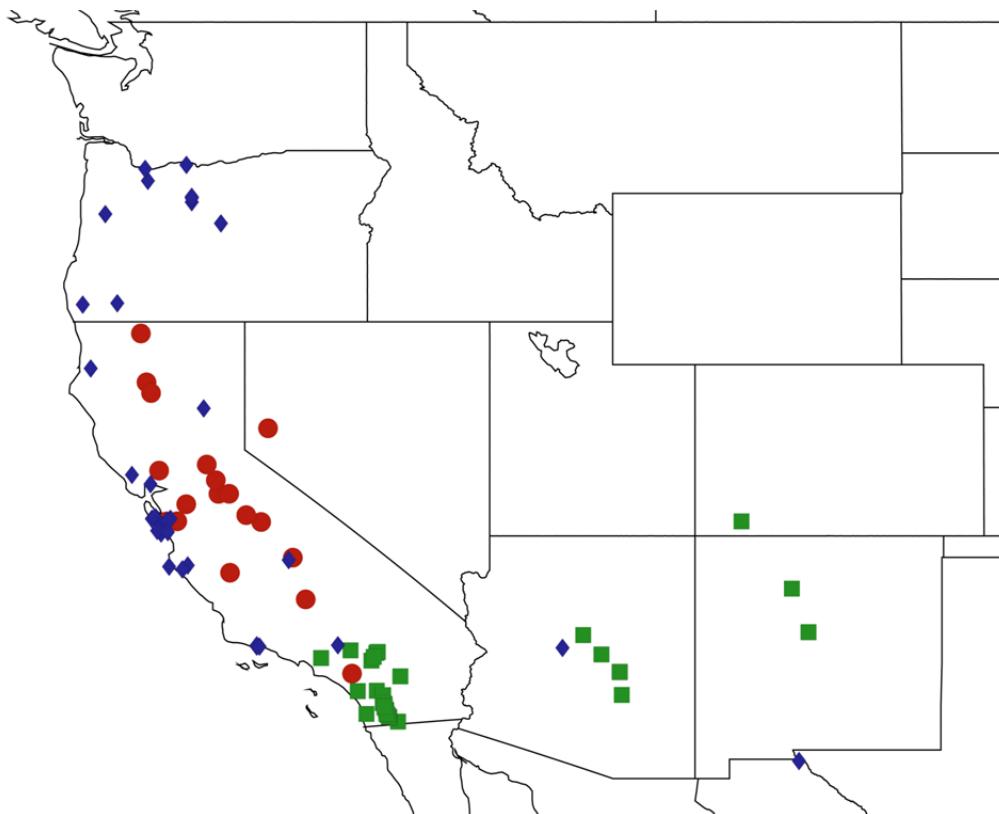
**Figure 37.** Distribution of *Platypedia areolata* (blue circles), *P. aperta* (orange diamonds), and *P. balli* (red triangles).





*Platypedia falcata* has a broad yet patchy distribution from Texas to Oregon (Figure 38). The type location is in far west Texas [166] and has since been found in Arizona, California and Oregon. It is another species found in several ecosystems including forests of the Chihuahuan Desert [73], the Pacific coastal/Cascadian forests [161], intermountain forests [76], California forests [71] and chaparral [74]. *Platypedia mariposa* is associated with the California forests [71] ecosystem with one location in the intermountain forests [76]. *Platypedia bernardinoensis* has a fairly broad distribution, found in chaparral [74] and Rocky Mountain forests [160] with populations separated by low elevation desert environments (Figure 38). The species has been associated with willows (*Salix* spp.), birch (*Betula* spp.) and maple (*Acer* spp.) [78].

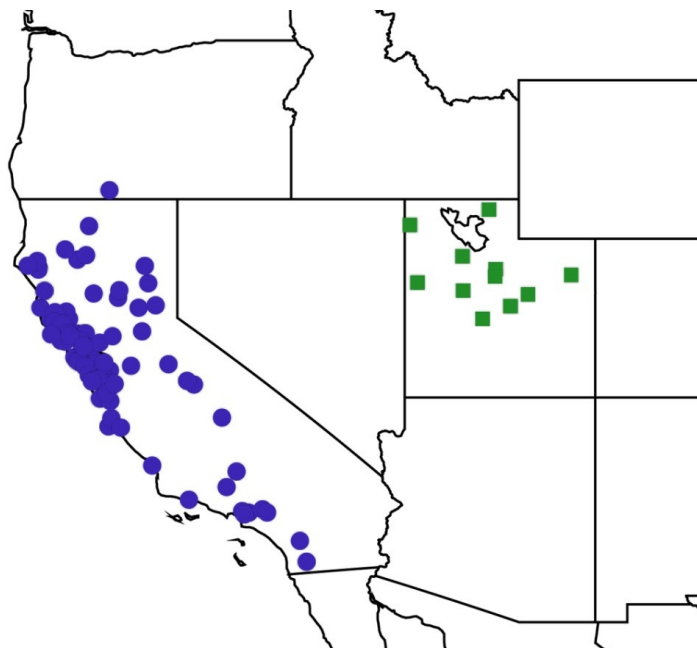
**Figure 38.** Distribution of *Platypedia falcata* (blue diamonds), *P. mariposa* (red circles), and *P. bernardinoensis* (green squares).



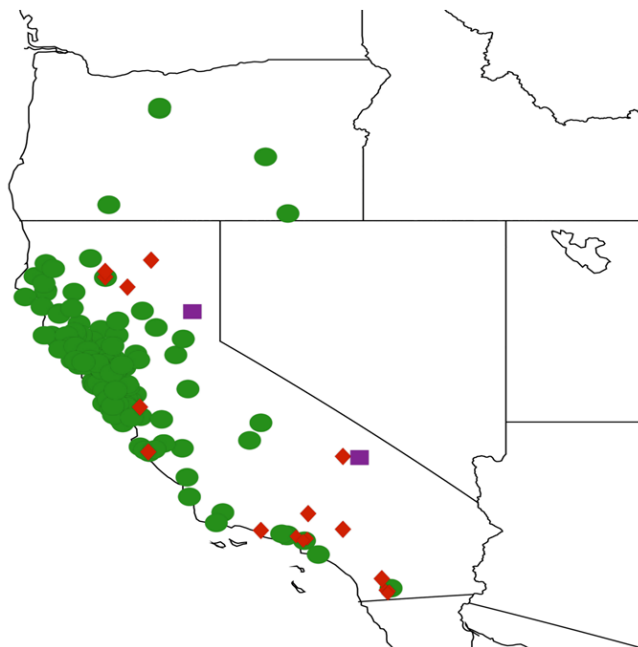
*Platypedia similis* is found in several ecosystems (Figure 39) including California forests [71] and chaparral [74]. *Platypedia affinis* is found in the intermountain forests [76] of Utah (Figure 39). We found it associated with Gambel's oak (*Quercus gambelii* Nuttall), manzanita (*Arctostaphylos* spp.) and Utah juniper (*Juniperus osteosperma*).

*Platypedia minor* is found across California with extensions into Oregon (Figure 40) and Mexico [8]. It is found in a variety of ecosystems including intermountain forests [76], Rocky Mountain forests [160], California forests [71] and chaparral [74] and has been associated with oaks (*Quercus* spp.), baccharis (*Baccharis* spp.), Pacific madrone (*Arbutus menziesii* Pursh), willow (*Salix* spp.) and fruit trees [44,69]. *Platypedia rufipes* is found in California forests [71], chaparral and woodlands [74]. *Platypedia sylvestri* is known from only two locations in the California forests [71] (Figure 40).

**Figure 39.** Distribution of *Platypedia similis* (blue circles) and *P. affinis* (green squares).

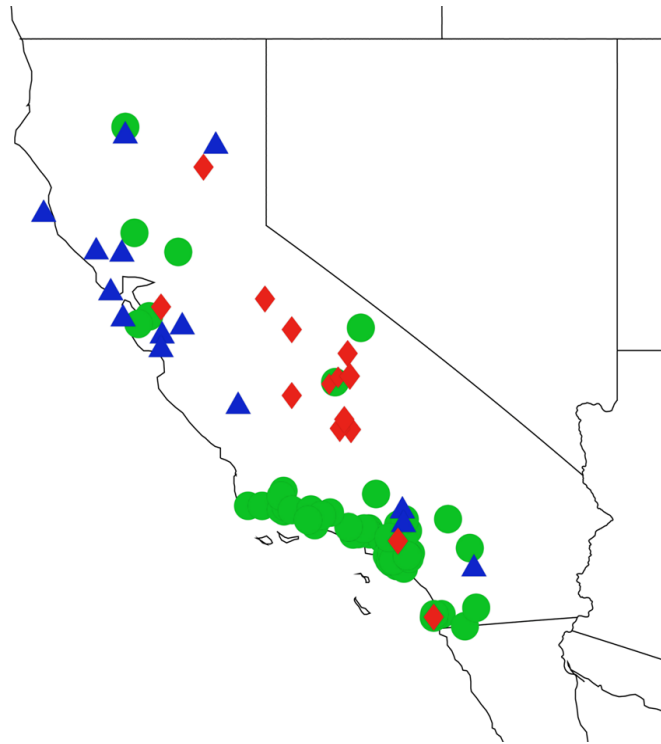


**Figure 40.** Distribution of *Platypedia minor* (green circles), *P. rufipes* (red diamonds), and *P. sylvestri* (purple squares).

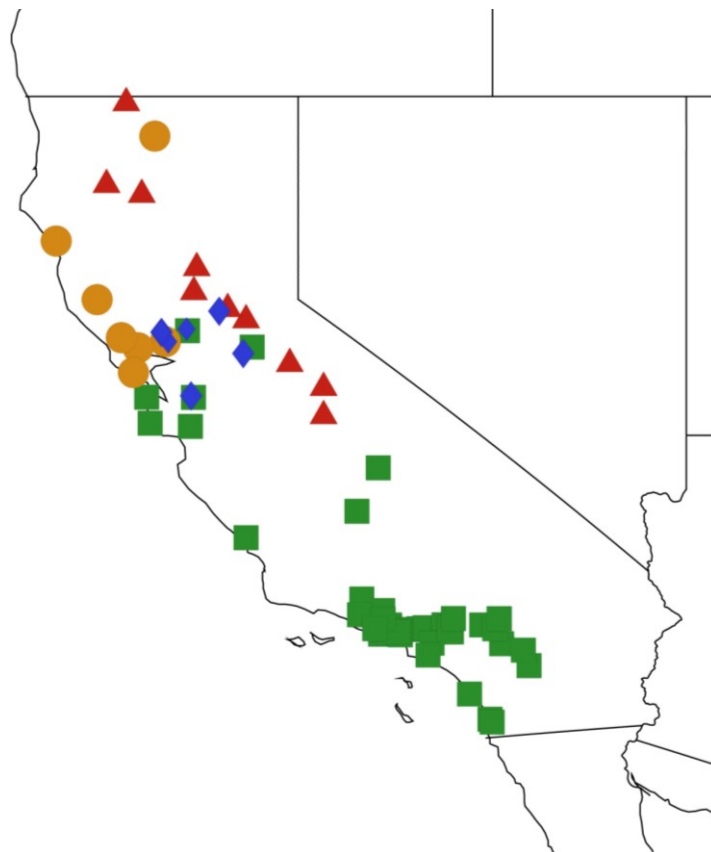


The remaining species of *Platypedia* are restricted to California. *Platypedia tomentosa*, *P. scotti*, *P. vanduzeei* (Figure 41), *P. laticapitata*, and *P. intermedia* (Figure 42) are found in California forests [71] and chaparral [74,75] ecosystems. *Platypedia tomentosa* has been associated with California juniper (*Juniperus californica* Carrière) [93], *P. scotti* with thick brush [158] and *P. vanduzeei* with grassy hillsides and sagebrush (*Artemisia* spp.) [64,158,166]. We collected *P. intermedia* in Pacific madrone (*Arbutus menziesii*). *Platypedia middlekauffi* and *P. usingeri* are found in California forests [71] (Figure 42).

**Figure 41.** Distribution of *Platypedia tomentosa* (blue triangles), *P. scotti* (red diamonds), and *P. vanduzeei* (green squares).



**Figure 42.** Distribution of *Platypedia laticapitata* (green squares), *P. intermedia* (orange circles), *P. middlekauffi* (red triangles), and *P. usingeri* (blue diamonds).

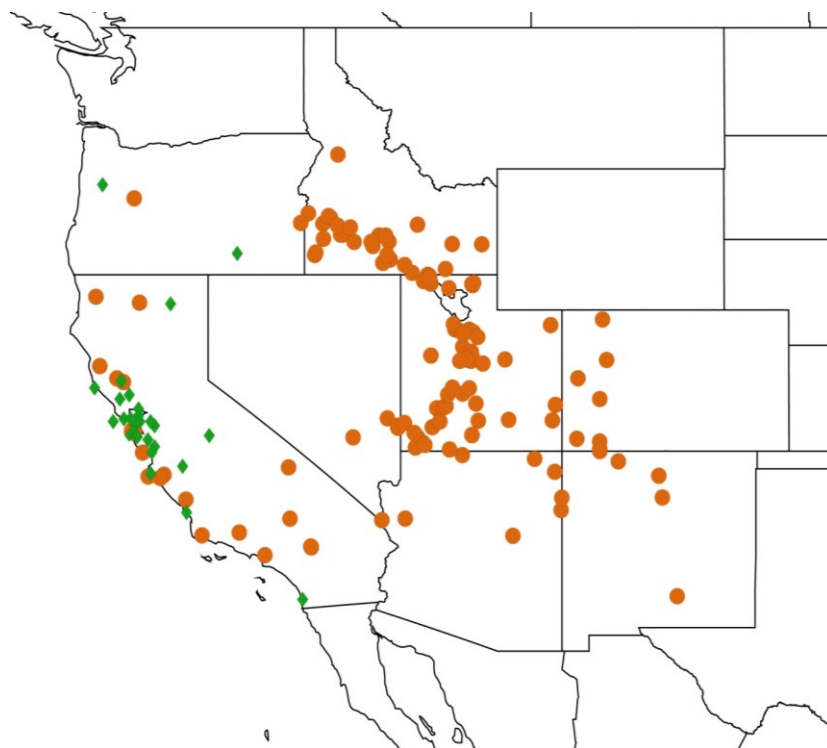


## 12. Biogeography of the *Neoplatypedia* Species

The genus *Neoplatypedia* is related to *Platypedia* differing primarily in the costal margin and number of apical cells in the fore wings and is the only other member of the Platypediini [26]. Both species are restricted to North America, north of Mexico.

*Neoplatypedia ampliata* is found in California and Oregon (Figure 43). *Neoplatypedia constricta* has a more extensive distribution being found in 8 western states (Figure 43). The species of *Neoplatypedia* are associated with the California upland forests and woodlands habitat [71], Pacific Northwest forests [161] and *N. constricta* also is found in the forests of the Rocky Mountains [160] and intermountain woodlands [76]. *Neoplatypedia constricta* has been associated with sagebrush (*Artemisia* spp.) [49,165,167] and rubber rabbitbush (*Ericameria nauseosa*) [49].

**Figure 43.** Distribution of *Neoplatypedia ampliata* (green diamonds) and *N. constricta* (orange circles).



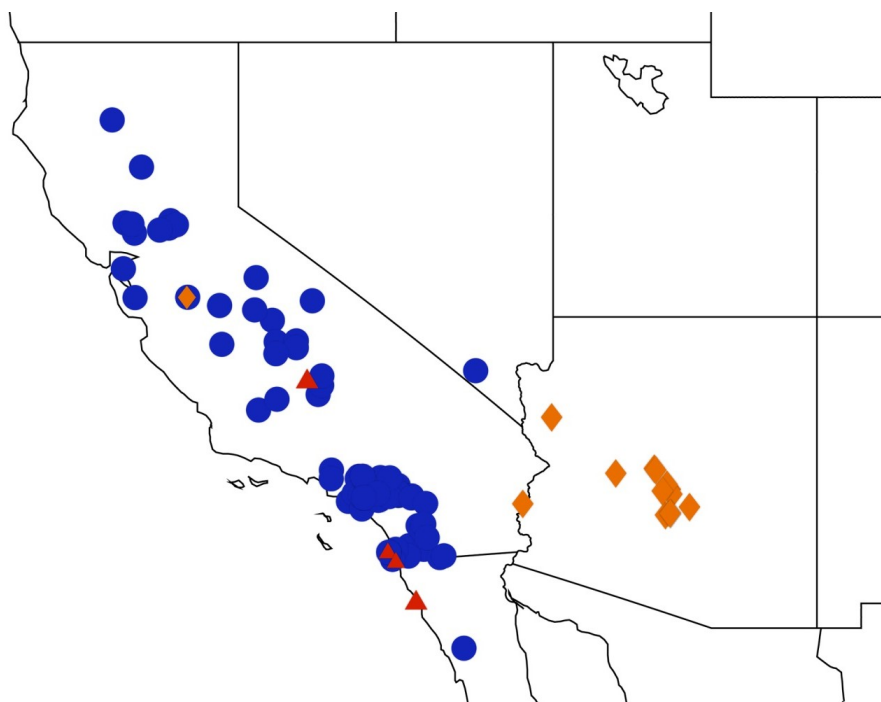
## 2.13. Biogeography of the *Clidophleps* Species

There are seven species and two subspecies of *Clidophleps* in North America, north of Mexico [26]. *Clidophleps* is related to *Okanagana*, *Okanagodes*, and *Tibicinoides* with these genera classified together in the Tibicinini. Other members of the tribe are found in Europe, Asia, India and northern Africa (the South American genus *Ahomana* Distant needs to be reexamined for its tribal placement).

The majority of *Clidophleps* species are found in California. *Clidophleps distanti distanti* and *C. distanti truncatus* are found in the California upland forests and woodlands [71] (Figure 44). The nominotypical subspecies has been reported from chaparral as well [66,74,75] and we found it associated with blue oak (*Quercus douglasii* Hooker & Arnott) but it has also been associated with live oak (*Quercus agrifolia* Née) [66]. The single record in Nevada for *C. distanti distanti* is suspect. The

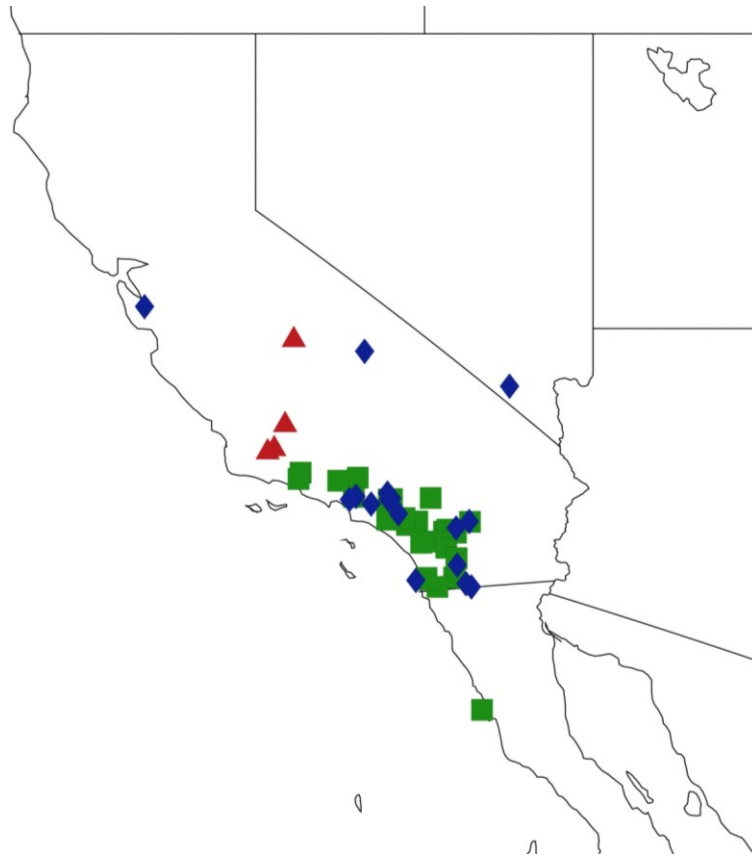
type locality of *C. vagans* (Figure 46) is unknown because the type specimen was collected off an automobile [87] and perhaps something similar happened with the *C. distanti distanti* specimen collected in Nevada as the location is between high population centers in southern California and southeastern Nevada. The overlap in the distributions of the subspecies suggests the status of the subspecies should be examined further using acoustic methods. The known range of *C. distanti distanti* and *C. distanti truncata* was recently extended into Mexico [8]. *Clidophleps rotundifrons* is currently known from Arizona (Figure 44), where the collection sites are found in the creosote bush-bur sage habitats [130] of the Sonoran Desert [73]. The location in Merced County, CA is questionable because even though the specimen was checked and has been properly identified, this record is in a different habitat and may have been mislabeled.

**Figure 44.** Distribution of *Clidophleps distanti distanti* (blue circles), *C. distanti truncata* (red triangles) and *C. rotundifrons* (orange diamonds).

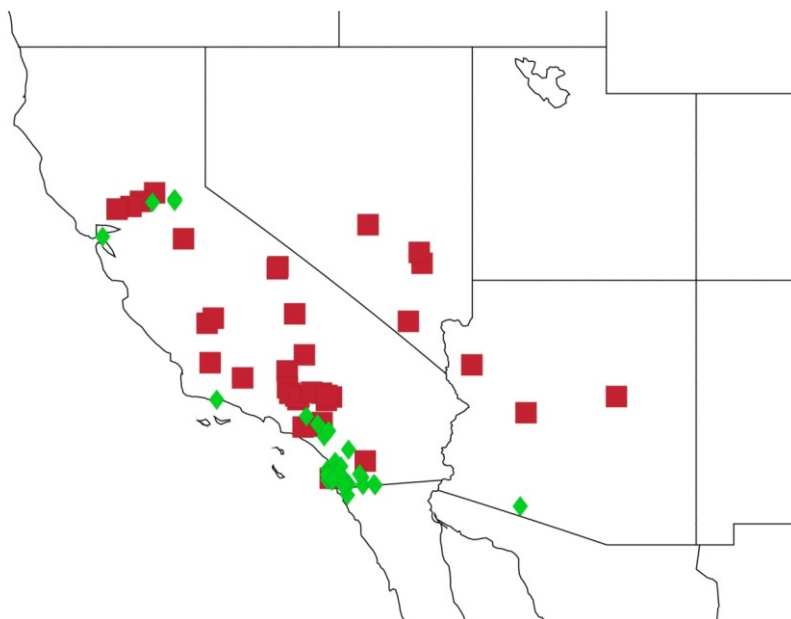


*Clidophleps wrighti*, *C. tenuis* (Figure 45) and *C. blaisdelli* (Figure 46) are also found in the California upland forests and woodlands [70] with *C. blaisdelli* also reported from chaparral [66,168]. *Clidophleps blaisdelli* and *C. wrighti* were reported to be restricted to chamise (*Adenostoma fasciculatum* Hooker & Arnott) in a southern California habitat [169]. There are also some suspect locations for *C. tenuis* in central California and southern Nevada and *C. blaisdelli* in northern California and southwestern Arizona. The known range of *C. wrighti* was recently extended into Mexico [8]. *Clidophleps beameri* has a more restricted distribution (Figure 45) and has been reported from chaparral [74,75] where we found it associated with an *Atriplex*-like plant (probably *Adenostoma* spp. based on appearance and distribution of the genus in California) on which it is cryptically colored and difficult to see.

**Figure 45.** Distribution of *Clidophleps beameri* (red triangles), *C. wrighti* (green squares) and *C. tenuis* (blue diamonds).



**Figure 46.** Distribution of *Clidophleps vagans* (red squares) and *C. blaisdelli* (green diamonds).



The most extensive range for a *Clidophleps* species is that of *C. vagans* (Figure 46). Specimens have been collected in California, Nevada and Arizona. Collection sites are found in the California upland forest and woodlands [71], chaparral [74], and intermountain deserts and shrub steppes [76].



#### 2.14. Biogeography of the *Okanagana* Species

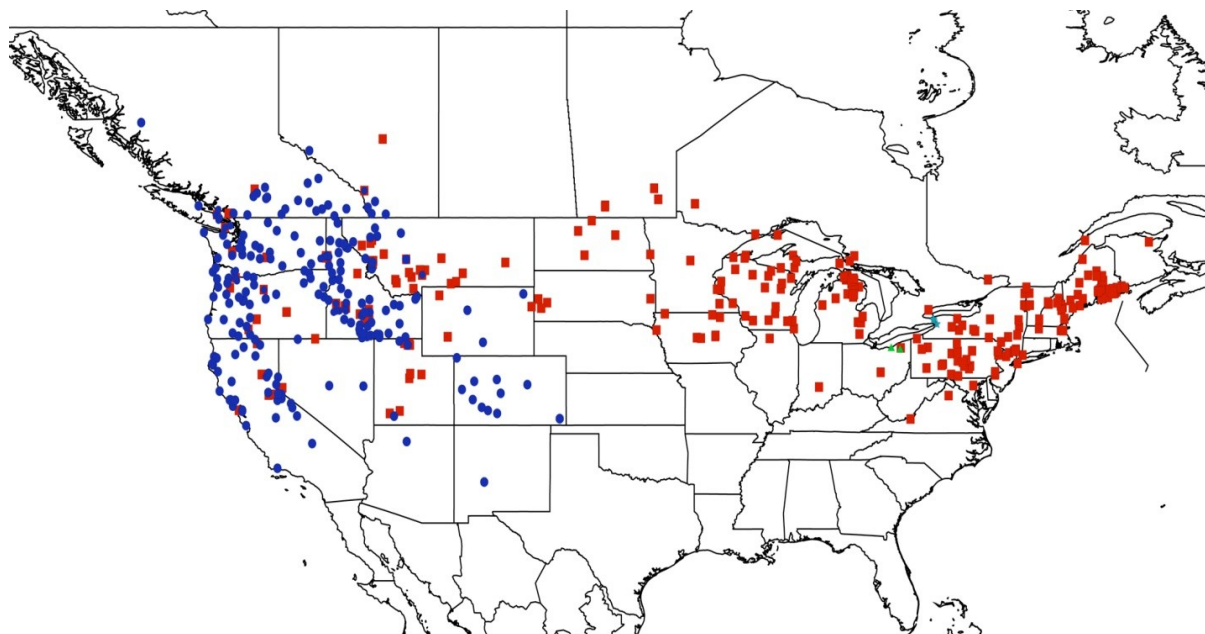
The genus *Okanagana* is the most diverse member of the Tibicinini found in North America. There are 57 species and four subspecies of *Okanagana* in North America, north of Mexico [26]. It is related structurally to *Okanagodes*, *Clidophleps* and *Tibicinoides* with *Okanagana* probably being the phylogenetic origin for these genera. The species of *Okanagana* are distributed over most of North America, north of Mexico except for southeastern states.

The first group of *Okanagana* to be discussed is a complex of species related to *Okanagana rimosa*. Several species and subspecies at one time or another were classified related to *O. rimosa* [26]. Many specimens also have been misidentified historically (e.g., [49]). *Okanagana rimosa rimosa* is found in northern regions of North America extending from New Brunswick to California (Figure 47) with the first documented records for New Jersey [170] being published recently. The species is found in a variety of habitats including eastern deciduous forests [94], central plains [70], Rocky Mountain forests [160], intermountain forests [76], Pacific coastal/Cascadian forests [161], and California forests [71]. The nominotypical subspecies has been reported from aspen trees (*Populus* spp.) [162], white birch (*Betula papyrifera* Marshall), maple (*Acer* spp.) [170,171], pine (*Pinus* spp.) [66], blueberry barrens (*Vaccinium* spp.) [85,96], bigtooth aspen (*Populus grandidentata* Michaux) and blackberries (*Rubus alleghaniensis* Porter) [172]. The subspecies *O. rimosa ohioensis* is only known from northeastern Ohio (Figure 47) and may simply be a localized color variation. It has been associated with white pines (*Pinus strobus* L.) and hemlocks (*Tsuga* spp.) [93]. The validity of *O. noveboracensis* was recently confirmed [12] with the known distribution in western New York and southeastern Ontario (Figure 47). *Okanagana occidentalis* has a more western distribution (Figure 47) with the type location determined to be Chilliwack, British Columbia [173]. It can be found in large numbers in sagebrush shrublands in Colorado [49]. It has been associated with cottonwoods (*Populus* spp.), trees, underbrush and flowers [174]. We found it associated with several bushy plants in a wash. It is restricted to mountainous environments and is associated with the Rocky Mountain forests [160], intermountain forests [76], Pacific coastal/Cascadian forests [161], and California forests [71].

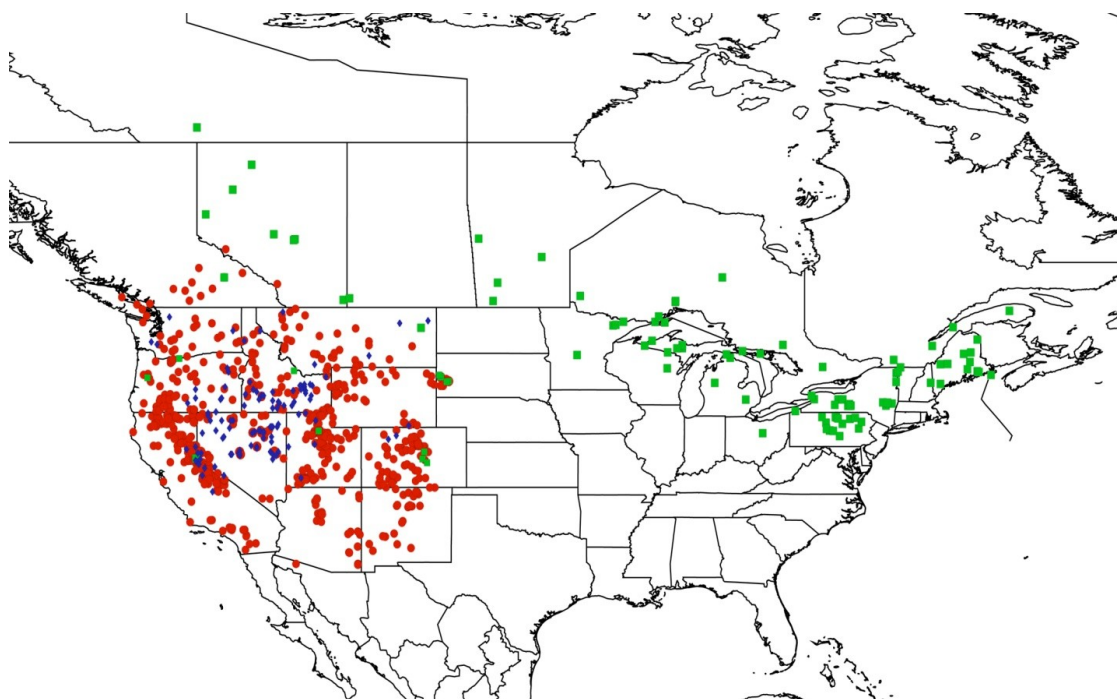
*Okanagana canadensis* has a similar range to *O. rimosa rimosa*; it is found in northern regions of North America extending from New Brunswick to California (Figure 48) in a variety of habitats including eastern deciduous forests [94], central plains [70], Rocky Mountain forests [160], intermountain forests [76], Pacific coastal/Cascadian forests [161], and California forests [71]. A specimen collected in Samba Deh Falls Territorial Park, Northwest Territory is the northernmost (61°N, 120°W) cicada we have recorded (Figure 48). It has been reported to use sagebrush (*Artemisia* spp.) [49,175], cedar trees (no species given), willows (*Salix* spp.) [174], cherry (*Prunus* spp.), Scots pine (*Pinus sylvestris* L.) and northern white cedar (*Thuja occidentalis* L.) [172] and we collected it in ponderosa pine (*Pinus ponderosa*). *Okanagana bella* has been reported to use various tree species [44,52,66] including ponderosa pine, piñon pines (*Pinus edulis*) [67], junipers (*Juniperus* spp.), aspens (*Populus* spp.), and willows (*Salix* spp.) [49] in the Rocky Mountain forests [160], intermountain forests [76], Pacific coastal/Cascadian forests [161], California forests [71] and chaparral [74]. We also found it in quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta* Douglas) and mountain mahogany (*Cercocarpus* spp.). *Okanagana annulata* has a distribution similar to that of *O. bella* (Figure 48) and has been associated with the Rocky Mountain forests [160], intermountain forests [76], Pacific

coastal/Cascadian forests [161], California forests [71] and chaparral [74,75]. We found it in oak (*Quercus* spp.), pine (*Pinus* spp.) and sequoia (*Sequoiadendron giganteum* (Lindley)J. Buchholz).

**Figure 47.** Distribution of *Okanagana rimosa rimosa* (red squares), *O. rimosa ohioensis* (green triangles), *O. noveboracensis* (light blue stars) and *O. occidentalis* (blue circles).



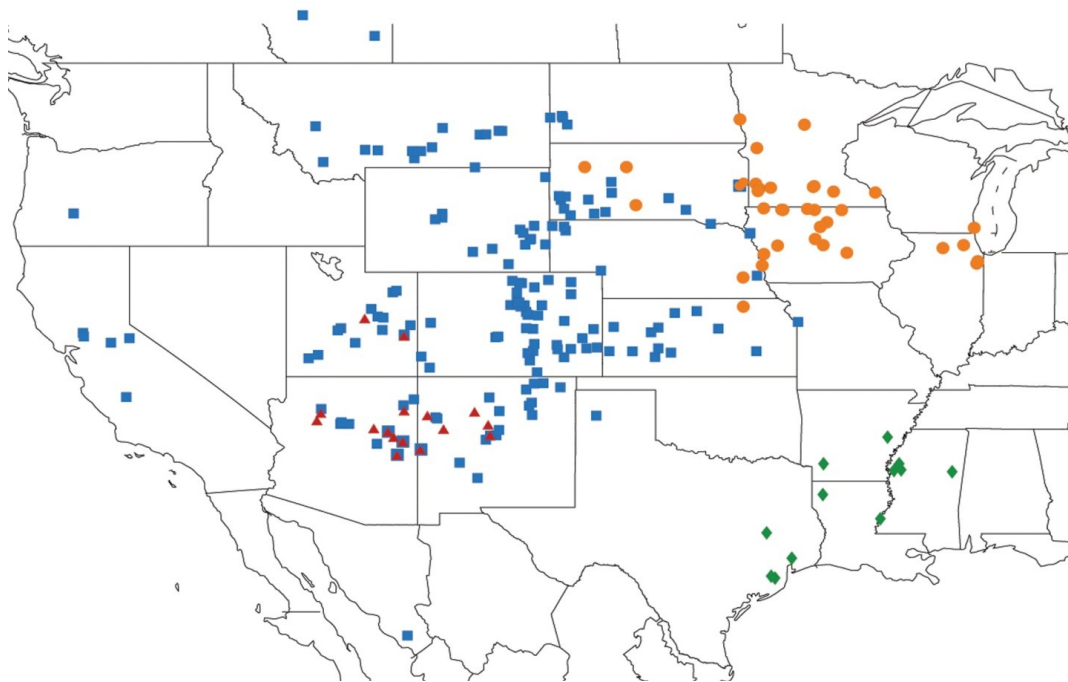
**Figure 48.** Distribution of *Okanagana canadensis* (green squares), *O. bella* (red circles) and *O. annulata* (blue diamonds).



*Okanagana synodica synodica* is found in grasses [36,92,129,162,174] in a wide variety of habitats but has also been reported to use sand sage (*Artemisia filifolia*) and low shrubs [49]. The host plants are probably grasses because we found specimens in habitats that had no vegetation other than short

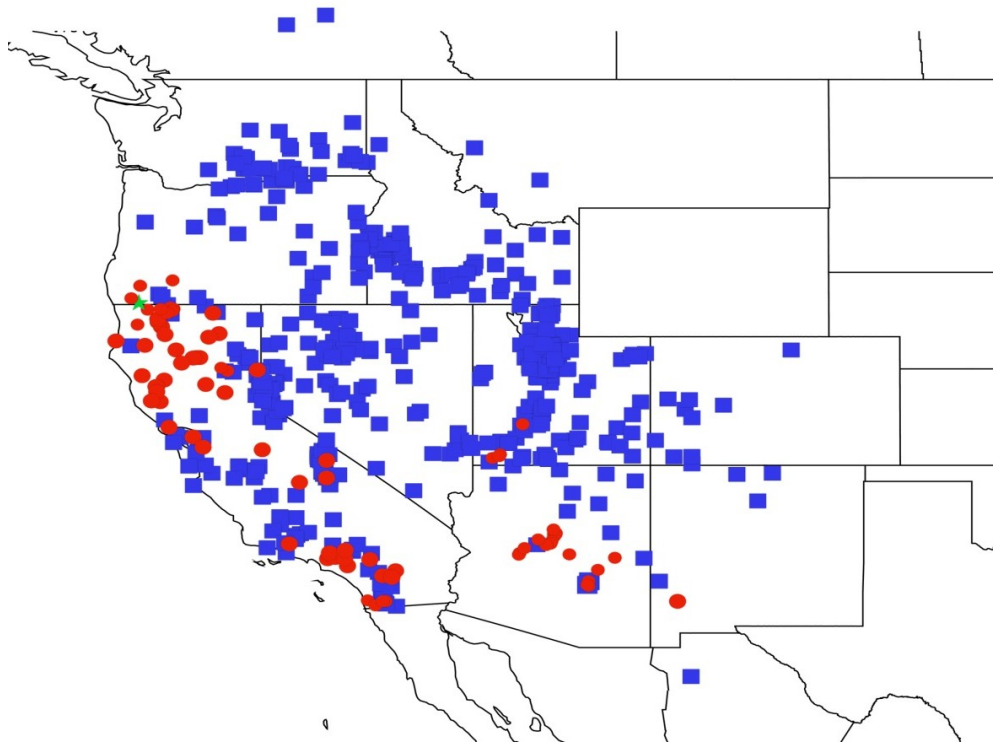
clumps of grass. The nominotypical subspecies is found in grasslands [70] and Rocky Mountain vegetation [160], intermountain areas [76] and California uplands [71] (Figure 49). *Okanagana synodica nigra* is also found in grasses but is more restricted in its distribution in southern areas (Figure 49). *Okanagana balli* is also a grass species that is distributed in the grasslands [70] of the northern Great Plains (Figure 49). It has been associated with weeds and grasses, lead plant (*Amorpha canescens* Pursh) [176] and stands of bluestem grass (*Andropogon gerardii* Vitman) [157]. We found specimens in remnants of prairie along railroad tracks in otherwise agricultural environments and on a remnant of tallgrass prairie in southern Minnesota. The only species of *Okanagana* to extend into the southern United States is *O. viridis* (Figure 49). We found it associated with hardwoods in the southeastern coastal plains vegetation [72] where the green coloration provided crypsis. It has also been reported to use blackjack (*Quercus marilandica*) and post oaks (*Quercus stellata*) [87].

**Figure 49.** Distribution of *Okanagana synodica synodica* (blue squares), *O. synodica nigra* (red triangles), *O. balli* (orange circles) and *O. viridis* (green diamonds).

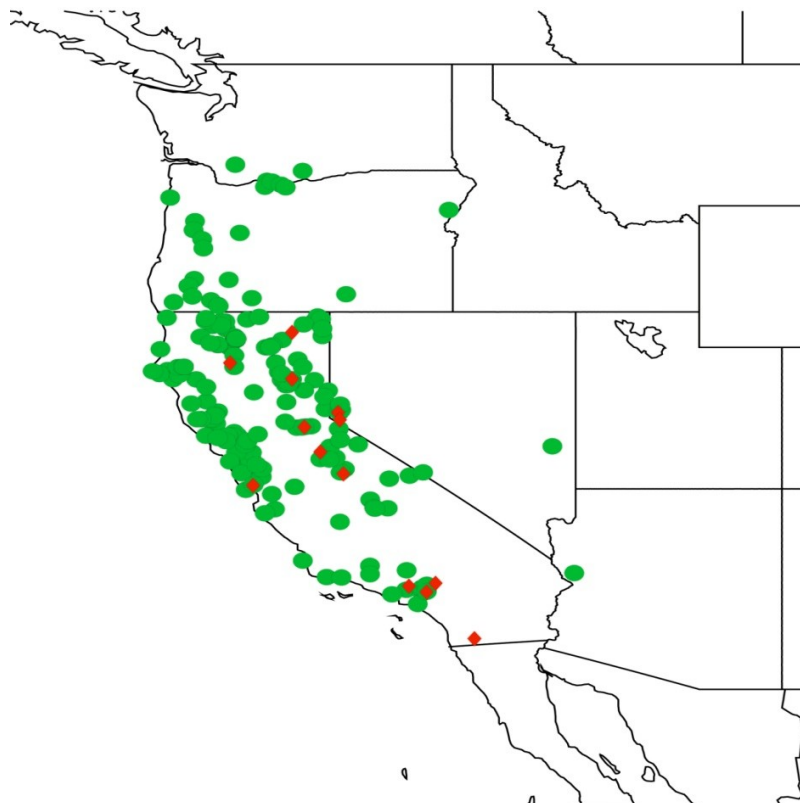


Another species of *Okanagana* to have subspecies is *O. mariposa* (Figure 50). The nominotypical subspecies has been associated with chaparral [74,75,92] and California forests [71]. It has been specifically associated with oak (*Quercus* spp.) [66] and we found it associated with Arizona cypress (*Cupressus arizonica* Greene), mountain mahogany (*Cercocarpus* spp.) and scrub oak (*Quercus turbinella*). *Okanagana mariposa oregonensis* is restricted to a single location in Oregon (Figure 50) near the northern border of the California forests [71] ecosystem. It is completely surrounded by the nominotypical subspecies which suggests it is highly localized color variation and further analyses to assess the status of the subspecies should be performed. A very common species of *Okanagana* in the west is *O. utahensis* (Figure 50). It is found in Great Basin sagebush (*Artemisia tridentata* Nuttall) [177] and sagebrush shrublands [49] in the Rocky Mountain forests [160], intermountain steppes [76], California forests [71], chaparral [74] and Palouse prairie [70].

**Figure 50.** Distribution of *Okanagana mariposa mariposa* (red circles), *O. mariposa oregonensis* (green star) and *O. utahensis* (blue squares).



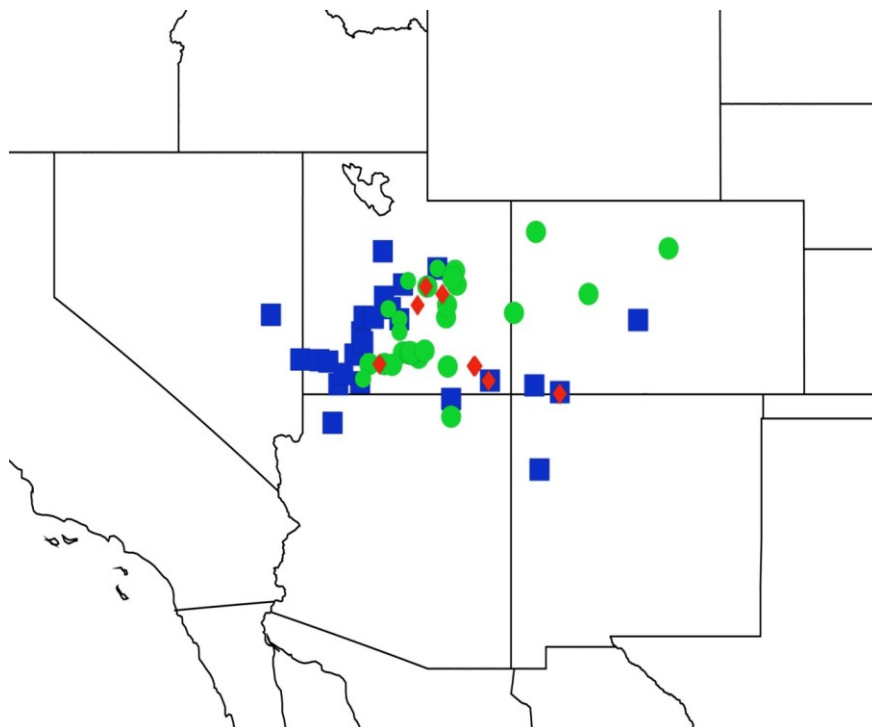
**Figure 51.** Distribution of *Okanagana tristis tristis* (green circles) and *O. tristis rubrobasalis* (red triangles).



*Okanagana tristis tristis* (Figure 51) is found using trees in a variety of habitats including chaparral [74,75], California forests [71], intermountain forests [76] and forests of the Pacific coasts [161]. *Okanagana tristis rubrobasalis* is restricted to California (Figure 51) in the California forests [71] and chaparral [74]. The significant overlap of the subspecies suggests it is a color variation and further analyses to assess the status of the subspecies should be performed.

*Okanagana tanneri* was originally described as a subspecies of *O. schaefferi* [60]. Both species (Figure 52) are found in intermountain forests [76] and Rocky Mountain forests [160]. *Okanagana schaefferi* has been reported in sagebrush (*Artemisia* spp.) [174,178] and sagebrush shrublands [49]. We found *O. schaefferi* in Great Basin sagebrush (*Artemisia tridentata*) and juniper (*Juniperus* spp.) and *O. tanneri* in sage (*Artemisia tridentata*) and oaks (*Quercus* spp.). *Okanagana sugdeni* (Figure 52) is found in intermountain forests [76] in Utah. We found it only on to piñon pine (*Pinus edulis*).

**Figure 52.** Distribution of *Okanagana schaefferi* (blue squares), *O. tanneri* (green circles) and *O. sugdeni* (red diamonds).



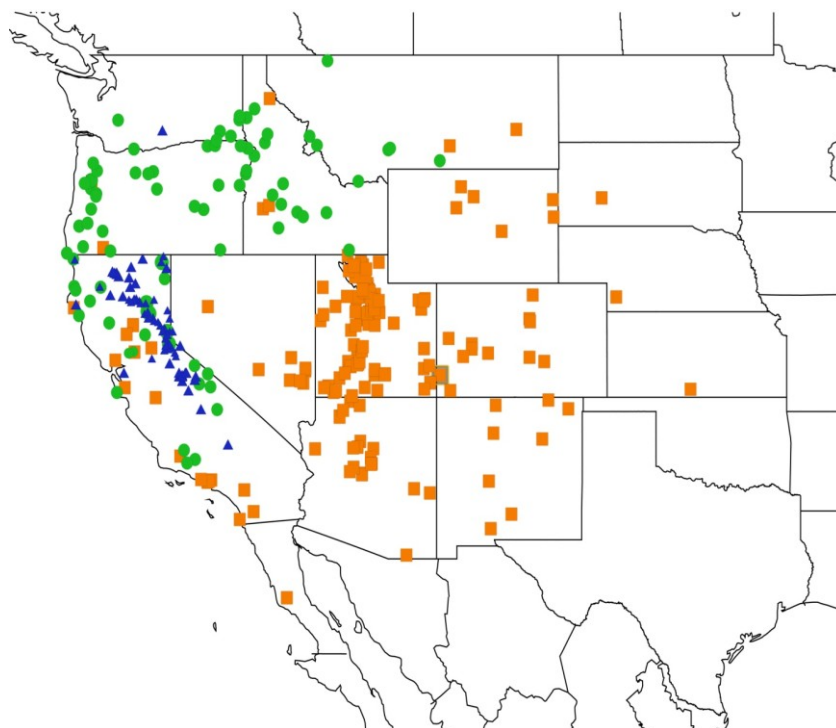
Another common species of *Okanagana* in the west is *O. striatipes* (Figure 53). It is found in Great Basin sagebrush (*Artemisia tridentata*) [78,177] and sagebrush shrublands [49] in the Rocky Mountain forests [160], intermountain steppes [76], California forests [71], chaparral [74], grasslands and Palouse prairies [70]. *Okanagana oregona* is found in trees in the California forests [71], chaparral [74,75], intermountain [76] and rocky Mountain forests [160] (Figure 53). We found it associated with white fir (*Abies concolor* (Gordon)Lindley ex Hildebrand) and also calling from grasses. *Okanagana nigrodorsata* is restricted to California upland forests [71] (Figure 53).

*Okanagana hesperia* (Figure 54) is a common grass species that has been associated with chaparral [74,75] and the Great Plains [49,70] but is also found in intermountain areas [76]. We found it associated with grasses and weedy plants such as rabbit bush (*Chlysothamnus* spp.) but it would also call from trees like ponderosa pine (*Pinus ponderosa*) and one-seed juniper (*Juniperus monosperma*).

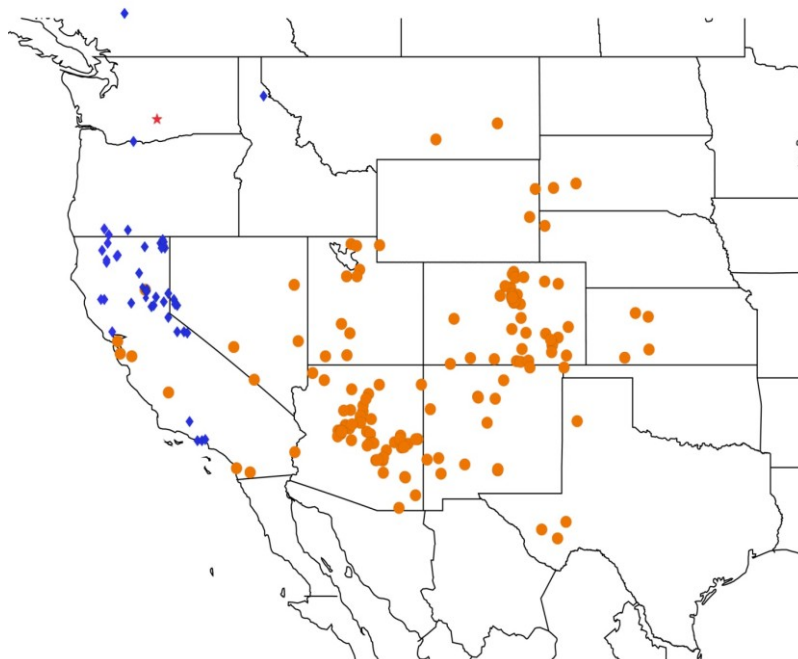


It has previously (as *O. striatipes beameri* Davis) been reported to oviposit in weeds [66]. *Okanagana yakimaensis* is restricted to the Palouse prairie [70] of central Washington (Figure 54). *Okanagana ornata* is primarily found in California forests [71] with a few records in chaparral [74] and forests of the Rocky Mountains [160]. It has been associated with oak bushes (*Quercus* spp.) [59].

**Figure 53.** Distribution of *Okanagana oregona* (green circles), *O. nigrodorsata* (blue triangles) and *O. striatipes* (orange squares).



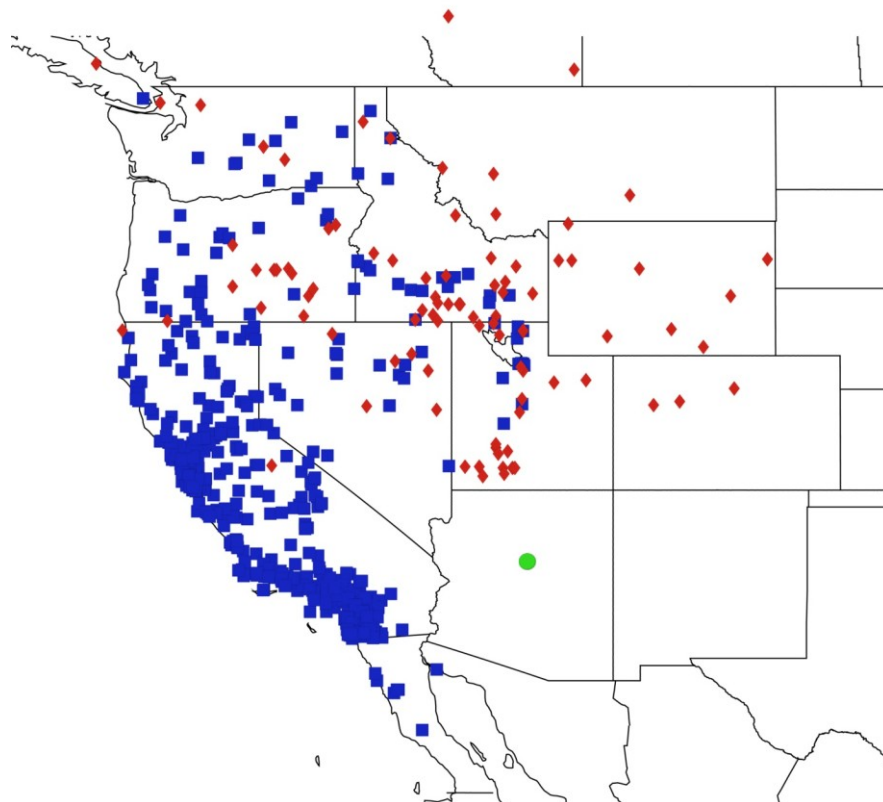
**Figure 54.** Distribution of *Okanagana yakimaensis* (red star), *O. ornata* (blue diamonds) and *O. hesperia* (orange circles).





One of the most common species of *Okanagana* in collections is *O. vanduzeei* (Figure 55). It has been reported to inhabit chaparral [64,74,75], California forests [71], intermountain areas [76], Rocky Mountain vegetation [160] and the Palouse prairie [70]. As previously reported [64,66], we collected it from a variety grasses and sage (*Artemisia* spp.) over a wide range of California and it has been associated with dry grasses in fields and hillsides of California [69]. It has also been known to use wild buckwheat (*Eriogonum* spp.), sage, *Baccharis* spp., goldenrod (*Solidago* spp.) and pines (*Pinus* spp.) [44,64] but is rarely found in trees [174]. The known range of *O. vanduzeei* was recently extended into Mexico [8]. *Okanagana fratercula* is found in intermountain regions [76], forests of the Rocky Mountains [160] and grasslands [70]. We found it in small bushes and it has been associated with sagebrush (*Artemisia* spp.) [178]. Perhaps the most restricted distribution of any species in North America, north of Mexico is that of *O. georgi* (Figure 55) which is currently known from a restricted section of chaparral [18,74,75] in northern Arizona. We found it associated with Arizona cypress (*Cupressus arizonica*), and Lowell ash (*Fraxinus anomala* var. *lowellii* (Sargent) Little).

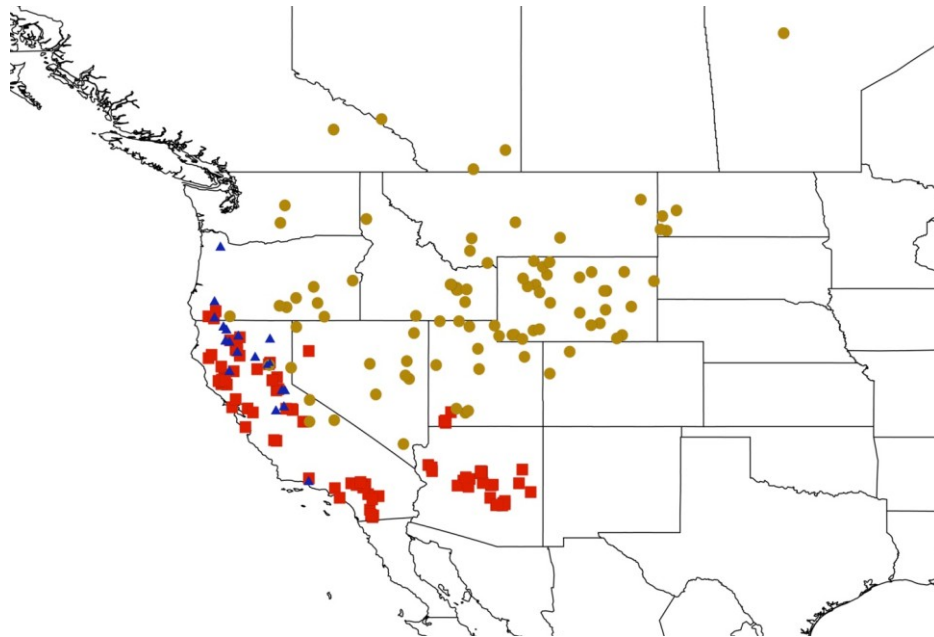
**Figure 55.** Distribution of *Okanagana vanduzeei* (blue squares), *O. fratercula* (red diamonds) and *O. georgi* (green circle).



*Okanagana luteobasalis* (Figure 56) has a wide distribution across much of the western states and southern Canada east of the Sierra Nevada Mountains. It is associated with several ecosystems including the intermountain vegetation [76], Rocky Mountain vegetation [160] and grassland environments [70]. We collected the species on sagebrush (*Artemisia* spp.) as has been reported previously [61]. *Okanagana rubrovenosa* is found in chaparral [74,75] and California forests [71] (Figure 56) on manzanita (*Arctostaphylos* spp.) [38,44,66,78,174] and was reported to be restricted to *Arctostaphylos pungens* in a southern California habitat [168] where their red coloration provides

crypsis. *Okanagana vandykei* is associated with the California forests [71] (Figure 56) and has been reported to be arboreal [44].

**Figure 56.** Distribution of *Okanagana luteobasalis* (gold circles), *O. rubrovenosa* (red squares) and *O. vandykei* (blue triangles).



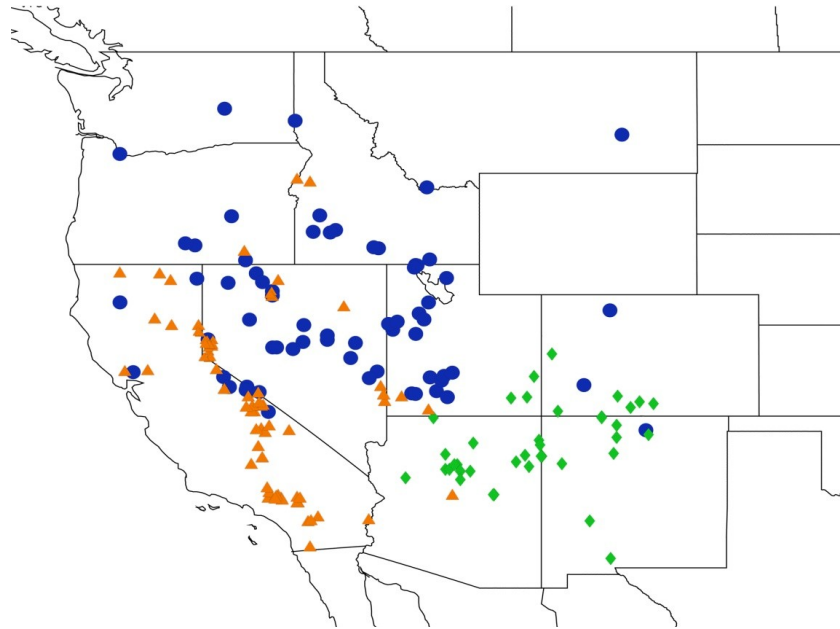
*Okanagana gibbera* (Figure 57) is found in intermountain areas [76], Rocky Mountain vegetation [160] and grassland environments [70]. *Okanagana fumipennis* has been associated with sagebrush-greasewood shrublands and juniper-sagebrush woodlands [49] and emergence holes have been found under big sagebrush (*Artemisia tridentata*) [78] and greasewood (*Sarcobatus vermiculatus* (Hooker) Torrey) [49]. We also collected the species on yellow menodora (*Menodora scabra* Gray). It is found primarily in the southern portions of the intermountain shrub steppes [76]. *Okanagana cruentifera* is found in the California forests [71] with some extensions into the intermountain forests [76] (Figure 57).

*Okanagana ferrugomaculata* is found in several forested areas of the northwest (Figure 58) and has been collected in chaparral [74,75], California forests [71], intermountain forests [76] and Pacific coastal forests [161]. We found it associated with lodgepole pine (*Pinus contorta*) and oaks (*Quercus* spp.). *Okanagana pallidula* is found in chaparral [74,75,179] primarily along the central valley of California (Figure 58) and has been associated with bushy weeds and grasses [66] and we also found it in grasses. *Okanagana lurida* is found in the Palouse prairies [70] and intermountain forests [76] and we found it associated with grasses and weeds. *Okanagana formosa* (Figure 58) is more restricted in its distribution and is found in trees in the intermountain forest ecosystem [76]. We found it associated with juniper (*Juniperus* spp.).

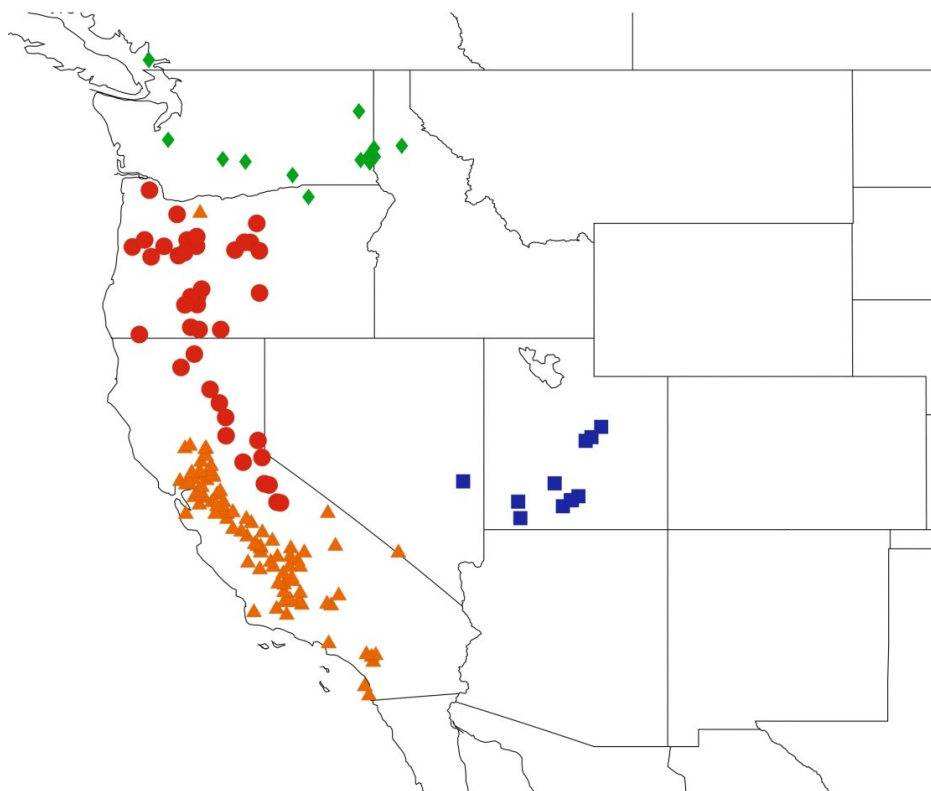
*Okanagana magnifica* is a large species that extends across much of the southwest (Figure 59). It has been reported in chaparral [75], pinyon-juniper woodlands [66,67,174], juniper (*Juniperus* spp.) [66,174], piñon pine (*Pinus edulis*) [67,164], sagebrush (*Artemisia* spp.), Gambel oak (*Quercus gambelii*, and cottonwood (*Populus* spp.) [36,174]. We found it in piñon pine and single leaf piñon pine (*Pinus monophylla* Torrey & Frémont). It inhabits the forests of the Rocky Mountains [160], chaparral [74,75], intermountain forests [76] and California forests [71]. *Okanagana simulata* (Figure

59) is also found in the California forests [71]. *Okanagana napa* has a scattered distribution and is found in California forests [71], chaparral [74] and intermountain forests [76] and has been associated with oak (*Quercus* spp.), other trees and shrubs in the hillsides coastal California mountain range [69].

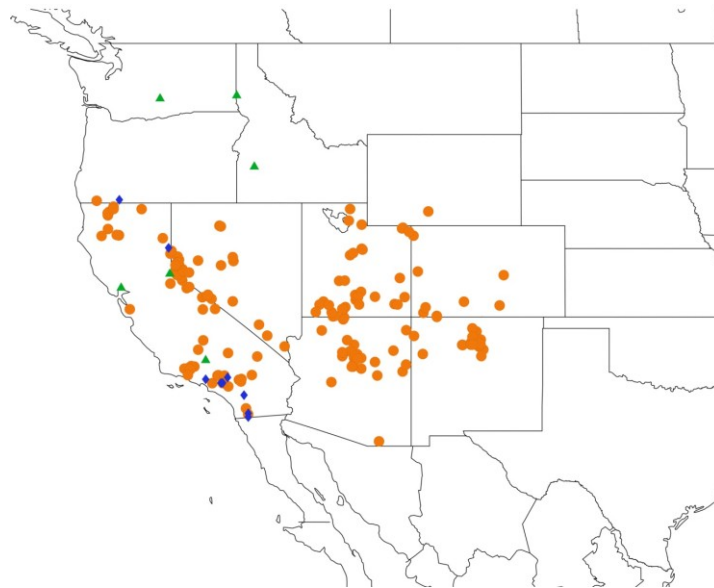
**Figure 57.** Distribution of *Okanagana gibbera* (blue circles), *O. cruentifera* (orange triangles) and *O. fumipennis* (green diamonds).



**Figure 58.** Distribution of *Okanagana formosa* (blue squares), *O. pallidula* (orange triangles), *O. ferrugomaculata* (red circles) and *O. lurida* (green diamonds).



**Figure 59.** Distribution of *Okanagana magnifica* (orange circles), *O. simulata* (blue diamonds) and *O. napa* (green triangles).



*Okanagana triangulata* is found in chaparral [74,75] and was recently reported from Mexico [8]. It has been associated with meadows and grasses [44,174] and we found it associated with large species of grasses. *Okanagana canescens* is found in chaparral [74,75] and California forests [71] (Figure 60) where we collected it on blue oak (*Quercus douglasii*). *Okanagana aurora* is found in California forests [71] and western regions of the intermountain forests [76]. *Okanagana sperata* (Figure 60) has a scattered distribution within the known range of the California upland forests [71].

Bliven [180] described several species of cicadas from northern California (Figure 61). *Okanagana orithya*, *O. vocalis*, *O. salicicola*, *O. sequoia* and *O. rhadine* are found at the southern end of the Pacific coastal forests [161]. *Okanagana pernix* is found in the northern end of the California upland forests [71]. No further information on the biology of these species is available.

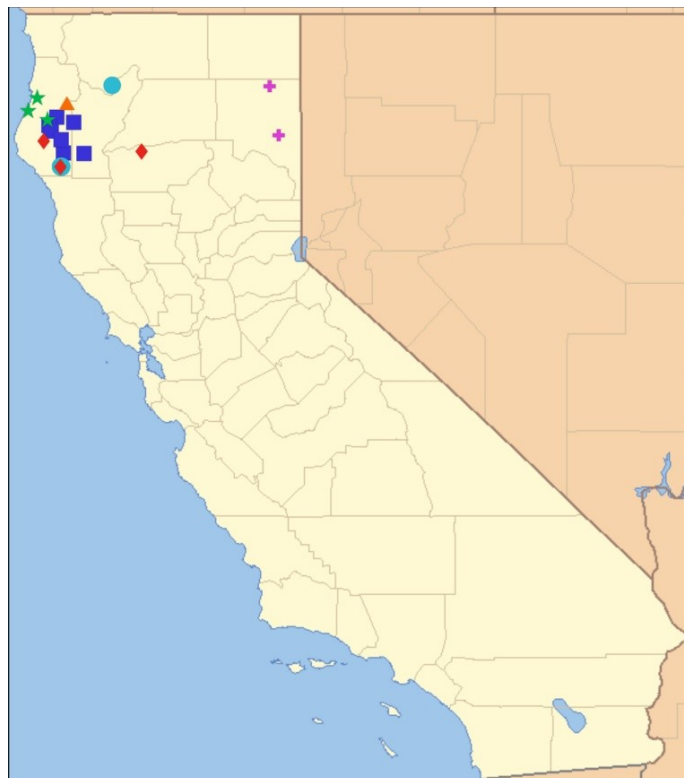
Another series of California cicadas related to chaparral [74] is *O. arctostaphylae*, *O. venusta*, *O. opacipennis* and *O. uncinata* [75] (Figure 62). *Okanagana arctostaphylae* was named for its affinity for manzanita (*Arctostaphylos* spp.) [181] and was reported to be restricted to *Arctostaphylos pungens* in a southern California habitat [168] in which the red coloration provides crypsis. We found only two locations for the species, one of which is Cajon Pass, a common collecting site in California. *Okanagana opacipennis* has also been associated with manzanita (*Arctostaphylos* spp.) [40,44,166,175] where its coloration would also provide crypsis. *Okanagana villosa* is restricted to high elevations in the California upland forests [71] (Figure 62).

The remaining species of *Okanagana* are also restricted to California (Figure 63). *Okanagana wymorei* is found in chaparral [74,75] and California forests [71] as is *O. arboraria*. We found *O. wymorei* in grasses. *Okanagana nigriviridis* is found in elevated chaparral [74] associated with shrubs [66] and was reported to be restricted to chamise (*Adenostoma fasciculatum*) in a southern California habitat [169]. Finally, *Okanagana hirsuta* is found in coastal chaparral and offshore islands and *O. catalina* is geographically isolated in the chaparral [74] of the Catalina Islands.

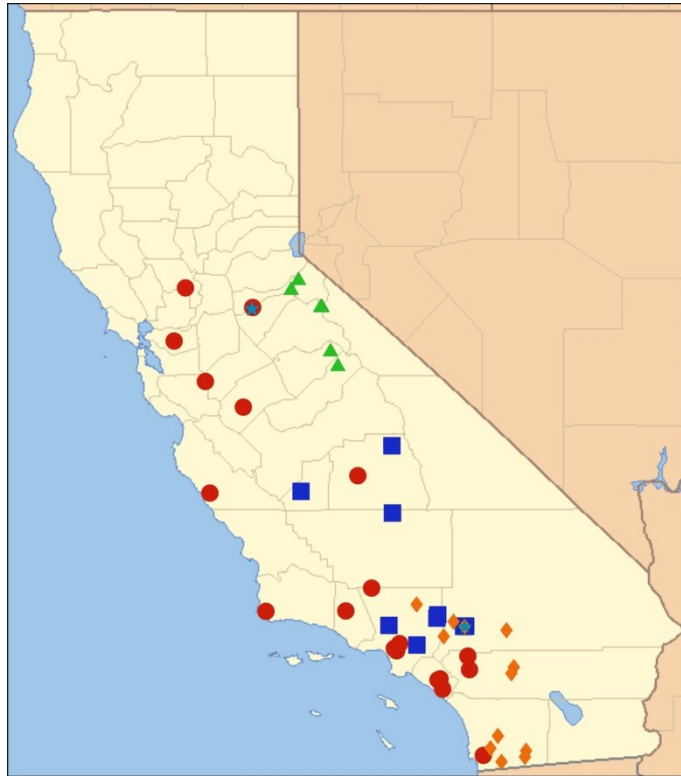
**Figure 60.** Distribution of *Okanagana triangulata* (green diamonds), *O. sperata* (orange circles), *O. canescens* (red squares) and *O. aurora* (blue diamonds).



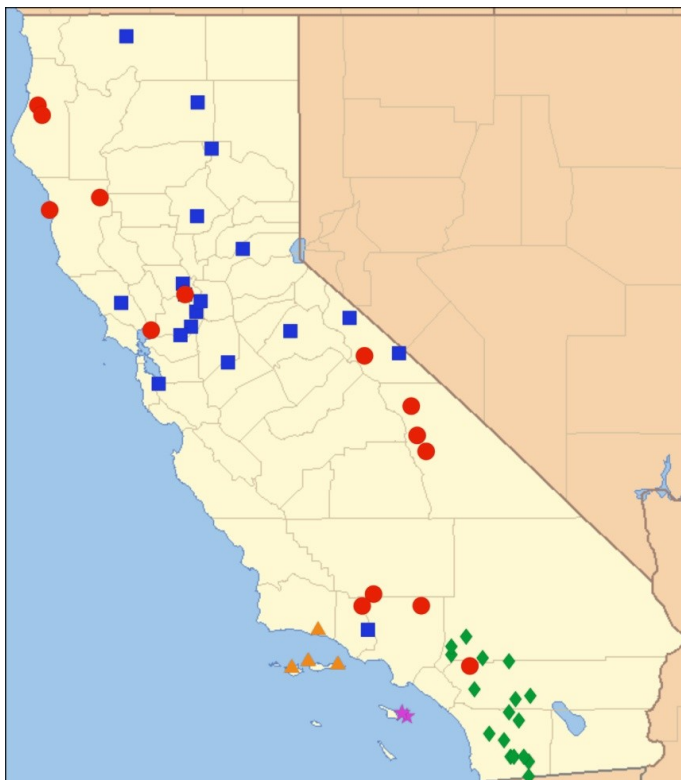
**Figure 61.** Distribution of *Okanagana orythia* (dark blue squares), *O. vocalis* (light blue circles), *O. rhadine* (orange triangle), *O. salicola* (red diamond), *O. pernix* (purple crosses) and *O. sequoia* (green stars).



**Figure 62.** Distribution of *Okanagana arctostaphylae* (light blue stars), *O. opacipennis* (orange diamonds), *O. uncinata* (red circles), *O. venusta* (dark blue squares) and *O. villosa* (green triangles).



**Figure 63.** Distribution of *Okanagana arboraria* (blue squares), *O. hirsuta* (orange triangles), *O. wymorei* (red circles), *O. catalina* (purple stars) and *O. nigriviridis* (green diamonds).





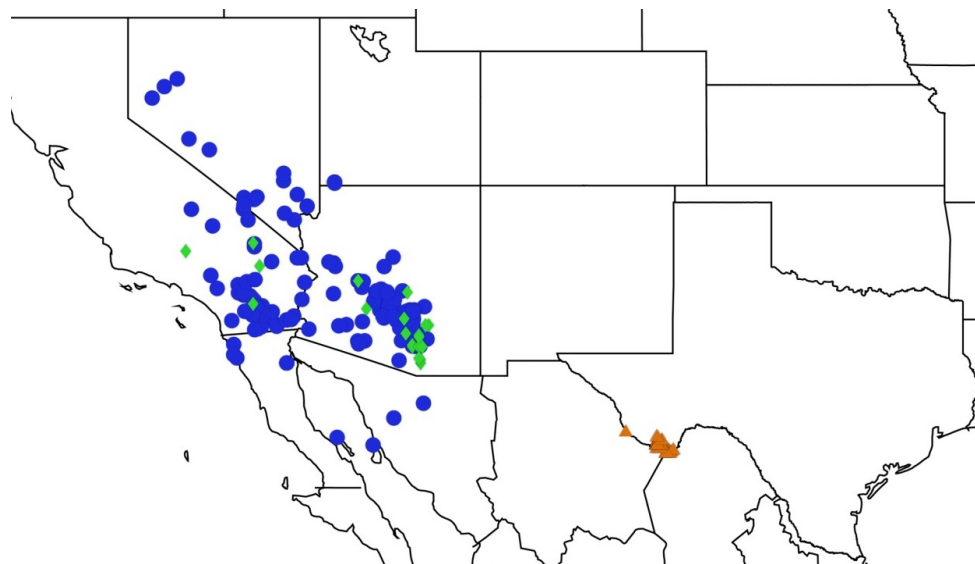
### 2.15. Biogeography of the *Okanagodes* Species

The genus *Okanagodes* is named for its relationship to *Okanagana* [92] but is most similar to *Tibicinoides* or *Clidophleps* in certain structural characteristics [26]. Although primarily distributed in North America, north of Mexico, one species of the genus have also been reported from Mexico [6,8].

Two species of *Okanagodes* are known, one of which has two subspecies. All species are associated with *Atriplex* spp. [52] on which they are cryptically colored and difficult to see. *Okanagodes gracilis gracilis* and *O. gracilis viridis* are found in salt flats of the Sonoran, Mohave, Colorado, and Great Basin deserts [52,73,88] (Figure 64). The nominotypical subspecies extends over four states and Mexico with *O. gracilis viridis* being found primarily in the southeastern portion of the species distribution with a few specimens recorded from California. The subspecies may in fact be a local variation in color. Further analysis of songs and morphology should be performed to determine the status of the subspecies.

*Okanagodes terlingua* is currently only known from the Big Bend region of Texas [52,56] (Figure 64) but should be found in Mexico with continued collecting. It is also restricted to the salt flats but is found in the Chihuahuan Desert [52,56,73].

**Figure 64.** Distribution of *Okanagodes gracilis gracilis* (blue circles), *O. gracilis viridis* (green diamonds) and *O. terlingua* (orange triangles).



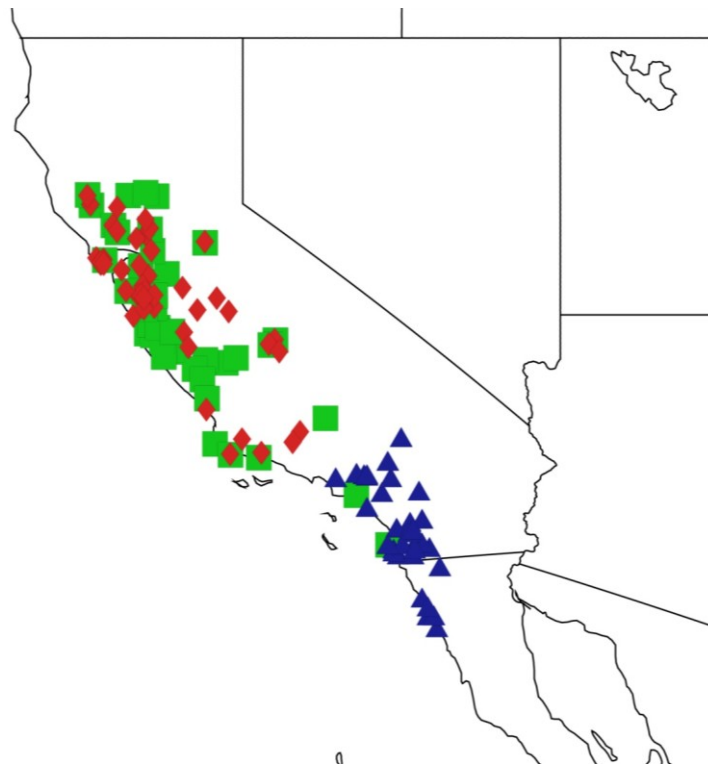
### 2.16. Biogeography of the *Tibicinoides* Species

The genus *Tibicinoides* is related to *Okanagana* and *Okanagodes* [26] and all three species are restricted to California. We collected *T. mercedita* in grasses and expect the other species to be associated with grass as well.

*Tibicinoides cupreosparsa* has the southernmost distribution extending into northern Mexico (Figure 65). *Tibicinoides mercedita* extends across the central two thirds of western California (Figure 65) in chaparral [74,75]. *Tibicinoides minuta* is generally more concentrated in central California (Figure 65). All three species are associated with the California upland forests and woodlands habitat [71] and their distributions coincide with this floristic region. All species have been

associated with grasses [44,70,175] with *T. minuta* associated with tarweed (probably *Holocarpha virgata* (A. Gray)D.D. Keck) [167] and *T. cupreosparsa* with tufted grasses (probably *Poa* spp.) [64].

**Figure 65.** Distribution of *Tibicinoides minuta* (green squares), *T. mercedita* (red diamonds) and *T. cupreosparsus* (blue triangles).



The North American cicada fauna show distributional patterns that are related to their phylogeny. The representatives of *Cacama*, *Diceroprocta*, *Cornuplura*, *Pacarina*, *Quesada* and *Neocicada* in North America, north of Mexico are the northernmost of their respective genera with greater diversity being found in Central and/or South America. Although the species of the genus *Beameria* are primarily found in North America, north of Mexico, they represent the northernmost extension of the tribe Fidicinini. The species of *Magacidada* are restricted to North America, north of Mexico and also represent the northernmost extension of the tribe Taphurini. The Tibicininae has its greatest diversity in the New World with a large number of species found in southern South America (the Tettigadini) along with the North American Platypediini and the Tibicinini with representatives from North America, Europe, North Africa and Asia. The genera of the Platypediini and the North American Tibicinini are primarily distributed in North America, north of Mexico with the distribution of only a few species extending southward into Mexico. Both the genera *Cicadetta* and *Tibicen* have expansive distributions in the Palearctic and Oriental regions with *Tibicen* extending southward into the Neotropical region. The relatively low diversity of *Cicadetta* species and their distribution on the eastern portion of North America suggests immigration from the Palearctic region where there is greater diversity. The distribution of the three species groups within *Tibicen* illustrate a geographical separation between the eastern and western species groups. The large *Tibicen* species are sympatric with many of the eastern and western species. Further analyses should be performed to determine if these species groups represent distinct genera.

California (89 species, 46.6% of taxa) is the state with the greatest alpha diversity. Texas (57 species, 29.8% of taxa), Arizona (49 species, 25.7% of taxa), Colorado (36 species, 18.8% of taxa), and Utah (35 species, 18.3% of taxa) complete the top five states in biodiversity. Maine (4 species, 2.1% of taxa), New Hampshire (4 species, 2.1% of taxa), and Rhode Island (5 species, 2.6% of taxa) exhibit the lowest alpha diversity containing only species that extend over much of the eastern or northern part of North America. Although there is a size effect to biodiversity [182], there is a good relationship between the diversity of habitats within these states and the observed diversity. Mountain terrain within these states also may increase the diversity as has been suggested for other regions of the world [8,13,183]. The variety of plant communities provides the opportunity to support a greater variety of cicadas if the insects specialize on particular types of plants as hosts.

Texas, Arizona, Colorado and Utah also illustrate how phylogeny can influence regional diversity. These states have representatives of genera that are unique to the Nearctic but also representatives of genera that have examples in the Neotropical and Palaearctic regions. California is an area noted for the high concentration of species from the genera *Platypedia*, *Okanagana*, and *Clidophleps* and is the only state in which the species of *Tibicinoides* is found. Only four California species are from genera that are found primarily in Mexico [26] and appear to have colonized southern California from the east or southeast.

California (35 species, 18.3% of taxa) is also the state with the greatest number of species found only in a single state. It is followed by Texas (15 species, 7.9% of taxa), Arizona (10 species, 5.2% of taxa), Utah (3 species, 1.6% of taxa) and Florida, Ohio, Oregon and Washington (1 species each, 0.5% of taxa each) for states with unique diversity. The same factors influencing alpha diversity are probably responsible for the single states in which particular species are found. Limited collecting and access to Canadian collections makes analysis of Canadian provinces difficult, so the summary comments are restricted to the lower 48 United States.

The known distribution of several species is limited due to the accessibility to collection sites. For example, 19 species from four genera have been recorded as collected at Cajon Pass in San Bernardino County, California and 14 species from four genera were collected at Buckman Springs, San Diego County, California. Both of these sites are found where major roadways cross mountain ranges and represent the only location in the geographic area where collecting is possible without hiking into areas without roadways. We can expect further range extensions with continued collecting.

Several regions need additional collection efforts. There are gaps in the distribution of species through central Nevada and within certain portions of the Rocky Mountains. The distance between the most northern examples of some species in Canada (e.g., *Platypedia areolata* (Figure 37)) and *Okanagana luteobasalis* (Figure 56) and the remaining distribution of the species suggests there are large areas of Canada that also need to be surveyed in more detail.

A review of the distributions of subspecies suggests that the status of the subspecies be re-evaluated. The current subspecies of cicadas were produced with the publication of the last edition of the *Code* [58] when varieties were converted to subspecies following Article 45.6.4. Although some subspecies appear to have geographic separation (e.g., the subspecies of *Tibicen lyricen* (Figure 11) and *Tibicen pronotalis* (Figure 21)), others are restricted to individual locations (e.g., *Okanagana mariposa oregonensis* (Figure 50)) or are surrounded by the nominotypical subspecies (e.g., *Okanagana tristis rubrobasalis* (Figure 51) or *Diceroprocta swalei castanea* (Figure 4)). We

have shown [27,29,30] that several taxa originally described as varieties are actually species. The distributions of the remaining subspecies illustrated here will hopefully stimulate further study to determine the status.

### 3. Experimental Section

Location data were collected from the cicada specimens housed in more than 110 institutional and private collections (see list in acknowledgements). These data were combined with data from our own field studies between 1985 and 2004 and specimens sent to AFS for determination. Label data were placed in spreadsheets and missing information, *i.e.*, counties or coordinates, was collected from maps and websites, particularly the USGS Geographic Names Information System [184] and Heavens-Above GmbH [185]. The distribution maps were produced with iMAP version 3.5 (Bioevolution, Leuven, Belgium). A limited number of specimens from Mexico are plotted on some of the figures even though the scope of the paper is north of Mexico to give a more complete illustration of the distribution of the species since the maps used often included the northern Mexican states. Specimens collected during agricultural inspections (e.g., a specimen of *Neocicada hieroglyphica* collected at an agricultural inspection site in California) were not included in the distribution map because the source of the specimen could not be verified and these specimens were transported to the state in question with agricultural products.

Species are grouped on maps to illustrate one of several potential concepts without making the map unclear or confusing with respect to the distributions of the species illustrated. Subspecies are placed on the same map in order to illustrate the comparative distribution of each subspecies. Species that form a complex of related taxa are also mapped on a single map when possible. The remaining species are grouped together based on the ability to demonstrate the distributions of the collected species without interference with one another.

### 4. Conclusions

We have shown that cicadas show an affinity for specific plant communities and are limited in their distribution by the plants within these communities. Most species have extensive ranges but the known range of some species is limited (e.g., *Okanagana georgi* and *O. rhadine*) either due to habitat isolation (e.g., *O. georgi*) or to limited collecting effort (e.g., *O. rhadine*). Some species with limited distributions north of Mexico (e.g., *Cornuplura nigroalbata* or *Diceroprocta lata*) have more extensive ranges into Mexico. The first look provided here for the distributions of subspecies suggests that several subspecies may simply be local color variations. Further collecting efforts in areas that have traditionally had limited access should fill in the distribution pattern for some western species. We hopefully have provided a useful tool for future researchers in locating the cicadas of North America, north of Mexico.

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