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Forum

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Whence and Whither the *Convolvulus* Psyllid? An Invasive Plant Leads to Diet and Range Expansion by a Native Insect Herbivore

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Abstract

Arrival and spread of nonnative plant species can lead to changes in structure and function of the native insect fauna that include shifts in host use by native insect herbivores. Well-documented examples showing that these host shifts also lead to range expansion of native herbivores are, however, surprisingly rare. Evidence for range expansion requires an understanding of the insect's distribution preceding arrival of exotic species. These data often are lacking. The North American psyllid *Bactericera maculipennis* (Crawford) (Hemiptera: Triozidae), a specialist herbivore on plants in the Convolvulaceae, has been hypothesized to have expanded its geographic range after colonizing the exotic field bindweed (*Convolvulus arvensis* L.; Convolvulaceae). Efforts to test this idea run into the same retrospective problems typical of these analyses, in that the psyllid's host plant and its geographic distribution preceding arrival of *C. arvensis* are uncertain. We used the psyllid's current association with *C. arvensis* to help identify its natal (pre-bindweed) host, reasoning that a host shift by this specialist herbivore would be more likely if natal and exotic species are closely related. Phylogenetic analyses of plants, rearing trials, and field records led us to target species of *Calystegia* R. Brown (hedge and false bindweeds; Convolvulaceae) as natal hosts of *B. maculipennis*. The current presence of *B. maculipennis* in regions lacking *Calystegia* but where *C. arvensis* is common supported the hypothesis that arrival of the exotic weed *C. arvensis* has indeed led to range expansion by this host-specialized psyllid.

Key words: field bindweed, *Calystegia*, morning glory, Psylloidea, phylogenetic tree

The North American psyllid *Bactericera maculipennis* (Crawford) (Hemiptera: Triozidae) was described in 1910 as *Trioza maculipennis* Crawford from adult specimens collected in San Mateo County, California (Fig. 1). The species was placed in *Bactericera* by Burckhardt and Lauterer (1997) in revising the genus. Horton et al. (2017) summarized the geographic distribution of *B. maculipennis* and reviewed its limited host records. *Bactericera maculipennis* is known from six states west of the Great Plains, with three of the states added to its range since 2015 (Horton et al. 2017).

Developmental hosts of *B. maculipennis* remained unknown until adults and immatures were collected in 1948 from plants identified as '*Convolvulus* sp.' (Palo Alto, Santa Clara County, CA) (Jensen 1957). Taxonomic reviews of the North American Psylloidea by Hodkinson (1988) and Percy et al. (2012) list *Convolvulus* sp. as the psyllid's host plant. Most of our new state and county records were obtained while sampling an introduced and invasive weed species, field bindweed (*Convolvulus arvensis* L; Convolvulaceae). It is unclear from historical records whether listing of '*Convolvulus* sp.' as the psyllid's host indicates the exotic *C. arvensis* or some other species. Our samples have shown widespread association of *B. maculipennis* with *C. arvensis*, and rearing trials have confirmed that the psyllid readily develops on this species (Horton et al. 2017). These observations

Fig. 1. Adults and immatures of *Bactericera maculipennis.* Lower panels: eggs showing characteristic pedicel; and, fifth instar nymph. Photo credits in Supp. Table S2.

have prompted us to hypothesize that colonization of *C. arvensis* has resulted in range expansion of *B. maculipennis* associated with spread of the invasive weed (Horton et al. 2017).

Knowledge of a native herbivore's natal (original) hosts can be used to make inferences about its geographic range before the arrival of an adventive plant species. Our objectives are twofold: to formally propose that introduction of field bindweed into North America allowed *B. maculpennis* to spread beyond its pre-bindweed distribution; and, to identify what plant taxa hosted *B. maculipennis* preceding arrival of field bindweed in western North America during the 1800s. Because historical records do not identify the pre-bindweed host of *B. maculipennis*, we used its current association with *C. arvensis* to help identify the natal host, reasoning that its pre-bindweed hosts are likely to be close relatives of field bindweed. Phylogenetic similarity of exotic and native plant species often is a prerequisite for a host shift to an exotic species by a native insect herbivore (Branco et al. 2015, Grandez-Rios et al. 2015), especially if the herbivore has a narrow host range (Gossner et al. 2009). The Psylloidea are highly host-specific (Eastop 1979, Ouvrard et al. 2015), and this trait may often limit host shifts to colonization of plant species closely related to the original hosts (Percy 2003, Percy et al. 2004, Ouvrard et al. 2015). Our analyses enabled us to propose that the natal hosts of *B. maculipennis* are plants in a genus closely related to *Convolvulus*, namely *Calystegia* (hedge bindweeds), and that historical association with *Calystegia* led to a pre-bindweed concentration of *B. maculipennis* in California where *Calystegia* is especially diverse. Examination of historical and contemporary geographic records for the psyllid and its host plants indicate that colonization of the exotic weed *C. arvensis* within the psyllid's natal range was followed by spread into regions of North America that lack other Convolvulaceae, including the presumed natal host (*Calystegia*) of the psyllid.

Materials and Methods

Biogeography of Native Convolvulaceae, Field Bindweed, and *B. maculipennis*

Diversity and distribution of native Convolvulaceae in Mexico, the United States, and southwestern Canada were determined using web-based resources and published taxonomic reviews (Table 1). To examine the role of *C. arvensis* in the spread of *B. maculipennis*, we used online herbarium records dating from the 1800s to describe geographic distribution of field bindweed in western North America. Herbarium records were cross-categorized by state, county, province (Canada), and year that the specimen was collected, allowing us to infer the rate and extent of geographic spread of field bindweed following its introduction into North America. Historical and contemporary geographic records for *B. maculipennis* were obtained

Table 1. Sources of biogeographic data for *Bactericera maculipennis* and Convolvulaceae

Bactericera maculipennis

Horton et al. (2017): summary of historical records

Records not included in Horton et al. (2017):

OREGON: Lake County, Bullard Canyon, A. Jensen, ex *Calystegia occidentalis*, 21 July 2016 (eggs, nymphs, adults); Lakeview, A. Jensen, ex*Convolvulus arvensis*, 10 June 2016 (1♀). CALIFORNIA: Los Angeles County, C. Lee, ex *Calystegia macrostegia*, 3 May 2016 (one adult unsexed; https://bugguide.net/node/view/1218784/bgimage); Bonelli Regional Park, San Dimas, C. Mallory, ex *Convolvulus* sp., 9 Aug. 2017 (one adult unsexed; https://bugguide.net/node/view/1423647/bgimage); Orange County, Bommer Canyon, J. Bailey, ex *Calystegia macrostegia*, 12 July 2017 (eggs, nymphs, adults; https://bugguide.net/node/view/1402495/bgimage); Little Sycamore Trail, Laguna Coast Wilderness, J. Bailey, ex *Calystegia macrostegia*, 24 June 2017 (eggs; https://bugguide.net/node/view/1391053/bgimage). COLORADO: Boulder County, Louisville, no collector record, no plant record, 20 June 2017 (one adult unsexed; https://bugguide.net/node/view/1388806/bgimage); Fremont County, Canon City, D. Jarrett, no plant record, 23 June 2008 (one adult unsexed; https://bugguide.net/node/view/194273/bgimage). ALBERTA, CANADA: Bow Island, D. Johnson, yellow sticky card in potato field, Aug. 2015 (one adult unsexed); yellow sticky card in potato field, Aug. 2017 (one adult unsexed); Grassy Lake/Bow Island, L. Kawchuk, yellow sticky card in potato, Aug. 2017 (one adult unsexed).

CALIFORNIA county records (and year first detected) not included in Horton et al. (2017) from specimens housed in American Museum of Natural History: San Luis Obispo (1982), San Bernardino (1945), Solano (1932), San Diego (1972), Santa Cruz (1967), Tulare (1954), Ventura (1949), Yolo (1965).

Convolvulaceae[a]

Mexico: Felger et al. (2012), Carranza (2007, 2008), Villaseñor (2016)

Web-based sources (North America)

Biota of North America Program (http://www.bonap.org)

CalFlora (http://www.calflora.org/)

Plants Database (https://plants.usda.gov/java/)

On-line herbaria

Consortium of Pacific Northwest Herbaria (http://www.pnwherbaria.org)

Consortium of Intermountain Herbaria Collection (http://intermountainbiota.org)

Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/)

Consortium of Northern Great Plains Herbaria (http://ngpherbaria.org/portal/collections)

University of Texas Plant Resources Center (http://prc-symbiota.tacc.utexas.edu/)

KU Biodiversity Inst. Nat. Hist. Museum (http://botany.biodiversity.ku.edu/botany/collections/)

TAMU Vascular Plant Specimens List (http://botany.csdl.tamu.edu/FLORA/tamu/tamucnv.htm)

[a] Our overview ignores the plant-parasitic genus *Cuscuta* (the dodders). *Cuscuta* is often included within the Convolvulaceae, although its exact systematic position remains unclear (Stefanović et al. 2002, 2003). Efforts to rear *B. maculipennis* on *Cuscuta indecora* Choisy were unsuccessful, to the extent that we struggled even in inducing egglaying on this plant (D.R.H. unpublished data). We believe that this genus has no role as a developmental host for this psyllid.

from the literature, examination of on-line records, and our own collecting (Table 1). Records include several new geographic observations since the synthesis in Horton et al. (2017), including the first record from Canada (Table 1).

Assays of Native Convolvulaceae for Development of *B. maculipennis*

We discovered that efforts to identify the natal host of *B. maculipennis* were hampered by a scarcity of field records associating the psyllid with plant species other than the exotic *C. arvensis* (Horton et al. 2017). We therefore were forced to work backwards from observations of the psyllid's current association with *C. arvensis* to infer host use preceding arrival of *C. arvensis*. After examining published phylogenetic trees to identify taxa systematically near *C. arvensis* (Stefanović et al. 2002, 2003; Williams et al. 2014), we focused on three genera: *Convolvulus*, *Calystegia*, and *Ipomoea*. We assessed the psyllid's development on 37 species of Convolvulaceae across nine genera and five tribes (Table 2), emphasizing species in the targeted genera. We limited assays mostly to taxa geographically sympatric or near sympatric with *B. maculipennis*, thus using species native to the western and central continental United States and to six political states of northern Mexico (Baja California Norte, Chihuahua, Coahuila, Nuevo León, Sonora, Tamaulipas). Because of difficulties in obtaining native representatives of certain genera found in the southwestern United States, a few species native to South America or to U.S. regions outside of the psyllid's known geographic range were also assayed (Table 2).

Plants were grown from seed, as rooted clippings, or were purchased as seedlings (Table 2). Seeds were obtained from commercial vendors, were donated by germplasm repositories, or were harvested locally. To improve germination, seeds were nicked using a scalpel and soaked for 24–48 h in gibberellic acid (1,000 ppm in water). Treated seeds were planted in 10-cm pots containing 4 parts commercial potting soil (Miracle-Gro Moisture Control Potting Mix, Scotts Company, Marysville, OH), 1 part perlite (Miracle-Gro Perlite, Scotts Company), and 1 part clean sand. Seedlings were grown in a greenhouse under ambient light supplemented with grow

Table 2. Species of plants used in assays, growth habit (perennial or annual), nativity, and sources of seeds or potted seedlings

Species (Tribe)	Annual Perennial	Native to North America?[a]	Seed and plant sources
Convolvuleae			
Calystegia macrostegia (Greene) Brummitt	P	Yes	Theodore Payne Foundation, Sun Valley, CA
Calystegia occidentalis (A. Gray) Brummitt	P	Yes	J.L. Hudson, Seedsman, La Honda, CA
Calystegia silvatica (Kit.) Griseb.	P	No? (Med.)[b]	Tillamook County, OR (rooted cuttings from field)
Convolvulus arvensis L.	P	No (Med.)	Prosser, WA (field-collected seed)
Convolvulus equitans Benth.	P	Yes	Western Region Plant Introduction Station, Pullman, WA
Convolvulus tricolor L.	A	No (Med.)	J.L. Hudson, Seedsman, La Honda, CA
Cresseae			
Cressa truxillensis Kunth	P	Yes	S&S Seeds, Carpinteria, CA
Evolvulus arizonicus A. Gray	P	Yes	Southwestern Native Seeds, Tucson, AZ
Evolvulus glomeratus Nees & Mart.	P	Yes	Select Seeds, Union, CT (potted seedling)
Dichondreae			
Dichondra sp.	P	Yes	Park Seed, Hodges, SC
Ipomoeaee			
Ipomoea alba L.	P	Yes	The Sample Seed Shop, Tonawanda, NY
Ipomoea batatas (L.) Lam.	P	No (S.A.)	Local grocery store (seedlings from fresh market tubers)
Ipomoea carnea Jacq.	P	No (S.A.)	Onalee's Seeds, Madeira Beach, FL
Ipomoea coccinea L.	A	Yes	Onalee's Seeds, Madeira Beach, FL
Ipomoea cordatotriloba Dennstedt	P	Yes	Georgia Vines, Claxton, GA
Ipomoea hederacea Jacq.	A	No (S.A.)	Onalee's Seeds, Madeira Beach, FL
Ipomoea hederifolia L.	A	Yes	Georgia Vines, Claxton, GA
Ipomoea imperati (Vahl) Griseb.	P	Yes	South Padre Island, TX (field-collected seed)
Ipomoea leptophylla Torr.	P	Yes	Georgia Vines, Claxton, GA
Ipomoea lindheimeri A. Gray	P	Yes	J.L. Hudson, Seedsman, La Honda, CA
Ipomoea muricata (L.) Jacq.	A	Yes	J.L. Hudson, Seedsman, La Honda, CA
Ipomoea nil (L.) Roth	A	Yes	The Sample Seed Shop, Tonawanda, NY
Ipomoea pandurata (L.) G. Mey.	P	Yes	Georgia Vines, Claxton, GA
Ipomoea parasitica (Kunth) G. Don	A	Yes	South Pines Seeds, Claxton, GA
Ipomoea pes-caprae (L.) R. Br.	P	Yes	The Sample Seed Shop, Tonawanda, NY
Ipomoea pubescens Lam.	P	Yes	J.L. Hudson, Seedsman, La Honda, CA
Ipomoea purpurea (L.) Roth	A	Yes	Park Seed, Hodges, SC
Ipomoea rupicola House	P	Yes	Weslaco, TX (field-collected seed)
Ipomoea sagittata Poiret	P	Yes	Weslaco, TX (field-collected seed)
Ipomoea ternifolia Cav.	A	Yes	Southwest Seeds, Dolores, CO
Ipomoea tricolor Cav.	A	No (S.A.)	J.L. Hudson, Seedsman, La Honda, CA
Ipomoea triloba L.	P	Yes	Taste.ecrater (https://taste.ecrater.com/)
Ipomoea violacea L.	P	Yes	The Sample Seed Shop, Tonawanda, NY
Ipomoea wrightii A. Gray[c]	A	Uncertain	J.L. Hudson, Seedsman, La Honda, CA
Turbina corymbosa (L.) Raf.	P	Yes	J.L. Hudson, Seedsman, La Honda, CA
Jacquemontieae			
Jacquemontia pentanthos (Jacq.) G. Don	A	Yes	The Sample Seed Shop, Tonawanda, NY
Merremieae			
Merremia tuberosa (L.) Rendle	P	Yes	Sheffield's Seed Company, Locke, NY

[a] Med., Mediterranean; S.A., South America.

[b] *Calystegia* is a taxonomically difficult genus often exhibiting confusing geographic variation in morphological traits within species (Brummitt 1963). The rooted cuttings collected from Tillamook County, OR and assayed in this study appear to be *Calystegia silvatica* (Kit.) Griseb. subsp. *disjuncta* Brummitt (Brummitt 1980, 2002). This species can be confused with another *Calystegia* that occurs in the Pacific Northwest, *Calystegia sepium* (L.) R.Br. subsp. *angulata* Brummitt (Brummitt 1980, 2002). The species are separated by leaf shape, size of flower corolla, and characteristics of the inflated bracteoles at the flower base (Brummitt 1963, 1980). However, these traits themselves may vary within species (Brummitt 1963, 1980). *Calystegia silvatica* and *C. sepium* hybridize in nature (Brummitt 1963, Brummitt and Chater 2000, Brown et al. 2009), which additionally complicates identifications. *Calystegia silvatica* subsp. *disjuncta* is thought to be of Mediterranean origin, although there have also been suggestions that it is native to North America (see discussion in Brummitt 2002).

[c] Uncertain taxonomy and nativity (see discussion by Felger et al. 2012)

Fig. 2. Examples of Convolvulaceae used in psyllid development assays: (A) *Convolvulus arvensis* (field bindweed); (B) *Ipomoea cordatotriloba*; (C) *Calystegia macrostegia*; (D) *Evolvulus glomeratus*; (E) *Jacquemontia pentanthos*; (F) *Ipomoea batatas* (sweet potato); (G) *Ipomoea ternifolia*; (H) *Ipomoea lindheimeri*. Photo credits in Supp. Table S2.

lights. No insecticides or fungicides were used in rearing plants. Plants were assayed once they had at least three fully expanded leaves. Egglaying *B. maculipennis* were collected from local *C. arvensis*. Psyllids were moved in mixed-sex groups of 10–20 insects to plants housed individually in ventilated plastic tubs (7.5 liters) and allowed to oviposit for 24–48 h, which was long enough generally to result in 20–60 eggs per plant. Egglayers were removed from plants following the 24–48 h oviposition period. Egg-laden plants and containers were moved to a controlled-environment room at 22°C and a 16:8 (L:D) h photoperiod. Lighting was provided by EnviroGro T5 light fixtures (Hydrofarm, Petaluma, CA).

We had 2–4 replicates for most plant taxa. It was not possible to screen all species simultaneously due to the large number of plants, irregularity in availability of seed, and difficulties in getting seed for some species to germinate. Thus, plants were assayed as they became available, generally in groups of 10–15 plants per round of screening. Each group of 10–15 plants was assayed with a control plant of *C. arvensis* to confirm that psyllids used as egglayers produced viable eggs and offspring. We follow Burckhardt et al. (2014) in defining a psyllid 'host plant' as a species that allows egg-to-adult development. We determined whether a plant species allowed egg-to-adult development (recorded as a yes/no variable); for species that supported development, we recorded the number of days from oviposition to eclosion of the first new adult (=minimum number of days required for a newly deposited egg to produce a new adult). We did not estimate survival rates beyond the 'yes/no' measure. Our objective was not to produce detailed life history statistics for *B. maculipennis* on each plant species, but rather to determine whether a full generation could be completed on a given plant species.

Plants were examined every 3 or 4 d for the first 2 wk after oviposition, and then daily until adult emergence. Once newly eclosed adults were observed on a plant, the assay for that plant was terminated. A leaf sample was taken from each assayed species to obtain DNA sequences for later phylogenetic analysis (see following section). One representative of each plant species also was returned to the greenhouse following assay to allow the plant to grow and flower to confirm plant identifications. Stem, leaf, and flowers from assayed species were pressed and are housed with D.R.H.

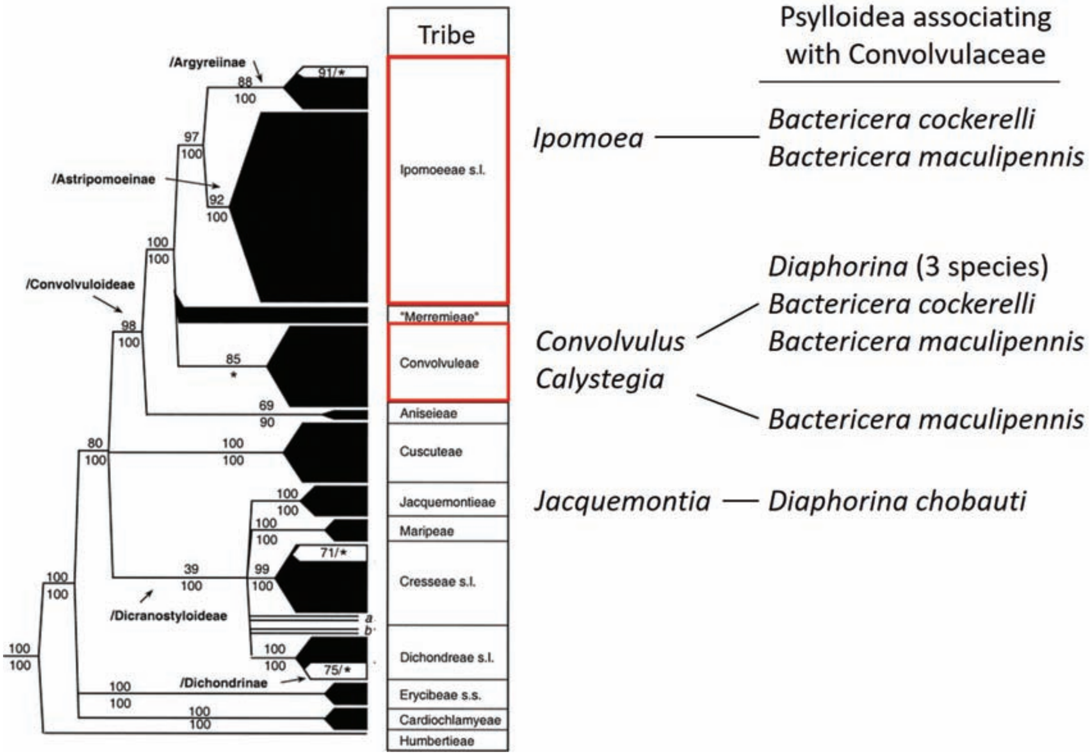

Fig. 3. Subfamily classification scheme for Convolvulaceae proposed by Stefanović et al. (2003) derived from DNA-sequence data. Figure modified and used here with permission of S. Stefanović. The bindweeds (Convolvuleae) and morning glories (Ipomoeeae) are shown in red boxes and group together in a single well-defined clade (Convolvuloideae). Plant species known to host psyllids currently are limited to species in four genera (of 56 genera worldwide) and three tribes. Psyllid species currently known to associate with Convolvulaceae are limited to two New World species of *Bactericera* and three Old World species of *Diaphorina* (from Ouvrard 2018).

Relationship Between Plant Phylogeny and Suitability to *B. maculipennis*

To examine our underlying assumption that species of Convolvulaceae closely related to *C. arvensis* are more likely to allow *B. maculipennis* development than less closely related species, we developed a phylogenetic tree for the 37 species used in our psyllid-rearing assays, and then overlaid results from the rearing assays on the tree. Development of a phylogenetic tree followed protocols of Kaur et al. (2018) whose tree included many of the same Convolvulaceae. Leaf samples from the screening assays were used to provide DNA sequences. DNA was extracted using the cetyltrimethylammonium bromide (CTAB) method of Zhang et al. (1998). Two universal plant barcoding primer sets were used. The first primer set targeted ~500 bp in internal transcribed spacer region (*ITS*) (Chen et al. 2010); the second primer set targeted ~684 bp region of the chloroplast maturase K gene (*matK*) (Yu et al. 2011). Extraction methods and polymerase chain reaction (PCR) conditions are summarized in Kaur et al. (2018). Bands from agarose gels were purified using GenElute minus EtBr spin columns (Sigma, St. Louis, MO) and cloned using a TOPO TA cloning kit with TOP10 *E.coli* chemical competent cells (Invitrogen, Carlsbad, CA). The QIAprep spin mini prep kit (Qiagen, Valencia, CA) was used to prepare plasmid DNA. Sequencing was done by MC laboratories (MC Lab, San Francisco, CA). DNA sequences were aligned and consensus sequences constructed using Geneious R10 software (North America Biomatters Inc, Newark, NJ). A phylogenetic tree was constructed with the combined sequences of *ITS* and *matK* regions using an underlying Tamura-Nei model and neighbor-joining method (Kearse et al. 2012). Sequences were deposited in GenBank (Supp. Table S1).

Results and Discussion

Convolvulaceae and Psylloidea: An Atypical Association

The Convolvulaceae comprise ~1,800 species in 56 genera, with more than one-third of the species in *Ipomoea* and *Convolvulus* (Stefanović et al. 2002). The family is found worldwide but has highest diversity in the tropics and subtropics (Staples and Brummitt 2007, Felger et al. 2012). Many species have a vining or twining habit, best shown by the bindweeds (*Convolvulus*, *Calystegia*), but the family includes everything from shrubby perennials to herbaceous annuals (Fig. 2). The Convolvulaceae include food crops (sweet potato; *Ipomoea batatas* L.), ornamentals (morning glories; *Ipomoea* spp.), medicinals (Staples and Brummitt 2007), and agricultural weeds (field bindweed; *C. arvensis*). The most thorough current family-level treatment resolves Convolvulaceae into 12 tribes, with the species-rich *Ipomoea* and *Convolvulus* in a single well-defined clade but in different tribes, Ipomoeeae and Convolvuleae (Fig. 3). The genus *Calystegia*, an important focus of the current synthesis, is placed in the Convolvuleae with *Convolvulus* and the only other member of this tribe, the Australian endemic *Polymeria*. The Convolvuleae is one of only two tribes (with the dodders; Cuscuteae) in this mostly

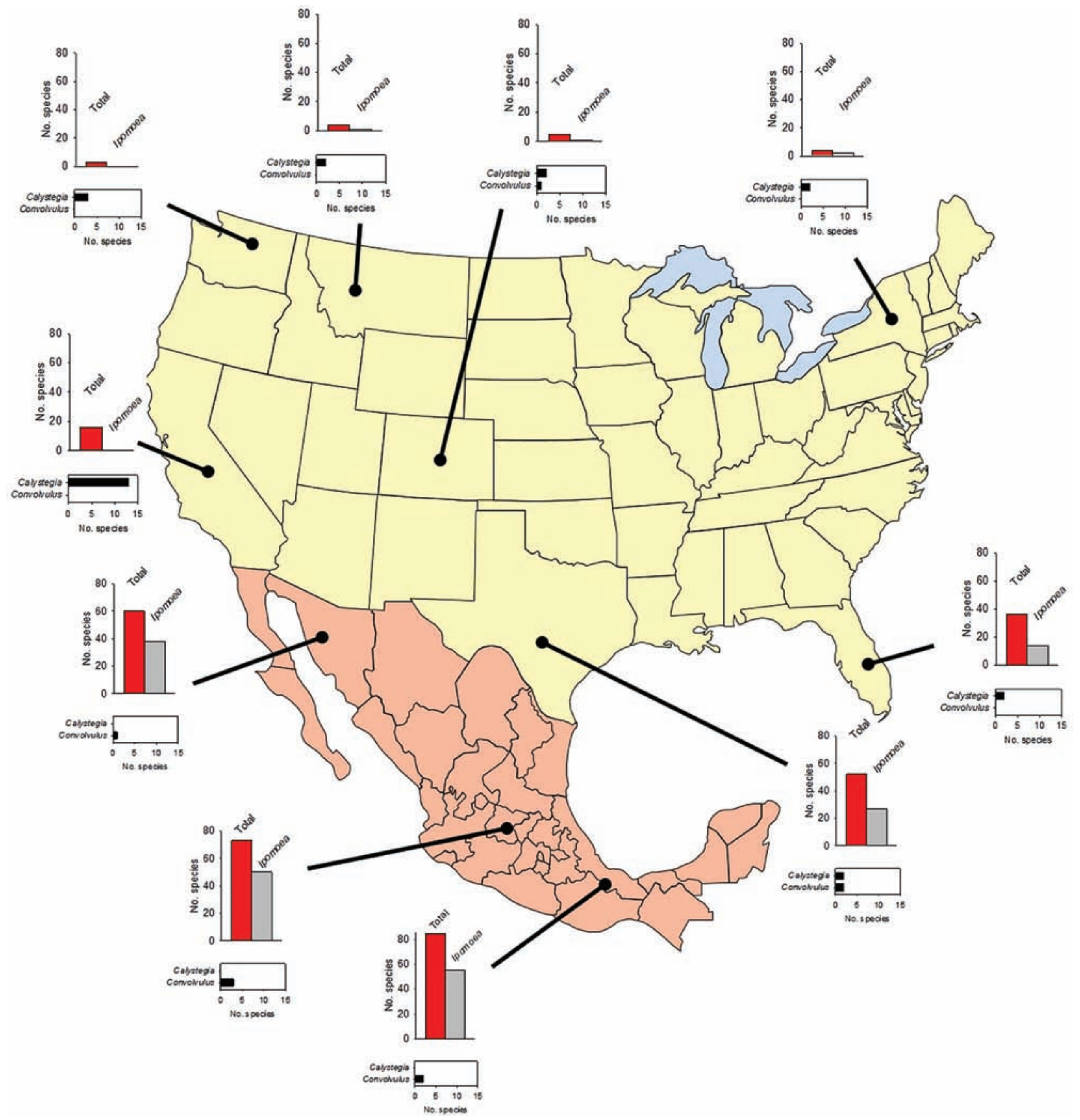

Fig. 4. Northern latitudinal decline in diversity of North American Convolvulaceae. Histograms indicate numbers of native species. Sources of biogeographic data are summarized in Table 1. The dodders (*Cuscuta*) excluded.

tropical and subtropical family to have widely colonized temperate regions (Mitchell et al. 2016).

Convolvulaceae are poorly represented as developmental hosts for Psylloidea, both in numbers of species associated with this plant family and in numbers of plant species that serve as hosts (Ouvrard 2018). Of the approximately 3,800 species of psyllids worldwide (Ouvrard et al. 2015), only five species are known to develop on Convolvulaceae (Fig. 3). Host records (from field observations or laboratory rearing) are limited to four genera (*Convolvulus*, *Calystegia*, *Ipomoea*, *Jacquemontia*) in three tribes (Fig. 3). Psyllid taxa that develop on convolvulaceous plants include three species of Old World *Diaphorina* (Liviidae) associated with Old World *Convolvulus* and an introduced New World *Jacquemontia* (Spodek et al. 2017, Ouvrard 2018), and two species of New World Triozidae, *Bactericera cockerelli* (Šulc) and *B. maculipennis* with records from *Convolvulus*, *Calystegia*, and *Ipomoea* (Martin 2008, Puketapu and Roskruge 2011, Horton et al. 2017). The apparent absence of psyllids from such a large percentage of genera within a single plant family is difficult to explain. The Solanaceae, a family considered sister

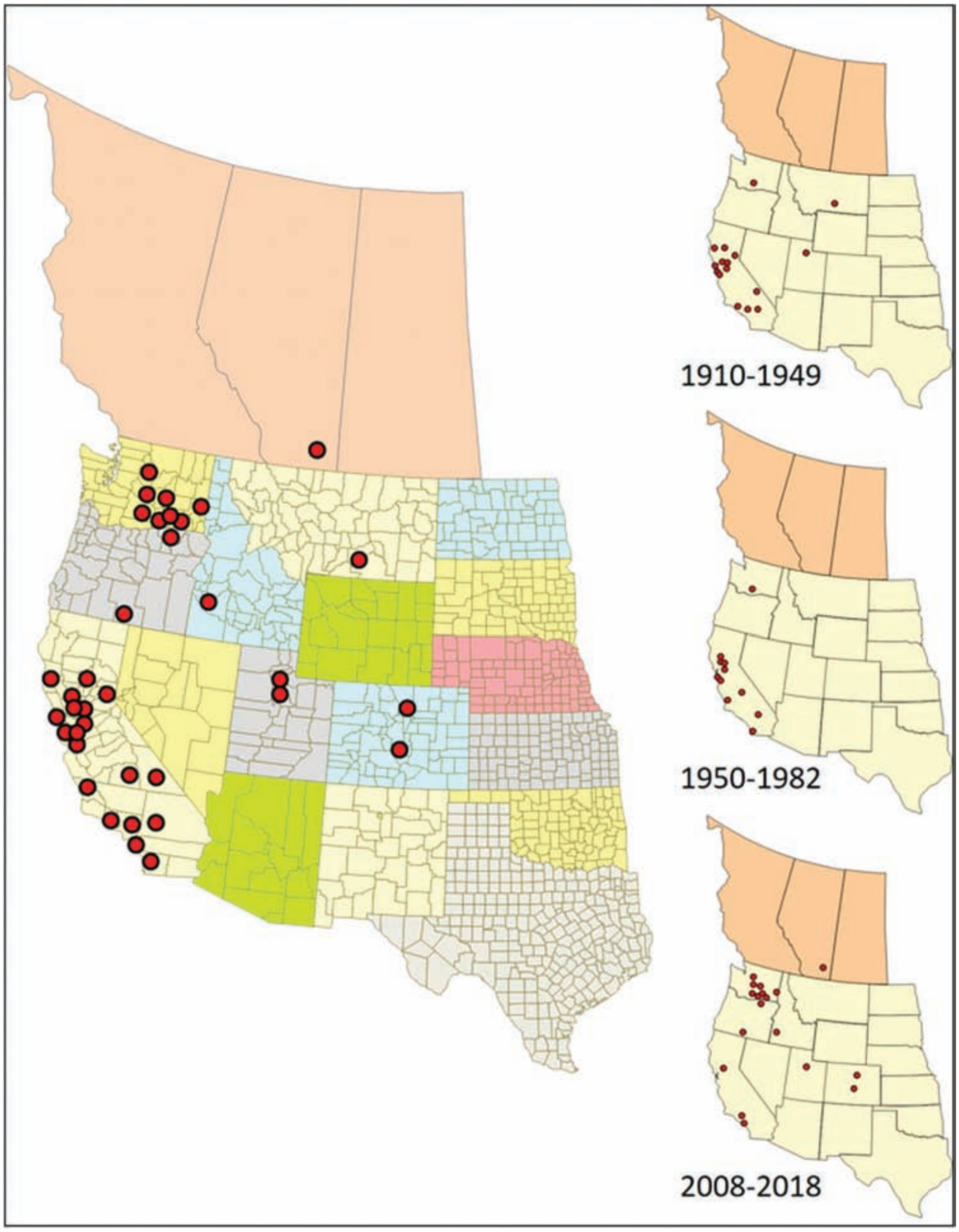

Fig. 5. County (United States) and province (Canada) records for *B. maculipennis*. Maps in column at right: red circles indicate U.S. counties (or Canadian province) in which the psyllid was collected during the specified year interval. Sources of records summarized in Table 1.

to the Convolvulaceae (Refulio-Rodriguez and Olmstead 2014), share plant chemistry with Convolvulaceae (Eich 2008) but are nevertheless widely attacked by Psylloidea. Psylloidea associated with Solanaceae include at least 31 species of psyllids in 10 genera, with Solanaceae records encompassing at least 14 plant genera and 50 species (Ouvrard 2018).

Biogeography of Convolvulaceae and *B. maculipennis*

Species diversity of Convolvulaceae in North America declines substantially between Central America/Mexico and the northern United States (Fig. 4). Our vertical histograms show total number of native species and number of species in the family's most species-rich genus *Ipomoea*. The northward distribution of the largely tropical and subtropical *Ipomoea* essentially ends in southern Arizona and New Mexico. *Ipomoea* is found eastward from its high-diversity region in coastal Texas through the Gulf Coast states and into Florida (Fig. 4). The horizontal histograms show diversity of *Convolvulus* and *Calystegia* (Fig. 4). Despite the high diversity of *Convolvulus* worldwide (~200 species; Wood et al. 2015), its presence in North America is limited (Wood et al. 2015, Mitchell et al. 2016). The relatively high diversity of Convolvulaceae in California is due to large numbers of endemic species of *Calystegia* (Fig. 4).

The latitudinal decline in diversity of Convolvulaceae in the northwestern United States broadly overlaps the geographic range of *B. maculipennis*, indicating that the psyllid encounters a much lower diversity of potential hosts in its known range than if it

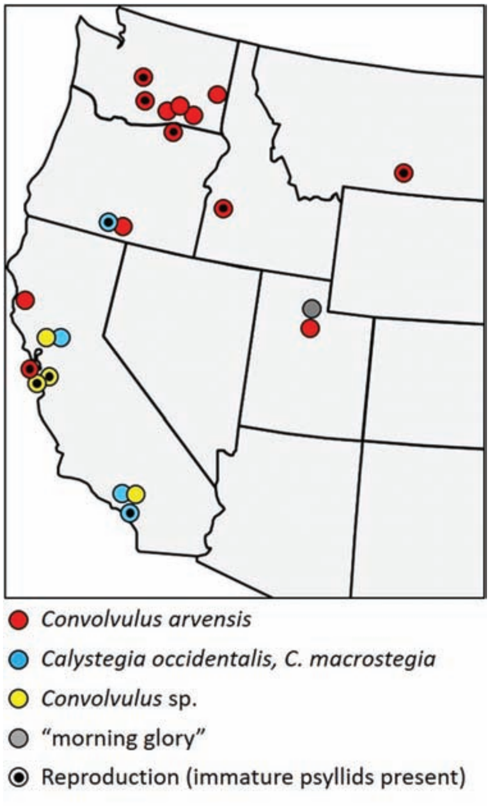

Fig. 6. Plant sources (Convolvulaceae) of *B. maculipennis* records. Red symbols: *Convolvulus arvensis*; blue symbols: *Calystegia* spp.; yellow or gray symbols: uncertain taxonomy. Symbols having black centers indicate immature psyllids were present.

occupied regions to the south. *Bactericera maculipennis* has been recorded from seven states and one Canadian province (Fig. 5), with all records west of the Rocky Mountains except the four from Colorado, Montana, and Alberta. Initial records summarized by county extend from the early 1900s to the present (2018), with a gap of 26 yr (1982–2018) in which no new counties were added (Fig. 5). The largest concentrations of records are from California (19 counties) and Washington (eight counties). Concentrations of records probably reflect the psyllid's widespread presence and intensity of collecting effort. Nearly all pre-1950s records pertain to the adult psyllid and provide few clues to host plant. Records that list Convolvulaceae are limited to two genera, *Convolvulus* and *Calystegia* (Fig. 6). In addition, adult psyllids were collected in Utah (in 1943) from a plant listed as 'morning glory' (Jensen and Knowlton 1951). This common name generally is applied to species of *Ipomoea*, but sometimes refers to field bindweed (Austin 2000). Some records from *C. arvensis* and *Calystegia* spp. indicate that nymphs or eggs of *B. maculipennis* were present (Fig. 6), verifying that these plants are developmental field hosts. Observations also suggest that *B. maculipennis* may overwinter on stems of *C. arvensis* beneath mats of dead leaf and stem material (Pletsch 1947, Jensen 1957, Horton et al. 2017); thus, this exotic plant may provide resources for year-round residence of *B. maculipennis* in the northern parts of its range.

A Search for the Natal Host of *B. maculipennis*

Evidence supporting the hypothesis that *Calystegia* species are the natal hosts of *B. maculipennis* includes biogeographic data for native Convolvulaceae, field host records, and psyllid-rearing assays. Native species within or near the known geographic range of *B. maculipennis* are found in 12 genera (Fig. 7). The only genus present in all states is *Calystegia*, with greatest diversity in California (Fig. 7). Native *Convolvulus* includes only *Convolvulus equitans* and the uncommon Texas endemic *Convolvulus carrii* B.L. Turner (Turner 2009). Presence of native *Ipomoea* in the western United States largely ends in southern Arizona and New Mexico despite extensive diversity in northern Mexico and southward (Fig. 4). The absence of native *Ipomoea* from California may be due in part to extreme aridity of the desert regions that separate southern California from high-diversity regions of southern Arizona and Sonora, Mexico (Austin 2006). Other taxa native within the psyllid's range include *Cressa*, *Dichondra*, and *Evolvulus* (Fig. 7).

Pre-1950s records for *B. maculipennis* are concentrated in California (Fig. 5) and suggest that *B. maculipennis* had a widespread presence in California by the early 1900s. Almost none of the old records provide meaningful host plant data. The only definitive early record for *Calystegia* is Crawford's (1914) report of adults of *B. maculipennis* associated with *Calystegia occidentalis* (as *Convolvulus occidentalis*) in Sacramento County, California. More recent observations of *B. maculipennis* and *Calystegia* include records of eggs, nymphs, and adults of *B. maculipennis* on *C. occidentalis* in southern Oregon and on *C. macrostegia* in southern California (Fig. 6).

The evolutionary histories of *Calystegia* and *Convolvulus* are entangled to the extent that debate has centered on whether the hedge bindweeds merit their own genus or instead should be included in *Convolvulus* with the other bindweeds (Brummitt 1963, Lewis and Oliver 1965, Brown et al. 2009, Williams et al. 2014, Wood et al. 2015). Almost 200 species of *Convolvulus* are recognized, with highest diversity in the Mediterranean region (Wood et al. 2015). *Convolvulus* is poorly represented in North America where it is replaced by *Calystegia*, also apparently of Mediterranean origin (Wood et al. 2015, Mitchell et al. 2016). *Calystegia* colonized western North America about 6 mya and experienced explosive speciation (Mitchell et al. 2016) that led to extraordinary diversity in California (Figs. 8 and 9). Of the approximately 26 species of *Calystegia* worldwide (Staples and Brummitt 2007), at least 12 are native to California, including several endemic to the state (http://www.calflora.org/).

Bactericera maculipennis was assayed on 37 species of Convolvulaceae to look for clues about host plant breadth and to obtain evidence of its developmental success on *Calystegia* (Fig. 10). Results of assays overlain on a phylogenetic tree enabled us to identify plant taxa that both allowed development and are phylogenetically near *C. arvensis* (Fig. 10). Our tree is consistent with similar treatments in the literature (Stefanović et al. 2002, 2003) in grouping *Convolvulus* and *Calystegia* (Convolvuleae) separately from *Ipomoea* (Ipomoeeae) and other tribe-level taxa (Cresseae, Dichondreae, Jacquemontieae). *Bactericera maculipennis* developed on all six Convolvuleae that were assayed (Fig. 10), which supports the hypothesis that close relatives of *C. arvensis* are likely to support development of this specialist psyllid.

Bactericera maculipennis unexpectedly also developed on *Jacquemontia* (cluster vine), which through molecular analysis is positioned in its own tribe distinct from Convolvuleae (Stefanović et al. 2002, 2003). In contrast, morphological treatments have placed *Jacquemontia* in the Convolvuleae with *Convolvulus* and *Calystegia* (Austin 1998; Stefanović et al. 2002, 2003). Results of the molecular analysis that removed this genus from Convolvuleae have been termed

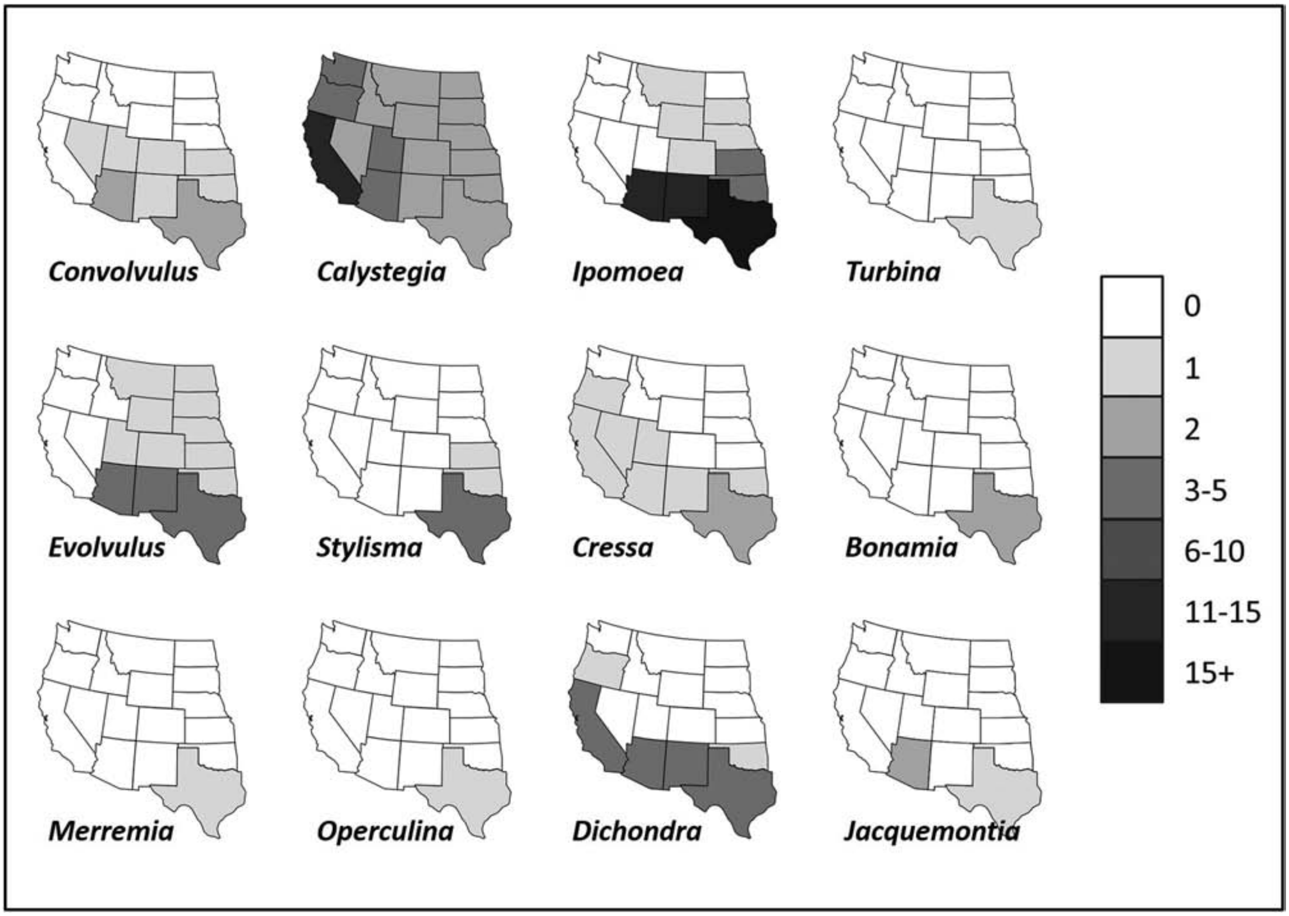

Fig. 7. Number of native species of Convolvulaceae for each of 12 genera summarized by state. Shading indicates numbers of species. Due to uncertainties about the eastern and southern geographic limits for *B. maculipennis*, the biogeographic summary extends to states neighboring the psyllid's most eastern and southern records. Sources of data are listed in Table 1.

'perplexing' (Stefanović et al. 2002). Our psyllid rearing data are more in line with the systematic placement of *Jacquemontia* defined by plant morphology than by DNA sequences. *Jacquemontia* has been recorded to be a field host of another psyllid, *Diaphorina chobauti* Puton; other records for this psyllid include *Convolvulus* (Zendedel et al. 2016, Spodek et al. 2017, Ouvrard 2018; see also Fig. 3).

Bactericera maculipennis failed to develop on any taxa outside of Convolvuleae and Ipomoeeae (except *Jacquemontia*), including *Merremia* (wood rose; Merremieae), *Evolvulus* (dwarf morning glory; Cresseae), *Dichondra* (ponysfoot; Dichondreae), and *Cressa* (alkaliweed; Cresseae). Depending on the correct systematic placement of *Jacquemontia*, assays failed to produce evidence that hosts might extend outside of Convolvuleae and Ipomoeeae, although diversity of species assayed was not extensive outside of *Ipomoea*. The species-rich *Ipomoea* included both host and non-host species (Fig. 10). On taxa allowing egg-to-adult survival, development rates were rapid (20–27 d) on *C. arvensis*, the other two *Convolvulus* species, and two of the *Calystegia* species (Fig. 11). Development was equally rapid on a few species outside of the Convolvuleae, including *Jacquemontia pentanthos* and the ornamental *Ipomoea alba* (moonvine). Developmental rates on other *Ipomoea* species often exceeded 30 d (Fig. 11).

Results of psyllid-rearing assays, phylogenetic analysis, biogeographic analyses, and field observations are consistent with the hypothesis that *Calystegia* is a viable choice as a natal host of *B. maculipennis*. Other taxa supporting rapid development of the psyllid, such as the native *C. equitans* or species of *Ipomoea* and *Jacquemontia*, might merit consideration, although they appear not to have extensive presence in western North America north of Mexico. *Convolvulus equitans* is found in Mexico, Texas, Arizona, and New Mexico (Turner 2009). There is no evidence that the species extends into California (Preston and Dempster 2012, http://ucjeps.berkeley.edu/consortium/, http://www.calflora.org/). *Jacquemontia* and *Ipomoea* are mostly tropical and subtropical. *Jacquemontia* is diverse in the Neotropics (Buril 2013), but is limited to the Gulf States, Texas, and southern Arizona in North America. The species we assayed (*J. pentanthos*) proved to be an excellent host for *B. maculipennis*, but its U.S. range is limited to Florida. *Ipomoea* extends farther north in the United States than many other genera (Fig. 7), but the species most widespread in the north (*Ipomoea leptophylla*) is not a host of *B. maculipennis* (Fig. 10). Additionally, no field records document presence of *B. maculipennis* on *Ipomoea*. We cannot exclude *Ipomoea* and *C. equitans* from consideration as natal sources of the psyllid, but our study indicates that species of *Calystegia* are the likely natal (pre-bindweed) hosts.

Field Bindweed as a Source of Geographic Spread by *B. maculipennis*

Field bindweed is of Mediterranean origin (Wood et al. 2015, Mitchell et al. 2016). Herbarium records show that the species has been in the eastern United States since the early 1700s and in the western United

Fig. 8. County presence of native *Calystegia* in California (from CalFlora; http://www.calflora.org/).

States since the early 1800s (Austin 2000). Field bindweed is found in every U.S. state and in several provinces in southern Canada (Austin 2000). Our grouping of *C. arvensis* records by 20-yr time intervals provides a historical snapshot of the plant's spread through the western United States (Fig. 12). Records of *B. maculipennis* were overlain on the maps to portray its range expansion from the early 1900s to 2018, and show that counties from which the psyllid were collected invariably occur within the expanding geographic range of field bindweed (Fig. 12). Canadian records for *B. maculipennis* comprise three specimens collected in 2015 and 2017 from sticky cards in potato fields near Bow Island, Alberta (east of Lethbridge). Herbarium records show that *C. arvensis* was present in this region by the 1950s.

Other evidence that field bindweed facilitated range expansion by *B. maculipennis* is the psyllid's presence in areas lacking other Convolvulaceae, shown for example by its widespread presence in Washington State. *Bactericera maculipennis* is regularly collected in counties lacking herbarium-based evidence for Convolvulaceae other than field bindweed. Figure 13 shows herbarium records for *Calystegia* spp. (the only native Convolvulaceae in Washington State) and field bindweed, with records for the two taxa obtained from the same herbaria. *Calystegia* records are concentrated on the coastal side of the Cascade Mountains (Fig. 13) or in riparian areas and higher elevation regions of inland sites. The maps show that *B. maculipennis* has been collected in counties having no herbarium records for *Calystegia* (Fig. 13). The absence of records is not due to a lack of collecting in those counties because field bindweed is well represented in records from the same herbaria used in searching for *Calystegia* (Fig. 13). Records of the psyllid from inland Washington are from lowland agricultural regions, where the weedy *C. arvensis* is widespread as an agricultural pest and *Calystegia* is absent.

Dietary Expansion Leading to Range Expansion of a Nearctic Psyllid

Our efforts to understand the role of field bindweed in distribution of *B. maculipennis* actually arose from ongoing efforts to understand geographic distribution of a related triozid, *B. cockerelli*. This species is a pest of potatoes in western North America, Mexico, and Central America, but the factors leading to its establishment and residence in the potato-growing regions of Washington, Idaho, and Oregon are unclear (Horton et al. 2015a,b). Field bindweed has been shown to allow development of *B. cockerelli* and may additionally act as a wintering reservoir of the psyllid (Pletsch 1947, Wallis 1955, Horton et al. 2017, Kaur et al. 2018), and it is possible that this weedy exotic has contributed to the pest's current geographic range. Our monitoring of field bindweed for presence of *B. cockerelli* led to the discovery of widespread association between field bindweed and the non-pest psyllid *B. maculipennis* (Horton et al. 2017), prompting the synthesis presented here.

Fig. 9. *Calystegia* species. (A) Hillside near Santa Monica, CA covered with flowering *Calystegia macrostegia*; (B) the coastal species *Calystegia soldanella*; (C) *Calystegia macrostegia* growing along chain-link fence; (D) *Calystegia* sp., western Oregon, showing characteristic aggressive growth and climbing ability; (E) *Calystegia occidentalis*, Lake County, Oregon (this stand infested with all stages of *B. maculipennis*); (F) *Calystegia silvatica* being grown as an ornamental, Yakima County, WA. Photo credits in Supp. Table S2.

The introduction of invasive plant species into regions previously free of those species can affect the evolutionary ecology of herbivorous insects by prompting changes in diet, shifts in life histories, and expansion of geographic range (Tabashnik 1983, Strauss et al. 2006, Branco et al. 2015, Schilthuizen et al. 2016). In our recent treatment of *B. maculipennis*, we updated collecting records to include four states (Washington, Idaho, Oregon, Montana) where the psyllid was not previously known to occur, and hypothesized that introduction of field bindweed into the western United States in the 1800s allowed the psyllid to expand its geographic range into these regions (Horton et al. 2017). *Convolvulus arvensis* is one of the world's 10 worst weeds due to its rapid spread and invasiveness (Holm et al. 1977). Field bindweed has more than 80 common names in 29 languages, evidence of its importance worldwide, including common names such as small-flowered morning glory, European bindweed, creeping Jenny, European twiner, common tangler, bearbind, and others (Austin 2000). *Convolvulus arvensis* is found in every U.S. state, which is evidence of its ability to flourish in multiple habitats under highly diverse climatic conditions.

Did the arrival of field bindweed in North America trigger range expansion by the native *B. maculipennis*? Despite extensive movement by exotic plants into regions outside of their native ranges, well-documented examples showing that introductions produce range expansion by native insect herbivores are rare. The largest difficulty is that proof of range expansion necessarily requires a retrospective look at how the target insect was distributed before arrival of the exotic plant. Those sort of historical records are often not available. Butterflies may provide the best examples of how exotic plants can lead to geographic range expansion of native insect herbivores (Shapiro 2002, Graves and Shapiro 2003). Their larger size and visibility, coupled with their attractiveness to both amateur and professional entomologists, have led to geographic records and host lists for butterflies often not available for other taxa (Graves and Shapiro 2003). The synthesis of Graves and Shapiro (2003) showed that presence of exotic plant species in California has led to dietary expansion by more than 80 species of native butterflies, accompanied by geographic range expansion by at least nine of the species.

Our claims that arrival of field bindweed in North America has led to geographic spread of *B. maculipennis* suffer from the same retrospective difficulties typical of this type of synthesis. Information that would assist in understanding the role of field bindweed in the current distribution of *B. maculipennis* would be identification of the natal host of the psyllid, as that knowledge would allow us to better define the insect's pre-bindweed distribution. We suggested that *Calystegia* is a candidate for designation as natal host, arriving at this conclusion in a somewhat indirect manner by arguing that dietary expansion to include an exotic host would be more likely if exotic and natal hosts were closely related rather than only distantly related (Gossner et al. 2009, Branco et al. 2015, Grandez-Rios et al. 2015). While this idea has been used to predict whether an exotic plant might be susceptible to colonization by native herbivores, we used it to proceed in the opposite direction: i.e., in using contemporary observations of association with an exotic host to identify candidate natal hosts. Phylogenetic data were used to

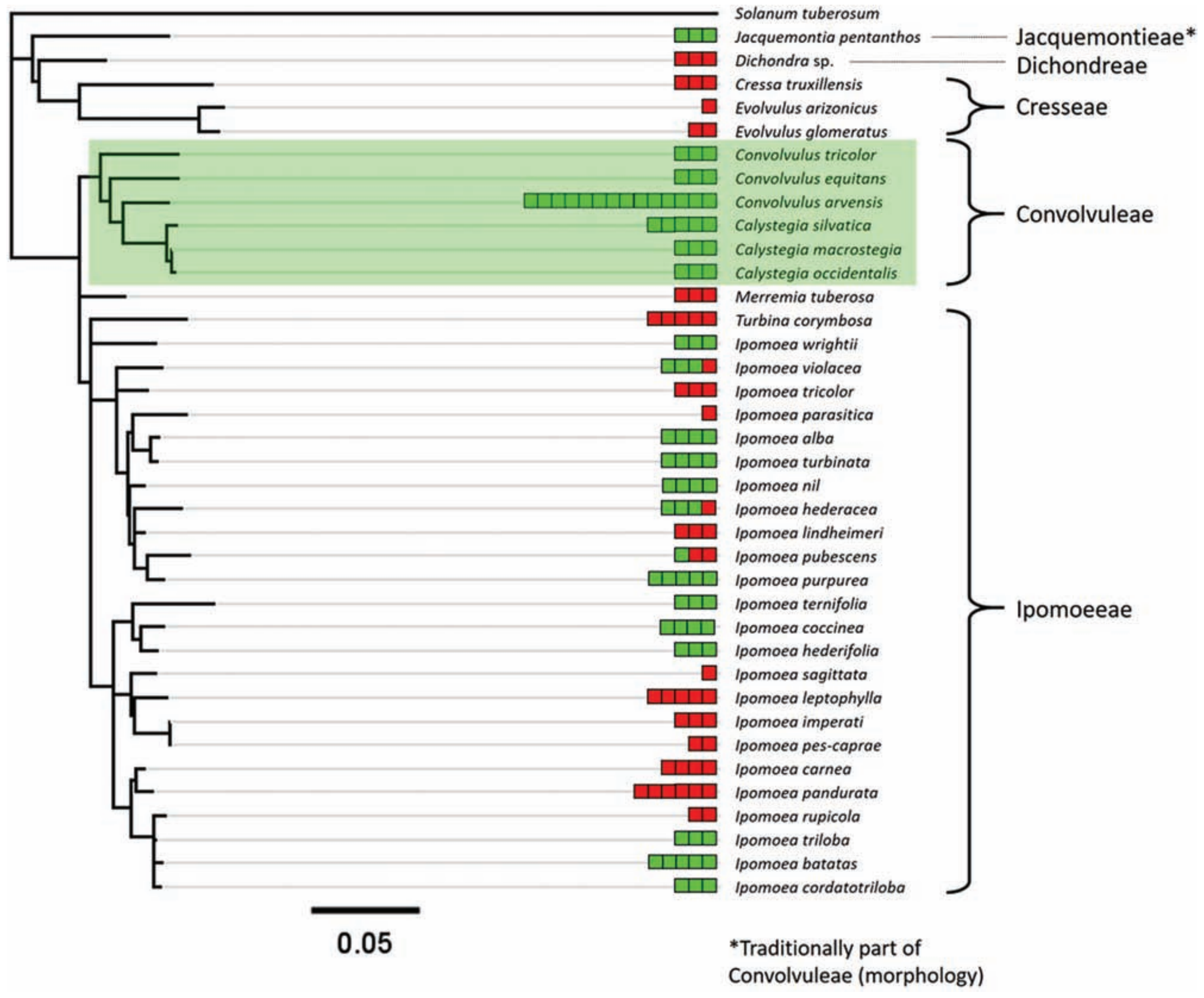

Fig. 10. Phylogenetic tree created from DNA-sequence data for 37 species of Convolvulaceae used in developmental assays. Potato (Solanaceae; *Solanum tuberosum* L.) used as an outgroup. Green and red squares show individual replications either allowing (green) or failing to allow (red) egg-to-adult-development. Green-shaded rectangle circumscribes species of *Convolvulus* and *Calystegia* (Convolvuleae).

guide our choices of plant species to be examined in rearing trials, and led us to focus particularly on *Calystegia* species in those assays. The assays showed that *Calystegia* species readily support egg-to-adult development of *B. maculipennis*.

The earliest records for *B. maculipennis* are concentrated in California, which is also where *Calystegia* is most diverse. Recent records for *B. maculipennis* extend into regions known from herbarium listings to be heavily infested by *C. arvensis*, which is correlative evidence that the psyllid has spread with field bindweed. Indeed, most of the newer psyllid records were obtained collecting from *C. arvensis*. More tellingly, *B. maculipennis* is common and abundant in geographic regions that are lacking Convolvulaceae other than the invasive field bindweed. Shapiro (2002) has shown that native Lepidoptera occur in some urban regions that lack native host species, through association with exotic species. In the absence of exotic hosts, Shapiro (2002) suggests that many of these butterflies would disappear from those urban locations. The presence of *B. maculipennis* in the northern United States and in southern Canada, regions in which native Convolvulaceae are rare or absent, may be evidence of a similar phenomenon.

In summary, despite the scarcity of field records for *B. maculipennis* that antedate arrival of field bindweed in the western United States, we have nonetheless been able to make a plausible case that distribution of *B. maculipennis* has expanded well beyond its historical distribution due to the psyllid's colonization of field bindweed. By assuming that the previously unknown natal host of *B. maculipennis* would likely be closely related to *C. arvensis*, plant taxa closely related to *C. arvensis* were targeted for biogeographic analysis and rearing assays. The rearing assays confirmed that *Calystegia* species are favorable hosts for *B. maculipennis*, while the biogeographic analyses showed that there is convincing evidence for historical geographic overlap between *Calystegia*, *C. arvensis*, and *B. maculipennis*. These conditions likely would have allowed a relatively simple dietary expansion by the psyllid from its hypothesized natal *Calystegia* hosts onto the introduced *C. arvensis*.

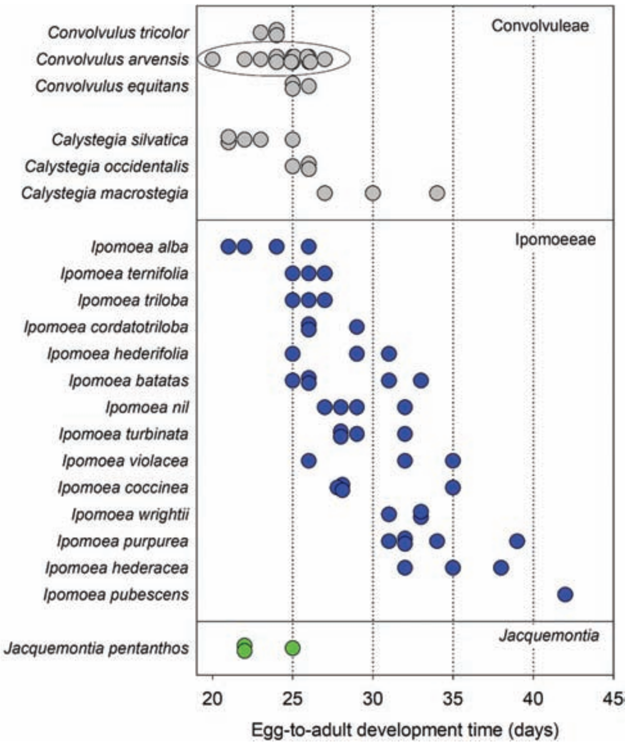

Fig. 11. Egg-to-adult development times (number of days) for those species and replications that allowed successful development. Each circle shows data for an individual replicate.

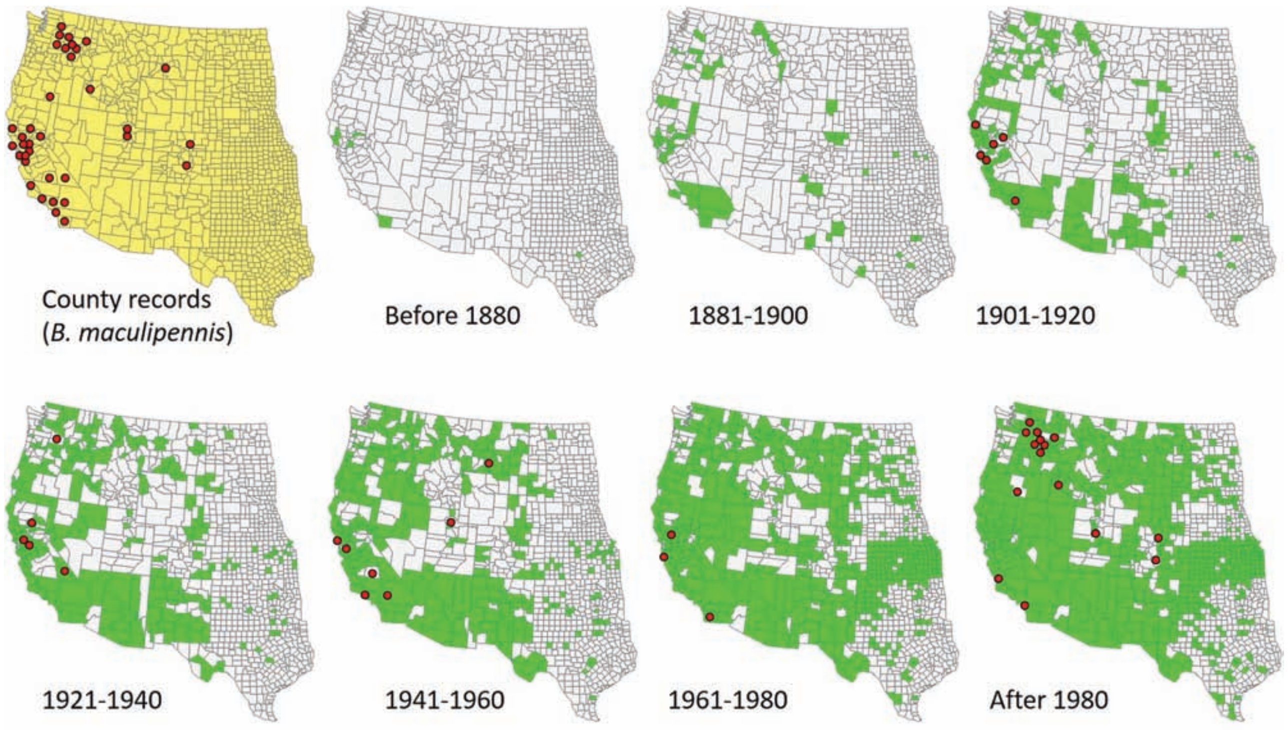

Fig. 12. Presence of *C. arvensis* accumulated across counties and decades (green shading). Red dots show *B. maculipennis* records by county for the time interval in which the initial record for that county was obtained. Sources of plant and insect records are summarized in Table 1.

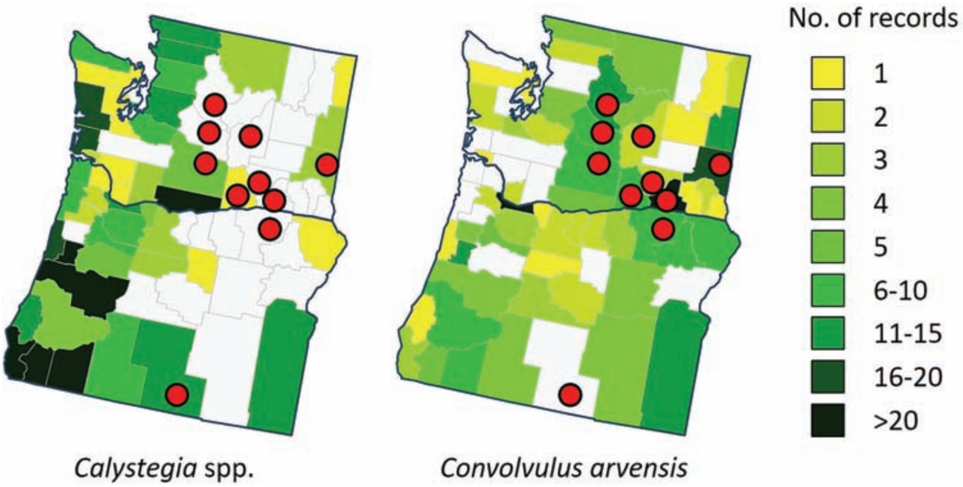

Fig. 13. Number of herbarium records by county for *Calystegia* species and *C. arvensis*, with county records for presence of *B. maculipennis* overlain as red dots. Darker shading indicates more records. Lack of shading indicates absence of herbarium records for that county. Sources of plant and insect records are summarized in Table 1.

Supplementary Data

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

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References Cited

Austin, D. F. 1998. Parallel and convergent evolution in the Convolvulaceae, pp. 201–234. *In* P. Matthews and M. Sivadasan (eds.), Diversity and taxonomy of tropical flowering plants. Mentor Books, Calicut, India.

Austin, D. F. 2000. Bindweed (*Convolvulus arvensis*, Convolvulaceae) in North America – from medicine to menace. J. Torrey Botanical Soc. 127: 172–177.

Austin, D. F. 2006. Noteworthy distributions and additions in southwestern Convolvulaceae. Canotia. 2: 79–106.

Branco, M., E. G. Brockerhoff, B. Castagneyrol, C. Orazio, and H. Jactel. 2015. Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. J. Appl. Ecol. 52: 69–77.

Brown, J. M., R. K. Brummitt, M. Spencer, and M. A. Carine. 2009. Disentangling the bindweeds: hybridization and taxonomic diversity in British *Calystegia* (Convolvulaceae). Bot. J. Linn. Soc. 160: 388–401.

Brummitt, R. K. 1963. A taxonomic revision of the genus *Calystegia*. Ph.D. thesis. University of Liverpool, Liverpool, United Kingdom.

Brummitt, R. K. 1980. Further new names in the genus *Calystegia* (Convolvulaceae). Kew Bull. 35: 327–334.

Brummitt, R. K. 2002. *Calystegia silvatica* (Convolvulaceae) in Western North America. Madroño. 49: 130–131.

Brummitt, R. K., and A. O. Chater. 2000. *Calystegia* (Convolvulaceae) hybrids in West Wales. Watsonia. 23: 161–165.

Burckhardt, D., and P. Lauterer. 1997. A taxonomic reassessment of the triozid genus *Bactericera* (Hemiptera: Psylloidea). J. Nat. Hist. 31: 99–153.

Burckhardt, D., D. Ouvrard, D. Queiroz, and D. Percy. 2014. Psyllid host-plants (Hemiptera: Psylloidea): resolving a semantic problem. Fl. Entomol. 97: 242–246.

Buril, M. T. 2013. Sistemática e filogenia de *Jacquemontia* Choisy (Convolvulaceae). Ph.D. thesis, Universidade Federal de Pernambuco, Recife, Brazil.

Carranza, E. 2007. Flora del Bajío y de Regiones Adyacentes. Familia Convolvulaceae. Fascículo 151, Instituto de Ecologia A.C., Centro Regional del Bajio, Pátzcuaro, Michoacán, México.

Carranza, E. 2008. Flora del Bajío y de Regiones Adyacentes. Convolvulaceae II. Fascículo 155, Instituto de Ecologia A.C., Centro Regional del Bajio, Pátzcuaro, Michoacán, México.

Chen, S., H. Yao, J. Han, C. Liu, J. Song, L. Shi, Y. Zhu, X. Ma, T. Gao, X. Pang, et al. 2010. Validation of the ITS2 region as a novel DNA barcode for identifying medicinal plant species. PLoS One 5: e8613.

Crawford, D. L. 1910. American Psyllidae I (Triozinae). Pomona College J. Entomol. 2: 228–237.

Crawford, D. L. 1914. A monograph of the jumping plant-lice or Psyllidae of the New World. Bulletin of the United States National Museum. 85: 1–186.

Eastop, V. 1979. Sternorrhyncha as Angiosperm taxonomists. Symbolae Botanicae Upsalienses. 22: 120–134.

Eich, E. 2008. Solanaceae and Convolvulaceae: secondary metabolites. biosynthesis, chemotaxonomy, biological and economic significance (a handbook). Springer, Berlin, Germany.

Felger, R. S., D. F. Austin, T. R. Van Devender, J. Jesús Sánchez-Escalante, and M. Costea. 2012. Convolvulaceae of Sonora, Mexico. I. *Convolvulus*, *Cressa*, *Dichondra*, *Evolvulus*, *Ipomoea*, *Jacquemontia*, *Merremia*, and *Operculina*. J. Botanical Res. Instit. Texas. 6: 459–527.

Gossner, M. M., A. Chao, R. I. Bailey, and A. Prinzing. 2009. Native fauna on exotic trees: phylogenetic conservatism and geographic contingency in two lineages of phytophages on two lineages of trees. Am. Nat. 173: 599–614.

Grandez-Rios, J. M., L. L. Bergamini, W. S. de Araújo, F. Villalobos, and M. Almeida-Neto. 2015. The effect of host-plant phylogenetic isolation on species richness, composition and specialization of insect herbivores: a comparison between native and exotic hosts. PLoS One 10: e0138031.

Graves, S. D., and A. M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biol. Cons. 110: 413–433.

Hodkinson, I. D. 1988. The Nearctic Psylloidea (Insecta: Homoptera): an annotated check list. J. Nat. Hist. 22: 1179–1243.

Holm, L. G., D. L. Plunknett, J. V. Pancho, and J. P. Herberger. 1977. The world's worst weeds: distribution and biology. University Press of Hawaii, Honolulu, HI.

Horton, D. R., W. R. Cooper, J. E. Munyaneza, K. D. Swisher, E. R. Echegaray, A. F. Murphy, S. I. Rondon, C. H. Wohleb, T. D. Waters, and A. S. Jensen. 2015a. A new problem and old questions: potato psyllid in the Pacific Northwest. Amer. Entomol. 61: 234–244.

Horton, D. R., W. R. Cooper, J. E. Munyaneza, K. D. Swisher, J. Thinakaran, C. H. Wohleb, T. D. Waters, and A. S. Jensen. 2015b. Non-potato host plants of potato psyllid in the Pacific Northwest: a year-round complication? Potato Progress. 15: 1–6.

Horton, D. R., E. Miliczky, T. M. Lewis, W. R. Cooper, J. E. Munyaneza, T. Mustafa, J. Thinakaran, T. D. Waters, C. H. Wohleb, and A. S. Jensen. 2017. New geographic records for the Nearctic psyllid *Bactericera maculipennis* (Crawford) with biological notes and descriptions of the egg and fifth-instar nymph (Hemiptera: Psylloidea: Triozidae). Proc. Entomol. Soc. Wash. 119: 191–214.

Jensen, D. D. 1957. Parasites of the Psyllidae. Hilgardia. 27: 71–99.

Jensen, D. D., and G. F. Knowlton. 1951. The psyllidae of Utah. Utah State Agricultural College Mimeograph Series 380, Logan, UT. 5pp.

Kaur, N., W. R. Cooper, J. M. Duringer, I. E. Badillo-Vargas, G. Esparza-Díaz, A. Rashed, and D. R. Horton. 2018. Survival and development of potato psyllid (Hemiptera: Triozidae) on Convolvulaceae: effects of a plant-fungus symbiosis (*Periglandula*). PLoS One 13: e0201506.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics. 28: 1647–1649.

Lewis, W. H., and R. L. Oliver. 1965. Realignment of *Calystegia* and *Convolvulus* (Convolvulaceae). Ann. Missouri Bot. Gard. 52: 217–222.

Martin, N. A. 2008. Host plants of the potato/tomato psyllid: a cautionary tale. The Weta. 35: 12–16.

Mitchell, T. C., B. R. M. Williams, J. R. I. Wood, D. J. Harris, and R. W. Scotland. 2016. How the temperate world was colonized by bindweeds: biogeography of the Convolvuleae (Convolvulaceae). BMC Evol. Biol. 16: 16.

Ouvrard, D. 2018. Psyl'list – the world Psylloidea database. http://www.hemiptera-databases.com/psyllist. Accessed multiple occasions 2015–2018.

Ouvrard, D., P. Chalise, and D. M. Percy. 2015. Host-plant leaps versus host-plant shuffle: a global survey reveals contrasting patterns in an oligophagous insect group (Hemiptera, Psylloidea). Syst. Biodiv. 13: 434–454.

Percy, D. M. 2003. Radiation, diversity, and host-plant interactions among island and continental legume-feeding psyllids. Evolution. 57: 2540–2556.

Percy, D. M., R. D. Page, and Q. C. Cronk. 2004. Plant-insect interactions: double-dating associated insect and plant lineages reveals asynchronous radiations. Syst. Biol. 53: 120–127.

Percy, D. M., A. Rung, and M. S. Hoddle. 2012. An annotated checklist of the psyllids of California (Hemiptera: Psylloidea). Zootaxa. 3193: 1–27.

Pletsch, D. J. 1947. The potato psyllid *Paratrioza cockerelli* (Sulc): its biology and control. Montana Experiment Station, Bulletin 446, Bozeman, MT. 95 pp.

Preston, R. E., and L. T. Dempster. 2012. Convolvulaceae, pp. 654–664. *In* B.G. Baldwin, D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken (eds.), The Jepson manual: vascular plants of California, 2nd ed. University of California Press, Berkeley, CA.

Puketapu, A., and N. Roskruge. 2011. The tomato-potato psyllid lifecycle on three traditional Maori food sources. Agron. New Zealand. 41: 167–173.

Refulio-Rodriguez, N. F., and R. G. Olmstead. 2014. Phylogeny of Lamiidae. Am. J. Bot. 101: 287–299.

Schilthuizen, M., L. P. Santos Pimenta, Y. Lammers, P. J. Steenbergen, M. Flohil, N. G. P. Beveridge, P. T. van Duijin, M. M. Meulblok, N. Sosef, R. van de Ven, et al. 2016. Incorporation of an invasive plant into a native insect herbivore food web. PeerJ 4: e1954.

Shapiro, A. M. 2002. The Californian urban butterfly fauna is dependent on alien plants. Divers. Distrib. 8: 31–40.

Spodek, M., D. Burckhardt, and A. Freidberg. 2017. The Psylloidea (Hemiptera) of Israel. Zootaxa. 4276: 301–345.

Staples, G. W., and R. K. Brummitt. 2007. Convolvulaceae, pp. 108–110. *In* V.H. Heywood, R.K. Brummitt, A. Culham, and O. Seberg (eds.), Flowering plant families of the world. Firefly Books, Richmond Hill, ON, Canada.

Stefanovic, S., L. Krueger, and R. G. Olmstead. 2002. Monophyly of the Convolvulaceae and circumscription of their major lineages based on DNA sequences of multiple chloroplast loci. Am. J. Bot. 89: 1510–1522.

Stefanović, S., D. F. Austin, and R. G. Olmstead. 2003. Classification of Convolvulaceae: a phylogenetic approach. Syst. Botany. 28: 791–806.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol. Lett. 9: 357–374.

Tabashnik, B. E. 1983. Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias philodice eriphyle*. Evolution. 37: 150–162.

Turner, B. L. 2009. *Convolvulus carrii*, a localized endemic from southernmost Texas. Phytologia. 91: 394–400.

Villaseñor, J. L. 2016. Checklist of the native vascular plants of Mexico. Revista Mexicana de Biodiversidad. 87: 559–902.

Wallis, R. L. 1955. Ecological studies on the potato psyllid as a pest of potatoes. United States Department of Agriculture, Technical Bulletin 1107, Washington, DC. 25 pp.

Williams, B. R. M., T. C. Mitchell, J. R. I. Wood, D. J. Harris, R. W. Scotland, and M. A. Carine. 2014. Integrating DNA barcode data in a monographic study of *Convolvulus*. Taxon. 63: 1287–1306.

Wood, J. R. I., B. R. M. Williams, T. C. Mitchell, M. A. Carine, D. J. Harris, and R. W. Scotland. 2015. A foundation monograph of *Convolvulus* L. (Convolvulaceae). PhytoKeys. 51: 1–282.

Yu, J., J. H. Xue, and S. L. Zhou. 2011. New universal matK primers for DNA barcoding angiosperms. J. Systematics Evol. 49: 176–181.

Zendedel, A., D. Burckhardt, L. Fekrat, S. Manzari, and H. S. Namaghi. 2016. An annotated checklist of the jumping plant-lice (Hemiptera: Psylloidea) of Iran. J. Entomol. Res. Soc. 18: 37–55.

Zhang, Y. P., J. K. Uyemoto, and B. C. Kirkpatrick. 1998. A small-scale procedure for extracting nucleic acids from woody plants infected with various phytopathogens for PCR assay. J. Virol. Methods 71: 45–50.