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Ployploidy in creosote bush (*Larrea tridentata*) shapes the biogeography of specialist herbivores

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Abstract

Aim: Whole-genome duplication (polyploidy) can influence the biogeography and ecology of plants that differ in ploidy level (cytotype). Here, we address how two consequences of plant polyploidy (parapatry of cytotypes and altered species interactions) shape the biogeography of herbivorous insects.

Location: Warm deserts of North America.

Taxa: Gall midges (*Asphondylia auripila* group, Diptera: Cecidomyiidae) that attack three parapatric cytotypes of creosote bush (*Larrea tridentata*, Zygophyllaceae).

Methods: We surveyed *Asphondylia* species diversity at 177 sites across a 2300-km extent. After noting a correspondence between the distributions of eight *Asphondylia* species and *L. tridentata* cytotypes, we fine-mapped *Asphondylia* species range limits with transects spanning cytotype contact zones. We then tested whether plant–insect interactions and/or abiotic factors explain this coincidence by (a) comparing attack rates and gall midge communities on alternative cytotypes in a narrow zone of sympatry and (b) using species distribution models (SDMs) to determine if climatically suitable habitat for each midge species extended beyond cytotype contact zones.

Results: The range limits of 6/17 *Asphondylia* species (including two novel putative species confirmed with *COI* sequencing) perfectly coincided with the contact zone of diploid and tetraploid *L. tridentata*. One midge species was restricted to diploid host plants while five were restricted to tetraploid and hexaploid host plants. Where diploid and tetraploid *L. tridentata* are sympatric, cytotype-restricted midge species more frequently attacked their typical host and *Asphondylia* community structure differed markedly between cytotypes. SDMs predicted that distributions of cytotype-restricted midge species were not constrained by climatic conditions near cytotype contact zones.

Main conclusions: Contact zones between plant cytotypes are dispersal barriers for many *Asphondylia* species due to plant–insect interactions. The distribution of *L. tridentata* cytotypes therefore shapes herbivore species ranges and herbivore community structure across North American deserts. Our results demonstrate that polyploidy in plants can affect the biogeography of ecological communities.

KEYWORDS

Asphondylia, Cecidomyiidae, creosote bush, gall midge, herbivory, *Larrea tridentata*, North American deserts, polyploidy, species distribution models, species interactions

1 | INTRODUCTION

Autopolyploidy (whole-genome duplication without hybridization) is common in vascular plants and can influence plant ecology and evolution (Barker, Arrigo, Baniaga, Li, & Levin, 2015; Barker, Husband, & Pires, 2016; Parisod, Holderegger, & Brochmann, 2010; Ramsey & Ramsey, 2014; Soltis et al., 2007; Van de Peer, Mizrahi, & Marchal, 2017). Related plants of different ploidy level (cytotype) are often reproductively isolated, which can limit local coexistence through reproductive interference (Levin, 1975) and drive rapid speciation (Coyne & Orr, 2004; Soltis et al., 2007). Cytotypes may also differ in a suite of traits including size, growth form, phenology, water use, cold-hardiness, and secondary metabolism (Levin, 1983; Ramsey & Schemske, 2002) due to genome doubling *per se* (e.g., Stebbins, 1949) and/or subsequent evolutionary divergence (e.g., Ramsey, 2011). Accordingly, abiotic niches differ between cytotypes in some plant taxa (McIntyre, 2012; Thompson, Husband, & Maherali, 2014). However, broadly overlapping climatic niches in other taxa indicate that cytotypes may be in direct competition (Glennon, Ritchie, & Segraves, 2014; Laport, Hatem, Minckley, & Ramsey, 2013). The joint effects of niche differentiation and population-level processes (reproductive interference and competition) likely underlie a common biogeographic consequence of polyploidy: cytotypes of many taxa have parapatric or allopatric distributions (Lewis, 1980).

The phenotypic effects of polyploidy can also influence interactions with other species, including herbivorous insects (Segraves & Anneberg, 2016; Thompson, Nuismer, & Merg, 2004; Thompson, Segraves, Cunningham, Althoff, & Wagner, 1997). In some systems, rates of herbivory are mediated by insect abundance in a cytotype's preferred microclimate (Arvanitis, Wiklund, & Ehrlén, 2007; Richardson & Hanks, 2011). Other insect herbivores consistently attack one host cytotype over others (Halverson, Heard, Nason, & Stireman, 2008a; Nuismer & Thompson, 2001; Thompson et al., 1997) or specialize exclusively on a single cytotype (Arvanitis, Wiklund, Münzbergová, Dahlgren, & Ehrlén, 2010). The herbivores that discriminate most strongly between host plant cytotypes tend to have highly specialized and intimate interactions with their host plants (e.g., gall-makers and other internal-feeding insects), which may make them especially sensitive to phenotypic differences among plant cytotypes (Segraves & Anneberg, 2016).

Given that polyploidy affects plant biogeography and species interactions, its influence on the biogeography of closely associated species is a notable gap in our understanding of polyploidy's ecological significance. Thompson et al. (1997) hypothesized that the geographic distribution of favourable plant cytotypes may constrain the distribution of herbivore species. The distribution of *Greya politella* moths on *Heuchera grossulariifolia* did not support this hypothesis (Thompson et al., 1997). However, *H. grossulariifolia* comprises cytotypes with broadly overlapping distributions (Segraves, Thompson, Soltis, & Soltis, 1999; Thompson et al., 1997), as do most plants for which the effect of polyploidy on species interactions has been studied (Arvanitis et al., 2007; Halverson, Heard, Nason, & Stireman,

2008b; Kao, 2008a; Mandáková & Münzbergová, 2006) (but see Münzbergová, Skuhrovec, & Maršík, 2015). Plants with sympatric cytotypes allow for natural experiments to parse the effect of cytotype from those of geography and environment, but any effect of plant–insect interactions is not necessarily expected to shape the geographic range of herbivore species. Instead, we hypothesized that plants with parapatric cytotypes could constrain herbivore distributions if cytotype contact zones serve as biotically mediated dispersal barriers.

To address this hypothesis, we tested if plant cytotype variation shapes the biogeography of herbivores of creosote bush (*Larrea tridentata* (DC.) Coville, Zygophyllaceae), a long-lived and dominant shrub in the warm deserts of North America. *Larrea tridentata* is a classical polyploid series comprising diploid ($2n = 2x = 26$), autotetraploid ($2n = 4x = 52$), and autohexaploid ($2n = 6x = 78$) cytotypes that roughly assort among the Chihuahuan, Sonoran, and Mojave Deserts (Barbour, 1969; Yang, 1970). Contact zones between *L. tridentata* cytotypes are well-characterized in multiple areas, including sites where cytotypes are sympatric (Laport & Minckley, 2013; Laport, Minckley, & Ramsey, 2012; Laport & Ramsey, 2015). These resources enable comparisons with the distributions of insect herbivores and direct tests for the effect of cytotype on species interactions. Diploid and tetraploid cytotypes meet in a short and well-defined contact zone in south-eastern Arizona, while a sinuous contact zone between tetraploids and hexaploids extends from central Arizona to southern California (Laport et al., 2012). Established tetraploid populations are hypothesized to have a single origin (Laport et al., 2012). The precise timing of polyploidy events is unknown, but some of the oldest macrofossils of *L. tridentata* from packrat (*Neotoma* spp.) middens were inferred to be tetraploid (25,600 cal. y.b.p.; Cole, 1986; Hunter et al., 2001). Hexaploid populations are hypothesized to have arisen from tetraploids in the Holocene (Holmgren et al., 2014; Hunter et al., 2001) and may have multiple origins (Laport et al., 2012). Macrofossil evidence suggests that contemporary cytotype distributions were established in the past 5,000 years during expansion from glacial refugia (Hunter et al., 2001).

The creosote gall midges (*Asphondylia auripila* group, Diptera: Cecidomyiidae) are an adaptive radiation of 15 species that attack leaves, stems, buds, and flowers of *L. tridentata* (Gagné & Waring, 1990). Remarkably, the *A. auripila* group diversified without host plant switching (Joy & Crespi, 2007) and comprises the majority of the gall-forming insect community on *L. tridentata*. As with most gall midges (Gagné, 1989; Tokuda, 2012), the life cycles of the *A. auripila* group are intimately associated with their host plant (Gagné & Waring, 1990). The small (2–5 mm) and short-lived adults emerge from their natal galls in one or two phenological windows per year. Many gall midges are weak fliers and actively disperse only short distances (i.e., a few meters, Highland, 1964), but wind-borne transport can enable passive dispersal over many kilometers (Miao et al., 2013; Yukawa & Rohfritsch, 2005; Yukawa, Uechi, Horikiri, & Tuda, 2003). After mating, females deposit eggs and spores of a symbiotic fungus (Tokuda, 2012) into a species-specific host plant organ (Gagné &

Waring, 1990). Larvae then induce the formation of an enclosed gall in which they develop to maturity. Although the ecology of the *A. auripila* group has been carefully studied at select sites (Huggins, 2008; Waring & Price, 1989, 1990), the distributions of *A. auripila* group species have not been previously characterized.

Our goal was to test whether interactions with *L. tridentata* cytotypes constrained the distributions of individual *Asphondylia* species and shaped broader patterns of *Asphondylia* diversity across North American deserts. We had three specific aims: (a) determine the geographic distributions of species in the *A. auripila* group, (b) identify concordance between the range limits of *Asphondylia* species and *L. tridentata* cytotypes, and (c) evaluate whether concordance is due to species interactions or confounding abiotic factors. In doing so, we link genome-scale mutational processes in plants to broad geographic patterns of herbivore diversity.

2 | MATERIALS AND METHODS

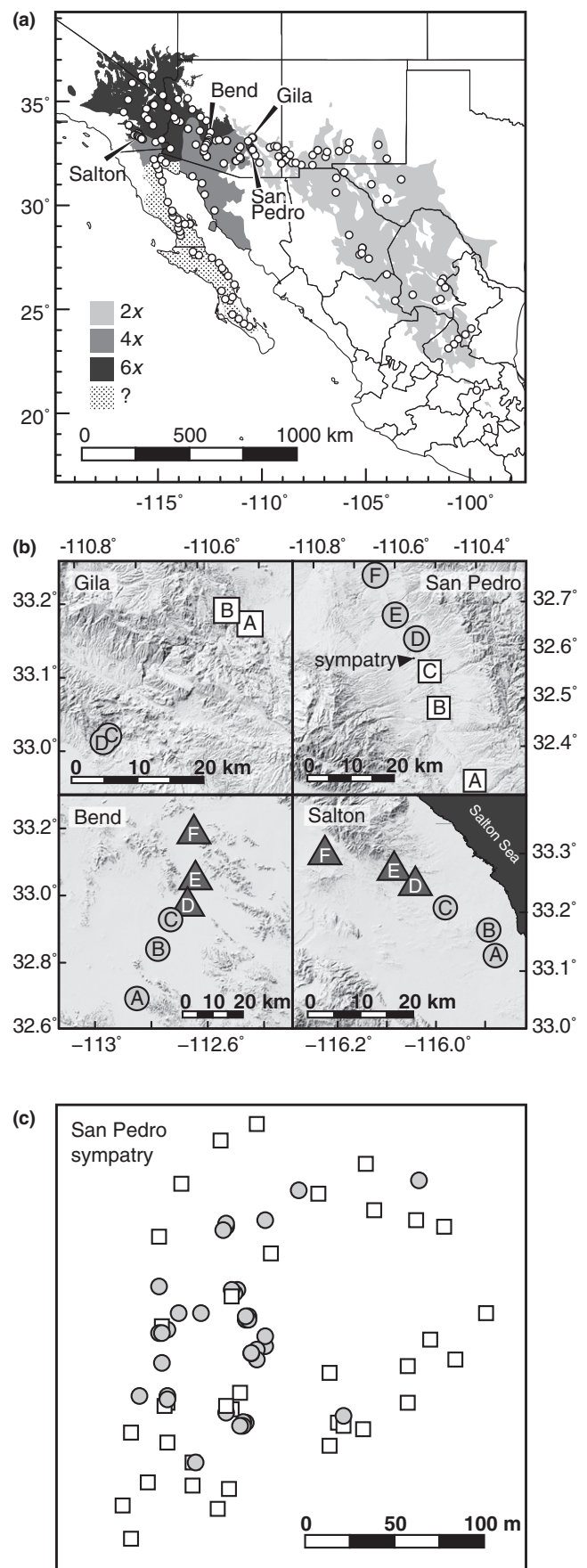
2.1 | Diversity and distributions of *Asphondylia auripila* group

We surveyed *Asphondylia* diversity on *L. tridentata* at 177 sites across the Chihuahuan, Sonoran, and Mojave Deserts between March 2015 and August 2016 (Figure 1). At most sites we haphazardly collected branch segments from 5 to 10 plants, transported them to the laboratory, and a single investigator (TKO) searched them for galls with the naked eye. Two sites near Tucson, AZ were surveyed more intensively (up to 15 plants/site), and three sites were represented by opportunistic collections from a single plant (Appendix S6). We sorted galls into morphotypes and identified the causative *Asphondylia* species using the original species descriptions (Gagné & Waring, 1990). Gall morphology is the most reliable diagnostic character for species of the *A. auripila* group (Gagné & Waring, 1990) and corresponds to species identity (Joy & Crespi, 2007).

2.2 | Contact zone transects

To evaluate concordance between the range limits of *Asphondylia* species and *L. tridentata* cytotypes, we sampled along four transects spanning cytotype contact zones (Figure 1). We used two diploid–tetraploid transects (Gila and San Pedro) and two tetraploid–hexaploid transects (Salton and Bend) previously established by Laport and

FIGURE 1 Map of sampling sites. (a) 177 total sites surveyed in this study. Shading shows the approximate distribution of diploid (2x), tetraploid (4x), and hexaploid (6x) *Larrea tridentata* (after Laport & Ramsey, 2015). *L. tridentata* cytotypes in the Lower Colorado River Valley and Baja California Peninsula have not been directly determined by flow cytometry and are unknown. Arrowheads indicate transect locations. (b) Four contact zone transects. Symbols indicate creosote bush cytotype: white squares = 2x, grey circles = 4x, dark grey triangles = 6x. (c) Site of diploid–tetraploid sympatry within San Pedro transect showing location of 72 surveyed plants. Symbols follow (b)



colleagues (Laport, Minckley, & Ramsey, 2016; Laport & Ramsey, 2015; Laport et al., 2012). Each transect includes 4–6 sites with permanently marked plants of known cytotype as determined by flow cytometry. In most transects, the transition between parapatric cytotypes has been delimited to within ≤ 8 km (except Gila transect: 19 km). We did not sample marked plants directly to protect ongoing research. Instead, we sampled plants found among marked plants (< 5 m away) or at sites near those of Laport and colleagues. Additional details are provided in Appendix S1.

In all transects, sampling sites were ≥ 10 m from the nearest paved road and embedded in regionally typical vegetation. We collected ≥ 10 branch segments (30 cm long) from throughout the canopy of 10 focal plants per site. All plants were separated by at least 5 m to reduce the chance of sampling from the same clone and limit spatial autocorrelation among samples. Collections were stored in airtight containers under cool conditions for up to 24 hr. We then clipped stems into 5 cm-long segments, thoroughly mixed them, and subsampled 50 g fresh mass. A single investigator (TKO) exhaustively searched subsamples for galls with the naked eye. It was often impossible to differentiate senesced galls of the current season from those of previous seasons, which may remain on the plant for months. We included all galls in analyses described below, and results may therefore integrate patterns of gall midge diversity over several generations.

We tested whether the prevalence of *Asphondylia* species differed between cytotypes in each transect using binomial generalized linear mixed models (GLMMs) with site as a random effect. We evaluated the significance of model terms with Wald *F*-tests and applied a 5% false discovery rate (FDR) correction to *P*-values to account for multiple testing. We only fit models for the 13 species found on > 5 plants in a given transect. Analyses were performed in the R Environment for Statistical Computing 3.4.2 (R Core Team, 2018) with packages “lme4” (Bates, Maechler, Bolker, & Walker, 2015) and ‘car’ (Fox & Weisberg, 2011).

2.3 | Diploid–tetraploid sympatry

To isolate the effect of cytotype from confounding factors, we next tested whether gall midge attack rates differed between sympatric diploid and tetraploid *L. tridentata* in the San Pedro River Valley (Figure 1). Only a single such site has been characterized along the diploid–tetraploid contact zone. We surveyed galls on 72 permanently marked plants of known cytotype (36 diploid, 36 tetraploid; Laport & Ramsey, 2015; RGL, unpublished data) near the peak of spring gall maturation in March–April 2016. To protect ongoing research on focal plants, we used a non-destructive field survey. A single investigator (TKO) inspected each plant for eight minutes under a standardized search routine and recorded all galls encountered. Although most plants were observed while blind to cytotype, morphological differences between diploids and tetraploids at this site (Laport & Ramsey, 2015) precluded a truly blind experiment. We measured mean diameter for 58/72 focal plants.

We used binomial generalized linear models (GLMs) to test whether the prevalence of *Asphondylia* galls differed between

sympatric diploid and tetraploid hosts. We constructed GLMs for the 13 *Asphondylia* species found on > 5 plants and assessed significance as for GLMMs. Initial models included cytotype, plant diameter, and their interaction as independent variables. Plant diameter did not differ between cytotypes (*t* test, $p > 0.2$), so we present models with cytotype as the only independent variable. The inferred effect of cytotype from GLMs including or excluding plant diameter was generally consistent (Table S4.1). Analyses were performed with base functions in R and the “car” package (Fox & Weisberg, 2011).

In addition to single-species analyses, we compared overall *Asphondylia* community structure between sympatric diploid and tetraploid *L. tridentata*. This analysis integrates over all *Asphondylia* species to test the hypothesis that interactions between *Asphondylia* species differ between *L. tridentata* cytotypes. We applied square-root and Wisconsin double-standardizations to gall abundance data (Bray & Curtis, 1957) and calculated Bray-Curtis dissimilarities among *Asphondylia* communities on individual plants. We analysed only plants with ≥ 10 galls ($N = 54$). We then visualized variation among communities with non-metric multidimensional scaling (NMDS) ordinations and tested if community structure differed between cytotypes with permutational MANOVA (PERMANOVA) (Anderson, 2001). Analyses were implemented with the R packages “MASS” (Venables & Ripley, 2002) and “vegan” (Oksanen et al., 2017).

2.4 | Species distribution models

As a complement to our field observations of *Asphondylia* distributions and abundance, we used species distribution models (SDMs) to assess whether abiotic factors or plant–insect interactions set the range limits of *Asphondylia* species. Our approach followed Anderson, Peterson, and Gómez-Laverde (2002), who compared the predicted extent of climatically suitable habitat for parapatric spiny pocket mice (*Heteromys*) species to their observed distributions. Because *Heteromys anomalus* was absent from climatically suitable areas that were occupied by *Heteromys australis*, the authors concluded that competition set the range limit of *H. anomalus*. We conducted an analogous comparison for *Asphondylia* species with range limits near cytotype contact zones. If climatically suitable *Asphondylia* habitat extended beyond the cytotype contact zone, we would conclude that plant–insect interactions limit *Asphondylia* distributions. If suitable habitat was instead confined to the observed species distribution, we would conclude that abiotic factors are sufficient to explain the location of *Asphondylia* species range limits.

We built SDMs using maxEnt (Phillips, Dudik, & Schapire, 2004). Models were fit using WorldClim 2.0 BioClim variables at 2.5 arc-minute resolution (Fick & Hijmans, 2017) and implemented with the R packages “dismo” (Hijmans, Phillips, Leathwick, & Elith, 2017), “ENMeval” (Muscarella et al., 2014), “maxnet” (Phillips, 2017), “MASS” (Venables & Ripley, 2002), “raster” (Hijmans, 2016), and “spThin” (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015). Expanded methods are reported in Appendix S2.

We selected eight uncorrelated BioClim variables ($|r| < 0.7$; Dormann et al., 2013) for modelling: Bio2 (mean diurnal temperature

range), Bio 4 (temperature seasonality), Bio10 (mean temperature of warmest quarter), Bio11 (mean temperature of coldest quarter), Bio15 (precipitation seasonality), Bio16 (precipitation of wettest quarter), Bio17 (precipitation of driest quarter), and Bio19 (precipitation of coldest quarter). We combined our collection data with published surveys of the creosote gall midge community (Gagné & Waring, 1990; Huggins, 2008; Schowalter, Lightfoot, & Whitford, 1999; Waring & Price, 1989; Werner & Olsen, 1973).

Sampling bias can substantially affect Maxent model predictions (Kramer-Schadt et al., 2013), so we applied and compared two methods to account for bias in our data set: spatial thinning of occurrence records (Aiello-Lammens et al., 2015; Pearson, Raxworthy, Nakamura, & Peterson, 2007) and biased background sampling (Dudík, Phillips, & Schapire, 2005). Spatially thinned analyses only included occurrences separated by ≥ 25 km, resulting in relatively uniform sampling across the range of each species. We randomly drew 10,000 background points from a species-specific background region (see below). The second set of SDMs used biased background sampling to match the bias in occurrence records. We modelled geographic variation in sampling intensity by estimating the two-dimensional kernel density of our 177 sampling sites then drew 10,000 background points with probability defined by local kernel density. To avoid model overfitting (Kremen et al., 2008), background regions for each species were defined as (a) within 100 km of the minimum convex polygon fit to occurrence records, and (b) within 100 km of the range of *L. tridentata*.

We tuned Maxent models by fitting 40 alternative combinations of feature classes and regularization multipliers and then selected the preferred model using the sample size-corrected Akaike information criterion (AICc) (Warren & Seifert, 2011). We fit final SDMs with MAXENT 3.4 (Phillips, Anderson, Dudík, Schapire, & Blair, 2017) using optimized model settings for each species. We predicted habitat suitability across North America and estimated model performance using geographically structured 4-fold cross-validation (Radosavljevic & Anderson, 2014; "block" method in "ENMeval"). We converted probabilistic predictions of habitat suitability to binary predictions with the commonly used 10% omission threshold (Pearson et al., 2007).

2.5 | Evaluating SDM transferability

Our approach to test whether *L. tridentata* cytotypes determine the range limits of *Asphondylia* species assumes that SDMs can predict habitat suitability in unoccupied areas (i.e., that models are transferable across space). However, an array of methodological and biological factors can reduce model transferability (reviewed in Petitpierre, Broenimann, Kueffer, Daehler, & Guisan, 2017). We addressed methodological challenges of inferring transferable SDMs using a limited number of uncorrelated, biologically meaningful predictors, as suggested by Petitpierre et al. (2017). Another persistent challenge is non-analogue conditions between training and prediction regions (Fitzpatrick & Hargrove, 2009). The diploid–tetraploid contact zone coincides with the ecotone of the Chihuahuan and Sonoran Deserts, and the contrasting temperature and precipitation regimes in each desert region (MacMahon & Wagner, 1985) may limit SDM transferability.

We therefore evaluated SDM transferability across the study extent to identify potential limitations of our hypothesis testing framework. First, we subsetted the occurrences of nine widespread *Asphondylia* species to include records only from the range of diploid *L. tridentata* ("diploid sites") or the range of polyploid *L. tridentata* ("polyploid sites"). These subsetted records mimicked the observed distributions of some *Asphondylia* species (see Results). For each species, we then trained SDMs on either diploid or polyploid sites using model tuning and sampling bias correction as described above. We applied a 10% omission threshold calculated from training data (e.g., polyploid sites) and calculated omission rates for occurrences on the other side of the contact zone (e.g., diploid sites). Omission rates greater than the expected 10% would indicate limited model transferability across desert regions. Finally, we compared habitat suitability predictions from models trained on complete versus subsetted occurrence records. By visualizing the agreement between these predictions across North American deserts, we identified where models trained on one region could be successfully transferred across the diploid–tetraploid contact zone and where they could not.

2.6 | Molecular phylogenetics

Three gall morphotypes identified in this study did not match any species descriptions. We collected gall midges from two of these galls ("acuminata" and "hirsuta"; informal names explained in Appendix S3) and used molecular phylogenetics to test the hypothesis that they correspond to novel *Asphondylia* species. Detailed molecular methods and specimen information are reported in Appendix S3. Briefly, we sequenced fragments of *cytochrome c oxidase subunit I* (COI) from novel gall morphotypes ("acuminata", $N = 8$; "hirsuta", $N = 5$) and combined them with a previously ungenotyped member of the *A. auripila* group (*Asphondylia discalis*, $N = 1$) and published sequences representing the other 14 described species in the group (Joy & Crespi, 2007). Following initial phylogenetic analyses, we sequenced more exemplars of *Asphondylia florea* ($N = 10$), *A. apicata*, ($N = 3$), *Asphondylia rosetta* ($N = 3$) and *Asphondylia silicula*, ($N = 4$) to provide additional phylogenetic context. Our final data set comprised 34 new COI sequences and 34 sequences from the literature representing all 15 described species in the *A. auripila* group, midges from two novel gall morphotypes, and seven out-groups (Table S3.2). We aligned sequences with MUSCLE (Edgar, 2004) using default parameters, trimmed sequences to a uniform length (432 bp), and estimated a maximum likelihood phylogeny with PHYML 3 (Guindon et al., 2010) under a GTR+G model. Branch support was estimated with 200 bootstrap replicates.

3 | RESULTS

3.1 | Diversity of the *A. auripila* group

We found 18 gall morphotypes from 177 total sites across a 2,300-km extent (Appendix S5). Among these were galls of all 15 species and three gall morphotypes that did not match any

species description (Figure S3.1). A large (10 mm-long) spade-shaped bud gall (“acuminata”) was widespread in the Chihuahuan Desert. A smaller (2.5–3 mm), oblong gall found on the abaxial leaf surface (“hirsuta”) resembled the gall of *A. silicula* but was densely covered in long trichomes. The “hirsuta” morphotype was also present in the Chihuahuan Desert but at lower frequency than “acuminata” galls. A third undescribed morphotype strongly resembled the gall of *A. silicula* but was attached to the adaxial leaf margin rather than the abaxial surface (“adaxial silicula”). The “adaxial silicula” galls were found in all contact zone transects, but because we did not record the position of *A. silicula* galls at most sites, the full distribution of this morphotype is unknown.

The *COI* phylogeny indicated that gall midges collected from “acuminata” and “hirsuta” galls represent distinct mitochondrial lineages in the *A. auripila* group (Figure 2). *A. sp.* “acuminata” was monophyletic (bootstrap support [BS] = 99) and found as sister to *A. rosetta* (*A. apicata* + *A. florea*) with moderate support (BS = 88). *A. sp.* “hirsuta” was strongly supported as monophyletic (BS = 100), but relationships with other *Asphondylia* species were poorly resolved. We considered *A. sp.* “acuminata” and *A. sp.* “hirsuta” to be novel undescribed species based on the distinctness of their gall morphology, their phylogenetic placement, and the extent of mitochondrial sequence divergence from sister lineages (uncorrected divergence: *A. sp.* “acuminata” $\geq 4.3\%$, *A. sp.* “hirsuta” $\geq 7.7\%$).

We did not design our phylogenetic analyses to re-evaluate relationships within the *A. auripila* group or uncover cryptic diversity. Nevertheless, we note that *A. florea* specimens from across Arizona and California formed a clade (BS = 84) that was strongly supported as sister to the clade of *A. rosetta* (*A. apicata* + *A. florea*) sequenced by Joy and Crespi (2007) (BS = 93; Figure 2). We also identified a divergent lineage of *A. silicula* from the southern Chihuahuan Desert (represented by samples MX D8S4P2G1 and MX D7S2P2G1, Figure S3.2) that renders the species paraphyletic with respect to *A. fabalis*. This lineage co-occurs with other *A. silicula* (MX D8S4P3G1) that are closely related to populations in the Sonoran Desert (*A. silicula* J&C1, Figure S3.2). Additionally, we found that *A. discalis* (not sequenced by Joy and Crespi (2007)) is sister to *Asphondylia bullata* with strong support (BS = 100, Figure S3.2).

3.2 | Concordance of *Asphondylia* and *L. tridentata* range limits

Nine of 17 *Asphondylia* species were found across portions of all the Chihuahuan, Sonoran, and Mojave Deserts and therefore attack all *L. tridentata* cytotypes (Appendix S5). No species had range margins near the tetraploid–hexaploid contact zone. The other eight species were initially found only in the Chihuahuan Desert (on diploid hosts) or in the Sonoran and Mojave Deserts (on polyploid hosts). We found six such species in diploid–tetraploid transects,

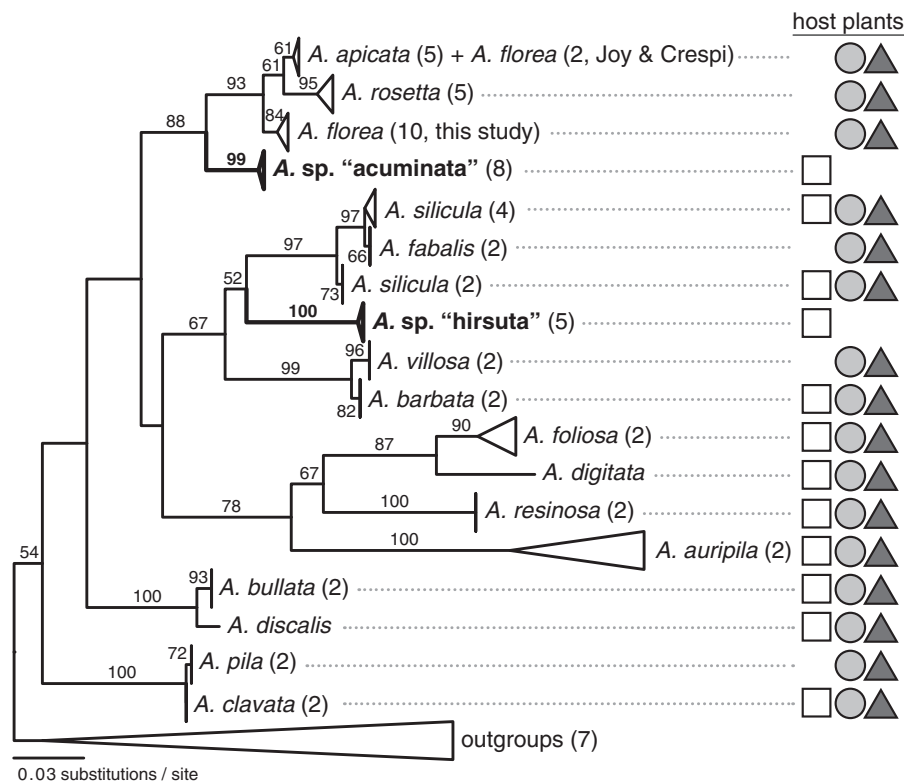


FIGURE 2 Maximum likelihood phylogeny of *Asphondylia auripila* group inferred from cytochrome *c* oxidase subunit I (*COI*) sequences. Two novel putative species (*A. sp.* “acuminata” and *A. sp.* “hirsuta”) are indicated in bold. Number of samples per species given in parentheses. Bootstrap support values $\geq 50\%$ are indicated above branches. Scale bar represents number of substitutions per site. Host plant use shown with symbols at right: white squares = 2x, grey circles = 4x, dark grey triangles = 6x

and each occurred on a single host cytotype. *A. sp. "acuminata"* was found in diploid sites while *A. apicata*, *A. florea*, *Asphondylia pila* (= "*A. pilosa*" of Gagné and Waring (1990) and Joy and Crespi (2007); see Gagné and Jaschof (2014)), *A. rosetta*, and *Asphondylia villosa* were found in tetraploid sites (Figure 3). "Adaxial silicula" galls were also found only in tetraploid sites. These species included all four bud-galling species, two leaf-galling species, and one leaf-galling morphotype (Table S5.1).

Concordance between *Asphondylia* range limits and the diploid–tetraploid contact zone is especially striking for *A. apicata*, *A. rosetta*, and "adaxial silicula" galls. Each was absent from diploid sites in the San Pedro transect but found at frequencies ≥ 0.5 in a tetraploid site < 8 km away (Figure 3). We found similarly striking trends in the prevalence of *A. apicata*, *A. florea*, *A. rosetta*, and *A. silicula* in the Gila transect, although diploid and tetraploid sites were more distant than in the San Pedro transect. All six species and the "adaxial silicula" gall morphotype were also found in the sympatric site within the San Pedro transect. The range limits of these species were thus perfectly concordant with those of their typical host plant cytotype, a pattern we describe as "cytotype-restricted." Note that Joy and Crespi (2007) reported *A. florea* 65 km east of the diploid–tetraploid contact zone, within the range of diploid *L. tridentata*. In light of our phylogeny, this likely represents a different species from the *A. florea* we consider here.

3.3 | Plant–insect interactions differ between *L. tridentata* cytotypes

All cytotype-restricted species attacked diploid and tetraploid hosts at different rates in sympatry. *A. pila* and *A. villosa* were rare in the sympatric site and found only on their typical tetraploid hosts ($N = 2$ and $N = 1$, respectively). *A. sp. "acuminata"*, *A. apicata*, *A. rosetta*, and "adaxial silicula" galls were more prevalent on their typical host cytotype (binomial GLM, $p < 0.05$; Table 1). *A. florea* was also more than twice as prevalent on its typical host (11/36 tetraploids vs. 5/36 diploids), but this was only a trend ($p > 0.1$). Mean gall intensity (gall abundance on plants with ≥ 1 gall) for these four species and the "adaxial silicula" morphotype was higher on the species' typical host plant cytotype (1.3–3.3 \times higher). However, we had limited power to statistically evaluate the differences between cytotypes because atypical cytotypes were rarely attacked.

Asphondylia community structure differed markedly between sympatric diploid and tetraploid *L. tridentata* (Figure 4, PERMANOVA $R^2 = 0.33$, $p < 0.001$). This is consistent with the tendency of cytotype-restricted species to attack their typical host cytotype. However, the correlation of *Asphondylia* community structure and host cytotype was nearly as strong when cytotype-restricted species were removed from the data set ($R^2 = 0.28$, $p < 0.001$). This indicates that some widespread *Asphondylia* species also attacked diploid and tetraploid hosts at different rates in sympatry. *A. discalis* was more prevalent on tetraploids in the sympatric site while *Asphondylia clavata*, *Asphondylia digitata*, and *A. silicula* were more prevalent on diploids

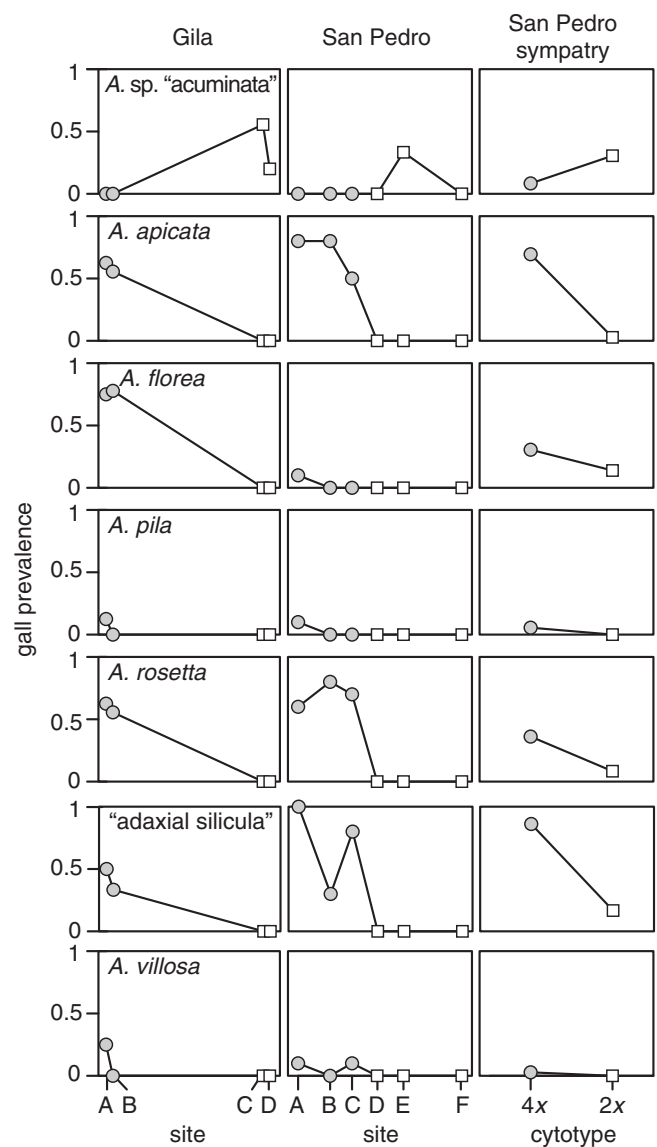


FIGURE 3 The range limits of six *Asphondylia* species and the "adaxial silicula" gall morphotype are concordant with the contact zone between diploid (white squares) and tetraploid (grey circles) *Larrea tridentata*. For each species or morphotype, the first two columns show gall prevalence (proportion of plants with a gall) in contact zone transects. Relative position along the transect is shown on the x-axis. The third column shows gall prevalence on each plant cytotype where they naturally occur in sympatry

(GLM, $p < 0.05$) (Table 1). The prevalence of *A. discalis* was also higher in tetraploid sites than diploid sites within the San Pedro transect (diploid = 0.07, tetraploid = 0.66; GLMM, $p < 0.001$), although not in the Gila transect. By contrast, *A. clavata*, *A. digitata*, and *A. silicula* did not show consistent bias in prevalence in the San Pedro or Gila transects (Table S1.2).

In general, gall prevalence was similar on both cytotypes at the tetraploid–hexaploid contact zone. However, one species (*Asphondylia foliosa*) was more prevalent on tetraploids in the Salton transect (GLMM, $p < 0.05$, Table S1.2). We also detected differences in prevalence for several other species (*A. auripila*, *A. florea* in the

TABLE 1 Summary of binomial generalized linear models and Wald *F*-tests for differences in prevalence of *Asphondylia* species between sympatric diploid (2x) and tetraploid (4x) *Larrea tridentata*. We fit models only for species found on ≥ 5 plants

Cytotype-restricted?	Species	N 2x	N 4x	<i>b</i> (\pm s.e.) ^a	O.R. (95% CI) ^a	<i>F</i> _{1,70} ^b	<i>p</i> ^b
Yes	<i>A. sp.</i> "acuminata"	11	3	-1.58 (\pm 0.70)	0.21 (0.04–0.74)	5.8	0.035
Yes	<i>A. apicata</i>	1	25	4.38 (\pm 1.08)	79.5 (14.3–1504)	39.6	<0.001
Yes	<i>A. florea</i>	5	11	1 (\pm 0.60)	2.73 (0.87–9.62)	2.87	0.137
Yes	<i>A. pila</i>	0	2	—	—	—	—
Yes	<i>A. rosetta</i>	3	13	1.83 (\pm 0.70)	6.22 (1.77–29.39)	8.3	0.014
Yes	"adaxial silicula" morphotype	6	31	3.43 (\pm 0.66)	31 (9.3–125.8)	37.24	<0.001
Yes	<i>A. villosa</i>	0	1	—	—	—	—
No	<i>A. auripila</i>	4	6	0.47 (\pm 0.69)	1.6 (0.42–6.78)	0.45	0.544
No	<i>A. barbata</i>	9	3	-1.30 (\pm 0.72)	0.27 (0.06–1.02)	3.64	0.099
No	<i>A. bullata</i>	15	15	0 (\pm 0.48)	1 (0.39–2.56)	0	1.000
No	<i>A. clavata</i>	17	5	-1.71 (\pm 0.59)	0.18 (0.05–0.54)	9.55	0.009
No	<i>A. digitata</i>	6	2	-1.22 (\pm 0.85)	0.29 (0.04–1.39)	2.28	0.176
No	<i>A. discalis</i>	3	28	3.65 (\pm 0.72)	38.5 (10.6–193)	38.53	<0.001
No	<i>A. foliosa</i>	0	2	—	—	—	—
No	<i>A. resinosa</i>	14	17	0.34 (\pm 0.48)	1.41 (0.55–3.63)	0.5	0.544
No	<i>A. silicula</i>	35	28	-2.30 (\pm 1.09)	0.10 (0.01–0.59)	6.78	0.024

^aCoefficients from GLM: *b*: estimated effect of cytotype, O.R.: odds ratio that galls of an *Asphondylia* species were found on a tetraploid rather than diploid plant. We report the inverse of the O.R. for *A. sp.* "acuminata" in the main text, which is the O.R. that this species was found on a diploid plant (its typical host) rather than a tetraploid.

^bResults of Wald *F*-tests. *P*-values reflect 5% false discovery rate correction.

Salton transect, *A. discalis* in the Bend transect), but these were not statistically different after FDR correction.

3.4 | Abiotic limits to *Asphondylia* species ranges

Accounting for sampling bias using a biased background yielded SDMs with visual fits that were generally better or comparable to those using spatial thinning. For simplicity we discuss only the results using biased background sampling, but we note where spatially thinned models differ.

Tuned SDMs for all cytotype-restricted species predicted suitable abiotic habitat beyond their observed range limit at the diploid–tetraploid contact zone (Figure 5). Nearly the full range of *L. tridentata* was predicted to be suitable for *A. sp.* "acuminata", which is found only in the Chihuahuan Desert. Suitability predictions for *A. apicata*, *A. florea*, and *A. rosetta* included most of the Sonoran and Mojave Deserts and regions of unoccupied habitat in the Chihuahuan Desert. Unoccupied Chihuahuan Desert habitat was contiguous with the observed distribution of *A. rosetta*, but was interspersed with larger unsuitable regions for *A. apicata* and *A. florea*. The *A. villosa* SDM based on biased background selection produced the biologically unrealistic prediction of suitable habitat in the coastal plains of Texas and Tamaulipas. Bias may have been more difficult to correct in this case due to limited occurrence records (*N* = 23) that were spatially clustered. The SDM based on spatial thinning resembled those of *A. apicata*, *A. florea*, and *A. rosetta*, although suitable habitat in the Chihuahuan Desert was smaller than in those species. The SDM for *A. pila* least resembled the other

cytotype-restricted species. Regions beyond the northern limit of *L. tridentata* were predicted to be suitable for *A. pila*, as were isolated patches of the south-eastern Chihuahuan Desert. Further details of model parameters, evaluation, and performance are reported in Appendix S2.

Transferability experiments for nine widespread *Asphondylia* species revealed that models trained with polyploid sites systematically under-predicted suitable habitat in the Chihuahuan Desert, suggesting that abiotically suitable habitat is more widespread than indicated by SDM predictions. Omission rate of diploid sites was well above the expected 10% for most species (up to 71%, Table 2), although *A. clavata* and *A. digitata* were exceptions to this trend. Under-prediction was even more pronounced in spatially thinned data sets (omission rates: 51–77%, Table S2.5). Notably, SDMs trained on polyploid sites predicted relatively small and non-contiguous regions of suitable habitat in the western Chihuahuan Desert (Figure S2.1), similar to those observed in models for cytotype-restricted species (*A. apicata*, *A. florea*, *A. rosetta*, and *A. villosa*). By contrast, models trained only with occurrences from diploid sites tended to predict the distribution in the Sonoran and Mojave Deserts well (Table 2). The species with the least transferable models (*A. auripila*, *A. bullata*, and *A. resinosa*) all have very limited distributions and/or sparse occurrence records confined to the Northern Chihuahuan Desert (Figure S5.1). Species with broader ranges in the Chihuahuan Desert had omission rates near or below the expected 10% (range: 0–12%), indicating good model transferability. Results were qualitatively similar for spatially thinned models.

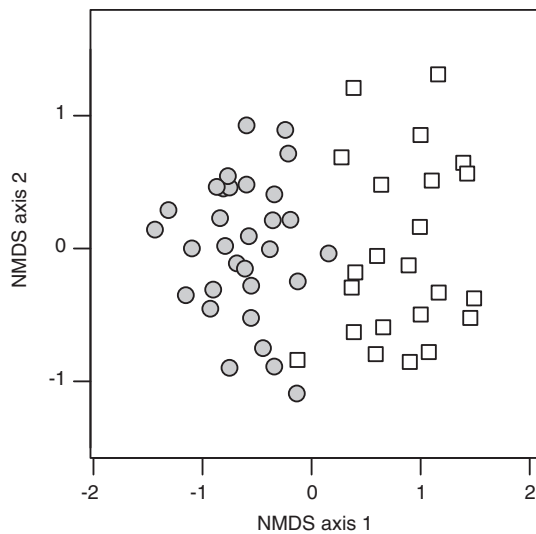


FIGURE 4 Non-metric multidimensional scaling (NMDS) ordination of *Asphondylia* communities on sympatric diploid (white squares) and tetraploid (grey circles) plants. Cytotype was a significant predictor of community structure (PERMANOVA, $R^2 = 0.33$, $p < 0.001$)

4 | DISCUSSION

There is an emerging consensus that cytotype variation is an important dimension of plant biodiversity (Barker et al., 2015; Laport & Ng, 2017; Ramsey & Ramsey, 2014; Soltis et al., 2007), and growing interest in how polyploidy affects interactions with other species (Segraves & Anneberg, 2016). Only one study has formally tested whether host plant polyploidy influences the biogeography of herbivorous insects (Thompson et al., 1997). Here, we tested if cytotype variation in creosote bush (*L. tridentata*) affects interactions with specialized herbivores and shapes herbivore biogeography.

The observed range limits of six *Asphondylia* species and an additional gall morphotype coincided perfectly with the contact zone of diploid and tetraploid *L. tridentata*. Although it is likely that cytotype-restricted species disperse beyond their observed distributions, they must occur at only low densities: among >5,800 galls identified from the San Pedro and Gila transects, cytotype-restricted species were only found on atypical host cytotypes where diploids and tetraploids are sympatric. Galls of all cytotype-restricted species were more prevalent on their typical host where diploid and tetraploid *L. tridentata* naturally co-occur, and overall *Asphondylia* community structure

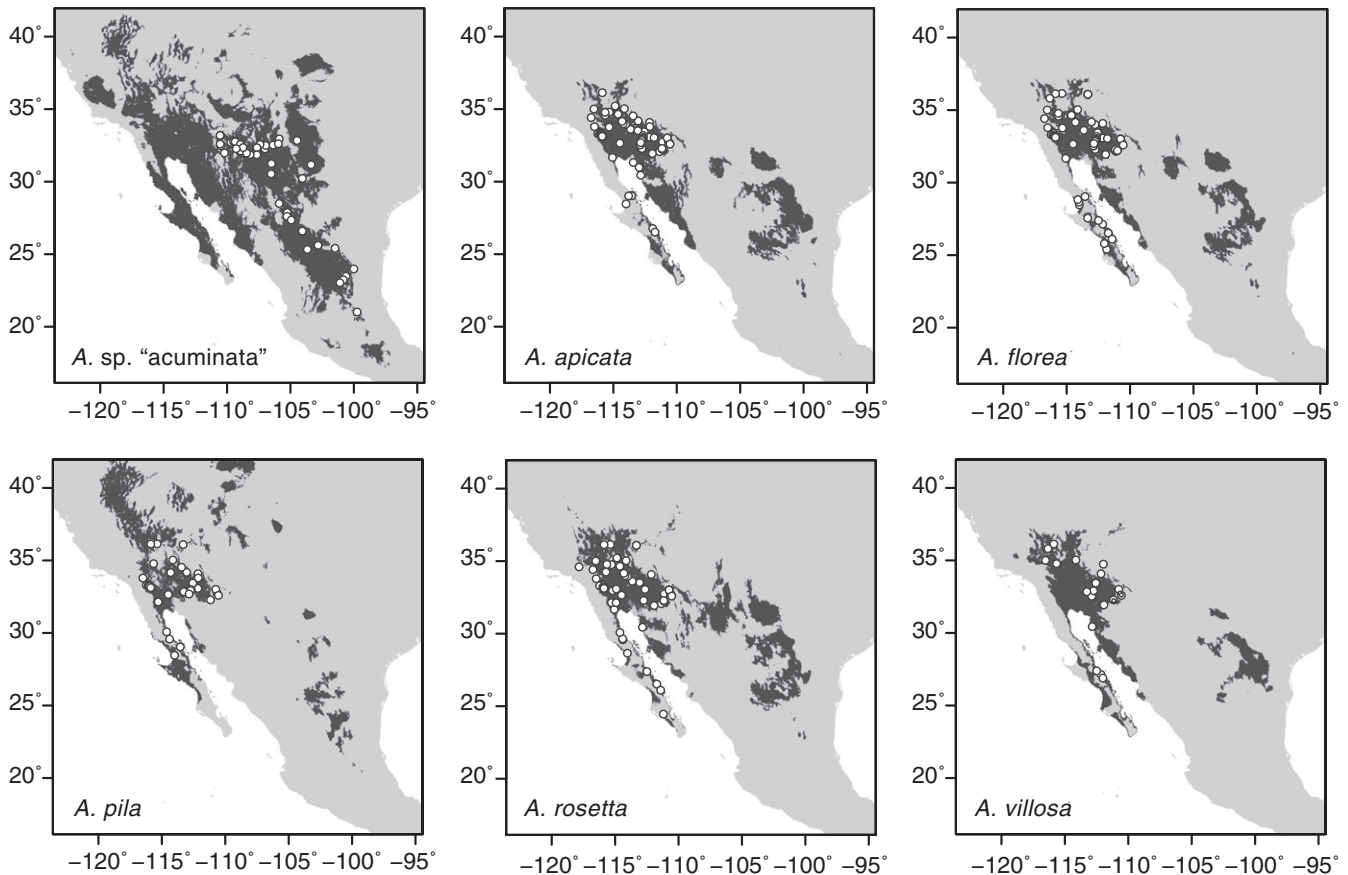


FIGURE 5 Species records and habitat suitability predictions for six cytotype-restricted species. Dark grey areas show suitable habitat when applying a 10% omission rate threshold. Habitat predicted to be suitable extends beyond the observed range limits of each species. For species found on polyploid *Larrea tridentata* (all but *Asphondylia* sp. "acuminata"), tests of model transferability (Appendix S2) suggest that species distribution models under-predict the extent of suitable habitat in the Chihuahuan Desert. Predictions for all species except *A. villosa* are based on models fit using biased background sampling; *A. villosa* predictions are based upon predictions from spatially thinned models

TABLE 2 Results of SDM transferability experiments with models employing biased background sampling. SDMs were trained with occurrences from the range of diploid or polyploid *Larrea tridentata*, then tested with occurrences from the opposite data set. Columns report mean omission rates when applying a 10% omission threshold calculated from the training dataset

Species	Training: polyploid Test: diploid	Training: diploid Test: polyploid
<i>A. auripila</i>	67%	38%
<i>A. barbata</i>	43%	3.3%
<i>A. bullata</i>	48%	57%
<i>A. clavata</i>	12%	2.8%
<i>A. digitata</i>	0%	8.3%
<i>A. discalis</i>	67%	5.2%
<i>A. foliosa</i>	71%	12%
<i>A. resinosa</i>	52%	45%
<i>A. silicula</i>	66%	5.9%

differed markedly between sympatric host plant cytotypes. In contrast, we found only modest differentiation in *Asphondylia* galling between tetraploid and hexaploid *L. tridentata*. The same pool of *Asphondylia* species attacked tetraploids and hexaploids, and while several species tended to attack these cytotypes at different rates near contact zones, prevalence differed statistically for only one species in one transect. Although our findings are generally consistent across contact zone surveys, we note that these results would be more compelling with further replication.

Species distribution models (SDMs) indicated that abiotic factors are unlikely to determine the range limits of most cytotype-restricted species. Suitable habitat for *A. sp.* “*acuminata*” was predicted across the full range of *L. tridentata*, while *A. apicata*, *A. florea*, *A. rosetta* were predicted to have large and nearly contiguous regions of suitable, but unoccupied, habitat in the Chihuahuan Desert. SDM transferability experiments demonstrated that models trained on occurrences from the range of polyploid creosote bush systematically underestimate suitable habitat in the northwest Chihuahuan Desert. Therefore, predicted distributions for *A. apicata*, *A. florea*, and *A. rosetta* on diploid *L. tridentata* are likely conservative. Both *A. pila* and *A. villosa* were predicted to have disjunct distributions separated by a broad region of unsuitable habitat in the western and central Chihuahuan Desert. It is unclear whether this reflects true abiotic tolerances or methodological bias, so we cannot exclude the possibility that abiotic and biotic factors jointly limit the distribution of these species.

It is possible that competition between *Asphondylia* species contributes to the parapatric distribution of some cytotype-restricted species (Sexton, McIntyre, Angert, & Rice, 2009), although we have limited data to test this hypothesis. This is most plausible among bud-galling species, which include *A. sp.* “*acuminata*” on diploid hosts and *A. apicata*, *A. florea*, and *A. rosetta* on polyploids. We consider this unlikely because we commonly find all three polyploid-restricted species on the same plant, some plants host all four species where

diploid and tetraploid *L. tridentata* are sympatric, and many buds remain ungalled.

The *Larrea-Asphondylia* system demonstrates that extreme specialization on a host plant cytotype (as seen in *Dasineura cardaminis* on *Cardamine pratensis*, Arvanitis et al., 2010) is not required for polyploidy to shape insect biogeography. *Asphondylia* herbivory was biased between sympatric *L. tridentata* cytotypes, but less so than insect herbivory on *Solidago altissima* (Halverson et al., 2008a), *Heuchera grossulariifolia* (Nuismer & Thompson, 2001), and *Arnica cordifolia* (Kao, 2008b). In the *A. auripila* group, a host plant with parapatric cytotypes and modest differences in herbivore preference or performance appear sufficient to constrain herbivore distributions. Because cytotype parapatry is common among autopolyploid plants (Lewis, 1980), our results may be generalizable to other systems. For example, the sister lineage to the *A. auripila* group attacks a geographically segregated complex of *Atriplex canescens* cytotypes (2x–20x) (Hawkins, Goeden, & Gagné, 1986; Sanderson & Stutz, 1994) and is a compelling system for future study.

Several plausible mechanisms may underlie specialized interactions between *Asphondylia* species and host plant cytotypes. Traits that differ among *L. tridentata* cytotypes such as volatile organic compounds (Bohnstedt & Mabry, 1979) and organ size and proportions (Laport & Ramsey, 2015) affect host plant preference in other gall midges (Hall et al., 2012; Kanno & Harris, 2000). Alternatively, cytotype-restricted species may perform better on typical host cytotypes due to differences in plant defence. Although the major constituent of *L. tridentata* resin (nordihydroguaiaretic acid, NDGA) is a defence against many chewing herbivores (Mabry, DiFeo, Sakakibara, Bohnstedt, & Siegler, 1977; Rhoades, 1977), internal-feeding *Asphondylia* spp. larvae are unlikely to encounter biologically meaningful levels of this compound. Moreover, NDGA levels are comparable between diploids and tetraploids (Zuravsky, 2014). We are unaware of any studies investigating inducible defences in *L. tridentata*, which are more likely to target internal parasites such as gall midges (e.g., Harris et al., 2003; Williams & Whitham, 1986).

Whether whole-genome duplication directly alters species interactions or potentiates their subsequent evolution is an unresolved question (Segraves & Anneberg, 2016). The limited evidence from other systems is mixed. *Eurosta solidaginis* flies tend to attack independently derived tetraploid plants over alternative cytotypes, suggesting that a trait directly affected by genome duplication *per se* might mediate plant–insect interactions (Halverson et al., 2008a). By contrast, although *Greya politella* moths prefer tetraploid *Heuchera grossulariifolia*, this is not due to pre-existing bias and likely evolved after polyploidization (Janz & Thompson, 2002). Comparisons between contact zone transects suggest an indirect effect of polyploidy in the *Larrea-Asphondylia* system. We found that while the prevalence of many *Asphondylia* species differed between adjacent diploid and tetraploid populations, few species attacked tetraploids and hexaploids at different rates. We hypothesize that this difference is due to 1) the more ancient divergence between tetraploids and diploids and 2) periods of allopatry between diploid and tetraploid *L. tridentata* during Pleistocene glacial cycles. However, we

cannot rule out the possibility that phenotypic differences accompanying transitions from diploidy to tetraploidy present a steeper adaptive gradient for *Asphondylia* than transitions from tetraploidy to hexaploidy (Laport & Ramsey, 2015; Madlung, 2013; Ramsey & Schemske, 2002).

Joy and Crespi (2007) found that the *A. auripila* group diversified without host plant switching, a remarkable pattern among herbivorous insects. Our results suggest at least some diversification in this group may be associated with switching among *L. tridentata* cytotypes. For example, the diploid-restricted species *A. sp.* "acuminata" shares a common ancestor with the clade comprising *A. rosetta*, *A. apicata*, and *A. florea*, all of which are restricted to polyploid *L. tridentata* (Figure 2). Robustly testing the hypothesis that speciation coincides with host cytotype switching will require greater phylogenetic resolution and elucidation of cryptic species in the *A. auripila* group.

Overall, our results are consistent with the hypothesis of Thompson et al. (1997) that polyploidy, by altering plant traits, can affect plant–insect interactions and impact herbivore distributions. The distribution of *L. tridentata* cytotypes indirectly contributes to the disparity in *A. auripila* group diversity between the Chihuahuan versus Sonoran and Mojave Deserts (max 11 species/site vs. max 15 species/site, Figure S5.2). Given the strong influence of plant polyploidy on many species interactions (Segraves & Anneberg, 2016), genomic variation at the primary trophic level may broadly affect the biogeography and composition of ecological communities. Future research on the community-wide effects of plant polyploidy (Laport & Ng, 2017; Segraves, 2017) should explicitly test for such biogeographic linkages.

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DATA ACCESSIBILITY

COI sequences have been deposited in GenBank (accession numbers: MK058365–MK058398). Collection records for all species are reported in Appendix S6.

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BIOSKETCHES

Timothy (Tim) O'Connor employs the methods of biogeography, evolutionary ecology, and population genomics to understand how species interactions generate biodiversity. His dissertation research addresses a variety of evolutionary questions using creosote bush and its herbivorous insect community as a model system.

Robert Laport is a plant evolutionary ecologist interested in the processes generating patterns of biodiversity. His research focuses on the population-level interplay between genome duplication (polyploidy), ecological processes, and speciation. Additional details can be found at: <https://robertlaport.com>.

Noah Whiteman studies the evolution of plant–herbivore and host–parasite interactions with a focus on the genomic basis of adaptation. He also has an interest in the assembly of host–parasite communities. His dissertation research was on the phylogeography of the Galápagos hawk (*Buteo galapagoensis*) and its parasite community. His research group's website can be found at: <https://noahwhiteman.org>.

Author contributions: TKO designed the research and led the writing with input from RGL and NKW; TKO collected and analyzed data.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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