Ecological niche modeling implicates climatic adaptation, competitive exclusion, and niche conservatism among *Larrea tridentata* cytotypes in North American deserts

Author(s): Robert G. Laport , Layla Hatem , Robert L. Minckley , and Justin Ramsey
Source: The Journal of the Torrey Botanical Society, 140(3):349-363. 2013.
Published By: Torrey Botanical Society
DOI: http://dx.doi.org/10.3159/TORREY-D-13-00009.1
URL: http://www.bioone.org/doi/full/10.3159/TORREY-D-13-00009.1

Journal of the Torrey Botanical Society 140(3), 2013, pp. 349–363

Ecological niche modeling implicates climatic adaptation, competitive exclusion, and niche conservatism among *Larrea tridentata* cytotypes in North American deserts[1,2]

Robert G. Laport[3], Layla Hatem, Robert L. Minckley, and Justin Ramsey

Department of Biology, University of Rochester, River Campus, Rochester, NY 14627

Laport, R. G., L. Hatem, R. L. Minckley, and J. Ramsey (Department of Biology, University of Rochester, 213 Hutchison Hall, River Campus, Rochester, NY 14627). Ecological niche modeling implicates climatic adaptation, competitive exclusion, and niche conservatism among *Larrea tridentata* cytotypes in North American deserts. J. Torrey Bot. Soc. 140: 349–363. 2013.—*Larrea tridentata* is a dominant and widespread shrub of North American warm deserts. The species comprises three ''chromosomal races,'' including diploids (Chihuahuan Desert), tetraploids (Sonoran Desert), hexaploids (Mojave and western Sonoran Deserts), as well as the geographically restricted tetraploid *L. tridentata* var. *arenaria*. Creosote bush is a recent arrival to the North American continent, and it is hypothesized that its geographic dispersion reflects rapid ecological divergence mediated by polyploidization. Here we use species distribution modeling to quantitatively evaluate alternate hypotheses for cytotype distributions, based on comprehensive field sampling of creosote bush populations over four years. Using ecological niche models and analyses of field-collected soils, we test whether (1) the climatic niche of the three cytotypes are differentiated; (2) there is evidence for strong climatic gradients at the distributional boundaries of the cytotypes; and (3) cytotype ranges are distinguished by edaphic features. Quantitative tests of niche equivalence indicated that distribution models for all cytotypes were significantly different from one other, suggesting that cytotype races occupy unique and distinctive habitats. However, tests of niche similarity suggest a pattern of niche conservatism, wherein cytotypes tend to occur in climatically similar regions of their respective deserts. Moreover, the modeled diploid distribution was projected to intrude into the geographic range of tetraploids, and the modeled tetraploid distribution was projected to intrude into the range of hexaploids, suggesting that intercytotype competition is a factor influencing cytotype distributions. The range boundary between the dune endemic *L. tridentata* var. *arenaria* and hexaploid *L. tridentata* was noteworthy for exhibiting a strong climatic gradient and striking differences in soil texture (increased sand, decreased gravel). More generally, soil texture differed statistically between sites occupied by diploid, tetraploid, and hexaploid *L. tridentata*, albeit with considerable overlap across the geographic ranges of the three cytotypes. Taken together, our findings suggest that multiple factors affect the distribution of creosote bush chromosome races, including but not limited to ecological divergence.

Key words: ecological speciation, edaphic endemic, genome duplication, polyploidy, range boundary, species distribution modeling.

Genomic analyses indicate that angiosperms have undergone repeated polyploidization through their evolutionary history (Soltis et al. 2009); among more recent speciation events, approximately 15% result from whole genome duplication events (Wood et al. 2009). Theoretical models and empirical data suggest that, in the absence of self-fertilization, polyploids require a marked fitness advantage or ecological barrier to escape frequency dependent selection (Levin 1975, Felber 1991, Rodriquez 1996). Physiological and genetic changes associated with polyploidization may enable rapid ecological adaptation, facilitating the demographic establishment of neopolyploids (Thompson and Lumaret 1992, Husband and Schemske 1998, Levin 2004, Soltis et al. 2007). For example, differences in ecologically important traits including size, drought tolerance, herbivore resistance, phenology, and reproductive systems have been observed between diploids and polyploids (Bretagnolle and Lumaret 1995, Segraves and Thompson 1999, Maherali et al. 2009, Ramsey 2011). Polyploids may thus be ''pre-adapted'' to invade novel habitats, or exhibit increased

[1] This research was supported by an NSF DDIG grant (DEB-1010738), a Torrey Botanical Society fellowship, and a Botanical Society of America student research grant to R. Laport, and an NSF CAREER grant (DEB-0953551) to J. Ramsey.

[2] The authors thank A. Kjolhede, C. Smigelski, H. Pullman, and L. Widener for assistance with soil analyses; S. Laport, M. Laport, J. Ng, M. Castiglione, and M. Strangas for assistance with field sampling; and M. Hatem and R. Glor for insightful advice regarding GIS and ENMs. B. McCarthy, J. Ng, T. Ramsey, and two anonymous reviewers provided helpful comments on a draft of this manuscript.

[3] Author for correspondence, E-mail: rob.laport@gmail.com

Received for publication February 1, 2013, and in revised form September 5, 2013.

phenotypic variability and ecological amplitude that enables them to expand their geographic range (Brochmann et al. 2004, Martin and Husband 2009, McIntyre 2012, *but see* Buggs and Pannel 2007). The underlying causes of ploidy effects are poorly understood, but probably reflect alterations in gene dosage, homologous chromosome recombination, the masking of genetic load, and/or cell size differences resulting from increased chromosome complements (Ramsey and Schemske 2002).

The North American creosote bush (*Larrea tridentata* (DC) Coville, Zygophyllaceae) is one of the most widespread plants in the warm deserts of the southwestern U.S. and northern Mexico, often occurring in uninterrupted stands for hundreds or thousands of hectares (Benson and Darrow 1981, Turner et al. 1995). Creosote bush is regarded as a defining element of the North American warm deserts (Solbrig 1977) and serves as habitat and a vital food resource for numerous specialist herbivores and pollinators (Hurd and Linsley 1975, Wells and Hunziker 1976, Greenfield et al. 1987). *Larrea tridentata* is also considered a classic example of a polyploid complex, comprising three chromosome races (including the tetraploid sand-dune endemic *L. tridentata* var. *arenaria* L.D. Benson) that occur allopatrically in the Chihuahuan, Sonoran, and Mojave Deserts (Yang 1967, Yang and Lowe 1968, Barbour 1969, Yang 1970, Lewis 1980): diploids ($2n = 2x = 26$) in the Chihuahuan Desert, tetraploids ($2n = 4x = 52$) in the Sonoran Desert, and hexaploids ($2n = 6x = 78$) in the Mojave Desert. However, recent analyses using guard cell measurements (Hunter et al. 2001) and flow cytometry (Laport et al. 2012) have shown cytotype distributions to be more geographically complex than previously thought. While diploids are limited largely to the Chihuahuan Desert and hexaploids are the only cytotype known from the Mojave Desert, tetraploids and hexaploids intermingle in the northern Sonoran Desert of central and western Arizona (Laport et al. 2012). The geographically restricted tetraploid *L. tridentata* var. *arenaria* is only known to inhabit the Algodones Dunes of southeastern California and adjacent Baja, Mexico.

Based on limited sampling, early workers documented non-overlapping spatial distributions for *L. tridentata* cytotypes and hypothesized that chromosome races were differentially adapted to environmental conditions of the Chihuahuan, Sonoran, and Mojave Deserts (Yang 1967, Yang and Lowe 1968, Hunziker et al. 1977). As a test of this hypothesis, Barbour (1969) showed that diploid, tetraploid, and hexaploid seedlings grown under controlled conditions differed in morphology and physiology, and that some soil features varied among sites occupied by the three cytotypes. Yang (1970) argued that the cytotypes could generally be distinguished on the basis of morphology, even when growing in close proximity, and Hunziker et al. (1972) discovered seed albumin expression differences among the cytotypes. More recently, Hunter et al. (2001) demonstrated a correlation between chromosome number and stomatal size, and speculated that differences in plant water relations contributed to the cytotype distributions. Though insightful, these data do not represent assessments of adaptation via field transplantation experiments or measurements of ecophysiological traits. Moreover, prior studies were performed at a broad geographic scale and with limited sampling, and thus did not include plants from cytotype range boundaries or the sand dune specialist, *L. tridentata* var. *arenaria* (Benson and Darrow 1981, Turner 1994). Thus, it is unknown whether the distributions of *L. tridentata* cytotypes reflect adaptation to contrasting environments, competitive exclusion at range boundaries, or other factors.

While common garden and reciprocal transplant experiments are typically employed to test ecological adaptation, these methods are not feasible for highly motile organisms (including most animals) and long-lived, slow-growing immobile organisms, like creosote bush. Ecological Niche Modeling (ENM) has recently emerged as a quantitative approach for evaluating ecological divergence within and among species, based on field distribution data sets that can be generated for almost any species (Hijmans et al. 2003). ENMs have also proven valuable for habitat assessments of economically important or rare species (Hijmans et al. 2003), susceptibility of geographic regions to invasion by exotic species (Roura-Pascual et al. 2004), past and future changes in distribution due to climate change (Oberhauser and Peterson 2003), and the degree of niche conservatism between closely-related species (Kozak and Wiens

2006). Glennon et al. (2012) and Godsoe et al. (2013) recently used ENMs to evaluate climatic divergence among ploidy levels of *Houstonia* (Rubiaceae) and *Heuchera cylindrica* (Saxifragaceae), respectively, but species distribution models have not been widely applied to the analysis of speciation events in polyploid plants (Sobel et al. 2009, McIntyre 2012). Because of the frequent spatial segregation of diploid and polyploid cytotypes, and widespread belief that polyploidization may drive ecological divergence, species distribution modeling seems well suited to polyploidy research.

Here, we combine Ecological Niche Models with analyses of field-collected soil samples to evaluate ecological divergence among the three cytotypes of *L. tridentata*. Specifically, we ask three questions: (1) Do species distribution models indicate climatic niche differentiation or niche conservatism among the cytotypes of *L. tridentata* and *L. tridentata* var. *arenaria*? (2) Is there evidence for strong climatic gradients at the distributional boundaries of interacting *L. tridentata* cytotypes? and (3) Are the ranges of diploid, tetraploid, and hexaploid *L. tridentata* distinguished by soil features, and do these soil attributes also distinguish *L. tridentata* var. *arenaria* sites from those of the other *L. tridentata* cytotypes?

Materials and Methods. Population Sampling. All localities used for distribution modeling and soil comparisons were sampled by the authors from 2007–2010. All plants were cytotyped using flow cytometry, based on DNA content estimates of 10–30 plants per population (Laport et al. 2012). Although *L. tridentata* cytotypes sometimes occur in close spatial proximity at the boundaries of their respective ranges, populations (including the study sites described here) rarely harbor more than one ploidy level (Laport et al. 2012). Sites included in our analyses were no closer than ca. 15 km to reduce bias resulting from spatial autocorrelation in the distribution models (Fig. 1). Exceptions to this rule were made for *L. tridentata* var. *arenaria*, which has a geographically restricted distribution (Laport et al. 2012). In total, 19 diploid, 22 tetraploid, 8 *L. tridentata* var. *arenaria*, and 22 hexaploid localities were included in distribution modeling and analyzed for soil attributes. The optimal number of localities for accurate ENM construction is dependent on spatial distributions and underlying environmental variation (Glor and Warren 2011). Although the number of localities included in our study is lower than some others (Papes and Gaubert 2007, Pearson et al. 2007, Glor and Warren 2011), our sampling represents approximately two-thirds of the geographic range of *L. tridentata* and includes representation of the three major warm desert floristic provinces (Fig. 1). Pearson et al. (2007) suggested this level of sampling was sufficient to generate accurate distribution models.

Ecological Niche Modeling. Bioclim environmental variables at 30 arcsecond resolution (ca. 1 km^2 at the equator) were obtained from the Worldclim database (www.worldclim.org, Hijmans et al. 2005) for the geographic areas that included the *L. tridentata* localities, and were assembled in Quantum GIS (ver. 1.7; www.qgis.org). Layers were trimmed to encompass only the sampling points of the three cytotypes (NW corner: 36.92°/−116.16°; SE corner: 25.45°/−101.62°). As bioclim variables are highly correlated, we performed Principal Component Analysis (PCA) on the environmental layers to reduce dimensionality and avoid over-fitting of distribution models to the collection sites. We retained a combination of variables that are important for desert plant survival (Bowers et al. 2004) and those with the highest loadings in PCA (accounting for 97.6% of the variance) for distribution modeling: annual mean temperature (Bio 1), temperature seasonality (Bio 4), temperature annual range (Bio 7), precipitation seasonality (Bio 15), precipitation of the warmest quarter (Bio 18), and precipitation of the coldest quarter (Bio 19).

The predicted distribution for each cytotype was determined using the program Maxent (v3.3.0 beta; www.cs.princeton.edu/~schapire/maxent/) with default parameter settings (Phillips et al. 2006). Maxent derives a probabilistic function for the species occurrence from the climatic variables at known localities to predict areas suitable for the species. Models for each cytotype were constructed using the same climate layers trimmed to encompass the sampling points of all three cytotypes. Twenty random replicates were run for each cytotype using the cross validation method to test each of the models. Consistency and accuracy of the averaged predictions were

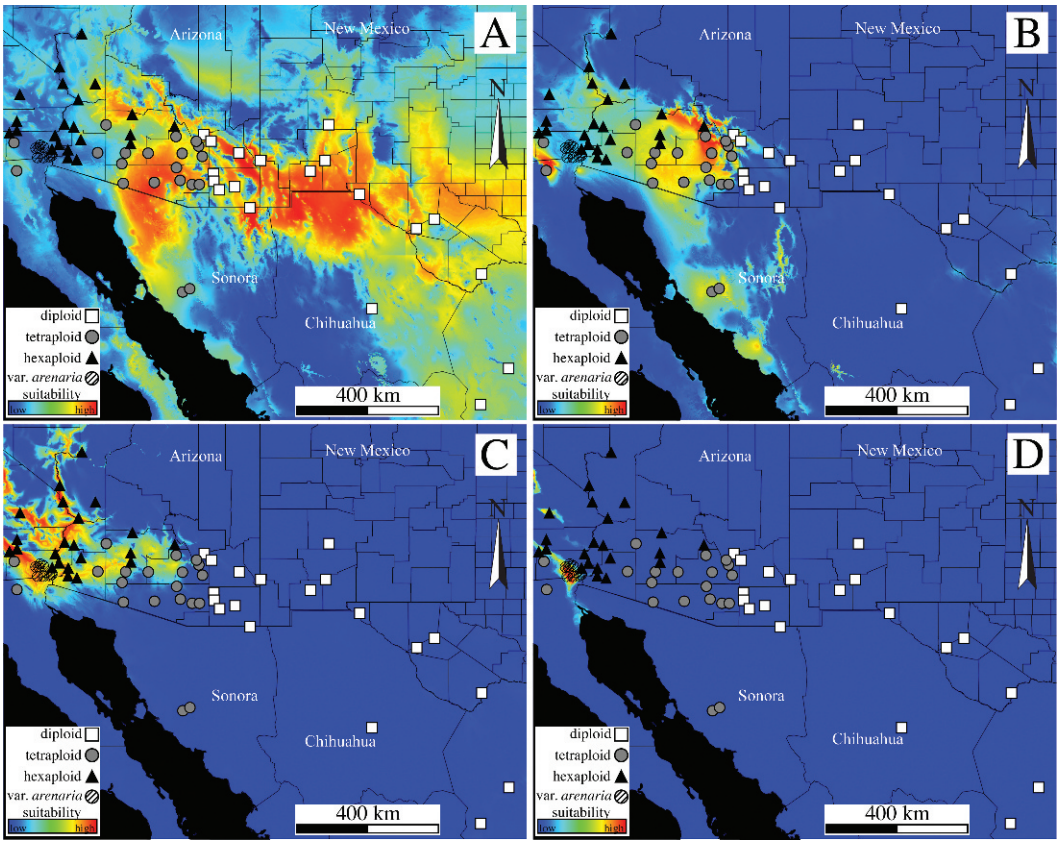

FIG. 1. Ecological Nice Model predictions for (A) diploid, (B) tetraploid, (C) hexaploid *L. tridentata*, and (D) *L. tridentata* var. *arenaria*. In each panel, collection sites used to make the distribution models are represented as white squares (diploids), grey circles (tetraploids), black triangles (hexaploids), and cross-hatched circles (*L. tridentata* var. *arenaria*). In all panels, warmer colors (more red) indicate higher predicted suitability.

assessed via the receiver operating characteristic (ROC) and the area under the ROC curve (AUC) following Warren et al. (2008) and Glor and Warren (2011). The predicted distributions for each cytotype were qualitatively reviewed in Quantum GIS prior to their use for quantitative analyses.

TESTS OF NICHE SIMILARITY. We tested whether predicted distributions (ENMs) were significantly different among cytotypes (''niche overlap,'' ''niche identity,'' and ''niche similarity'') and if there was a stronger than expected ecological gradient at cytotype boundaries (''range-breaking'') using the program ENM Tools (enmtools.blogspot.com, Warren et al. 2008, Glor and Warren 2011). The niche overlap test makes multiple pairwise comparisons between the ENMs of two taxa to determine their observed similarity using Schoener's statistic of niche overlap ($D_{(pX,\ pY)} = 1 - \frac{1}{2}\ \Sigma|p_{X,i} - p_{Y,i}|$ where $p_{X,i}$ and $p_{Y,i}$ are probability distributions assigned by the Ecological Niche Models for species X and Y, at each particular grid cell, i, in the models.). Values of D range from 0 (niche models are completely different or have no overlap) to 1 (niche models are identical) (Warren et al. 2008).

The niche identity test determines if distribution models produced for two species (or other taxonomic unit) differ in their climatic attributes by pooling the locality data for both species and sampling randomly from the pooled occurrences to create pseudoreplicate datasets (100 in our analyses) of equal size. New distribution models are constructed from each pseudoreplicate data set in Maxent, producing a null distribution of D values. The observed values of D (from the niche overlap test) were compared to these values to test the null hypothesis that distribution

models did not differ significantly from the pseudoreplicate models (Warren et al. 2008).

The niche similarity test (''background similarity'' test in ENMTools) determines whether distribution models of two species (or populations) are more or less similar than expected given the underlying environmental backgrounds in which they occur (Smith and Donoghue 2010, Glor and Warren 2011). Though comparable to the niche identity test, the niche similarity test is a more conservative test as it compares environmental attributes from collection sites of one species to randomly drawn background points from the range of another species. Because implementation involves a focal taxon and the abiotic background of a second taxon, asymmetric differences between species or populations may be observed. The random background points of each cytotype were limited to an area defined by a minimum convex polygon that included all sampling sites of that cytotype.

The range-breaking test determines if an observed distributional boundary between species or populations is associated with a significant environmental gradient (Glor and Warren 2011). Here we employ both ''linear'' and ''blob'' methods for comparison. The linear method is employed when a distributional boundary occurs in a sharply defined linear boundary. New linear boundaries are randomly selected (500 in our analyses) between pseudoreplicate data sets and ENMs are constructed for the newly split populations. The blob method is used when species or population distributions clearly replace each other on the landscape, but do not do so at a defined linear boundary (Glor and Warren 2011). Centered on a randomly selected sampling locality, new boundaries are randomly drawn (500 in our analyses) to generate pseudoreplicate data sets. Overlap metrics are calculated for the pseudoreplicate ENMs in both cases to create null distributions to which the observed overlap is compared. If the observed boundary occurs within a significant abiotic gradient the observed overlap value will fall outside the null distribution.

Soil Analyses. Because mature plants of *L. tridentata* have an extensive lateral root system, and the roots of seedlings only penetrate 5–10 cm into the upper horizon (Chew and Chew 1965), soil sampling was performed at the surface level ($\leq$ 20 cm in depth) using a hand trowel and soil corer. Sampling was performed at 2–3 haphazardly-selected locations at 71 sites in spring 2008, generating a total of 211 soil collections (Table 1). Soil samples were air-dried after collection and returned to the University of Rochester for analysis. Gravel content was determined as percentage of soil mass screened from samples with a 2 mm sieve (#10 mesh, Hubbard Scientific, Chippewa Falls, WI). Soil particle size determinations were made using the Bouyoucos sedimentation method to determine the amount of sand (1.0–0.05 mm), silt (0.05–0.005 mm), and clay ($<$ 0.005 mm) in each soil sample using an ASTM 152-H soil hydrometer (Fisher Scientific, Pittsburgh, PA, USA) (Bouyoucos 1936). We compared soil texture attributes across the *L. tridentata* cytotypes using MANOVA, with ploidy level and population (nested under ploidy) as model effects. We then used univariate ANOVA and Tukey HSD post-hoc tests (Tukey 1953, Kramer 1956) to analyze soil texture attributes individually. All statistical analyses were performed with the JMP statistical package (v9; SAS Institute, Cary, North Carolina, USA).

Macronutrient analyses were performed using a LaMotte Soil Outfit (model STH-4) configured for nitrate, phosphate, potassium, and pH (LaMotte Company, Chestertown, MD, USA), based on a single soil sample per study site. Macronutrient data were analyzed by MANOVA with ploidy level as a model effect; univariate ANOVA and Tukey HSD post-hoc tests were then used to evaluate individual macronutrients.

Results. Ecological Niche Models and Niche Similarity Tests. Distribution models for diploid, tetraploid, and hexaploid *L. tridentata*, and *L. tridentata* var. *arenaria*, predicted the published distributions of the individual cytotypes fairly well (Yang 1967, Barbour 1969, Yang 1970, Turner et al. 1995, Felger 2000, Hunter et al. 2001, Laport et al. 2012), with average AUCs (standard deviation) of 0.801 (0.086), 0.961 (0.014), 0.979 (0.008), and 0.999 (0.000), respectively (Fig. 1). Precipitation of the warmest quarter (46.1%) and mean annual temperature (34.3%) made the largest contributions to the diploid model, mean annual temperature (49.2%) and precipitation of the coldest quarter (23.7%) made the largest contributions

Table 1. Elevation, soil texture, macronutrient, and pH means (with standard deviations) for sites occupied by diploid, tetraploid, and hexaploid *L. tridentata*, and *L. tridentata* var. *arenaria*.

Cytotype	# of Sites	Mean elev. (SD)	Mean gravel (SD)	Mean sand (SD)	Mean silt (SD)	Mean clay (SD)	Mean N (SD)	Mean P (SD)	Mean K (SD)	pH (SD)
Diploid	14	1072.15 m (179.99)	23.97% (14.62)	66.43% (10.75)	23.84% (8.54)	9.73% (5.35)	7.68 ppm (6.68)	61.71 ppm (25.59)	130.21 ppm (45.03)	8.00 (.49)
Tetraploid	23	545.85 m (287.92)	17.81% (13.18)	67.29% (12.45)	24.90% (10.92)	7.84% (3.62)	10.43 ppm (16.90)	83.15 ppm (23.72)	143.4 ppm (34.46)	8.05 (.55)
Hexaploid	27	248.34 m (180.94)	26.53% (14.63)	75.61% (13.86)	18.98% (11.96)	5.41% (4.08)	7.69 ppm (4.85)	84.72 ppm (21.46)	132.31 ppm (41.68)	8.12 (.51)
L. tridentata var. *arenaria*	8	52.53 m (37.35)	7.39% (9.38)	88.56% (7.68)	8.46% (5.54)	2.99% (3.65)	7.50 ppm (2.67)	75.00 ppm (26.73)	134.38 ppm (19.90)	8.36 (.45)

to the tetraploid model, while mean annual temperature (39.6%) and precipitation of the warmest quarter (37.1%) made the largest contributions to the hexaploid model. Precipitation of the warmest quarter (44.7%) and annual mean temperature (24.7%) made the largest contributions to the *L. tridentata* var. *arenaria* model.

DIPLOID-TETRAPLOID COMPARISON. Visual inspection of the distribution models revealed high predicted suitability of both diploids and tetraploids near their distributional boundary, but suggested these cytotypes differed overall in their predicted distributions (Fig. 1A, B). The predicted distribution of diploids extended throughout areas where they are known to occur in the northern Chihuahuan Desert (Chihuahua, Coahuila, Texas, New Mexico), and further west than where they are currently present into the eastern Sonoran Desert (eastern and central Arizona; Fig. 1A). In contrast, the predicted tetraploid distribution was essentially restricted to the Sonoran Desert (northern Baja, Sonora, central Arizona, eastern California; Fig. 1B), where this cytotype is presently found.

Observed niche overlap between the diploid and tetraploid distribution models was $D = 0.381$. The niche identity test indicated a high degree of climatic niche identity, with values ranging from $D = 0.590$ to 0.910 (Fig. 2A). The observed value of overlap for diploid and tetraploid distribution models fell well below this distribution of expected values of similarity ($P < 0.01$), indicating the climatic niches of these cytotypes are different (Glor and Warren 2011). However, pairwise comparisons of the cytotype ranges from the niche similarity test indicated that diploid and tetraploid sites were climatically similar. The observed value of overlap was not significantly different from the range of pseudoreplicate comparisons between diploid sites and random background points drawn from the tetraploid range ($D = 0.254$ to 0.558, $P > 0.05$; Fig. 2D), but indicated tetraploid sites were climatically more similar to diploid sites than expected from comparisons to random points drawn from the diploid range ($D = 0.135$ to 0.298, $P < 0.01$; Fig. 2E). The observed distributional boundary between diploid and tetraploid cytotypes was not correlated with a significant climatic gradient in the variables used for ENM construction.

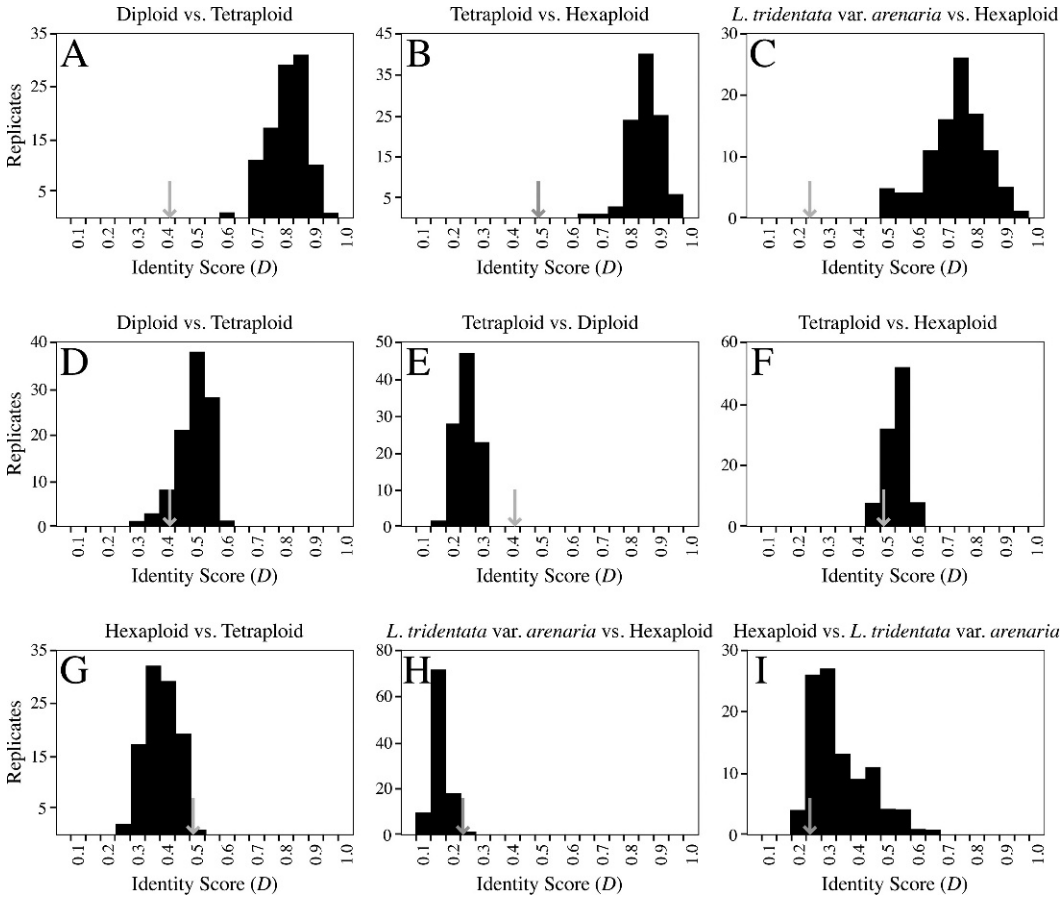

FIG. 2. ENM Tools analyses of observed niche overlap vs. niche identity between (A) diploids and tetraploids, (B) tetraploids and hexaploids, and (C) *L. tridentata* var. *arenaria* and hexaploids. ENM Tools analyses of niche similarity (background test) between (D) diploid sites and the tetraploid range, (E) tetraploid sites and the diploid range, (F) tetraploid sites and the hexaploid range, (G) hexaploid sites and the tetraploid range, (H) *L. tridentata* var. *arenaria* sites and the hexaploid range, and (I) hexaploid sites and the *L. tridentata* var. *arenaria* range. Histograms represent null distributions of niche overlap among ENMs generated from pseudoreplicate data sets randomly drawn from pooled locality data. Gray arrows on each graph indicate the observed niche overlap between ENMs. In all cases, if the observed niche overlap falls outside the null distribution of niche overlap, it is taken to represent a significant difference.

The observed statistic of overlap fell within the range of randomly-generated pseudoreplicate overlap values from the linear ($D = 0.336$ to 0.583, $P > 0.05$) and blob ($D = 0.333$ to 0.517, $P > 0.05$) range-breaking tests.

TETRAPLOID-HEXAPLOID COMPARISON. Visual inspection of distribution models revealed similar predicted climatic suitability of tetraploids and hexaploids throughout much of south-central Arizona and southern California. However, as noted above, the predicted tetraploid distribution was generally restricted to the Sonoran Desert throughout Sonora, Mexico and southern Arizona, and southeastern California (Fig. 1B). The predicted hexaploid distribution was generally concordant with their known occurrence along the lower Colorado River and north throughout the Mojave Desert in eastern California, southern Nevada and northwestern Arizona (Fig. 1C).

Niche overlap between the tetraploid and hexaploid distributions was $D = 0.467$, which fell below the range of randomly-generated pseudoreplicate data generated in the niche identity test, indicating these two cytotypes occur under different climatic regimes ($D = 0.632$ to 0.916, $P < 0.01$; Fig. 2B, Glor and Warren 2011). In contrast, niche similarity comparisons revealed that tetraploid and hexaploid sites were climatically similar. The

observed value of overlap was not significantly different from the range of pseudoreplicate comparisons between tetraploid sites and random background points drawn from the hexaploid range ($D = 0.403$ to 0.573, $P > 0.05$; Fig. 2F), but indicated hexaploid sites were climatically more similar to tetraploid sites than expected from comparisons to random points drawn from the tetraploid range ($D = 0.246$ to 0.460, $P < 0.05$; Fig. 2G). Neither the linear ($D = 0.278$ to 0.579, $P > 0.05$) or blob ($D = 0.277$ to 0.743, $P > 0.05$) range-breaking analyses suggested the presence of a significant climatic gradient in the variables used for ENM construction at the distributional boundary between tetraploid and hexaploid *L. tridentata*.

L. tridentata var. *arenaria*-Hexaploid Comparison. Both *L. tridentata* var. *arenaria* and hexaploids were predicted to have high suitability throughout southeastern California. The predicted *L. tridentata* var. *arenaria* distribution is restricted to a narrow strip in southeastern California and northeastern Baja, Mexico, while the predicted distribution of hexaploid *L. tridentata* stretches throughout the lower Colorado River drainage and includes the entire observed distribution of *L. tridentata* var. *arenaria* (Fig. 1C, D).

Observed niche overlap between the modeled *L. tridentata* var. *arenaria* and hexaploid distributions was $D = 0.213$, which fell below the identity values of randomly-generated pseudoreplicate data in the niche identity test ($D = 0.460$ to 0.919, $P < 0.01$; Fig. 2C), indicating significant niche differentiation. The niche similarity test revealed that *L. tridentata* var. *arenaria* sites were climatically more similar to hexaploid sites than expected from comparisons to random points drawn from the hexaploid range ($D = 0.068$ to 0.201, $P < 0.01$; Fig. 2H), and the observed value of overlap was not significantly different from the range of pseudoreplicate comparisons between hexaploid sites and random background points drawn from the *L. tridentata* var. *arenaria* range ($D = 0.169$ to 0.610, $P > 0.05$; Fig. 2I). The observed statistic of overlap fell below the range of randomly-generated pseudoreplicate overlap values from the linear ($D = 0.309$ to 0.690, $P < 0.01$) and blob ($D = 0.383$ to 0.828, $P < 0.01$) range-breaking tests, indicating the presence of a strong climatic gradient in the variables used for ENM construction associated with the distributional boundary of *L. tridentata* var. *arenaria* and hexaploid *L. tridentata*.

Soil Analyses. Texture of soils sampled from field sites were classified as sand (44 samples), loamy sand (32 samples), sandy loam (121 samples), silty loam (4 samples), loam (8 samples), loamy clay sand (1 sample), and clay loam (1 sample). Although none of the soil types was exclusive to particular ploidy level(s), sites occupied by the different *L. tridentata* cytotypes were distinguished significantly by texture characteristics (MANOVA, Wilks' lambda = 0.335, $F_{12,360} = 15.369$, $P < 0.001$). Univariate ANOVA indicated significant ploidy associations for several individual texture attributes following correction by sequential Bonferroni (Rice 1989; Table 1). For example, diploid and hexaploid sites had soils with more gravel content than tetraploid and *L. tridentata* var. *arenaria* sites ($F_{3,68} = 21.854$, $P < 0.001$; Table 1, Fig. 3A). Diploid and tetraploid sites had greater clay content than hexaploid and *L. tridentata* var. *arenaria* sites ($F_{3,68} = 18.557$, $P < 0.001$; Table 1). The sand dune-endemic *L. tridentata* var. *arenaria* was found at sites where soil sand content was substantially greater than for any cytotype of *L. tridentata* ($F_{3,68} = 42.086$, $P < 0.001$; Table 1, Fig. 3A).

Soil nutrient content varied substantially among sites (nitrogen, range = 5.0–75.0 ppm; phosphorus, range = 12.5–100.0 ppm; potassium, range = 50.0–250.0 ppm; pH, range = 7.1–9.2), and differed significantly among the *L. tridentata* cytotypes (MANOVA, Wilks' lambda = 0.722, $F_{12,169} = 1.856$, $P = 0.043$). In univariate ANOVA tests, only phosphate ($F_{3,68} = 3.184$, $P = 0.029$; Table 1, Fig. 3B) and pH ($F_{3,68} = 2.859$, $P = 0.042$; Table 1) were found to differ significantly between sites occupied by the cytotype races, with diploids inhabiting environments with less phosphorus and lower pH than polyploid populations.

Discussion. With three cytotypes broadly distributed throughout the Chihuahuan (diploid), Sonoran (tetraploid and hexaploid), and Mojave Deserts (hexaploid) (Fig. 1), *Larrea tridentata* inhabits both the hottest, driest areas on the North American continent below sea level along the lower Colorado River, as well as relatively mesic areas at elevations > 1500 m in the northern Mojave Desert and

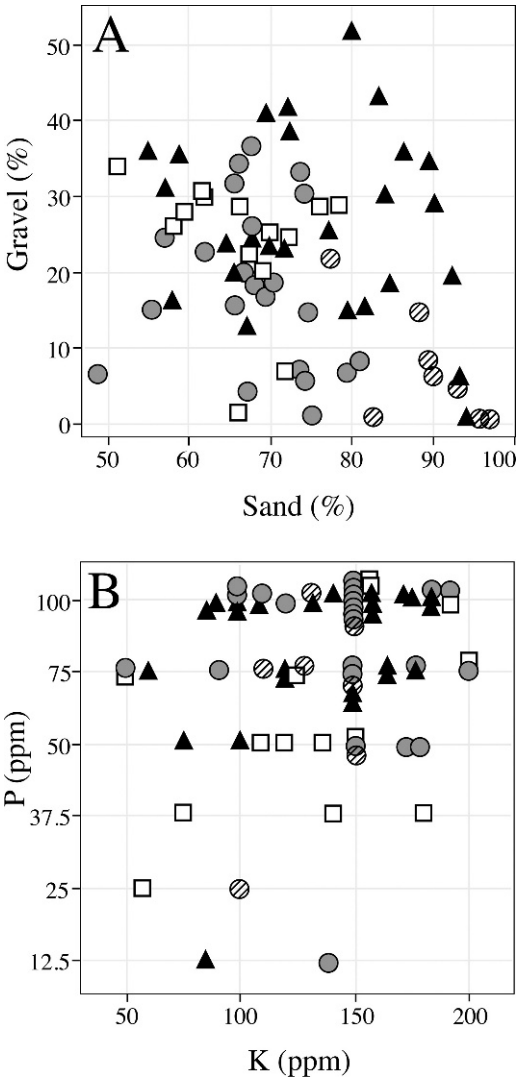

FIG. 3. Biplots showing (A) soil texture and (B) soil nutrients of field sites inhabited by diploids (open squares), tetraploids (grey circles), hexaploids (black triangles), and the narrowly distributed tetraploid endemic, *L. tridentata* var. *arenaria* (cross-hatched circles).

along the Sierra Madre Occidental in central Mexico (Turner et al. 1995). This broad geographic distribution is even more remarkable given the relatively recent arrival of creosote bush to the North American continent. Five species of *Larrea* reside in Chile and Argentina, and the North American *L. tridentata* originated via long distance dispersal from South America in the Pleistocene or late Pliocene (Laport et al. 2012). Polyploidy is thought to be a factor mediating the rapid ecological expansion of creosote bush across the warm deserts of the U.S. and Mexico (Barbour 1969, Hunter et al. 2001). The Ecological Niche Models and soil analyses presented here suggest that cytotype distributions are structured by ecological adaptation, but that competitive exclusion and niche conservatism may also play a role.

The Chihuahuan and Sonoran Deserts, where diploid and tetraploid *L. tridentata* occur (Fig. 1A, B), differ in a suite of physical and climatic features, including mean annual rainfall, mean annual temperature, and mean elevation (Russell 1931, Ackerman 1941, Schmidt 1979, Bahre 1995, Turner et al. 1995, MacEwen et al. 2005). In addition, many species of plants (Shreve 1942, 1951, Henrickson and Straw 1976, McLaughlin 1986), mammals (Riddle 1998, Riddle et al. 2000), reptiles (Morafka 1977), and bees (Rozen 1992, Danforth 1994) also reach their distributional limits at the boundaries of these deserts. Combined, these climatic and biotic discontinuities suggest an abrupt transition between the deserts, and Ecological Niche Models also indicate the boundary between diploid and tetraploid *L. tridentata* occurs in the uplands of southeastern Arizona (Fig. 1A, B, Laport and Minckley 2013). Analyses of niche identity further support that the ranges are climatically distinct (Fig. 2A), and that climate contributes significantly to their distributional limits. The aforementioned results are consistent with the hypothesis of ecological divergence among *L. tridentata* cytotypes. Further support can be inferred from the composition and spatial structuring of populations at cytotype range boundaries (Laport et al. 2012 and unpublished data). Based on intensive sampling in these areas, we have identified pure diploid and tetraploid populations in close proximity without clear geological barriers separating them. Such population structuring seems unlikely to occur in the absence of environmentally mediated fitness differences between cytotypes, though demographic stochasticity (Holt et al. 2005) and frequency dependent selection (i.e., minority cytotype exclusion; Levin 1975) may also play a significant role in establishing a zone of ''tension'' between reproductively incompatible diploid and polyploid populations.

On the other hand, analyses of niche similarity suggest that tetraploids occupy sites

that are climatically more similar to the diploid range than expected given the overall climatic differences between the ranges, and that diploid sites are not climatically distinguished from the tetraploid range (Fig. 2D, E). Moreover, despite the climatic, floral, and faunal indications of a clear border between the Chihuahuan and Sonoran Deserts, range-breaking analyses suggest the boundary is represented by a relatively modest climatic gradient. These findings suggest that intercytotype competition is an important factor restricting the spatial distributions of diploids, which otherwise would seem able to extend beyond their current range boundary. Overall similarities between diploid-occupied sites of the Chihuahuan Desert and tetraploid-occupied sites of the Sonoran Desert suggest an element of niche conservatism, in which the tetraploid *L. tridentata* shares climatic requirements with its progenitor.

The Sonoran and Mojave Deserts, where tetraploid and hexaploid *L. tridentata* occur (Fig. 1B, C), also differ climatically. The Sonoran Desert tends to be wetter and warmer than the Mojave Desert, which receives winter rainfalls originating from the Pacific Ocean (Turner 1994). However, unlike the general consensus regarding the boundary between the Chihuahuan and Sonoran Deserts, there is considerable disagreement over the location of the boundary between the Sonoran and Mojave Deserts. There are no obvious topographic barriers demarcating a boundary between the deserts and the uniqueness of the Mojave Desert has even been questioned (Turner 1994). However, based upon floristic (McLaughlin 1986) and faunal (Wood et al. 2012) assemblage patterns, contemporary opinion is that the deserts represent unique habitat. Distribution models and analyses of niche identity presented here suggest the distributions of tetraploid and hexaploid *L. tridentata* differ climatically (Fig. 1B, C) despite the broad overlap between the tetraploid and hexaploid ranges throughout the north-central and western portions of the Sonoran Desert (Laport et al. 2012).

The climatic differentiation between the tetraploid and hexaploid ranges appears to be less, however, than the climatic differentiation between the diploid and tetraploid ranges (Fig. 2B). Moreover, niche similarity analyses suggest that tetraploid sites are not climatically distinguished from the hexaploid range (Fig. 2F), and hexaploids tend to occupy sites that are more climatically similar to the tetraploid range than expected given the overall climatic differences between the ranges (Fig. 2G). The climatic similarity between the tetraploid and hexaploid ranges suggests that cytotype distributions in the western Sonoran Desert may be influenced as much by stochastic climatic variability (e.g., in the timing of summer monsoon and winter rainfall; Turner 1984, McLaughlin 1986), population processes (Holt et al. 2005), and intercytotype interactions (e.g., competition and minority cytotype exclusion; Levin 1975) as by ecological divergence, resulting in a geographic mosaic of sites occupied by tetraploid and hexaploid cytotypes in this region.

The Algodones Dunes, where *L. tridentata* var. *arenaria* occurs (Fig. 1D), comprise wind-blown deposits resulting from repeated inundations of the sub-sea level Salton Basin of southeastern California and northern Baja, Mexico over the last several thousand years (Brown 1923, Norris and Norris 1961). Despite their recent origin, the dunes harbor a suite of endemic plant and animal taxa (Luckenbach and Bury 1983, California Native Plant Society 2001, Van Dam and Van Dam 2008), including the tetraploid dune creosote, *L. tridentata* var. *arenaria*. This taxon is thought to be adapted to the peculiar edaphic habitat of the Algodones Dunes (Benson and Darrow 1981, Turner 1995), and niche identity analysis indicated that models for *L. tridentata* var. *arenaria* and hexaploid *L. tridentata* are climatically distinct.

However, both tetraploid and hexaploid *L. tridentata* occur in areas surrounding the Algodones Dunes, and our climatic distribution models did not suggest hexaploids should be excluded from the Algodones Dunes (Fig. 1C). Moreover, niche similarity analyses suggest *L. tridentata* var. *arenaria* and hexaploid *L. tridentata* sites are climatically similar (Fig. 2H, I). Relative site location and range size probably influenced these results; the range of *L. tridentata* var. *arenaria* occurs within the range of hexaploid *L. tridentata* and represents a subset of the hexaploid climatic niche (Hijmans 2012). Thus, it appears *L. tridentata* var. *arenaria* occurs in areas climatically similar (a subset and not identical) to hexaploid *L. tridentata*, with a sharp distributional boundary between the two taxa. Range-breaking analyses indicated a strong climatic

gradient at this range boundary, though this too may result from the relative locations of the ranges and the range sizes, as there are a limited number of ways to randomly draw the boundary between a small range contained within the larger range of a second species (McIntyre 2012). The boundary—whether climatically abrupt or not—is probably reinforced by edaphic factors that distinguish the Algodones Dunes from the adjacent stretches of Sonoran Desert (Table 1, Fig. 1C, D, Fig. 3A). Indeed, hexaploids are gradually replaced by dune creosote on the eastern flank of the dune system as the soil becomes sandier (Benson and Darrow 1981, Turner et al. 1995, Laport personal observation).

Soil characteristics are known to have a strong impact on desert plant species distributions (Gates et al. 1956, Ehleringer and Cooper 1988, Casper and Jackson 1997, Ogle and Reynolds 2004). The relationship between soil texture and moisture has been studied at multiple life-history stages in *L. tridentata* (Barbour 1969, McAuliffe 1994, Hamerlynck et al. 2002, Ignace and Huxman 2009) and found to influence plant survival and growth. Given the large-scale variation in soil texture observed in this study, and the statistical associations between soil features and cytotype distributions, it seems likely that soil texture is an important environmental factor for the system (Table 1, Fig. 3A). For example, hexaploid sites on average had very high gravel content, with significant differences to sites occupied by tetraploids and *L. tridentata* var. *arenaria*. Sites harboring the dune endemic *L. tridentata* var. *arenaria* had high sand content (Fig. 3A), in all likelihood contributing to its abrupt distributional boundary with the more widespread hexaploid cytotype.

Other things being equal, soils comprising large particles hold less moisture than soils comprising small particles, and it is tempting to speculate that soil texture differences across the Chihuahuan, Sonoran, and Mojave deserts reinforce the decrease in yearly precipitation across these regions, creating an east-west soil moisture gradient. Diploid sites from the Chihuahuan Desert have relatively fine-textured soils and experience relatively high amounts of rainfall, for example, while hexaploid sites from the Mojave Desert have rocky soils and relatively low amounts of rainfall (Figs. 1, 3). However, further work on the biological significance of soil texture on *L. tridentata* cytotypes would be illuminating. While texture is a major factor affecting water availability, and is likely to affect seedling survival, belowground competition and seasonally distributed (monsoon) rainfall may also be important for long-term survival. Moreover, the hydrology of desert soils is profoundly affected by the occurrence and depth of surface and sub-surface soil horizons, including the surface Av horizon, the argillic B horizon, and caliche—these structural features influence infiltration of precipitation and temporal persistence of soil moisture, probably to a greater degree than soil texture per se (McAuliffe 1994, Hamerlynck and McAuliffe 2008, 2010, McAuliffe and Hamerlynck 2010).

The survival and growth of *L. tridentata* plants is fundamentally affected by soil moisture (Ignace and Huxman 2009, McAuliffe and Hamerlynck 2010). In evaluating ecological divergence between chromosome races, we have focused on climatic variation (including precipitation, as inferred from climate models) and surface soil attributes (which influence soil moisture), but not topography, soil horizon structure, and other localized environmental features that influence soil hydrology, yet are logistically difficult to survey across a large geographic area. Future comparisons of the *L. tridentata* chromosome races may most profitably be focused on cytotype boundaries, where field experiments and comprehensive environmental sampling could be conducted across a smaller number of sites.

The ecological niche modeling and soil analyses presented here suggest that the distribution of *L. tridentata* cytotypes is influenced by multiple factors, representing a more complex situation than envisioned by classical work in the system. At face value, these findings seem consistent with recent experimental studies of polyploidization, which reveal that neopolyploids have some, but not all, features of established polyploid populations (Bretagnolle and Lumaret 1995, De Kovel and De Jong 2000, Maherali et al. 2009, Ramsey 2011). Although polyploidy appears to confer novel features to plants — potentially including "pre-adaptive" physiological and life-history traits — the trajectory of polyploid populations through niche space is probably influenced by natural selection (e.g., adaptation to local environmental factors via changes in gene frequencies), species

interactions (e.g., competition with progenitor cytotypes), and evolutionary constraints (e.g., failure to respond to natural selection because of genetic correlations or absence of genetic variation). Species distribution modeling may be particularly useful for highlighting the latter issue, in the context of niche conservatism.

Discussions of polyploid ecology often emphasize the potential for rapid divergence, because genome duplication affects many phenotypic and genetic traits simultaneously and because polyploids tend to have markedly different spatial distributions from diploids (Müntzing 1936, Levin 1983, Ramsey and Schemske 2002). Yet in most classical examples, related diploids and polyploids appear to have fundamental similarities in life form, habitat association, and phenology (Lewis 1980). This suggests that polyploidy may be a mechanism of rapid speciation and ecological divergence, while not so profoundly changing a species' phenotypic traits and genetic attributes as to shift its fundamental bauplan. Despite the very broad geographic distribution of *L. tridentata* cytotypes, for example, they all occur in warm desert environments and are absent from cooler and wetter areas; in South America, as well, *Larrea* taxa occur in arid environments (Barbour 1969, Hunziker et al. 1972). The tendency of related species to share ecological affinities (niche conservatism, Ricklefs and Latham 1992, Peterson et al. 1999) has been documented using species distribution models and quantitative tests of niche identity and similarity, especially in animals (Peterson et al. 1999, Peterson and Vieglais 2001, Graham et al. 2004, Wiens and Graham 2005, Kozak et al. 2008), yet is rarely discussed in the context of polyploidy (but see McIntyre 2012, Glennon et al. 2012, Godsoe et al. 2013). Together with experimental studies of neopolyploids and field investigations of established polyploid populations, niche modeling may be very useful for understanding the role(s) of polyploidy in ecological diversification.

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