AREAS OF ENDEMISM OF PLANTS IN THE SOUTH-CENTRAL AND SOUTHWESTERN NEARCTIC REGION[1]

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ABSTRACT

The history and connections of the flora of south-central/southwestern (SC/SW) North America have been studied and summarized in biogeographic regionalization. However, some studies show contrasting delineations of the SC/SW North American provinces that could be better determined using quantitative methods. We aimed to find spatial patterns of a set of plants in the SC/SW United States by conducting endemicity analysis (EA) on different scales. We first built a dataset with 81,965 specimen point records of 400 species from 174 genera and 61 families of angiosperms and two genera of gymnosperms using digitized specimen data from iDigBio. We then performed EA at four different scales to identify the areas of endemism (AoEs).

We obtained 28 AoEs with different cell sizes by selecting each AoE under the grid size that yielded the highest number of high-scoring species. The study region split into two significant centers of accumulation of nested or partially overlapping AoEs: the SW and SC consensus areas. In these parts of the Nearctic region, many genera/clades, among those in the dataset, showed a geographic split into western and eastern clades. The split corresponded to an environmental and physical barrier known as Cochise Filter Barrier. The Sonora–Mojave arid center, parts of South Texas, and the Chihuahuan Desert harbor basally branching taxa of several genera and even families, based on the observations of some species, which allowed identification of the AoEs.

Key words: Areas of endemism, biogeographic patterns, floristic regionalization, Madrean region, Nearctic, southwestern deserts.

By defining areas of homogeneous species composition, biogeographical frameworks provide spatial units of analysis that are useful in macroecological, evolutionary, and systematic studies of the processes that shape or maintain species distributions (Morrone, 2018). Congruent species distributions define units of different ranks (choria) in a hierarchical floristic regionalization system (Takhtajan, 1978). Choria are distinct from the units of ecological regionalization (ecoregions), which define biomes, such as those in the monumental work by A. Engler (1879). The biotic provinces by L. Dice (1943) attempted to map the major ecological divisions of North America. More recently, the inclusion of widespread species in the statistical biogeographic analysis resolves the patterns of biomes, rather than historical areas (Murphy et al., 2019). Conversely, regionalization systems based on endemic species (e.g., Rzedowski, 1978; Cronquist, 1982; Takhtajan, 1986; Morrone, 2014; Morrone et al., 2017) rather than biomes resolve historical areas.

The history and connections of the flora of south-central/southwestern (SC/SW) North America have long been a subject of research (Cooper, 1859; Engler, 1879; Harshberger, 1911; Axelrod, 1958, 1975; Udvardy, 1975; Raven & Axelrod, 1978; Felger, 1980; Axelrod & Raven, 1985; Rzedowski, 1993; Wen & Ickert-Bond, 2009; Rundel, 2011; Sosa & De-Nova, 2012; Baldwin, 2014; Baldwin et al., 2017; Graham, 2018; Sosa et al., 2018, 2020; Vásquez-Cruz & Sosa, 2019; Mishler et al., 2020). One of the major and long recognized biotic boundaries in North America is the east to west boundary (Katinas et al., 2004; Escalante et al., 2013; Gámez et al., 2016; Mishler et al., 2020). In the southern United States, it passes through Texas (Saghatelyan, 2009, 2015, 2017), where it separates almost adjacent floras (Supplementary Appendix S1), the flora of Big Bend National Park (BB) from the floras of Edwards Plateau (EP) and South Texas Plains (S TX). Texas lies on the intersection of the Madrean and Atlantic regions in Takhtajan's (1986) floristic system, as

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well as close to the Nearctic/Neotropical Mexican Transition Zone of Morrone (2010) and Halffter and Morrone (2017).

While there is a consensus in the delimitation of the northern provinces in temperate North America, there are some contrasting hypotheses concerning southern floristic units. In particular, in Takhtajan (1986), the Chihuahuan and Tamaulipan subprovinces are in the Madrean region of the Madrean subkingdom, and the Prairies province is in the Atlantic region of the Boreal subkingdom. Some other authors do not delineate these subkingdoms in the Holarctic kingdom as well as refer the Tamaulipan chorion to the Atlantic region of the Nearctic (Escalante et al., 2007, 2021). In the McLaughlin (2007) floristic system, EP falls in the Comanchian province (not recognized and included in the Prairie province in Takhtajan, but delineated in Dice [1943]). However, McLaughlin placed the Comanchian province and the entire Prairie province in his Southwestern (Madrean by Takhtajan) region.

These contrasting physiographic delineations could now be resolved with the application of quantitative methods of biogeographic analysis using ample digitized distributional data of North American plants. The search for biogeographic patterns starts with finding areas of endemism (AoEs), which are fundamental entities of analysis in biogeography, and a key step for biogeographical regionalization (Morrone, 1994; Linder, 2001; Mercado-Gómez & Escalante, 2019; Liria et al., 2021). The first explicitly defined and detailed methods for finding AoEs were proposed by Morrone (1994, 2009), with an AoE defined as a monophyletic group of geographic units that share at least two endemic species (biogeographic synapomorphies). Another widely used method is endemicity analysis (EA), which identifies patterns of non-random co-occurrence in the geographical distribution of different taxa (Szumik et al., 2002; Szumik & Goloboff, 2004). While this method is well established, studies using EA in the Americas have mostly focused on animals rather than plants. There is only one EA study in North America (Weirauch et al., 2017) that includes plants but only as hosts of the main object of their analysis, North American Miridae insects. The patterns derived from that analysis are mostly Miridae patterns.

Bertelli et al. (2017) argued that studies that have sought to discover patterns of endemism generally have not been sufficiently spatially refined and have not undertaken the discovery process in a manner that minimizes assumptions and biases. We conducted an EA on different scales aiming to identify AoEs of 400 mostly angiosperm species, in order to help resolve the controversy over the regionalization of SC/SW North America. We addressed the following questions: (1) where are the AoEs of these plants in SC/SW North America? (2) Are these AoEs congruent with the spatial patterns identified in previous phytogeographical studies? (3) What are the global ranges of the genera and connections of some of the high-scoring species that define these AoEs? (4) Do the AoEs support a subdivision to the Boreal and Madrean subkingdoms and Atlantic and Western regions in North America?

Materials and Methods

STUDY AREA

The study area includes the U.S. parts of the SC/SW North American warm deserts and adjacent xeric areas, previously identified as biogeographic units (Dice, 1943; Takhtajan, 1978; Cronquist, 1982; Axelrod & Raven, 1985; McLaughlin, 1986, 2007; Morrone et al., 2017). Two areas in southern Texas (Supplementary Appendix S1), BB and S TX, represent the northern parts of the Chihuahuan and Tamaulipan subprovinces of Takhtajan (1986) respectively. S TX and EP (of the Prairie province) also represent an ecotone between the floras of the southwestern (Madrean) and eastern (Atlantic) regions (Saghatelyan, 2015, 2017). The floras of the Sonoran and Mojave Deserts in southwestern Arizona, northwestern Mexico, and southeastern California represent the Sonoran province/subprovince of all authors. Additionally, Dice (1943) and McLaughlin (2007) delineated the uplands of southeastern Arizona, southwestern New Mexico, and northwestern Sonora as the Apachian (Navahonian) province.

We assembled the spatial dataset based on the species data downloaded from the iDigBio database. We did not trim the specimen point records merely to the study area in order to include the global ranges of the species in our dataset. Consequently, the combined species occurrence points extended from 50° to 18° latitude and –125° to –75° longitude (Supplementary Appendix S2). For comparison with the cold Great Basin Desert, we included additional species from the Bear River flora in northeastern Utah.

The Sonoran Desert is the most varied in species diversity and life forms of the North American deserts. It is also the lowest in elevation (sea level to 900 m) and rainfall (Graham, 2010). It prominently differs from the other three North American deserts by having mild winters. Two visually dominant life forms of plants distinguish the Sonoran Desert from the other North American deserts: legume trees and columnar cacti. Approximately half of the biota is of tropical origin (Dimmitt et al., 2015). The Apachian province represents the enclaves of the Madrean pine-oak woodlands (Madrean sky-islands) at higher elevations, surrounded at lower elevations by the Sonoran and Chihuahuan Deserts.

The Big Bend in Trans Pecos, southwest Texas (Chihuahuan Desert), is distinct from the surrounding areas because of its numerous mountain systems and low arid basins with elevations ranging from 1000 to 7835 ft. (Powell, 1998; Powell & Worthington, 2018). Lower elevations are dominated by shrubs, leaf-rosette semi-succulents (such as yuccas, agaves, and sotols), and desert grasslands. In the central Trans Pecos, the largest mountain systems are increasingly mesic and dominated by woodlands at mid to higher elevations. This is the easternmost edge of the Madrean sky-islands. The EP of the Prairies province in south-central Texas has elevations ranging from 450 to 3000 ft. Its climax vegetation (before European settlement) was an open temperate grassland, with shrubs and low trees along rocky slopes. South Texas Plains, located to the south of the EP, support extensive subtropical dryland Tamaulipan thorn scrub and mesquite-grassland vegetation (Correll & Johnston, 1970). This mostly sandy area in the Rio Grande Plain supports representatives of genera and even families not found indigenous elsewhere in North America north of Mexico (Thorne, 1993). Sixty-six woody species reach their northern limit of distribution in S TX (Lonard et al., 1991).

DATA

We compiled a dataset with 400 mostly xerophytic species belonging to 174 genera and 61 families of angiosperms, and two genera in two families of gymnosperms from the floras of the study area (Supplementary Appendix S3). The simultaneous analysis of different unrelated co-distributed taxa is a powerful approach that may reveal patterns that are not apparent from single taxon analyses (Gámez et al., 2016). Members of recently studied genera/families of angiosperms with published molecular phylogenies (Table S2 in Supplementary Appendix S4) were preferentially included in the dataset for the study area. Seven of the families comprise 254 species in the dataset (63.5% of all the sp.): Asteraceae (111 sp.), Fabaceae (43 sp.), Apocynaceae (28 sp.), Hydrophyllaceae (23 sp.), Boraginaceae (19 sp.), Cactaceae (19 sp.), and Nyctaginaceae (11 sp.). More than half of the species came from the checklists of BB, EP, and S TX, where they were classified into geographic elements (species with congruent distributions). We also consulted SEINet Portal Network (2020) and the Jepson Flora Project (2021) for inclusion of mostly desert species from southern Arizona and California.

To sample the central Rocky Mountains/Great Basin area we included species from the checklist of the Bear River flora, Utah (L. Shultz, Utah State University, pers. comm.). We downloaded digitized herbarium specimen data for all the species from iDigBio, the Integrated Digitized Biocollections (<https://www.idigbio.org/portal>, last accessed 28 April 2020). All geographic coordinates derived from coordinates of the original data. We checked the nomenclature based on the International Plant Name Index (<https://www.ipni.org/>). During data cleaning, we eliminated all duplicates, records on university campuses or botanical gardens, and erroneous records such as “0” or “NA” values for latitude and longitude. The maps were contrasted with those documented by the Biota of North America Program (Kartesz, 2016), online databases (e.g., EOL: <https://eol.org/>), and literature (e.g., Turner et al., 2003). The final cleaned dataset included 81,851 specimen point records unique for each of 400 species with seven to 800 points per species. The species list with authorities is in Supplementary Appendix S3.

ENDEMICITY ANALYSIS

We searched for AoEs using the NDM and VNDM vers. 3.1 programs (Goloboff, 2016), which applies the method proposed by Szumik et al. (2002) and Szumik and Goloboff (2004). As input data, NDM uses a list of species that includes georeferenced locations for each specimen, automatically transformed into a presence/absence matrix in cells of a user-defined grid. The method searches for areas (sets of cells) that are congruent with the distribution of as many species as possible. It identifies an AoE as the congruent distribution of two or more species. Based on an optimality criterion, NDM evaluates a candidate area (an area set) by assigning a score to each species depending on how well the species fits the area, with absence in parts of the area and presence in cells outside the area being penalized.

Each area of endemism receives an endemicity score (E) that is calculated as the sum of the endemicity scores (*e*) of all the species that supported the area. The E value depends on the number of species concordant with the area and the degree of concordance between the area and those species (Aagesen et al., 2013). As the E value increases, the support for the AoE is higher.

We performed preliminary analyses with varying grid sizes to explore different analytical options and increase the chances of finding different areas. Additionally, the areas that survive changes in grid size can be more strongly supported by the data (Casagranda et al., 2009; Elías & Aagesen, 2019). The search for optimal parameters showed a better outcome with rectangular rather than square cells in our study region. In addition, analyses with cells that are larger than frequently used in other regions, cells of 1° × 1° and 2° × 2° latitude-longitude, showed a better resolution.

We analyzed the dataset with 81,965 points of 400 species with four different cell sizes and three minimum species scores to explore the distribution patterns at different scales and the robustness of the resulting areas to changes in grid size and shape. Grids at latitude-longitude cell sizes of 3.3° × 2.5°, 4° × 4°, 2.5° × 4°, and 3° × 4°, origin at 11° latitude and –60° longitude, were used. To facilitate the presentation of the results, we computed the consensus areas of endemism (CAs) by combining all areas (sets of cells) that shared endemic taxa with a loose consensus rule and cut-off values at 40% similarity. The loose consensus rule combines all area sets that share a user-defined percentage of their defining species with at least one other area set in the consensus (Aagesen et al., 2013). To define the AoEs, we combined similar CAs from the different analyses based on their endemicity score E.

Final EAs were performed using NDM ver. 3.1 (Goloboff, 2016), saving all sets with scores higher than or equal to 2.0 with two or more defining species. The search was performed 100 times using edge proportions, and we retained overlapping subsets if 98% of their defining species were unique. We used different minimum species scores (*e*) to find more areas. From the sets obtained at cell sizes 3.3° × 2.5° and 4° × 4°, we selected the species with the minimum score $e = 0.8$, while for the analysis at cell sizes 2.5° × 4° and 3° × 4°, we selected the endemic species with a minimum score $e = 0.68$ and 0.7 respectively, and calculated the consensus areas to identify candidate AoEs.

We examined the results using VNDM (Goloboff, 2016), converted the CAs of all grid sizes into shapefiles (.shp), and mapped with QGIS vers. 3.6.3 (QGIS, 2021). Several CAs produced by the analyses with varying cell sizes had a similar outline with differences of only one or two endemic species. We intersected all CAs of different cell sizes to produce the AoEs and named them after known floristic provinces or geographic terms. We compared the outlines of the AoEs with previous regionalization units, particularly those in Takhtajan (1986) and McLaughlin (2007).

In addition, considering that Escalante et al. (2021) recently proposed a new map and synonyms of the hierarchical regionalization of the Nearctic region, we overlapped our AoEs with the subregions, dominions, and provinces of Escalante et al. (2021), in order to analyze the equivalence between our AoEs and that classification.

Finally, to reveal the floristic sources of the identified AoEs, we consulted molecular phylogenetic literature (Table S2 in Supplementary Appendix S4) on the genera represented in the AoEs to clarify vicariance relationships of some of the high-scoring endemic species in the AoEs or trace migration routes of their ancestors.

Results

We summarized the results of NDM analyses (Goloboff, 2016) at different cell sizes in Tables 1 and 2 and Figures 1–5 (see also Tables S1 and S2 in Supplementary Appendix S4, and Figs. S1–S6 in Supplementary Appendices S5 and S6). The CAs of the 2.5° × 4° and 3° × 4° cells had many similar areas, with the first group (25 CAs) providing finer results than the second group (13 CAs). We used the CAs selected from the analyses with 2.5° × 4° and 3° × 4° cells, combined with the ones selected from the analyses with 4° × 4° and 3.3° × 2.5° cells to define the AoEs. We identified 28 AoEs, including two candidate AoEs, which, although had a score of 1.75–2.0 each, had two and four endemic ($e = 1.0$) taxa. Several of the AoEs were nested or partially overlapping, and there was a clear split into two significant centers of accumulation of such AoEs in the study region, the SW and SC consensus areas, shown on Figure S1 (j2) and (j4) (see Supplementary Appendix S5).

All four analyses (Figs. 1–4) recovered AoEs with the highest scores in the SW (E = 6.78–17.35). The total number of species that supported an area under at least one grid size was 240 (Table S1 in Supplementary Appendix S4). We considered 28 AoEs obtained with different cell sizes, selecting each AoE under the grid size that yielded the highest number of high-scoring species. The list of final AoEs and their supporting species in Table 2 starts from the northernmost area, moving southward, and then eastward. The comparison with the hierarchical regionalization of Escalante et al. (2021) is shown in Table 3. Although there are some equivalences with that proposal, most of our AoEs probably correspond to intermediate categories (between the main categories, like subdominions; Escalante, 2009). Our other AoEs could correspond to two or more biogeographic units or be located between two biogeographic units, named as “unions” and “transitions” respectively, by Noguera-Urbano and Escalante (2015). All the AoEs are described below and shown in Figure 5 (see also Tables S1 and S2 in Supplementary Appendix S4; Figs. S1 and S2 in Supplementary Appendix S5).

AoE 1. Mid Rocky Mountains (47 to 37 lat., –116 to –110 long.) and **AoE 2. East Great Basin–Rocky Mountains** (41 to 33 lat., –137 to –109 long.) embrace parts of the Rocky Mountain and Great Basin provinces of Takhtajan (1986). Four (AoE 1) and three (AoE 2) species of broadly northern temperate (*Astragalus* L., *Androsace* L., and *Angelica* L.) and western North American (*Balsamorhiza* Hook. ex Nutt.) genera define these AoEs. Eleven species total ($e < 0.88$)

Table 1. Number of sets and consensus areas of endemism (CAs) for different cell sizes, their ranges of endemicity scores (E), and number of endemic taxa in them.

Cell size (latitude × longitude)	Number of sets	Number of CAs	E	Number of endemic species
3.3° × 2.5°	98	20	2.07–6.78	2 to 15
4° × 4°	61	15	2.00–11.49	4 to 17
2.5° × 4°	106	25	2.42–15.96	4 to 26
3° × 4°	80	13	2.69–23.57	3 to 61

of temperate genera support these AoEs in different analyses.

AoE 3. South Rocky Mountains–Colorado Plateau–East Madrean (38 to 22 lat., –118 to –98 long.) is a large AoE defined by five widespread species in open, arid, mountainous areas (*e* = 0.80–0.84), like *Gutierrezia microcephala* (DC.) A. Gray, *Allionia incarnata* L., *Baileya multiradiata* Harv. & A. Gray, *Thymophylla pentachaeta* (DC.) Small, and *Juniperus monosperma* (Engelm.) Sarg. Nine species total support AoE 3 in different analyses. They are either in mostly northern/SW North American genera (*Asclepias* L., *Baileya* Harv. & A. Gray ex Torr.) or in western/SW North American clades of mostly temperate families, e.g., Rosaceae (*Cercocarpus montanus* Raf., *Fallugia paradoxa* (D. Don) Endl. ex Torr.) and Fagaceae (*Quercus grisea* Liebm.). The latter taxa are among the core elements of the Cordilleran Floristic Province sensu Axelrod and Raven (1985). AoE 3 coincides with the Great Basin and Southern Rocky Mountains sectors of that province with the species extending to the east and south.

AoE 4. Great Basin–Colorado Plateau (42 to 33 lat., –120 to –109 long.) includes the western and southern parts of the Great Basin province and the western portion of the Colorado Plateau. It coincides with the Great Basin and western part of the Colorado element of McLaughlin's (1986) analysis. Three species of SW North American/amphitropical genera (*Hymenoxys cooperi* (A. Gray) Cockerell, *H. lemmonii* Cockerell, and *Cryptantha recurvata* Coville) support the area (*e* = 0.71–1.00). A nested area, **AoE 4.1 South Great Basin–Mojave**, is supported by three species (*Ephedra nevadensis* S. Watson, *Cryptantha recurvata*, and *Hymenoxys cooperi*) with *e* = 0.86–1.00.

AoE 5. Southern California Floristic Province–Southeast Great Basin–Mojave–North Sonora (42 to 31 lat., –121 to –113 long.) embraces the Mojave Desert, parts of Southern California Floristic Province (CFP), and the adjacent provinces. At least four species of mostly SW North American/amphitropical genera (*Phacelia* Juss., *Encelia* Adans., and *Thamnosma* Torr. & Frém.) support this AoE with scores *e* > 0.813.

AoE 6. Mojave–North Sonora (36 to 30 lat., –117 to –110 long.) is supported by 12 species (*e* = 0.81–1.00) of the xerophytic clades in SW North American genera, including a monotypic endemic genus *Hesperocallis* A. Gray. A nested **AoE 6.1 Mojave–South Great Basin** is supported by three species (*Cryptantha mohavensis* (Greene) Greene, *Brickellia incana* A. Gray, and *Phacelia austromontana* J. T. Howell) with *e* = 0.83–1.00. Another nested **AoE 6.2 Mojave** has four endemic species of *Cryptantha* and *Phacelia* and subendemic in AoE 6 monotypic genus *Stephanomeria* Nutt. AoE 6 coincides with the Mojavian element of McLaughlin (1986).

AoE 7. South Great Basin–Mojave–North Sonora (39 to 33 lat., –119 to –112 long.) is supported by six species (*e* = 0.81–0.94) of western/SW North American genera (*Cryptantha* Lehm. ex G. Don, *Argemone* L., *Phacelia*, *Brickellia* Elliott., and *Stephanomeria*). Their ranges extend from the Mojave Desert across the southern Great Basin and northern Sonoran province.

AoE 8. South Sierra Nevada–Mojave (37.6 to 34 lat., –119 to –116 long.) coincides with the Mojave subprovince and southeastern mountains in the CFP, including south high Sierra-Nevada. It has three endemic species (all with *e* = 1.0) of the mostly SW North American/amphitropical genera *Phacelia* and *Cryptantha*.

AoE 9. Sonoran (36 to 23 lat., –117 to –106 long.) coincides with the Sonoran chorion of all authors and is supported by six species of the Sonoran Desert with *e* scores > 0.89, including the monotypic endemic genus *Olneya* A. Gray and the monotypic endemic family Simmondsiaceae Nutt. The other species represent two subtropical to warm temperate genera with disjunctive Old World/New World distribution (*Lycium fremontii* A. Gray subsp. *viscidum* Wiggins and *Fagonia laevis* Standl.), a tropical/subtropical American genus (*Porophyllum gracile* Benth.), and a SW North American genus (*Psilostrophe cooperi* (A. Gray) Greene).

AoE 10. Southwest North American (39 to 28 lat., –121 to –110 long.) is a larger area (E = 10.9) that includes several partially overlapping or nested areas: AoE 4 to AoE 9. It is supported by 17 species

Table 2. Areas of endemism (AoEs) obtained from the consensus areas of endemism of all analyses including different cell sizes with their endemicity score (E), the endemic species with their score (*e*), and the number of sets.

AoE	E	Endemic species (*e*)	Number of sets
1. Mid Rocky Mountains	2.17–2.42	*Astragalus cibarius (0.700–0.868)* *Astragalus utahensis (0.000–0.714)* *Balsamorhiza macrophylla (0.684–0.733)* *Androsace filiformis (0.000–0.700)*	4
2. East Great Basin–Rocky Mountains	2.26–2.51	*Astragalus argophyllus (0.780)* *Astragalus kentrophyta (0.778)* *Angelica pinnata (0.707)*	1
3. South Rocky Mountains–Colorado Plateau–East Madrean	3.26–3.51	*Gutierrezia microcephala (0.821–0.833)* *Allionia incarnata* var. *incarnata (0.000–0.800)* *Baileya multiradiata (0.827–0.840)* *Thymophylla pentachaeta (0.808–0.820)* *Juniperus monosperma (0.000–0.804)*	2
4. Great Basin–Colorado Plateau	2.53–2.78	*Hymenoxys cooperi (1.000)* *Hymenoxys lemmonii (0.706)* *Cryptantha recurvata (0.824)*	1
4.1 South Great Basin–Mojave	2.61–2.86	*Ephedra nevadensis (0.000–0.955)* *Cryptantha recurvata (0.864–1.000)* *Hymenoxys cooperi (0.841–0.856)*	2
5. Southern California Floristic Province–Southeast Great Basin–Mojave–North Sonora	3.31–3.56	*Encelia actoni (0.875)* *Chorizanthe corrugata (0.813)* *Phacelia curvipes (0.813)* *Phacelia lemmonii (0.813)*	1
6. Mojave–North Sonora	4.07–4.42	*Hesperocallis undulata (0.000–1.000)* *Grusonia kunzei (0.833–1.000)* *Gaillardia arizonica (0.833–1.000)* *Brickellia desertorum (0.000–0.917)* *Cylindropuntia acanthocarpa (0.000–0.917)* *Baileya pauciradiata (0.000–0.833)*	3
6.1 Mojave–South Great Basin	2.67–2.92	*Cryptantha mohavensis (1.000)* *Brickellia incana (0.833)* *Phacelia austromontana (0.833)*	1
6.2 Mojave	2.50–2.75	*Stephanomeria parryi (0.000–1.000)* *Cryptantha mohavensis (0.800–0.875)* *Phacelia parishii (0.800–0.875)* *Phacelia neglecta (0.000–0.800)*	3
7. South Great Basin–Mojave–North Sonora	5.25–5.50	*Cryptantha utahensis (0.938)* *Phacelia rotundifolia (0.938)* *Argemone corymbosa (0.938)* *Phacelia curvipes (0.813)* *Brickellia desertorum (0.813)* *Stephanomeria parryi (0.813)*	1
8. South Sierra Nevada–Mojave	3.00–3.25	*Cryptantha mohavensis (1.000)* *Phacelia mojavensis (1.000)* *Phacelia austromontana (1.000)*	1
9. Sonoran	3.36–3.61	*Porophyllum gracile (0.000–0.988)* *Simmondsia chinensis (0.000–0.972)* *Lycium fremontii (0.000–0.902)* *Fagonia laevis (0.000–0.898)* *Olneya tesota (0.000–0.889)* *Psilostrophe cooperi (0.000–0.898)*	5
10. Southwest North American	10.87–11.49	*Centrostegia thurberi (0.864–1.000)* *Chorizanthe rigida (0.864–1.000)* *Eschscholzia minutiflora (0.000–0.808)* *Cylindropuntia acanthocarpa (0.000–0.813)* *Cylindropuntia echinocarpa (0.000–0.864)*	3

AoE	E	Endemic species (*e*)	Number of sets
		Cylindropuntia ramosissima (0.818–0.939)	
		Grusonia parishii (0.000–0.813)	
		Phacelia cryptantha (0.000–0.909)	
		Phacelia fremontii (0.000–0.818)	
		Brickellia atractyloides (0.818–0.938)	
11. Mogollon	2.00–2.25	*Tiquilia latior (1.000)*	1
		Encelia resinifera (1.000)	
12. Colorado Plateau–Mojave	1.75–2.00	*Brickellia incana (0.833–1.000)*	4
		Brickellia longifolia (0.000–1.000)	
		Phacelia neglecta (0.000–1.000)	
		Phacelia parishii (0.000–1.000)	
13. Madrean Region Montane	6.77–7.02	*Rhus virens (0.892)*	1
		Rhus microphylla (0.775)	
		Cologania angustifolia (0.816)	
		Cylindropuntia leptocaulis (0.786)	
		Tiquilia canescens (0.750)	
		Juniperus deppeana (0.738)	
		Nama hispida (0.714)	
14. Apache–North Chihuahuan	2.96–3.29	*Pinaropappus parvus (0.700–1.000)*	6
		Acleisanthes chenopodioides (0.000–1.000)	
		Porophyllum scoparium (0.000–0.857)	
		Tiquilia gossypina (0.000–0.821)	
		Hedeoma hyssopifolia (0.000–0.821)	
		Leuciva dealbata (0.000–0.729)	
15. Sonoran–Chihuahuan	5.20–5.45	*Thamnosma texana (0.813)*	1
		Aloysia wrightii (0.806)	
		Acleisanthes longiflora (0.806)	
		Thymophylla pentachaeta (1.000)	
		Acourtia wrightii (0.969)	
		Berberis haematocarpa (0.813)	
16. Chihuahuan (to South Prairie)	9.15–9.58	*Carlowrightia texana (0.694–0.833)*	4
		Asclepias brachystephana (0.711–0.806)	
		Asclepias texana (0.000–0.733)	
		Dalea pogonathera (0.000–0.789)	
		Telosiphonia macrosiphon (0.000–0.767)	
		Tiquilia greggii (0.750–0.767)	
		Guaiacum angustifolium (0.000–0.767)	
		Cryptantha mexicana (0.000–0.706)	
		Jefea brevifolia (0.719–0.733)	
		Lygodesmia texana (0.000–0.711)	
		Boerhavia linearifolia (0.694–0.706)	
		Linum vernale (0.000–0.700)	
17. North Chihuahuan	3.19–3.44	*Cynanchum pringlei (0.688–1.000)*	3
		Tiquilia gossypina (0.000–1.000)	
		Acleisanthes crassifolia (0.000–1.000)	
		Thymophylla micropoides (0.000–0.833)	
		Funastrum torrei (0.000–0.833)	
18. Central Texas	3.02–3.38	*Lupinus texensis (0.000–0.925)*	5
		Matelea biflora (0.000–0.864)	
		Amblyolepis setigera (0.000–0.864)	
		Desmanthus velutinus (0.000–0.829)	
		Carlowrightia torreyana (0.000–0.833)	
		Brickellia dentata (0.000–0.806)	
18.1 Southeast-central Texas	2.25–2.50	*Brickellia dentata (0.750–1.000)*	3
		Dalea lasiathera (0.750–1.000)	
		Mimosa latidens (0.000–0.813)	

Table 2. *Continued*

AoE	E	Endemic species (*e*)	Number of sets
19. South Texas–Coahuila	3.14–3.50	*Funastrum torrei (0.000–1.000)* *Tiquilia gossypina (0.000–1.000)* *Brickellia cylindracea (0.000–1.000)* *Chamaesaracha edwardsiana (0.000–0.833)* *Acleisanthes acutifolia (0.000–1.000)*	6
20. North Chihuahuan–Tamaulipan	2.54–2.79	*Johnstonella mexicana (0.875)* *Viguiera stenoloba (0.833)* *Boerhavia linearifolia (0.833)*	1
21. Chihuahua–Tamaulipas–Sierra Madre Oriental	10.48–10.73	*Condalia ericoides (0.833)* *Peganum mexicanum (0.778)* *Heliotropium confertifolium (0.833)* *Acleisanthes obtusa (0.778)* *Asclepias brachystephana (0.775)* *Cynanchum barbigerum (0.750)* *Brickellia laciniata (0.750)* *Vachellia rigidula (0.722)* *Forestiera angustifolia (0.705)* *Justicia pilosella (0.705)* *Psilostrophe gnaphalodes (0.700)*	1
22. East Madrean–Tamaulipan	9.57–9.82	*Cynanchum barbigerum (0.906)* *Menodora heterophylla (0.781)* *Cordia podocephala (0.750)* *Heliotropium confertifolium (0.750)* *Matelea reticulata (0.750)* *Justicia pilosella (0.725)* *Gochnatia hypoleuca (0.722)* *Mimosa malacophylla (0.719)* *Acleisanthes obtusa (0.694)* *Chaptalia texana (0.694)* *Helietta parviflora (0.694)* *Tiquilia mexicana (0.688)*	1
23. South-central U.S.A.–East Madrean	8.82–10.00	*Cynanchum maccartii (0.000–1.000)* *Dalea lasianthera (0.000–1.000)* *Menodora heterophylla (0.000–1.000)* *Guaiacum angustifolium (0.000–1.000)* *Asclepias texana (0.000–1.000)* *Acleisanthes crassifolia (0.000–1.000)* *Yucca constricta (0.000–0.857)* *Triodanis coloradoensis (0.000–1.000)* *Dermatophyllum secundiflorum (0.000–1.000)* *Serjania brachycarpa (0.000–0.900)* *Tiquilia gossypina (0.000–0.833)* *Linum vernale (0.000–0.800)* *Viguiera stenoloba (0.000–0.900)* *Krameria ramosissima (0.000–0.900)* *Ruellia corzoi (0.000–1.000)* *Mimosa malacophylla (0.000–0.900)* *Brickellia cylindracea (0.000–0.929)* *Brickellia dentata (0.000–0.100)* *Jefea brevifolia (0.000–0.929)* *Thymophylla micropoides (0.000–1.000)*	16
24. Prairie	3.06–3.31	*Tetraneuris scaposa (0.833)* *Asclepias arenaria (0.788)* *Dalea aurea (0.731)* *Senecio ridellii (0.705)*	1

AoE	E	Endemic species (*e*)	Number of sets
25. Comanchian	10.07–9.94	*Senecio ampullaceus (0.692–1.000)*	6
		Liatris elegans (0.708–0.900)	
		Baptisia sphaerocarpa (0.000–0.909)	
		Baptisia nuttalliana (0.000–0.818)	
		Thelesperma flavodiscum (0.731–0.875)	
		Matelea cynanchoides (0.000–0.850)	
		Triodanis texana (0.692–0.813)	
		Silphium radula (0.000–0.692)	
		Vernonia texana (0.000–0.864)	
		Krigia wrightii (0.000–0.750)	
		Mimosa roemeriana (0.000–0.813)	
		Phacelia glabra (0.000–0.800)	
		Phacelia strictiflora (0.000–0.818)	
		Vernonia lindheimeri (0.000–0.708)	
		Tradescantia edwardsiana (0.000–0.750)	
		Tradescantia humilis (0.692–0.813)	
26. Edwards Plateau	1.75–2.00	*Tradescantia edwardsiana (0.900–1.000)*	2
		Mimosa roemeriana (0.000–1.000)	
27. Gulf Coastal Plain	2.20–2.45	*Sabatia brevifolia (0.773)*	1
		Chaptalia tomentosa (0.773)	
		Zigadenus glaberrimus (0.692)	
28. Appalachian	3.12–3.37	*Corydalis flavula (0.844–0.851)*	2
		Camassia scilloides (0.771–0.845)	
		Cotinus obovatus (0.000–0.759)	
		Cynanchum laeve (0.000–0.700)	

(*e* scores > 0.81), including a monotypic endemic genus *Centrostegia* A. Gray.

AoE 11. Mogollon (38 to 34 lat., –116 to –108 long.) overlaps the southern Great Basin province in southern parts of Nevada and Utah and in northern Arizona. It coincides with the Mogollon area of McLaughlin (1986). Two species of amphitropical genera, *Tiquilia latior* (I. M. Johnst.) A. T. Richardson and *Encelia resinifera* C. Clark, support AoE 11 with scores *e* = 1.0 each.

AoE 12. Colorado Plateau–Mojave (39 to 33 lat., –119 to –107 long.) stretches from the Mojave Desert to the Colorado Plateau along the Mogollon Rim, where it overlaps AoE 11 Mogollon. It coincides with the Colorado Plateau element of McLaughlin (1986). Four species of two SW North American genera, *Brickellia* and *Phacelia*, support this AoE (each species with *e* = 1.0).

AoE 13. Madrean Region Montane (37 to 18 lat., –117 to –97 long.) encompasses more elevated portions of the study region from the Mojave, Apachian, and Colorado Plateau areas to the Mexican Transition Zone of Morrone et al. (2017)/Mexican highlands province of Takhtajan (1986). It overlays AoE 3. Woody species with broad distribution in these xeric mountains, like *Rhus virens* Lindh. ex A. Gray (of a tropical to warm temperate genus) and *Juniperus deppeana* Steud. (of a Madro-Tethyan genus), as well as the species of SW North American genera *Nama* L. and *Cylindropuntia* (Engelm.) F. M. Knuth, are among the seven supporting this AoE (*e* = 0.71–0.89).

AoE 14. Apache–North Chihuahuan (34 to 26 lat., –112 to –101 long.) coincides with the Apachian subprovince of McLaughlin (2007) and northern elevated part of the Chihuahuan subprovince from southeast Arizona to southwestern Texas and the northeastern Mexican Plateau. Six species, including those from a mostly Apache–Chihuahuan genus *Chamaesaracha* (A. Gray) Benth. & Hook. f. and a monotypic genus *Leuciva* Rydb., support this AoE (*e* = 0.73–1.00). In all the analyses, 23 species of mostly SW North American genera supported AoE 14.

AoE 15. Sonoran–Chihuahuan (36 to 23 lat., –116 to –97 long.) is a large area that overlaps with the mountainous AoE 3; however, it is in lower elevations. Six species (*e* = 0.81–1.00) of wide distribution in the Sonoran and Chihuahuan provinces of Morrone et al. (2017)/subprovinces of Takhtajan (1986) are endemic in this area. They are mostly in the genera of broad distribution in the SW United States/Mexico/Mesoamerica (*Acourtia wrightii* (A. Gray) Reveal & R. M. King, *Thymophylla pentachaeta*) and in a broadly temperate/subtropical genus (*Berberis haematocarpa* Wooton). In all the analyses, 24 species, including those

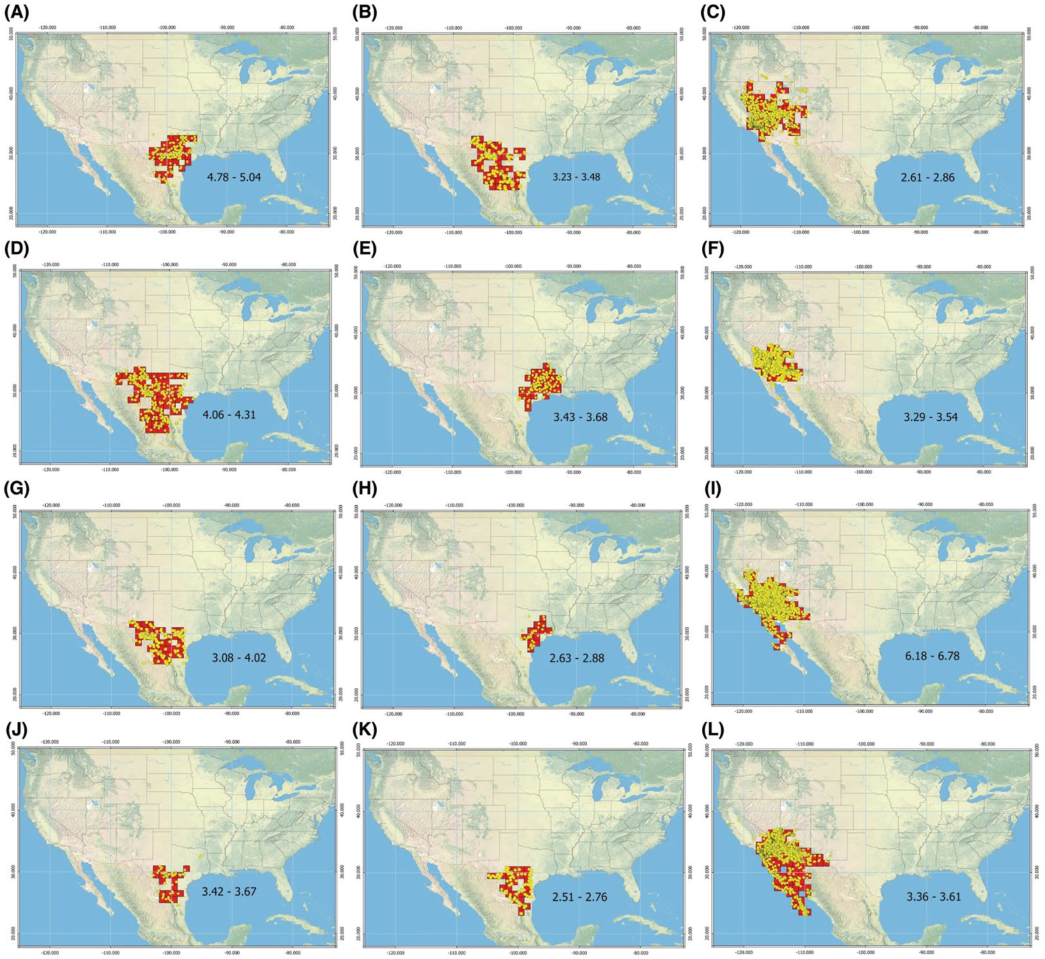

Figure 1. Selected consensus areas of endemism (CAs) recovered for angiosperm and *Ephedra* L. species found in the south-central and southwestern United States during endemicity analysis (EA) with various cell sizes. CAs recovered with cells 3.3° × 2.5°: (a) Central Texas; (b) North Chihuahuan; (c) South Great Basin–Mojave; (d) Chihuahuan–South Prairie; (e) Comanchian; (f) Mojave–North Sonora; (g) North Chihuahuan–Tamaulipan; (h) Southeast Texas; (i) SW North American; (j) South Texas–Coahuila; (k) South Texas–Coahuila–Tamaulipan; (l) Sonoran.

in the iconic amphitropical genera *Koeberlinia* Zucc. and *Larrea* Ortega, and an endemic genus *Cottsia* Dubard & Dop., supported AoE 15.

AoE 16. Chihuahuan (to South Prairie) (35 to 21 lat., –110 to –97 long.) encompasses the Chihuahuan province with some species (*Alloberberis trifoliolata* (Moric.) C. C. Yu & K. F. Chung) extending to the Prairie province. It is supported by 14 species (e = 0.71–0.83), including a monotypic endemic genus *Talinopsis* A. Gray and the only New World species of the Madro-Tethyan genus *Peganum* L., *P. mexicanum* A. Gray. Of the 19 species supporting this area in different analyses, many are in large tropical/warm temperate genera (e.g., *Phyllanthus* L., *Eryngium* L.).

AoE 17. North Chihuahuan (32 to 24 lat., –107 to –98 long.) is nested in AoE 16 and embraces northern/northeastern parts of the Chihuahuan province and Texas Edwards Plateau. Three of the five species supporting it have the highest score (e = 1.0): two in the American-African genera (*Cynanchum pringlei* (A. Gray) Henrickson and *Acleisanthes crassifolia* A. Gray), and *Tiquilia gossypina* (Wooton & Standl.) A. T. Richardson of an amphitropical genus.

AoE 18. Central Texas (32 to 27 lat., –102 to –96 long.) is supported by six species (e = 0.81–0.93) of widespread genera (*Desmanthus* Willd.) and a monotypic endemic genus *Amblyolepis* DC. **AoE 18.1 Southeast-Central Texas** is a small area with three edaphic en-

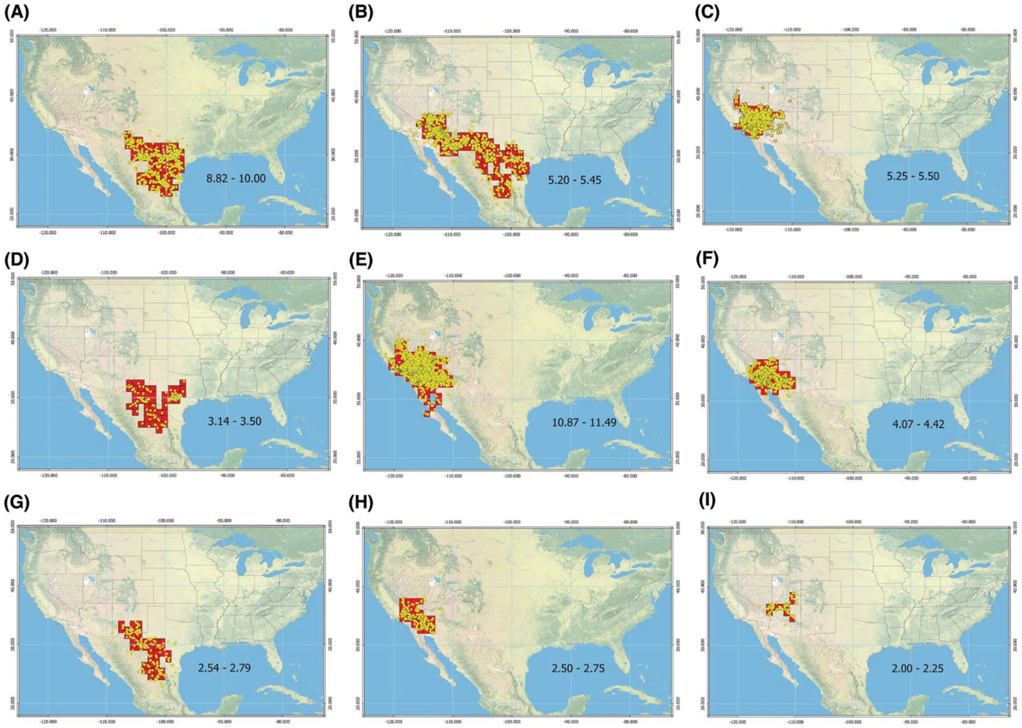

Figure 2. Selected consensus areas of endemism (CAs) recovered for angiosperm and *Ephedra* L. species found in the south-central and southwestern United States during endemicity analysis (EA) with various cell sizes. CAs recovered with cells 4° × 4°: (a) South-central U.S.A.–East Madrean; (b) Sonoran–Chihuahuan; (c) South Great Basin–Mojave–North Sonora; (d) South Texas–Coahuila; (e) SW North American; (f) Mojave–North Sonora; (g) North Chihuahuan; (h) Mojave; (i) Mogollon.

demics (*e* = 0.8–1.0) in southeastern Texas Sand Sheet (*Mimosa latidens* (Small) B. L. Turner, *Brickellia dentata* Sch. Bip., and *Dalea lasiathera* A. Gray).

AoE 19. South Texas–Coahuila (32 to 25 lat., –106 to –98 long.) is nested in AoE 16 as a part of the Chihuahuan province in Coahuila and Nuevo Leon in Mexico, stretching to Trans Pecos and Edwards Plateau in southern Texas. It has five edaphic endemics on gypsum or sandy soils (e.g., *Acleisanthes acutifolia* Standl., *Funastrum torreyi* (A. Gray) Schltr.), as well as on limestone (*Brickellia cylindracea* A. Gray & Engelm.). Four of these species have a score *e* = 1.0.

AoE 20. North Chihuahuan–Tamaulipan (34 to 24 lat., –108 to –98 long.) is supported by three species: *Johnstonella mexicana* (Brandegee) M. E. Mabry & M. G. Simpson and *Boerhavia linearifolia* A. Gray, which are mostly Chihuahuan extending to Tamaulipas, and *Viguiera stenoloba* S. F. Blake, which is found in Tamaulipan and Chihuahuan Desert scrub (*e* = 0.83–0.88).

AoE 21. Chihuahua–Tamaulipas–Sierra Madre Oriental (33 to 19 lat., –111 to –98 long.) is supported by 11 species found in the Chihuahuan Desert, Tamaulipas, and Sierra Madre Oriental provinces of Morrone et al. (2017). Most of them are in tropical/subtropical American genera (e.g., *Condalia* Cav., *Acleisanthes* A. Gray) and tropical to warm temperate genera with transatlantic disjunction (e.g., *Heliotropium* L., *Vachellia* Wight & Arn.). None of the species' *e* scores are > 0.83.

AoE 22. East Madrean–Tamaulipan (32 to 18 lat., –105 to –98 long.) is mostly in the Sierra Madre Oriental and Tamaulipas provinces of Morrone et al. (2017), extending to the Chihuahuan Desert province. It is supported by 13 species of American tropical/subtropical (e.g., *Gochnatia* Kunth, *Chaptalia* Vent.) and transatlantically disjunct (e.g., *Cynanchum* L., *Cordia* L.) genera.

AoE 23. South-central U.S.A.–East Madrean (34 to 20 lat., –110 to –97 long.) is a large area (E = 10) that overlaps with the northeastern Chihuahuan Desert and Tamaulipas provinces of Morrone et al. (2017), including all of their Unites States parts, plus Central Texas, and extending southward to the Sierra Madre Oriental province. Several of the AoEs are overlapping or nested in it (AoEs 12–21). Of the 21 species support-

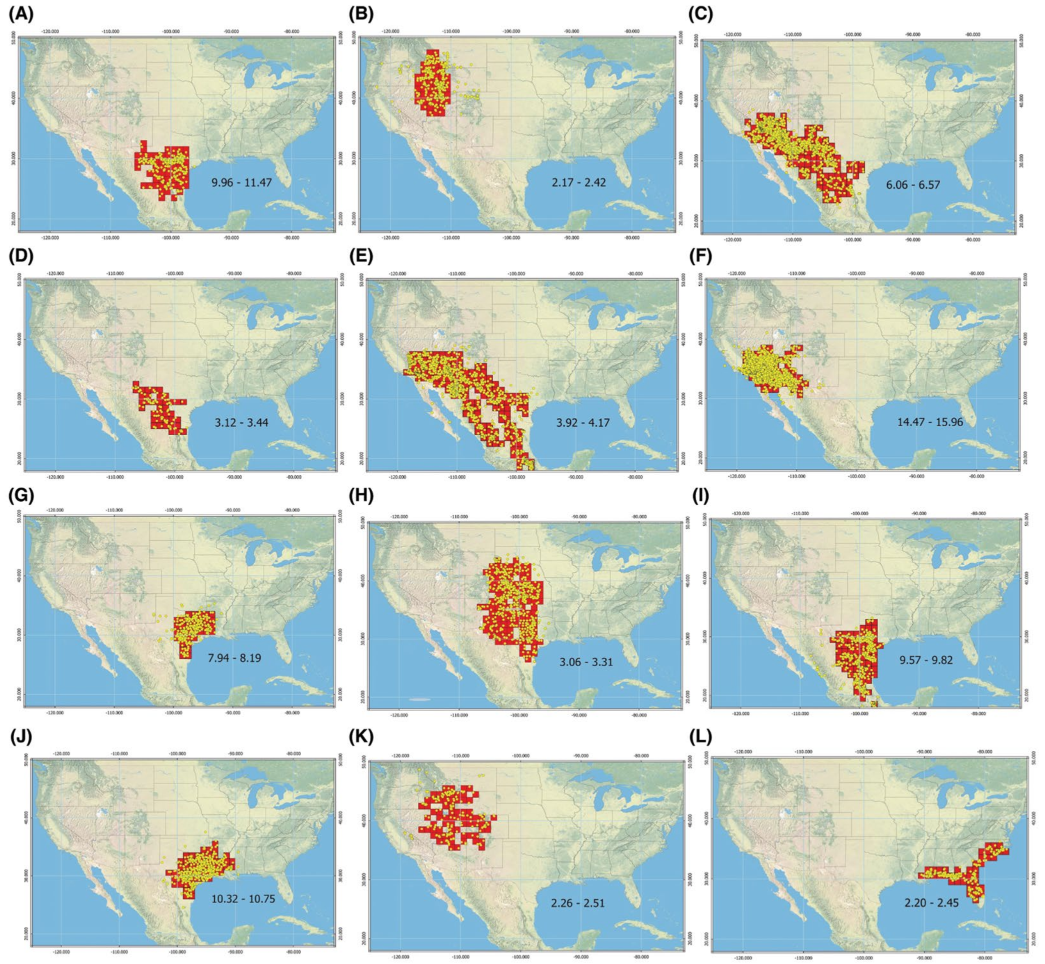

Figure 3. Selected consensus areas of endemism (CAs) recovered for angiosperm and *Ephedra* L. species found in the south-central and southwestern United States during endemicity analysis (EA) with various cell sizes. CAs recovered with cells 2.5° × 4°: (a) South Texas–Coahuila; (b) Mid Rocky Mountains; (c) Apache–North Chihuahuan; (d) North Chihuahuan; (e) Madrean Region Montane; (f) Mojave–North Sonora; (g) Southeast-Central Texas; (h) Prairie; (i) East Madrean–Tamaulipan; (j) Comanchian; (k) East Great Basin–Rocky Mountains; (l) Gulf Coastal Plain.

ing it ($e > 0.8$), 11 have $e = 1.0$. They are in the genera with tropical/subtropical American (e.g., *Guaiacum* L., *Serjania* Plum. ex Mill.), Mexican-Mesoamerican (*Viguiera* Kunth), or American-African (*Mimosa* L.) ranges. AoEs 20 and 21, which are nested in AoE 23, have one endemic species each in the tropical families of the Boraginales II clade of Luebert et al. (2016), Cordiaceae and Ehretiaceae, found only in S TX in North America north of Mexico.

AoE 24. Prairie (42 to 27 lat., –105 to –95 long.) includes southern/middle parts of the Prairie province of Takhtajan (1986) and is supported by species of mostly temperate genera (e.g., *Tetraneuris scaposa* (DC.) Greene, *Senecio riddellii* Torr. & A. Gray). Other species extend northward to the Prairie province from the center of origin of their genera in SW North America, e.g., *Asclepias* (Fishbein et al., 2018) and *Dalea* Juss. (Cardoso et al., 2013).

AoE 25. Comanchian (36 to 26 lat., –101 to –91 long.) partly coincides with the Comanchian subprovince of McLaughlin (2007). It is supported by 16 species (E = 10) found throughout central/east Texas to south/central Oklahoma. Most species are in the temperate eastern North American herbaceous genera (e.g., *Liatris* Gaertn. ex Schreb., *Krigia* Schreb., *Baptisia* Vent.), or in tropical/subtropical genera (*Vernonia* Schreb.). A nested area, **AoE 25.1 South Texas**, stretches from S TX and EP to BB (not shown).

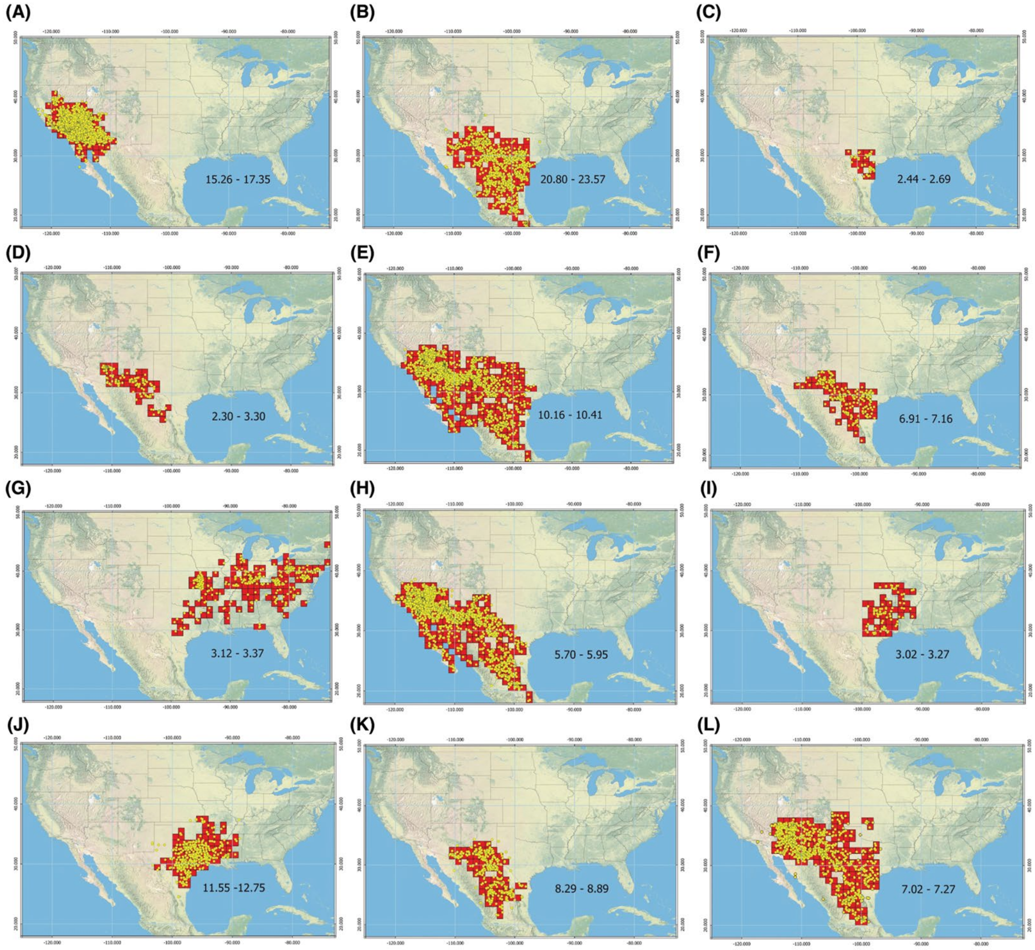

Figure 4. Selected consensus areas of endemism (CAs) recovered for angiosperm and *Ephedra* L. species found in the south-central and southwestern United States during endemicity analysis (EA) with various cell sizes. CAs recovered with cells 3° × 4°: (a) SW North American; (b) South-central U.S.A.–East Madrean; (c) Southeast-Central Texas; (d) Apache–North Chihuahuan; (e) Madrean Region Montane; (f) North Chihuahuan; (g) Appalachian; (h) Sonoran–Chihuahuan; (i) Comanchian; (j) Southeast Prairie; (k) Chihuahuan; (l) South Rocky Mountains–Colorado Plateau–East Madrean.

AoE 26. Edwards Plateau (33 to 29 lat., –101 to –95 long.) is a small AoE in northern Central Texas and the Edwards Plateau nested in AoE 25. It coincides with the Comanchian subprovince of McLaughlin (2007). Two endemic species, *Mimosa roemeriana* Scheele and *Tradescantia edwardsiana* Tharp, of American-African genera support the area (each with *e* = 1.0).

AoE 27. Gulf Coastal Plain (36 to 26 lat., –90 to –76 long.) encircles the Atlantic and Gulf Coastal Plain province of Takhtajan (1986) and is supported by two species of SE North American/Central American genera, *Sabatia brevifolia* Raf. and *Chaptalia tomentosa* Vent. (*e* = 0.773), and a monotypic endemic genus *Zigadenus* Michx. (*e* = 0.692).

AoE 28. Appalachian (42 to 31 lat., –100 to –72 long.) encircles the namesake province of Takhtajan (1986) and is supported by four species (*e* = 0.76–0.85) of broadly temperate (*Corydalis* DC.), North American temperate (*Camassia* Lindl.), and tropical/subtropical (*Chaptalia*) genera.

Discussion

The analysis of the dataset resulted in the recognition of 28 AoEs (Table 2), including two large areas, with several nested and overlapping AoEs, such as SW AoE 9 and SC AoE 22. Two major observations consistently emerged from all the analyses: a dramatic east/

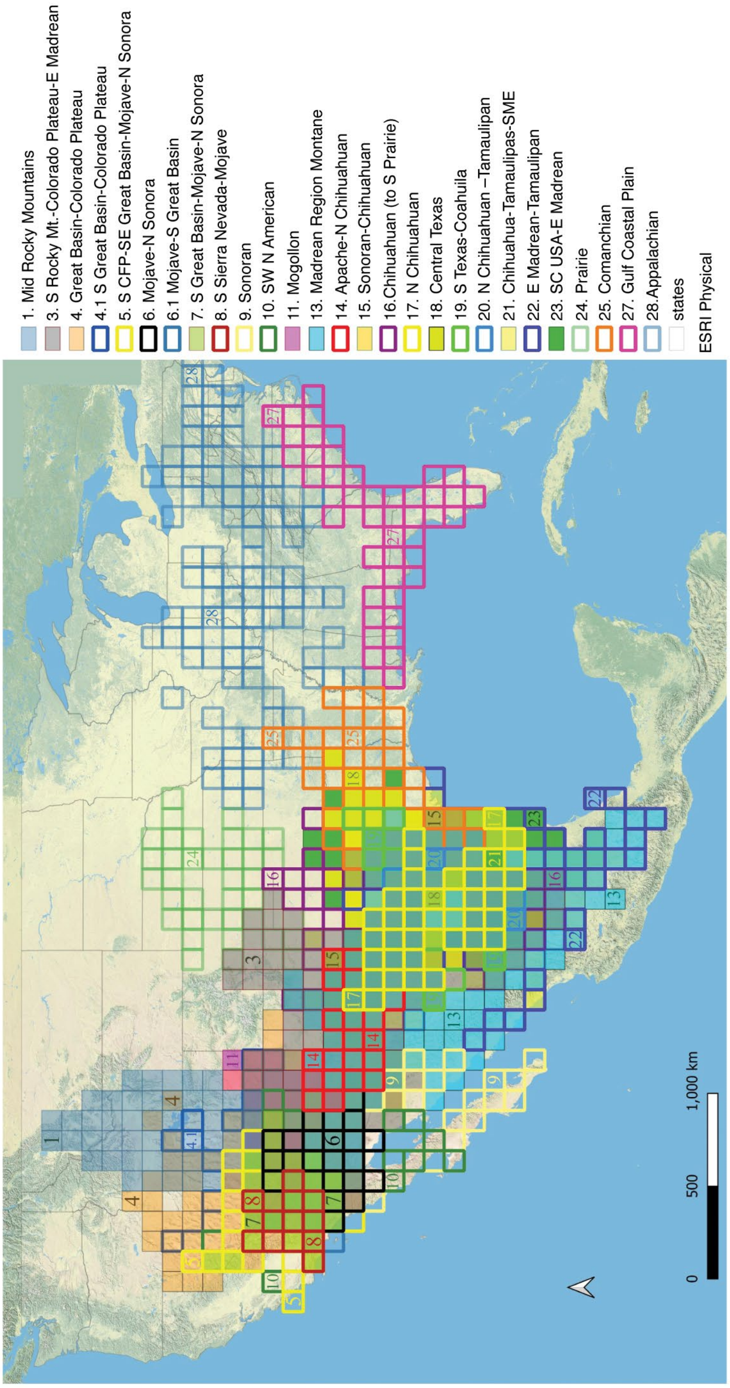

Figure 5. Areas of endemism (AoEs) based on consensus areas of endemism (CAs) recovered for angiosperm and *Ephedra* L. species found in the south-central and southwestern United States during endemicity analysis (EA) with cut-off 40%, various cell sizes, and minimum species scores.

west split and a significant partial overlap or nestedness among the adjacent AoEs within each of the two disjunctive groups—the two "super areas." The east/west split has been documented by several authors, corresponding to a division to Western and Alleghany subregions, and posteriorly to the Californian and Rocky Mountain dominions inside the Western subregion (Escalante et al., 2021). Szumik et al. (2018), using a dataset of mammals of North America, demonstrated that AoEs consistently overlap. This finding agrees with the patterns of some of our AoEs, especially in the SW "super area," which could not be assigned to a particular hierarchical category in the system of Escalante et al. (2021). While these overlapping and intermediate patterns could have resulted from the laxity of the method, documented by Escalante (2015), there is abundant evidence of such patterns in many of the 250 endemic genera listed for the Madrean region in Takhtajan (1986). "The Sonoran Province is linked to all the other provinces of the Madrean Region by endemic genera common to two or more provinces. Moreover, there are a great many species, among both endemic and more widespread genera, that occur in two or more of the provinces but are restricted to the Madrean Region" (Takhtajan, 1987: 164). Many of the sampled genera/clades in this part of the Nearctic region (see Table S2 in Supplementary Appendix S4), e.g., *Tiquilia* Pers. (Moore & Jansen, 2006), Cactaceae: Cylindropuntieae (Majure et al., 2019), *Nolina* Michx. (Ruiz-Sanchez et al., 2019), *Garrya* Douglas ex Lindl. (Burge, 2011; Nesom, 2012), and *Cryptantha/Johnstonella* Brand (Simpson et al., 2019) showed a geographic split into western, mostly southwestern, and southeastern clades. The split demonstrated by many taxa corresponds to an environmental and physical barrier, the Cochise Filter Barrier, which is a known transition zone between two biotas that divides the Sonoran and Chihuahuan Deserts (Provost et al., 2021). By synthesizing phylogeographic data for the Cochise Filter Barrier, Provost et al. (2021) estimated that the biota turns over approximately between ca. –109° and –106° longitude and for the maximum number of species the barrier overlapped –108.6°, which is close to our findings. Many of the taxa they analyzed showed a Pleistocene divergence time, and it appeared to be a combination of forces, ranging from allopatric isolation to ecological speciation.

The endemic species that define AoEs 1–4 (Table 2; Table S1 in Supplementary Appendix S4) have north temperate connections. They are either in the genera of Eurasian (mostly Tethyan) origin and migration via the Bering Land Bridge (BLB; Wen et al., 2016), e.g., *Astragalus* (Scherson et al., 2008), or in western North American clades, such as the Amsinckieae of Boraginaceae. The latter clade derived by long-distance dispersal from the northeastern Palearctic, where the earliest divergence events in the subfamily Cynoglossoideae occurred (Otero et al., 2019). The Cynoglossoideae are centered in the Irano-Turanian region, especially in the Central Asian subregion. In the Rosaceae, a western North American clade Dryadoideae derived from a Holarctic arcto-alpine genus *Purshia* DC. ex Poir. (Sun et al., 2016). *Fallugia paradoxa*, of a monospecific genus in Dryadoideae, is endemic in the AoE 3 South Rocky Mountains–Colorado Plateau–East Madrean.

Many species of the SW group of partially overlapping/nested areas, AoEs 5–11, diversified in the great SW North American arid center. Axelrod and Raven (1985: 27) wrote: "The woodland taxa originated in the southwestern United States and adjacent Mexico, in a region inferred earlier as a probable source area for the Madro-Tertiary Geoflora (Axelrod, 1958)." It is a well-known hotspot and the center of both paleo- and neo-endemism (Thornhill et al., 2017; Sosa et al., 2018; Mishler et al., 2020). The species that supported these AoEs are in the local genera with extensive radiation in the Sonoran and Mojave Deserts (Table S2 in Supplementary Appendix S4). Most of their connections extend along the western backbone of the Americas, especially to western Mexico and to deserts in South America as amphitropical disjunction. Examples of amphitropical disjunction in angiosperms have become established via multiple asynchronous "events" with the most estimated examples occurring within the last five Ma (Simpson et al., 2017). Some of the endemics of our SW AoEs represent the families that have originated and diversified in this center, e.g., Hydrophyllaceae and Namaceae, which are successively sister families to the remainder of the mostly tropical (to warm temperate) Boraginales II clade (Luebert et al., 2016). Other endemics supporting the SW AoEs are early-derived members of their families, such as the genera *Mortonia* A. Gray of Celastraceae (Sun et al., 2016) and *Eucnide* Zucc. of Loasaceae (Hufford, 2016), or the species of early lineages of such genera as *Matelea* Aubl. (McDonnell, 2015) and *Thamnosma*. All recent species of *Thamnosma*, whose ancestor could have dispersed from Asia to western North America via the BLB (Appelhans et al., 2016), are a part of the succulent biome, and the North American species "may have been members of the arid Neogene Madro-Tertiary Geoflora" (Thiv et al., 2011: 82). Within the large American genus *Asclepias* of Apocynaceae, the Sonoran Desert clade (nine species) and Incarnatae clade are successive sisters to the remaining American *Asclepias* species (Fishbein et al., 2018). Thus, phylogenetic evidence, high endemism, and the spatial patterns resulting from our analysis support the delineation of the Madrean chorion at a high rank in the western half of the Nearctic. It was delineated as the Madrean region

Table 3. Areas of endemism of plants in south-central/southwestern (SC/SW) North America, compared with Escalante et al. (2021) and their equivalent hierarchical category.

Area of endemism (AoE)	Name of the AoE	Comparison with Escalante et al. (2021)	Equivalent hierarchical category
AoE 1	Mid Rocky Mountains	partially in the Artemisian, Montanian, Coloradan, and Navahonian provinces	dominion
AoE 2	East Great Basin–Rocky Mountains	partially in Artemisian, Montanian, Navahonian, and Coloradan provinces	dominion
AoE 3	South Rocky Mountains–Colorado Plateau–East Madrean	mostly within the Mohavian, Sonoran, Navahonian, and Chihuahuan; partially in the Tamaulipas, Californian, Artemisian, Coloradan, Comanche, and Kansas provinces	
AoE 4	Great Basin–Colorado Plateau	mostly in the Artemisian, Mohavian, and Navahonian provinces	subregion
AoE 4.1	South Great Basin–Mojave	mostly in the Artemisian, Californian, Mohavian, and Navahonian provinces	subregion
AoE 5	Southern California Floristic Province–Southeast Great Basin–Mojave–North Sonora	within the Californian and Rocky Mountain dominions; this AoE includes mostly the Californian, Mohavian, Sonoran, and a tiny part of the southern Artemisian provinces	subregion
AoE 6	Mojave–North Sonora	mostly concentrated in the Californian, Mohavian, and Sonoran provinces	subregion
AoE 6.1	Mojave–South Great Basin	mostly in the Mohavian province, but partially in the Californian and northern part of the Sonoran provinces	
AoE 6.2	Mojave	mostly in the Mohavian province	
AoE 7	South Great Basin–Mojave–North Sonora	within the Californian and Rocky Mountain dominions; this AoE includes mostly the Californian, Mohavian, Sonoran, and a tiny part of the southern Artemisian and western Navahonian provinces	subregion
AoE 8	South Sierra Nevada–Mojave	within the Californian and Rocky Mountain dominions; this AoE includes mostly the Californian, Mohavian, Sonoran, and a tiny part of the southern Artemisian provinces	subregion
AoE 9	Sonoran	occupies the Baja Californian, Californian, Mohavian, Sonoran, and tiny parts of the Navahonian, Chihuahuan, and Neotropical provinces	
AoE 10	Southwest North American	within the Californian and Rocky Mountain dominions; this AoE mostly includes the Californian, Mohavian, Sonoran, partially the southern Artemisian, some parts of the northern Baja Californian, and the western Navahonian provinces	subregion
AoE 11	Mogollon	occupies only the Mohavian and Navahonian provinces	dominion
AoE 12	Colorado Plateau–Mojave	partially in Mohavian, Californian, Sonoran, and Navahonian provinces	
AoE 13	Madrean Region Montane	includes the Mohavian, Navahonian, Sonoran, Chihuahuan, Sierra Madre Occidental, Sierra Madre Oriental, and Transmexican Volcanic Belt provinces	Mexican transition zone
AoE 14	Apache–North Chihuahuan	just includes the Chihuahuan and Navahonian provinces; also, a quadrant in the Tamaulipas province	

Area of endemism (AoE)	Name of the AoE	Comparison with Escalante et al. (2021)	Equivalent hierarchical category
AoE 15	Sonoran–Chihuahuan	mostly in the Sonoran and Chihuahuan provinces; partially in the Mohavian, Navahonian, Tamaulipas, Comanche, and southern Texas provinces; including some part in the northern Sierra Madre Oriental	
AoE 16	Chihuahuan (to South Prairie)	mostly in the Chihuahuan and Comanche provinces; partially in the southern Kansas, Illinoian, and Texas provinces. Also includes the Tamaulipas and some parts of the Sierra Madre Occidental and Oriental	
AoE 17	North Chihuahuan	partially in the Chihuahuan, southern Comanche, northern Sierra Madre Oriental, and western Tamaulipas provinces	
AoE 18	Central Texas	mostly in the Comanche and Texas provinces; partially in the southern Illinoian, Kansas, and northern Tamaulipas provinces	
AoE 18.1	Southeast-central Texas	mostly in the Comanche and Texan provinces; partially in the northern Tamaulipas and southern Austroriparian and Illinoian provinces	
AoE 19	South Texas–Coahuila	includes the Chihuahuan and Comanche provinces; also, a couple of quadrants in the Tamaulipas province	
AoE 20	North Chihuahuan–Tamaulipan	partially in the Chihuahuan, northern Tamaulipas, and northern Sierra Madre Oriental provinces	
AoE 21	Chihuahua–Tamaulipas–Sierra Madre Oriental	within the Chihuahuan, Comanche, Tamaulipas, and Sierra Madre Oriental provinces; partially including southern Kansas and Illinoian provinces	
AoE 22	East Madrean–Tamaulipan	mostly in the Comanche, Tamaulipas, Sierra Madre Oriental, and Chihuahuan provinces; partially in the southern Texan, Illinoian, and Kansas provinces	
AoE 23	South-central U.S.A.–East Madrean	mostly in the Chihuahuan, Tamaulipas, Comanche, Sierra Madre Oriental, Texan, and southern Illinoian and Kansas provinces	
AoE 24	Prairie	mostly in the Kansas, Comanche, southern Illinoian, and northern Tamaulipas provinces; partially in the Texan and northern Chihuahuan provinces	
AoE 25	Comanchian	mostly in the Comanche and Texan provinces; partially in the northern Tamaulipas, southern Illinoian, and western Austroriparian provinces	province
AoE 25.1	South Texas		
AoE 26	Edwards Plateau	partially in the Comanche, Texan, and southern part of Illinoian provinces	
AoE 27	Gulf Coastal Plain	only in the Austroriparian province	province
AoE 28	Appalachian	mostly in the Carolinian province; partially in the Austroriparian and central Illinoian provinces	

of the Madrean subkingdom in Takhtajan (1969, 1978) and, with the inclusion of the Prairie province, as the Southwestern region in McLaughlin (2007). The Madrean flora is the richest in the Nearctic and is supported by two small endemic families, Simmondsiaceae and Fouquieriaceae, dated by 70–80 Ma and 61–65 Ma respectively (Christenhusz et al., 2017), and the nearly endemic family of four genera, Crossosomataceae, with the Mojave–Sonora–South California genus *Crossosoma* Nutt. sister to the remainder of the family (Sosa & Chase, 2003), and the monotypic genus *Apacheria* C. T. Mason, endemic to the Apachian subprovince.

Some species of the Sonoran Desert element (e.g., in *Boerhavia* L. and *Funastrum* E. Fourn.) extend eastward to the Chihuahuan Desert (mostly to Val Verde County in southwestern Texas) and Mexico, while some Chihuahuan species extend to the Sonoran Desert. This supports the hypothesis of niche conservatism (Wiens & Graham, 2005; Murphy et al., 2019), which states that endemic species will expand their range into similar environments and ecological niches. Laport et al. (2012) suggested a recent origin of the North American *Larrea tridentata* (DC.) Coville via long-distance dispersal from Argentina to the Chihuahuan Desert with establishment of polyploid populations accompanying its rapid spread through the Sonoran and Mojave Deserts. A hyper-diverse clade corresponding to the tribe Cacteae started diversification in the Sierra Madre Oriental around 15 Ma, after a long-distance dispersal event from South America. It subsequently dispersed to the Mexican Plateau, where it reached its maximum diversity (Hernández-Hernández et al., 2014).

The endemic species of the SC super area (AoEs 12–22) have mostly East Madrean/Mesoamerican affinities or transatlantic connections, including those with the Tethyan subkingdom. Interestingly, the only New World species of mostly Tethyan family Nitrariaceae, *Peganum mexicanum* A. Gray, is endemic to the Chihuahuan Desert. Nitrariaceae includes 13 species diversified during the Cretaceous and was placed in a sister position to the Sapindales (Chi et al., 2020). Nitrariaceae and its sister family Biebersteiniaceae (four species in the Irano-Turanian region and one in the eastern Mediterranean) have the longest stem lineages observed in Sapindales, indicating that extinction may have had a greater role in shaping their extant diversity than elsewhere within the order (Muellner-Riehl et al., 2016). *Ephedra* L. is present in all North American and Tethyan subkingdom deserts. The deepest divergences in *Ephedra* indicated a basal grade of species distributed in the Mediterranean area (Rydin & Korall, 2009). According to Graham (2018: 423), "affinities between the southwestern U.S./northern Mexico and the Mediterranean (ca. 15 genera of trees and shrubs; e.g., *Ephedra*, *Juniperus*, *Pinus*, *Quercus*, *Styrax*; the Madrean Tethyan vegetation) is more likely the result of parallel evolution and long-distance transport than continuity of land and continuous hot and arid conditions across the northern regions anytime during the Tertiary."

A strong representation of broadly tropical/subtropical genera (e.g., *Vachellia*, *Diospyros* L.), American tropical/subtropical genera (e. g., *Funastrum*, *Guaiacum*), and Madrean/Mesoamerican genera (e.g., *Telosiphonia* (Woodson) Henrickson, *Garrya*) is characteristic of the SC areas of endemism, especially the Tamaulipan thorn scrub. *Diospyros* is one of the boreotropical (Wolfe, 1975)/Paleotropical (Mai, 1995) genera of the Northern Hemisphere with intercontinental distribution in the Paleogene still present in the forests of the eastern United States. It was connected with the Antilles, the Bahamas, and Mesoamerica. Many of the other such genera, e.g., *Nothofagus* Blume, became extinct with late Cenozoic cooling and drying (Graham, 2018). *Diospyros texana* Scheele, which is endemic in AoE 23, is a member of a Mesoamerican-Caribbean clade of four species and is branching basally to the other species in the clade (Duangjai et al., 2006).

AoE 24 Comanchian is supported by the species of the temperate genera of the Atlantic region (e.g., *Baptisia*, *Silphium* L.), amphi-Atlantic disjunct genera (e.g., *Desmanthus*, *Mimosa*), and those that arrived by long-distance dispersal from western Eurasia/Mediterranean, e.g., *Linum* L. (McDill et al., 2009) and *Triodanis* Raf. (Crowl et al., 2014). All our analyses support delineation of the Comanchian chorion, close to that in McLaughlin (2007); however, we consider it at the subprovincial level in the Prairie province of the Atlantic region sensu Takhtajan (1986) and Katinas et al. (2004), rather than in the Southwestern region sensu McLaughlin's system. We did not find enough evidence for delineation of the Texan province, and its separation from the Comanchian, as in Dice (1943); it could be described at a lower rank in the Comanchian subprovince of the Prairie province.

Affinities of the forest flora of the Atlantic region across the Northern Hemisphere (AoE 28) have been extensively discussed in the literature and reviewed by Manchester (1999), Manchester et al. (2009), Harris et al. (2013), and Manos and Meireles (2015).

Our analysis supports the placement of the BB in the Chihuahuan Desert province of Morrone et al. (2017), as well as the delineation of the northeastern subprovince in it, as shown by the AoEs 17 and 19. The S TX, which is a part of the Tamaulipas province, shows SE North American affiliation (southern Atlantic region) in our analysis, which was also supported by the analysis of Katinas et al. (2004). Most of the prairie species in our dataset also show the Atlantic region affiliation. Some of the sampled species found in southwestern low prairies are those that extend northward in connection with recent aridification and expansion of deserts from the Sonoran/Mojave center, e.g., species of *Asclepias* (Fishbein et al., 2018) and *Dalea* (Cardoso et al., 2013), or from the Chihuahuan Desert, e.g., *Alloberberis* C. C. Yu & K. F. Chung (Angulo et al., 2017).

Our analysis with this particular dataset supports the Alleghany (Atlantic) and Western choria of high rank in the Nearctic of Escalante at al. (2021), as well as splitting of the Western into the Californian, Rocky Mountain (in the boundaries of Takhtajan, 1986), and Madrean (Mohavian, Sonoran, Baja Californian, Chihuahuan, and Mexican Transition Zone of Morrone et al. [2017], and Apachian of McLaughlin [2007]) choria. The affinities of the taxa supporting AoEs 5–23 are with the southern floras, while those in AoEs 1–4 and AoEs 24–28 showed north temperate connections. A sharp north/south climatic boundary along the Mogollon Rim makes the Cordilleran Floristic Province of Axelrod and Raven (1985), which includes the Artemisian (Great Basin) and Coloradan (Southern Rocky Mountains) provinces of Dice and Takhtajan respectively, more temperate, depauperate, and transitional with the Rocky Mountains chorion and the Sierra Nevada of CFP. Some of the AoEs could be used to delineate the choria of lower rank, for example the Mogollon, Edwards Plateau, Comanchian, and Apachian. The latter has been delineated in McLaughlin (2007: 27) as the subprovince "as a relatively recently assembled one, with taxa derived primarily from areas both to the north and east (the Great Plains Province), and also to the south (Madrean Province)."

CONCLUSION

Our analysis is the first attempt, to the best of our knowledge, to apply an EA to identify distribution patterns of only plant species in the United States. This study has an advantage over previous classifications in that the units were analyzed using species distribution data provided by the current plant specimen records. It is a step toward resolving discordances in the floristic regionalization of the SC/SW United States. Inclusion of more species into the dataset in the future, expansion of the area of study, as well as application of additional methods of analysis of species distribution patterns should produce improved outcomes.

CONFLICT OF INTEREST

No conflict of interest.

DATA AVAILABILITY STATEMENT

The data underlying this article are available in the Dryad Digital Repository at https://dx.doi.org/10.5061/dryad.7pvmcvdrz:

- XYD file containing point records (coordinates) for each of the species analyzed
- Supplementary list of occurrence data downloads from GBIF

SUPPORTING INFORMATION

Additional supporting information may be found online on the main article page: Supplementary Appendix S1 (Texas map); Supplementary Appendix S2 (all points map); Supplementary Appendix S3 (list of species with authorities by family used in the analyses); Supplementary Appendix S4 (list of species that supported the areas of endemism) including Table S1 and Table S2 (inferred source areas/relationships of the clades with endemic species); Supplementary Appendix S5 (disjunctive and overlapping areas of endemism), including Figures S1 and S2; and Supplementary Appendix S6 (maps of consensus areas of all analyses), including Figures S3–S6.

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