Areas of Endemism of Selected Seed Plants in Southcentral and Southwestern USA

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Abstract

Areas of endemism (AEs) are fundamental entities of analysis in biogeography and a key step for biogeographical regionalization. Even though many studies have contributed to the biogeographical knowledge of southern USA flora, no endemicity analysis (EA) has been conducted that would include a large number of native seed plant species from different families. A new analysis of plant spatial patterns is important as a first step for a future updated floristic regionalization of North America North of Mexico. It has become easier to accomplish owing to the increased availability of large-scale digitized distributional data and statistical methods of biogeographic analysis. Here we identify the AEs in SC/SW USA using digitized plant specimen data available from IDigBio. We built a database with 81,851-specimen point records of 400 selected mostly angiosperm species and applied the NDM/VNDM method of endemicity analysis. We then compare the established 26 AEs in the area of study with the floristic provinces in two comparatively recent regionalization systems of USA. To understand the spatial patterns, we also pay attention to the information on relationships of the endemic species found in phylogenetic literature.





1. Introduction

By defining areas of relatively homogeneous species composition, biogeographical frameworks provide spatial units of analysis that are useful in macroecological, evolutionary and systematic studies of the processes, which shaped or maintain species distributions (Morrone, 2018). The search for congruent species distributions ultimately defines choria, which are, according to Takhtajan (1978), units of different ranks in a hierarchical floristic regionalization system. They are distinct from the units of ecological regionalization (ecoregions), which define biomes. The inclusion of widespread species in the biogeographic analysis resolves the patterns of biomes, rather than historical areas, as was recently shown for Australia (Murphy et al., 2019). Conversely, regionalization systems based on endemic species (e.g., by Cronquist, 1982; Takhtajan, 1986; Rzedowski, 1978; Morrone, 2014; Morrone et al., 2017), rather than biomes, resolve historical areas.

The search for floristic patterns starts with finding areas of endemism (AE), which are fundamental entities of analysis in biogeography, and this is a key step for biogeographical regionalization (Morrone, 1994; Escalante, 2009; Linder, 2001; Mercado Gomez & Escalante, 2018; Liria et al., 2020). An adequate regionalization reflects the history of the assembly of a flora. Immigrant species/ancestors to local radiations enter a flora from different directions and at different times. Early studies (Popov, 1963, 1983; Kamelin, 1973, 1998; Raven and Axelrod, 1995) provided insight into history of a complex flora by subdividing a flora into species complexes of different ages and origins. More recently, analysis of cenocrons (Morrone, 2009, 2010; Corral-Rosas & Morrone, 2017; Halffter & Morrone, 2017; and Ferro et al., 2017), based on advances in phylogenetic systematics and historical biogeography, resulted in time slicing of the biota into sets of taxa that share the same biogeographic history.

The history and connections of the flora of southcentral/southwestern (SC/SW) North America have long been a subject of research (Axelrod, 1958, 1975; Raven & Axelrod, 1995; Rzedowski, 1993; Sosa & De-Nova, 2012; Graham, 2018; Sosa et al., 2018; Sosa et al., 2020; Baldwin, 2014; Baldwin et al., 2017; Vasquez-Cruz & Sosa, 2019; Mishler et al., 2020). The widely accepted major biotic boundary in North America, Nearctic/Neotropical, is defined as the Mexican transition zone (Morrone, 2010, 2015, 2018; Halffter & Morrone, 2017). A second major boundary is east to west boundary (Katinas et al., 2004; Escalante et al., 2013, Gamez et al., 2016; Mishler et al., 2020). In southern USA, it passes through Texas (Saghatelyan 2009, 2015, 2017), where it separates almost adjacent floras of Big Bend National Park (BB) and the Edwards Plateau (EP) (Map 1, Supplemental Information 1). In the floristic regionalization system of North America by Takhtajan (1987), BB falls in the Madrean region (MR) while EP falls in the Atlantic region (ER) of the Madrean and Boreal subkingdoms respectively. McLaughlin (2007) regionalization system identifies the MR as the Southwestern region (SW), including the North American Prairies province. The latter province is a part of the ER in the Takhtajan scheme. Disagreements in some aspects of these two more recent floristic systems necessitate a new analysis of geographic patterns of plants with more comprehensive species distribution data across SC/SW USA. This has become easier owing to the increased availability of largescale digitized distributional data and novel statistical methods of biogeographic analysis. Many authors search biogeographic units using clustering algorithms (McLaughlin, 2007; Linder et al., 2012; Munguio-Lina et al., 2016; Ye et al., 2019; Wang et al., 2019), e.g., the McLaughlin system resulted from a principal component analysis applied to a large set of local floras. The Takhtajan system used thresholds of endemism at successively finer taxonomic ranks to distinguish choria at different ranks.

A widely used method of endemicity analysis searches for areas of endemism (AE)s, which are patterns of co-occurrence in the geographical distribution of endemic taxa defined by the non-random congruence of occurrences between different taxa (Szumik et al., 2002). The first explicitly defined and detailed methods for finding AEs were proposed by Morrone (1994, 2009), with an AE defined as a group of geographic units that share at least two species. The studies on endemicity analyses in the Americas mostly use animals rather than plants and with the abundance of digitized distribution data for plants, it is feasible to use them for finding AEs.

Bertelli et al. (2017) argue that studies that have sought to discover patterns of endemism generally have not been sufficiently fine grained spatially and have not undertaken the 'discovery' process in a manner that minimizes assumptions and biases. To understand the biogeographic patterns in SC/SW USA, we first aim to identify the "unbiased" AEs using digitized plant specimen data available from IDigBio. We built a database with 81,851-specimen point records of 400 selected vascular plant species and applied the NDM/VNDM method of endemicity analysis (Szumik et al., 2002; Szumik & Goloboff, 2004) on different resolution scales. We then compare the established AEs with the floristic provinces/subprovinces and search for the relatives of the species that are endemic to these AEs in phylogenetic literature.

2. Materials and Methods

2.1 Study Area

The study area was determined to be from -125° to -75deg longitude and 20deg to 45deg latitude to accommodate the global ranges of most species included in the database. The native floras of three regions, BB, EP, and South Texas Plains (S TX) in southern Texas (Map 1, Appendix 1) were the sources of the majority of species in the database. Additional species were selected from the floras of northern Sonora and Mohave Deserts, the Great Basin, and the southern California Floristic province (CFP).

The Big Bend in West Texas 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). It is part of the Chihuahuan subprovince. The Edwards Plateau in south-central Texas, with elevations ranging from 450 to 3000 ft., is situated in the southern Prairies province. 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 Edwards Plateau, support extensive subtropical dryland thorn scrub and mesquite-grassland vegetation (Correll & Johnston 1970). This mostly sandy area in the Rio Grande Plain accommodates 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).

2.2 Sources of Data

We compiled the database with 81,851 records of 400 species in 174 genera and 61 families of angiosperms, and 2 genera in 2 families of gymnosperms. More than half of the species were selected, using the classification of geoelements (species with congruent distributions) from the checklists of BB, EP, and S TX (Saghatelyan, 2009, 2015, 2017) to represent the different floristic regions and provinces which intersect in Texas. Also included are species of the western parts of the Madrean region in the USA from the floras of southern

Arizona, New Mexico, and California (SENet Portal: http://swbiodiversity.org/seinet/; The Jepson Flora Project; https://ucjeps.berkeley.edu/jepsonflora/). To sample the central Rocky Mountains/Great Basin area we included species from Bear River flora, Utah (L. Shultz, Utah State University, personal communication). Widespread species with ranges covering most of the study area were avoided, while the species well represented in the dry areas of southern USA were included. The members of extensively studied families of eudicots with molecular phylogenies of their representative genera published in recent years were preferentially included in the database. Seven such families comprise 254 species (63.5% of all the species): Asteraceae (111 sp.), Fabaceae (43 sp.), Apocynaceae (28 sp.), Hydrophyllaceae (23 sp.), Boraginaceae (19 sp.), Cactaceae (19 sp.), and Nyctaginaceae (11 sp.).

The species of the sonoran, madrean, madro-tethyan, and tropical/subtropical genera were selected over species of widespread temperate genera. The species of temperate genera connected with the Old World via Bering Land Bridge (BLB), e.g. Astragalus L., are mostly from the temperate Bear River flora checklist. Digitized herbarium specimen data were downloaded from the Integrated Digitized Biocollections (http://www.idigbio.org/portal), last accessed January –April 2020. The nomenclature was checked with International Plant Name Index (IPNI). During the cleaning we eliminated duplicates, records on university campuses or botanical gardens, erroneous records, such as "0" or "NA" values for latitude and longitude; occasional points in southern or eastern hemisphere; in cases with ample occurrence points per species, older than 1950 records were purged. The maps were contrasted with those documented by the Biota of North America Project (BONAP; https://bonap.org, accessed April–May 2020), online databases (e.g., EOL: https://eol.org/), and literature (Turner at al., 2003). The final database included 81, 851 specimen point records of 400 species with 7 – 800 points per species. The species list is in the Appendix 3.

2.3 Endemicity Analysis

We searched for AEs using the NDM/VNDM v.2.7 program (2004, 2016), which applies the method proposed by Szumik et al. (2002) and Szumik & 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 AE 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.

All the areas receive an endemicity score (E), which is the sum of the scores of the supporting species. The E value improves with both the number of species concordant with the area and the degree of concordance between the area and those species (Aagesen et al., 2013).

Preliminary analyses were performed with varying grid sizes to explore different analytical options and to increase the chances of finding different areas. Additionally, the areas that survive changes in grid size can be considered to be more strongly supported by the data (Elias & Aagesen, 2019).

We analyzed the dataset with 81, 851 points of 400 species with three different cell sizes to explore the distribution patterns at different scales and the robustness of the resulting areas to changes in grid size. Grids at cell sizes of 2.5deg latitude x 1.5deg longitude, 3deg latitude x 1.5deg longitude, and 3deg latitude x 2.5deg longitude; R fill: 5×5 ; and R to assume 10 x10 were used.

A separate NDM/VNDM analysis was carried out with a subset of the database comprised of 259 more southern species (from the floras of southern Texas, Arizona, and New Mexico). This smaller database comprising 49, 290 point occurrences was analyzed with grids: 1.8deg x 1.8deg, 2.7deg latitude x 2.4deg longitude, 2.6deg x 2.6deg, 4.5deg x 4.5deg, and 5deg x 5deg.

Final endemicity analyses 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 run 100 times, and overlapping subsets were retained if 98% of their defining species were unique. Each search was executed using edge

proportions. From the sets obtained with the larger database at cell sizes 2.5deg x 1.5deg and 3deg x 1.5deg we chose the endemic species with a minimum score 0.68, and for the analysis with 3deg x 2.5deg cells we chose the species with the minimum score 0.75 and calculated the consensus areas (CAs) at 40% similarity. We used the loose rule, which 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). From the sets obtained with the smaller database, we chose only the endemic species with a minimum score of 0.7 and calculated the consensus areas (CAs) at 50% similarity for 1.8deg cells; 70% and 40% similarity for medium and larger (4.5deg x 4.5deg, and 5deg x 5deg) cell sizes respectively.

The results were examined using VNDM. The CAs of all grid sizes were converted into shapefiles (.shp) and mapped with QGIS version 3.6.3 (http://qgis.osgeo.org). Several CAs produced by the analyses with varying cell sizes had a similar outline and only one or two endemic species differences. We kept only one such CA as an AE (Table I; Table S1, Appendix 2) and named the AEs after known floristic provinces or using geographic terms. We compared the outlines of the AEs with the units in the floristic regionalization of Takhtajan (1987) and McLaughlin (2007).

3. Results

3.1 Endemicity Analysis

The results of endemicity analysis of the database with 400 species are summarized in Fig. 1, Table 1, and Table S1, Appendix 2. NDM analysis with grids 2.5deg latitude x 1.5deg longitude produced 19 CAs from 80 sets with the endemicity scores from 1.21 (supported by 1 species) to 23.57 (supported by 61 species). Two more CAs had high scores: 17.36 (supported by 33 species) and 12.75 (supported by 20 species.)

The analysis with grids 3deg latitude x 1.5deg longitude produced 43 CAs from 106 sets. Scores ranged from 1.25 (supported by one species) to 15.95 (supported by 26 species). The CAs of both analyses produced many similar areas, with the second group providing finer results. Therefore, after omitting 14 CAs with lower scores, we chose the CAs mostly from the analysis with 43 CAs in order to define the AEs. The selected CAs were those intersected with the 19 CAs from the former analysis.

The analysis with 3deglatitude x 2.5deglongitude cells produced 26 CAs from 61 sets. The endemicity scores ranged from 2.066 (supported by two taxa) to 11.49 (supported by 17 taxa). Since we run the last analysis with a higher cut off, it had fewer species endemic to each CA, but their scores were higher. To define the areas of endemism, we combined the CAs from that analysis with the ones selected from the first two analyses based on their endemicity score. We summarize results in Table 1, Fig. 1, and columns 2, 3, and 4 in Fig. S1, Appendix 2.

All three analyses produced several nested and overlapping CAs and a clear split to two significant centers of endemism in the study area: the SW and the SC main consensus areas, shown of Fig. 1 (j) 2 and (j) 4.

The results of the NDM analysis with the second dataset comprising 259 species are shown in Table S1, Fig. S2. Preliminary analyses identified 22 CAs from 60 sets at grid size 1.8deg x 1.8deg; 29 CAs from 36 sets at grid size 2.7deg latitude/2.4deg longitude; 12 CAs at grid size 2.6deg x 2.6deg; 12 CAs at grid size 4.5deg x 4.5deg; and nine CAs at grid size 5deg x 5deg. Many CAs were partially overlapping and/or nested, especially in the south-central part of the study area. We found more nested CAs with the smaller cells, while larger cells yielded results with more overlap between the CAs. The results using different cell sizes with 259 species showed little variation in the CAs; therefore, we chose the EA with more CAs to supplement our discussion based on the combined analyses of the larger database with 400 species. Column 5 in Table S1, Appendix 2 includes the endemic species of 29 CAs at cell size 2.7deg x 2.4deg from the smaller database.

We discuss 27 AEs obtained for 400 species from three different cell sizes, selecting each AE under the grid size that yielded the highest number of supporting species. We present the AEs starting from the northernmost one moving southward and then eastward. A total number of species that supported an area under at least one grid size is 230. The remaining 170 species that did not support any of the obtained AEs, are mostly widespread in parts of the study area species, e.g. *Calochortus nuttalii* in the western or *Asclepias* *viridis*in the SC/SE parts. Several species that are landscape forming in their provinces, like *Ungnadia* speciosa, Fallugia paradoxa, and *Diospyros texana*, emerged as endemics only from the analysis of smaller database with larger cells of 4.5deg x 4.5deg (Fig. S1, column 5).

3.2. The Areas of Endemism

AE 1. Mid Rocky Mountains (Fig. 1, a1) and **AE 2. E Great Basin - Rocky Mountains** (Fig. 1, k1) embrace parts of the Rocky Mountain and Great Basin provinces. AE 1 is defined by four and AE 2 by three species of broadly north temperate and western North American genera. Each AE (Table 1) is supported by two species of *Astragalus*, a genus of Eurasian origin and migration via the BLB (Scherson et al. 2008). Eight species total (Table S1) supporting AE1 grow mostly in sagebrush scrublands, grasslands, and open conifer woodlands. Two species of *Astragalus* and *Angelica pinnata*, defining AE 2 grow in sagebrush scrublands, subalpine forests, meadows, and wetlands.

AE 3. South Rocky Mountains-Colorado Plateau-E Madrean is a large AE (Fig.1, f1) defined by four species widespread in open arid mountainous areas (Table 1). They are in SW North American genera and a madro-tethyan genus Juniperus L. Six more species of grasslands, rocky slopes, and woodland support this area in the analysis with smaller database (Table S1). In the phylogeny of Fishbein et al. (2011), Asclepias asperula endemic in AE 3 and its sister species A. viridis, which supports AE 24 South Prairie, are in the Temperate North American clade of Asclepias L. Several other species of this clade grow on the Colorado Plateau. In the phylogeny of Fishbein et al. (2018), the Sonoran Desert and Incarnatae clades are successive sisters to the remaining American Asclepias species. Another endemic in AE 3 Asclepiadaceae species, Matelea producta, is a member of the arid-adapted clade found in SW USA and northern Mexico (McDonnell et al., 2018). Several other species supporting AE 3 (Table S1) are members of SW North American clades in the genera with southern connections (e.g. Dalea). North temperate connections among the endemics of AE3 have representatives of mostly temperate families (e.g. Rosaceae, Fagaceae). For example, the monotypic Apachian genus of montane scrublands Fallugia Endl. has a western North American ancestry (Kalkman, 2004) and the two five-species genera Petrophytum (Nutt.) Rydb. and Cercocarpus Kunth are present in western North America (C. ledifolius supports AE 1, Table S1). Within Dryadoideae of Rosaceae, a Holarctic arcto-alpine genus Dryas L., and then Purshia Raf., are successive sisters to the western North American genera Chamaebatia Benth. + Cercocarpus (Sun et al., 2016). An oak species Quercus grisea endemic in AE 3 (Table S1) is a member of a small 'Arizona/North Mexico' clade in white oaks, which returned north to the USA from Mexico. Mexico has 154 species of *Quercus* that diversified since 14–20 Ma from an eastern North American ancestor (Hipp et al., 2018). Another example of north temperate connections comes from the genus Garrya Douglas ex Lindl. Endemic to AE 3 G. wrightii, together with two species supporting AE 20, G. ovata and G. glaberrima, are a part of a complex in the Mexican highlands/N Chihuahua (Nesom, 2012). All three species are in the subgenus Fadyenia (Endl.) Dahling, which is sister to the CFP subgenus Garrya (Burge, 2011). The genus Garrya is sister to the East Asian genus Aucuba Thunb. in the family Garryaceae, which are sister to an arctotertiary, according to Mai (1995), family Eucommiaceae. Today, Eucommiaceae consists of a single species from China, but has a wide fossil distribution in the Northern Hemisphere (Manchester et al., 2009; Soltis et al., 2018).

AE 4. Great Basin-Mohave (Fig 1, d1) includes the Mohavian subprovince and western parts of the Great Basin province. It is supported by three species of western North American or amphitropical genera found in sagebrush or creosote bush scrub, Joshua-tree woodlands, or pine forests. *Eucnide urens* which supports this AE in the analysis with smaller database (Table S1) represents a SW USA-Mexico-Mesoamerican genus, which was placed as the sister to the rest of the family Loasaceae (Moody et al., 2001).

AE 5. S CFP-SE Great Basin-Mohave-N Sonora (Fig.1, j1). AE 5 embraces the Mohavian subprovince and parts of the adjacent subprovinces/provinces. Four species of SW N American /amphitropical genera, which grow in open areas, sandy to rocky slopes, chaparral, and oak/pine woodlands, support this AE. Two of them are in the genus*Phacelia* Juss., the largest (207 sp.) and most diverse member of the family Hydrophyllaceae (Vasile et al., 2020). The family is distributed mainly in western North and South America. Hydrophyllaceae and Namaceae both appear to have originated in North America and are successively sister

families to the remainder of the Boraginales II (Bor II) clade (Luebert et al. 2017). Another species supporting this AE in the analysis with the smaller database, *Nolina bigelovii*, represents the genus with 32 species half of which are endemic to Mexico (Ruiz-Sanchez et al., 2019). Geographical distribution of *Nolina*Michx. is split into the western and eastern ranges. The western range extends south from Utah in the north, through Baja California and the Sierra Madre Occidental. *N. bigelovii*, as well as *N. microcarpa*, which is endemic in AE 3 (Table S1), have western ranges. The eastern range of *Nolina* extends from Florida in the north, through the Sierra Madre Oriental south to Oaxaca in Mexico (Ruiz-Sanchez et al., 2019).

AE 6. Mohave-Sonora (Fig 1, b1). Six species, including a monotypic genus *Hesperocallis* A.Gray, found in the Mohavian and Sonoran subprovinces are endemic to AE 6 (Table 1). They are members of xerophytic clades of mostly SW North American genera (e.g. Cylindropuntia [Engelm.] F.M.Knuth). The Cylindropuntieae originated in the Chihuahuan Desert during the mid-Miocene and then migrated into other North American deserts. They show a consistent split between the Sonoran and Chihuahuan deserts exemplified by several Sonoran-Chihuahuan desert species pairs (Majure et al., 2019). Tiquilia plicata is another species supporting AE 6 (Table S1). It is a member of an amphitropical desert genus of the Bor II tribe Ehretieae (Gottschling et al., 2014), which is sister to the two tropical sister genera in America/Africa. Several dwarf species of *Tiquilia* Pers. are split between the Sonoran (subgenus Tiquilia) and Chihuahuan (subgenus Eddya) deserts. In the subgenus Tiquilia, T. plicata clade is sister to T. palmeri clade (Moore and Jansen, 2006) with T. palmeri supporting AE 7 of this study. An interesting example comes from Stephnomeria parryi of Cichorieae, Asteraceae, which is endemic to AE 6. All the principal American genera of Cichorieae radiated from a single common ancestor Phalacroseris A.Gray (Lee et al. 2003; Kilian et al. 2009), a monotypic local endemic genus in the wet meadows and upper montane forests of the Sierra Nevada Mountains. *Phalacroseris* is nested within the intercontinentally disjunctive Cichoriinae where it branches basally to a clade with a genus from the Horn of Africa and a mostly Mediterranean-Frontal Asian genus Cichorium L.

AE 7. South Great Basin- Mohave-N Sonora (Fig.1, g1; Table 1) is supported by three species of SW North American genera found on sandy plains and hillsides (e.g. Mohave prickly poppy), rocky slopes, creosote-bush scrub, Joshua-tree and pinyon/juniper woodlands. They are centered in the Mohave Desert extending across southern Great Basin province and northern Sonoran subprovince.

AE 8. South Sierra Nevada-Mohave (Fig. 1, 11) has three endemic species (Table 1) found on open, sandy, gravelly to rocky areas, in pinyon/juniper woodland. The area overlaps the Mohave subprovince and southern mountains in CFP, including south high Sierra-Nevada. The species supporting it are in amphitropical, mostly western North American genera (*Phacelia* and *Cryptantha* Lehmann ex G.Don). Several species of these genera are endemic in the areas partially overlapping in the super area AE 9, from AE 4 to AE 9. The majority of *Phacelia* species (176 spp.) is distributed in western North America (Walden et al., 2014). The center of diversity for the genus is the CFP, where a third of described taxa occur (ca. 70 spp., 40 spp. endemic). Raven and Axelrod (1995) suggest that the annual phacelias originated with the CFP during the Pliocene as early as 5.3 mya, and their ranges spread following the Eocene as more land became arid (Walden et al., 2014). An endemic to AE 7 species *Cryptantha utahensis* (A.Gray) Greene and two other species of series Pterocaryae form a clade with endemic to AE 8 *C. mohavensis* and *C. gracilis* Osterh (Mabry et Simpson, 2018).

AE 9. SW North American (Fig 1, j2). This super-area includes several overlapping or nested areas described above. Its endemicity index is nine, and the area is supported by 10 endemic species, including a monotypic genus *Centrostegia* A.Gray in Benth of Erigonoideae, Polygonaceae.

AE 10. Colorado Plateau (Fig. 1, i1). This AE overlaps southern Great Basin province in south Nevada, south Utah, and north Arizona. Two species found in semi-deserts, sandy, clayish or rocky places support this AE. One of them *Tiquilia latior* is sister to the endemic in AE 3 (Table S1) *T. hispidissima*. In the phylogeny of Moore and Jansen (2006), these species are in the subgenus Eddya, whereas endemic to AEs 6 and 7 species are in the western subgenus Tiquilia.

Moore and Jansen (2006) suggest that the Ehretioid ancestors of Tiquilia inhabited dry tropic scrub in SW North America during the Paleocene. All current major lineages of Tiquilia likely arose in the early to mid-Miocene, perhaps evolving allopatrically in locally arid or semi-arid pockets.

AE 11. Colorado Plateau-Mohave-Colorado Desert (Fig.1, c1). This AE has a score four and is supported by two species in each of SW North American genera *Brickellia* Elliott and *Phacelia*.

AE 12. Madrean Region Montane (Fig.1, h) coincides with the Mexican Highlands province and overlays the AE 3. Seven species of broad distribution in the mountainous region are endemic to this area, among them woody species, like alligator juniper and evergreen sumac.

AE 13. Apachian-North Chihuahuan (Fig.1, 1 2). The area overlays the Apachian subprovince of McLaughlin (2007) and northern part of the Chihuahuan subprovince from SE Arizona to SW Texas and northern Mexican plateau. It is supported by six species (Table 1) found on dry sandy, gravelly, rocky, and gypseous clay areas in low to mid elevations. Their ranges stretch southeastward along the northeastern Chihuahuan Subprovince to Sierra Madre Oriental. The species are members of the SW North American desert genera with tropical-subtropical American connections. A species of a mega-Mexico-Mesoamerican genus, in terms of Rzedowski (1993), Pinaropappus parvus, and Acleisanthes chenopodioides scored 1.0 each in AE 13. Acleisanthes A.Gray is a member of the North American xerophytic clade of mostly tropical/subtropical family Nyctaginaceae. It has a number of species living on gypsum-rich soils characteristic of the Chihuahuan Desert (Douglas & Manos, 2007; Escudero et al., 2015). An endemic to this AE Thamnosma texana of an American-African genus in Rutaceae, grows on dry rocky slopes and flats. For the ancestor of Thamnosma Torr. & Frem. a migration via the BLB from South Asia to western North America was proposed by Appelhans et al. (2016). Early diverging clades of *Thamnosma* were in SW North America and may have been present in the succulent biome of arid Neogene Madro-Tertiary geoflora about 34–2 Ma (Thiv et al., 2011). A single Somalian Thamnosma species that resulted from long-distance dispersal (LDD) is nested within the American clade of 15 species. In the American clade, T. texana is sister to T. montana that is endemic in AE 5. Another interesting example comes from SW USA-Mexican genus Mortonia A.Gray, whose several species are endemic in different AEs (Table S1). Within Celastraceae, Mortonia is sister to the rest of Celastraceae, with strong support (Sun et al., 2016). In the phylogeny of Simmons et al. (2012), M. scabrella (AE 13) and M. greggii (AE 14) form a clade, which is sister to a clade with two Mexican species in southern Sierra Madre Oriental-Sierra Madre Del Sur provinces of Morrone et al. (2017).

AE 14. Sonoran-Chihuahuan (Fig. 1, f 2). This large area is nested in the mountainous AE 3; however, it is in lower elevations. Six species of wide distribution in both subprovinces of the Sonoran province give score of 5.45 (Table 1). Highest scoring species Thymophylla pentachaeta, Asteraceae frequently grows on calcareous outcrops, scrublands or deserts (FNA, v. 21). A monotypic genus *Cevallia* Lag. of Loasaceae is sister to a clade of two small genera in Mexico-Mesoamerica. This family has two main centers of diversity: the Andes and SW North America (Hufford, 2016), with the SW North American genus Eucnide Zucc. (E. urens supports AE 4) branching basally to the rest. Twenty-four species total support AE 14 in different analyses (Table S1). Among them are species of amphitropical genera (Larrea Cav., KoeberliniaZucc.), a Sonoran-Chihuahuan endemic genus (Cottsia Dubard & Dop), and Ephedra. The latter genus has long been a symbol of the Tethyan flora or "flora *Ephedra*" (Popov, 1963). It is characterized by a Madro-Tethyan disjunction pattern and is found in all North American deserts, including in AEs 14, 15, and 23. The deepest divergences in *Ephedra* indicated a basal grade of species distributed in the Mediterranean area (Rydin & Corrall, 2009). Some species of tropical-subtropical American genera (BoerhaviaL., Fuastrum E.Fourn.) in this area extend from the Sonoran subprovince northward to the western prairies and eastward to the eastern Mexican Plateau. One of them, Boerhavia spicata is a member of the North American xerophytic clade of the genus, which diversified in the deserts of SW North America (Douglas & Manos, 2007).

AE 15. Chuhuahuan (to S Prairie). This AE (Fig. 1, d 2) encompasses the Chihuahuan subprovince, with some species extending to adjacent areas. The species supporting this area are in large genera of tropical to warm temperate regions (*Phyllanthus* L., *Eryngium* L.), American/African (*Mimosa* L.), or SE North American (*Lindheimera* A.Gray & Engelm.) genera. Many of the species extend north from the

Chihuahuan Desert to south-central parts of the Prairie province. Specifically, an important element of the Madro-Tertiary chaparral vegetation, the Chihuahuan Desert species *Mahonia trifoliolata* (Table S1) had a dynamic distribution range related to the Pliocene/Pleistocene climatic fluctuations (Angulo et al., 2017). It currently occupies the largest area in its history, with its northern limits reaching NE Texas. *Asclepias brachystefana* of AE 15 (Table 1) is in the Mexican Highands clade of the genus (Fishbein et al., 2018), while the species of *Asclepias* endemic to AE 3 and AE 24 are in the temperate North American clade of the genus.

AE 16. North Chihuahuan-South Texas (Fig.1 e). The area embraces northeastern part of the Chihuahuan subprovince and Texas Edwards Plateau. Three of the five species, which support this AE, have the highest score of 1.0 (Table 1). *Cynanchum pringlei* is in the New World clade of this tropical to warm temperate genus. It is sister to a clade across the Atlantic with center of distribution in NE Africa and Arabia. All Asclepiadeae, including *Asclepias, Matelea*Aubl., and *Cynanchum* L. have an "out-of-Africa" distribution pattern (Khanum, 2016). *Tiquilia gossypina* is in the Chihuahuan desert subgenus Eddya (Moore and Jansen, 2006). *Acleisanthes crassifolia* is a species of conservation concern, found on rocky, calcareous soils in cenizo shrublands and grasslands in Coahuila, Mexico, and Texas (FNA, v.4).

AE 17. South-East Texas (Fig 1, k 2). This small area is supported by three species with narrow ranges in SE Texas. They grow on the South Texas Sand Sheet (*Mimosa latidens;* Carr, 2007), on limestone hills and flat open ground (*Dalea lasiathera*), and on gravel of limestone streambeds (*Brickellia dentata*) (FNA Vol. 21). *Dalea* is the largest and extensively radiated in the Sonoran Desert genus in the predominantly North American temperate clade Amorpheae of the legumes (Cardoso et al., 2013). Several species of *Dalea* support different AEs of this study (Table S1).

AE 18. South Texas-Coahuila (Fig. 1, i 2). This area is nested in AE 16 and is a part of the Chihuahuan subprovince in Coahuila and Nuevo Leon in Mexico and south Texas. It has five endemic species, including edaphic endemics on sandy soils (*Funastrum torreyi*) and calcareus or gypsum rich soils (*Acleisanthes acutifolia*).

AE 19. Chihuahuan-Tamaulpan (Fig. 1, j 3) is nested in the super area AE 22. It is supported by three species (Table 1): *Viguiera stenoloba*, found in Tamaulipan and Chihuahuan Desert scrub, and mostly chihuahuan, extending to Tamaulipas species *Jonstonella mexicana* and *Boerhavia linearifolia*, found in arid grasslands or shrublands and on calcareous soils. *J. mexicana* represents one more tribe with the west/east split in the area of study. It is one of the four *Cryptantha* species of an eastern Mexico/Texas series Albidae, recently transferred to the new genus *Johnstonella* Brand (Simpson et al., 2019).

AE 20. Chihuahuan wide (Fig.1, a 2). This AE is supported by 11 species (Table 1) found in the Chihuahuan subprovince, sometimes extending to the east and south. They are mostly in

tropical/subtropical American genera (e.g. a common component of Chihuahuan desert scrub *Condalia* ericoides), tropical/subtropical (*Vachellia* [Wight & Arn.] Kuntze), and tropical/warm temperate genera with transatlantic connections (*Cynanchum, Heliotropium* L.). The only New World species of the Madro-Tethyan genus *Peganum* L. is restricted to the Chihuahuan Desert. *Peganum* is a member of a small, mostly Tethyan family Nitrariaceae of Sapindales, which includes 13 species and which diversified during the Cretaceous (Muellner-Riehl et al., 2016). The authors found that East Mediterranean-Irano-Turanian family Biebersteiniaceae (five species) and the family Nitrariaceae form a grade and have the longest stem lineages observed in Sapindales, possibly indicating that extinction may have had a greater role in shaping their extant diversity than elsewhere within the order. A good indicator of chihuahuan desert, a monotypic endemic genus *Talinopsis* A.Gray (Table S1) grows in desert scrub of Mexican Plateau and Trans Pecos in Texas. It is one of the four genera of a small family, which is sister to Cactaceae (Christenhusz et al., 2017), with widely disjunctive distribution in Southern Hemisphere and in the Chihuahuan Desert.

AE 21. E Madrean-Tamaulipan (Fig. 1, g 2). This AE is supported by eight species with E score of 7.04 (Table 1), found in the Sierra Madre Oriental and Tamaulipas provinces of Morrone (2017). They are in the genera with transatlantic disjunctions with the Old World, such as tropical/subtropical (*Cynanchum*)

, Mimosa, Cordia L.), or in tropical/subtropical American (Gochnatia Kunth, Chaptalia Vent.) genera.

AE 22. SC USA-E Madrean (Fig.1, j 4). This is a broad super area where several other areas (from AE 12 to 21) partially overlap. Twenty-one species, eleven of which have score of 1.0 support this area; E score of the area is 10 (Table 1). They are in mostly tropical/subtropical American (Guaiacum, Serjania Plum. ex Mill.), Mexican-Mesoamerican (Viguiera Kunth), or American-African (Mimosa) genera. The tropical Cordiaceae, Ehretiaceae, and Heliotropiaceae of Bor II clade have 1 species each in AEs 20 and 21, which overlap in the super area AE 22. A vegetation dominant *Dermatophyllum secundiflorum*, which supports AE 22, is the only widely distributed species of a small legume genus found mostly in the Chihuahuan and Sonoran subprovinces. Another woody species supporting AE 22, Diospyros texana (Table S1), is a member of a Mesoamerican-Caribbean clade of four species and is branching basally to the other species in the clade, whereas two species from its sister clade are distributed in SE Asia (Duangjai et al., 2006). Diospyros L. is one of the boreotropical (Wolfe, 1975)/paleotropical (Mai, 1995) genera of the Northern Hemisphere with intercontinental distribution in the Paleogene. The pantropical genus Ehretia L. has mostly an East Madrean-Mesoamerican range in the New World. Its single species in the USA E. anacua supports AE 22. Currently pantropical, Ehretieae species have diversified from an American ancestor in the Early Paleogene (Luebert et al., 2016). Another species supporting this AE represents the genus Menodora Bonpl., which is the New World counterpart of Jasminum L. It is a member of the mostly Old World tropical to warm temperate tribe Jasmineae, which has a disjunction between South Africa and xeric warm temperate/subtropical North and South America (Wallander & Albert, 2000). One more endemic, *Linum vernale*, belongs to the North American clade of vellow-flowered flax species derived by LDD from a western Eurasian ancestor at least 20 Mya (McDill et al., 2009).

AE 23. S Prairie (Fig. 2, b) is located north of the Apachian and Chihuahuan subprovinces and includes southern parts of the Prairie Province. It is supported by several species of North American genera (*Tetraneuris* Greene), with some of them extending northward from their center of origin in the SW North America/Madrean subkingdom (*Asclepias, Dalea*).

AE 24. Comanchian (Fig.1, b 2) partly coincides with the Comanchian chorino of McLaughlin (2007). It is supported by 16 species found throughout central/east Texas to south/central Oklahoma. The endemicity index of AE 24 is 10.07 (Table 1). Most species are in eastern North American temperate genera (*Liatris*) Gaertn. ex Schreb., Krigia Schreb., Baptisia Vent.), or in tropical/subtropical genera (Vernonia Schreb.). An eastern North American genistoid genus *Baptisia* is allied with the mostly western North American genus Thermopsis R.Br. in the Thermopsideae clade of the legumes; it had some exchange with Asia around the Bering Strait (Wang et al., 2006). Matelea is a mega-Mexico-Mesoamerican genus. With 200 species, Matelea is one of the largest genera within the Apocynaceae (McDonnell, 2015). The sister species M. biflora and M. cynanchoides , which support AE 24, are in the subgenus with 30 milkweeds of arid habitats centered in North Mexico (McDonnel, 2015). The genus Triodanis Raf., with two endemic species in AE 24, has a North American-Mediterranean disjunction due to an LDD event. Clade I of the Campanuloideae phylogeny of Crowl et al. (2014) contains the paraphyletic Mediterranean genus Legousia Durande and one North American clade. The Mediterranean-Frontal Asian L. falcata (Ten.) Fritsch is sister to the North American clade containing *Triodanis* species and a Texas endemic species *Campanula reverchonii* A.Gray. Some other species supporting AE 24 are endemic to a nested area that embraces S TX, EP, and BB. They are members of amphiatlantically disjunctive genera (Mimosa) or eastern North American genera (Baptisia and Silphium L.).

AE 25. Edwards Plateau (Fig. 1, c 2). This small AE is in North Central Texas and on the Edwards Plateau. It is supported by two endemic species of American-African genera, *Mimosa* and *Tradescantia* L. (Table 1).

AE 26. Atlantic and Gulf Coastal Plain (Fig. a 3). This AE is supported by three species of SE North American/Central American herbaceous genera, e.g. a monotypic genus *Zygadenus* Michx (Table 1). Our database containes only a few southeastern species. Analyzing in detail the woody flora of the southern Appalachians, Manos & Meireles (2015) found mostly low-diversity clades connected to the Old World and

a minority of New World clades.

4. Discussion

The analysis of the database resulted in the recognition of 26 AEs, including two super areas: SW superarea AE 9, and SC super-area AE 22. Two major observations consistently emerged from all the analyses: a dramatic east/west split and a significant overlap or nestedness among the adjacent AEs within each of the two disjunctive groups – the two super-areas. Szumik et al., (2018) using a dataset of mammals of North America demonstrate that AEs consistently overlap and are rarely characterized by sister taxa. Many genera (e.g. *Tiquilia, Nolina*, and *Cylidropuntia*) show a geographic split into western and eastern clades. The split to two super-areas corresponds to an environmental and physical barrier, Cochise Filter Barrier (CFB). Provost et al. (2021) studied community phylogeographic patterns of plants and animals across the CFB, which is a known transition zone between two biotas that divides the Sonoran and Chihuahuan Deserts. By synthesizing phylogeographic data for the CFB, the authors estimated that for the maximum number of species the barrier overlapped 108.6degW. Many of the taxa they surveyed show a Pleistocene divergence time, and divergence throughout the region appeared to be a combination of forces, ranging from allopatric isolation to ecological speciation.

The endemic species of AEs 1-4 are in north temperate or western North American genera. Many species of the SW group of overlapping areas, AEs 5 - 11, diversified in the great SW North American arid center, which Sosa et al. (2018) referred to as the center of both paleo- and neoendemism. They include members of the local xerophytic genera with extensive radiation in the Sonoran and Mohave deserts. The majority of their connections extend along the western backbone of the Americas, especially to western Mexico and to deserts in South America as amphitropical disjunctions (AAD). AAD examples throughout the angiosperms have become established via multiple asynchronous "events" with most estimated examples occurring within the last 5 Myr (Simpson et al., 2017). Some of the endemics of the SW AEs represent the families originated in this center (e.g. Hydrophyllaceae and Namaceae). Other endemics are early-derived members of their families, such as the genera Mortonia of Celastraceae and Eucnide of Loasaceae, or early-derived members of their genera (e.g. of Asclepias, Matelea, and Thamnosma). The Sonoran Desert element (e.g. Boerhavia) extends eastward to the Chihuahuan Desert into western Texas (mostly to Val Verde County) and Mexico. 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. The same is true for the chihuahuan element, which extends westward to Sonora/Mohave [Larrea tridentata (Laport et al., 2012)] and eastward to Tamaulipas (Carlowrightia torreyana).

Many sampled species are included in the SW North American genera extending northward to South Rocky Mountains and western prairies. BLB served as the migration route to western North America (e.g., for *Astragalus, Artemisia,* and the ancestor of *Thamnosma*).

The endemic species of SC super area (AEs 12-22), have mostly East Madrean/Mesoamerican affinities or transatlantic connections, including with the Tethyan subkingdom (*Peganum*). According to Graham (2018), affinities between the SW USA/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 tropical-subtropical genera (*Vachellia, Diospyros*), American tropical-subtropical genera (*Funastrum, Guaiacum*), and Madrean/Mesoamerican genera (*Telosiphonia, Garrya*) are characteristic of the SC AEs, especially of the Tamaulipan thorn scrub. The Antilles between NE South America, the Yucatan region of Mexico, and the SE USA via the Bahamas served as a filtering discontinuous stepping stone route for southern warm temperate to subtropical lineages into North America throughout their existence from about the middle Eocene to the present (Graham, 2018). Some of these made the trip but subsequently became extinct in northern North America with late Cenozoic cooling and drying (*Podocarpus, Nothofagus*). An example of one taxon that persisted is *Diospyros*, which is the only genus of the Ebenaceae known

in the forests of the eastern USA. Raven & Axelrod (1974) suggest the family originated in West Gondwana and migrated into Eurasia and North America during the Paleogene (Graham, 2018). AE 24 (Comanchian) is supported by the species of the genera of E region (*Baptisia, Silphium*), amphiatlantically disjunctive genera (*Desmanthus, Mimosa*), and those arrived by LDDs from the Mediterranean (*Lechea, Triodanis*). The Comanchian chorion of McLaughlin's system is strongly supported by our analysis, however it falls in the Prairie Province of the ER of Takhtajan's system, rather than the SW of McLaughlin. Affinities of the ER across the N hemisphere have been extensively discussed in the literature and reviewed by Manchester (1999), Harris et al. (2013), and Manos & Meireles (2015).

Our analysis supports the placement of BB in the Chihuahuan subprovince of the Sonoran province of the SW, while S TX flora, which is a part of the Tamaulipas province, shows SE North American affiliation (ER). The majority of sampled prairie species also show ER affiliation. Some sampled species found in southwestern low prairies are those that extend northward from the Sonoran/Mohave deserts (in Asclepias, Dalea) or the Chihuahuan desert (Alloberberis) in connection with recent aridification and expansion of deserts.

5. Conclusion

The Sonora-Mohave arid center is among the greatest centers of xerophytic diversification and is of high conservation importance. Some very rare species are found in S TX, and this area is also highly important from the conservation perspective, as is the unique desert flora of SW Texas, already protected in two National Parks.

Our analysis is the first attempt, to the best of our knowledge, to apply NDM analysis of endemism to study distribution patterns of plant species in USA. This study has an advantage over previous qualitative classifications that the units were analyzed using species distribution data provided by the current plant specimen records. It is a step towards resolving discordances in the floristic regionalization of the SW/SC USA. The inclusion of additional species into the database in the future, expansion of the area of study, as well as additional methods for analyzing species distribution patterns should produce improved outcomes.

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

-XYD file containing point records (coordinates) for each of the species analyzed

-Excel file containing all specimen point records

-supplementary list of occurrence data downloads from GBIF

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Table 1. Areas of endemism, numbers of species and species supporting each AE obtained for 400 sp. under cell sizes 3deglat. x 2.5deglong., 3deglat. x 1.5deglong, and 2.5 deglat. x 1.5deglong.

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
1. Mid Rocky Mt	2	3 x 1.5	2.16875 - 2.41875	4	Astragalus $cibarius$ $(0.700-$ $0.868)$ $Astragalus$ $utaensis$ $(0.000-$ $0.714)$ $Bal-$ $samorhyza$ $macrophylla$ (0.684733) $Androsace$ filiformis (0.000- $0.700)$	4	Fig .1 (a) 1
2. E Great Basin – Rocky Mt	27	3 x 1.5	2.26467 – 2.51467	3	Astragalus agrophyllus (0.780) Astragalus kentrophyta (0.778) Angelica pinnata (0.707)	1	Fig .1 (k) 1
3. S Rocky Mt -Colorado Plateau-E Madrean	15	3 x 2.5	2.45162 - 2.68962	4	Gutierrezia microcephala (0.821- 0.833) Allionia incarnata var. incarnata (0.000- 0.800) Baileya multiradiata (0.827- 0.840) Juniperus monosperma (0.000- 0.804)	2	Fig. 1 (f) 1

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
4. Great Basin –Colorado Plateau- Mohave-N Sonora	16	3 x 1.5	2.52975 - 2.77975	3	Hymenoxys cooperii (1.000) Hymenoxys lemmonii (0.706) Cryptantha recurvata (0.824)	1	Fig. 1 (d) 1
5. S CFP-SE Great Basin - Mohave - N Sonora	5	3 x 2.5	3.31250 – 3.56250	4	Encelia actoni (0.875) Chorizanthe corrugata (0.813) Phacelia curvipes (0.813) Phacelia lemmonii (0.813)	1	Fig. 1 (j) 1
6. Mohave - Sonora	8	3 x 2.5	4.07143 – 4.41667	6	$\begin{array}{l} Hesperocallis\\ undulata\\ (0.000-\\ 1.000)\\ Grusonia\\ kunzei\\ (0.833-\\ 1.000)\\ Gaillardia\\ arizonica\\ (0.833-\\ 1.000)\\ Brickellia\\ desertorum\\ (0.000-\\ 0.917)\\ Cylindrop-\\ untia\\ acanthocarpa\\ (0.000-\\ 0.917)\\ Baileya\\ pauciradiata\\ (0.000-\\ 0.833)\\ \end{array}$	3	Fig. 1 (b) 1

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
7. S Great Basin – Mohave – N Sonora	9	3 x 2.5	3.37400 – 3.06100	3	Cryptantha utahensis (0.938) Phacelia rotundifolia (0.938) Argemone corymbosa (0.938)	1	Fig. 1 (g) 1
8. S Sierra Nevada - Mohave	43	3 x 1.5	3.00000 – 3.25000	3	Cryptantha mohavensis (1.000) Phacelia mohavensis (1.000) Phacelia austromon- tana (1.000)	1	Fig. 1 (l) 1

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
9. SW N America	6	3 x 2.5	9.09774 - 8.90200	10	Centrostegia thurberi (0.864 - 1.000) $Chorizanthe$ rigida (0.864 - 1.000) $Eschscholzia$ minutiflora (0.000 - 0.808) $Cylindrop$ - untia acanthocarpa (0.000 - 0.813) $Cylindrop$ - untia echinocarpa (0.000 - 0.864) $Cylindrop$ - untia 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)	3	Fig. 1 (j) 2 Fig. 2 (a)

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
10. Colorado Plateau	23	3 x 2.5	2.00000 - 2.25000	2	Tiquilia latior (1.000) Encelia resinifera (1.000)	1	Fig. 1 (i) 1
11. Colorado Plateau – Mohave - Colorado Desert	4	3 x 2.5	1.75000 – 2.00000	4	Brickellia incana (0.833 -1.000) Brickellia longifolia (0.000- 1.000) Phacelia neglecta (0.000- 1.000) Phacelia parishii (0.000- 1.000)	4	Fig. 1 (c) 1 blue
12. Madrean Region Montane	25	3 x 1.5	6.77443 – 7.02443	7	Rhus virens (0.892) Rhus microphylla (0.775) Cologania angustifolia (0.816) Cylindrop- untia leptocaulis (0.786) Tiquilia canescens (0.750) Juniperus deppeana (0.738) Nama hispida (0.714)	1	Fig. 1 (h)

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
13. Apache- N Chi- huahuan	6	2.5 x 1.5	2.96429 – 3.29167	6	$\begin{array}{c} Pinaropappus\\ parvus\\ (0.700-\\ 1.000)\\ Acleisanthes\\ chenopodi-\\ oides\\ (0.000-\\ 1.000)\\ Porophyllum\\ scoparium\\ (0.000-\\ 0.857)\\ Tiquilia\\ gossypina\\ (0.000-\\ 0.821)\\ Hedeoma\\ hyssopifolia\\ (0.000-\\ 0.821)\\ Hedeoma\\ hyssopifolia\\ (0.000-\\ 0.821)\\ Leuciva\\ dealbata\\ (0.000-\\ 0.720)\\ \end{array}$	6	Fig. 1 (l) 2
14. Sonoran – Chi- huahuan	24	3 x 2.5	5.20486 – 5.45486	6	Thamnosma $texana$ (0.813) $Aloisya$ $wrightii$ (0.806) $Acleisanthes$ $longiflora$ (0.806) $Thymophylla$ $pentachaeta$ (1.000) $Acourtia$ $wrightii$ (0.969) $Berberis$ $haemato-carpa$ (0.813)	1	Fig. 1 (f) 2

AE	CA	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
15. Chi- huahuan -(to S Prairie)	10	3 x 1.5	8.20985 - 8.11247	12	Carlowrightia texana (0.694- 0.833) Asclepias brachys- tephana (0.711- 0.806) Asclepias texana (0.000- 0.733) Dalea pogonathera (0.000- 0.739) Telosiphonia macrosiphon (0.000- 0.767) Tiquilia greggi (0.750- 0.767) Tiquilia greggi (0.750- 0.767) Guaiacum angusti- folium (0.000- 0.767) Guaiacum angusti- folium (0.000- 0.767) Cryptantha mexicana (0.000- 0.767) Cryptantha mexicana (0.000- 0.767) Cryptantha mexicana (0.000- 0.733) Lygodesmia texana (0.000- 0.711) Boerhavia linearifolia (0.694- 0.706) Linum vernale (0.000- 0.700)	4	Fig. 1 (d) 2
			26				

AE	CA	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
16. N Chi- huahuan	14	3 x 1.5	3.18750 – 3.43750	5	$Cynanchum pringlei \\ (0.688- \\ 1.000) \\ Tiquillia \\ gossypina \\ (0.000- \\ 1.000) \\ Acleisanthes \\ crassifolia \\ (0.000- \\ 1.000) \\ Thymopyilla \\ micropoides(0 \\ 0.833) \\ Funasrum \\ torrei \\ (0.000- \\ 0.822) \\ \end{bmatrix}$	3	Fig. 1 (e)
17. SE Texas	13	3 x 1.5	2.2500 – 2.5000	3	Brickellia dentata (0.750- 1.000) Dalea lasiathera (0.750- 1.000) Mimosa latidens (0.000- 0.813)	3	Fig. 1 (k) 2

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Map
18. S Texas – Coahuila	2	3 x 2.5	3.1428 – 3.50000	5	Funastrum torrei (0.000- 1.000) Tiquilia gossypina (0.000- 1.000) Brickellia cylindracea (0.000- 1.000) Chamae- saracha edwardiana (0.00-0.833) Acleisanthes acutifolia (0.000- 1.000)	6	Fig. 1 (i) 2
19. Tamauli- pan - Chihuahuan -	19	3 x 2.5	2.54167– 2.79167	3	Cryptantha mexicana (0.875) Viguiera stenoloba (0.833) Boerhavia linearifolia (0.833)	1	Fig. 1 (j)3

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
20. Chi- huahuan – Tamaulipan -SME	34	3 x 1.5	9.70358 – 10.48258	11	Condalia ericoides (0.833) Peganum mexicanum (0.778) He- liotropium conferti- folium (0.833) Acleisanthes obtusa (0.778) Asclepias brachys- tephana (0.775) Cynanchum barbigerum (0.750) Brickellia laciniata (0.750) Brickellia laciniata (0.750) Vachellia rigidula (0.722) Forestiera angustifolia (0.705) Justicia pilosella (0.705) Psilostrophe gnaphalodes (0.700)	1	Fig. 1 (a) 2

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
21. E Madrean - Tamauli- pan	33	3 x 1.5	6.97000 – 7.04000	8	Cynanchumbarbigerum(0.906)Menodoraheterophyla(0.781)Cordiapodocephala(0.750) He-liotropiumconferti-folium(0.750)Mateleareticulata(0.750)Justiciapilosella(0.725)Gohnatiahypoleuca(0.722)Mimosamalacophylla(0.719)	1	Fig. 1 (g) 2

AE	CA	Cell: Lat° x Long°	Endemicity Score (E)	End Ser	Species Giving Score (endemicity score)	Ind	AFs	Man
22. SC USA – E Madrean	0	3 x 2.5	8.82143 - 10.0000	21	Cynanchum maccartii (0.000-1.000) Dalea lasianthera (0.000-1.000) Menodora heterophylla (0.000-1.000) Guaiacum angusti-folium (0.000-1.000) Asclepias texana (0.000-1.000) Asclepias texana (0.000-1.000) Acleisanthes crassifolia (0.000-1.000) Acleisanthes crassifolia (0.000-1.000) Yucca constricta (0.000-0.857) Triodanis coloradoensis (0.000-1.000) Dermatophyllum secundiflorrum (0.000-1.000) Dermatophyllum secundiflorrum (0.000-1.000) Serjania brachycarpa (0.000-1.000) Tiquilia gossypina (0.000-0.833) Linum vernale	16		 Fig. 1 (j) 4
			31		0.800) Viguiera stenoloba (0.000-			

ramagiagima

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
23. S Prairie	30	3 x 1.5	3.05711 – 3.30711	4	Tetraneuris $scaposa$ (0.833) $Asclepias$ $arenaria$ (0.788) $Dalea aurea$ (0.731) $Senecio$ $ridellii$ (0.705)	1	Fig. 2 (a)

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
24. Co- manchian	9	3 x 1.5	10.06817 - 9.938750	16	Senecio ampullaceus (0.692- 1.000) 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 cy- nanchoides (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-	6	Fig. 1 (b) 2
			33		0.800) Phacelia strictiflora (0.000- 0.818) Vernonia lindheimeri (0.000-		

AE	СА	Cell: Lat° x Long°	Endemicity Score (E)	End. Ssp.	Species Giving Score (endemicity score)	Ind. AEs	Мар
25. Edwards Plateau	17	3 x 1.5	1.75000 - 2.0000	2	Tradescantia edwardsiana(0 1.000) Mimosa roemeriana (0.000- 1.000)	2 9.900-	Fig. 1 (c) 2
26. Gulf Coast - Atlantic	41	3 x 1.5	2.19837 – 2.44837	3	Sabatia brevifolia (0.773) Chaptalia tomentosa (0.773) Zigadenus glaberrimus (0.692)	1	Fig. 1 (a) 3

Table 1.Mt-mountains, Gr-Great, Plt-Plateau, Chih-Chihuahua, Tam-Tamaulipas, Comanch-
Comanchian, TX-Texas, S-South, N-North, E-East, W-West, sp-species, lat-latitude, long-longitude.

Fig. 1 Legend

Abreviations: Chih - Chihuahuan; Moh - Mohave; Son - Sonoran; Co l- Colorado; Plt - Plateau; Des - Desert; Edw - Edwards; Gr Bas - Great Basin; Prair - Prairie; TX - Texas; Madr - Madrean Reg - Region; Mont - Montane; Coah - Coahuila; CFP - California Floristic Province; Am - American; Tam - Tamaulipan; Sier Nev - Sierra Nevada; Apach - Apachian

Fig. 2 Legend

(a). AE9. SW N Am; (b). AE23. S Prairie

Appendix 1. Texas map.

Appendix 2. Table S1.

Appendix 3. List of species with authorities used in the analyses.



