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Long-term trends in the plant community in three habitats in the Big Bend of Texas

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Abstract.—In 1959, the plant community and abiotic environment of three 2.2-ha Chihuahuan Desert plots were studied in Big Bend National Park, Texas. In 2019 and 2020, we continued the study of these plots using the same methods with the goal of evaluating the long-term trends in the perennial plant communities of 3 different habitats within the park. Our study assessed species composition, density, and ground cover, which were compared with the same parameters reported from 1959. At a rocky site in the foothills of the Chisos Mountains, plant density decreased during the 61 years of the study (1959–2020) but remained high compared with the other sites. Many of the perennial plant species persisted, but the relative proportions of some species had changed over time. Another study plot was situated on a gently sloping alluvial fan at Panther Junction. Plant density and ground cover increased substantially on this desert pavement habitat. Much of the increased density can be attributed to grasses, particularly Lehmann lovegrass (*Eragrostis lehmanniana*), an exotic invasive species likely introduced as a result of human activity surrounding the nearby park headquarters at Panther Junction. A third plot was a level sandy habitat on Tornillo Flat. The density and species composition of the plant community at Tornillo Flat were remarkably stable between the 1959 and 2019 surveys. Factors likely affecting the plant community at the 3 plots include periodic drought, invasive species, fire, climate change, and secondary succession following past overgrazing of livestock that ended with the establishment of the national park in 1944.

Resumen.—En 1959, se estudió la comunidad vegetal y el entorno abiótico de tres parcelas de 2.2 ha del Desierto Chihuahuense en el Parque Nacional de Big Bend, Texas. En 2019 y 2020, continuamos el estudio utilizando los mismos métodos con el objetivo de evaluar las tendencias a largo plazo en las comunidades de plantas perennes de tres hábitats diferentes dentro del Parque. Nuestro estudio evaluó la composición de las especies, la densidad y la cobertura del suelo, y comparó dichos parámetros con los registrados en 1959. En un lugar rocoso de las estribaciones de las montañas Chisos, la densidad de las plantas disminuyó durante los 61 años del estudio (1959–2020) pero se mantuvo alta en comparación con los otros lugares. Muchas de las especies de plantas perennes persistieron, no obstante, las proporciones relativas de algunas especies han cambiado con el tiempo. Otra parcela de estudio fue situada en un abanico aluvial de pendiente suave en Panther Junction. La densidad de las plantas y la cobertura del suelo aumentaron sustancialmente en este hábitat de pavimento desértico. Gran parte del aumento de la densidad se puede atribuir a las gramíneas, en particular a la hierba *Eragrostis lehmanniana*, una especie exótica invasora probablemente introducida como resultado de la actividad humana en torno a la cercana sede del parque en Panther Junction. Una tercera parcela se ubicó en un hábitat arenoso llano en Tornillo Flat. La densidad y la composición de especies de la comunidad vegetal se mantuvieron notablemente estables entre los muestreos de 1959 y 2019. Entre los factores que probablemente afectan a la comunidad vegetal en las tres parcelas se incluyen la sequía periódica, las especies invasoras, el fuego, el cambio climático y la sucesión secundaria tras el sobrepastoreo del ganado en el pasado, que terminó con el establecimiento del parque nacional en 1944.

The Chihuahuan Desert is centered in the Mexican state of Chihuahua but extends north into southwest Texas and southern New Mexico. The Chihuahuan Desert is characterized by hot summers and cool winters, with a plant community including desert scrub and desert grassland and distinguishing species including creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), honey mesquite (*Prosopis gladulosa*), yucca (*Yucca* spp.), ocotillo (*Fouquieria splendens*), lechuguilla (*Agave lechuguilla*), green sotol (*Dasylirion leiophyllum*), and black grama grass (*Bouteloua eriopoda*) (Wauer 1977, Wauer and Fleming 2002).

Big Bend National Park (BBNP) is located in the U.S. side of the Chihuahuan Desert where the Rio Grande bends far to the south around the Chisos Mountains (Fig. 1). The Chisos range is an igneous intrusion of Eocene age surrounded by Cretaceous sediments (Page et al. 2008). The

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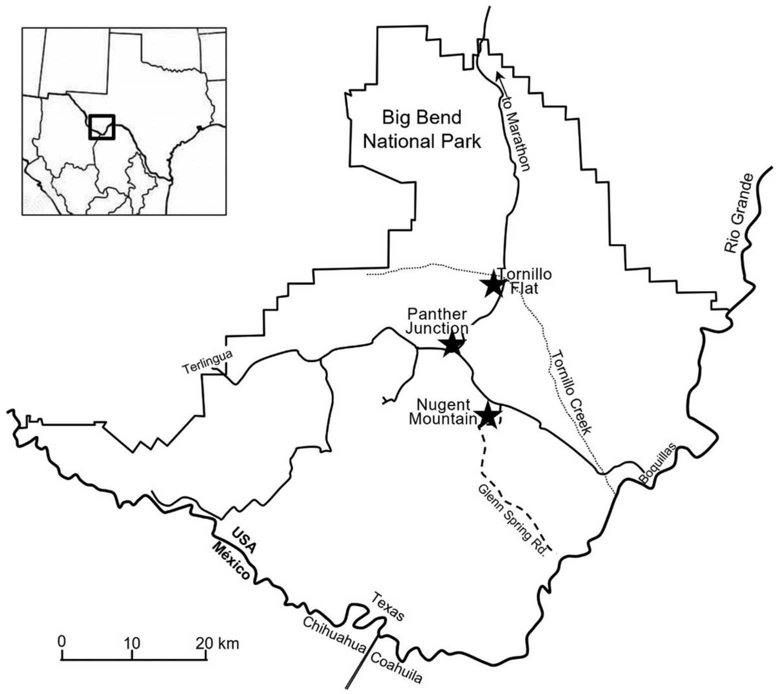

Fig. 1. Map of Big Bend National Park, Texas. Locations of the 3 study plots are indicated by stars.

Chisos rise to an elevation of 2385 m, having a pine-oak-juniper (*Pinus*, *Quercus*, and *Juniperus*) woodland at the higher elevations. Foothills of the Chisos are characterized by cobbles and boulders eroded from the volcanic intrusions that created the mountains and from older surrounding sediments. Away from the mountains, the habitat of boulders gives way to extensive alluvial fans of Quaternary age. The alluvium closer to the mountains consists of sandy soil and closely packed coarse gravel, known as desert pavement. Still farther from the Chisos, the substrate often becomes largely rock-free and sandy. Extensive weathering, erosion, and deposition have thus created a gradient of sediment sizes and a variety of habitats. Distinctive plant and animal communities are found in each of these desert environments. Porter (2011) recognized 9 habitat types in BBNP based on substrate, soil texture, vegetation, and fauna. The climate is dry, with annual precipitation at Panther Junction fluctuating most years between 25 and 45 cm, reaching a high of 65 cm in 1941 and a low of 5 cm in 2011 (Fig. 2). Precipitation is highest during the period of May through September (Porter 2011).

The ecosystems of Big Bend and the larger Trans-Pecos region have been greatly influenced by a variety of human impacts, including fire suppression, ranching, invasive species, water diversion, habitat fragmentation, pollution, and climate change (Richardson 2003, Schmidly et al. 2022). These and other factors have contributed to a decrease in grassland habitats, replaced by desert scrub (Wondzell and Ludwig 1995, Schmidly et al. 2022). Heavy grazing (mainly cattle and goats) occurred in the Big Bend area until the establishment of the national park in 1944 (Maxwell 1985). In the final year before grazing of livestock was scheduled to end on 1 January 1945, ranchers increased livestock populations, resulting in particularly heavy overgrazing at the beginning of the National Park Service (NPS) control of the region. (Baccus 1971, Wauer and Fleming 2002). Subsequently, NPS made efforts to reseed native grass on Tornillo Flat (Maxwell 1985). The potential recovery was also influenced by drought conditions (Baccus 1971, Wondzell 1984) during the period of 1950–1957 when annual precipitation remained under 30 cm and fell as low as 15 cm in 1953 (Fig. 2).

Vegetation is a major determinant of the structure, function, and biodiversity of a given ecosystem (Gardner et al. 2009). The complexity

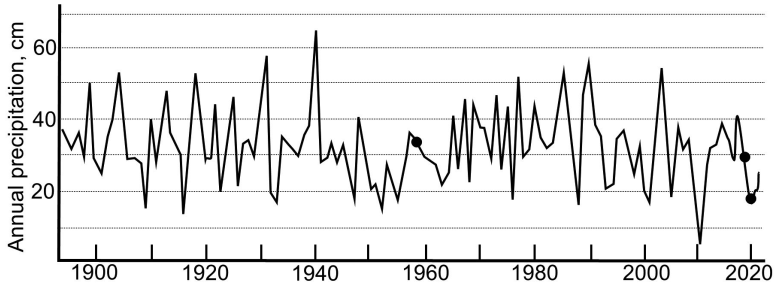

Fig. 2. Annual precipitation at Panther Junction for the years 1895–2022. The dots represent the sampling years of 1959, 2019, and 2020. During the same period, precipitation averaged about 12 cm/year less at Nugent Mountain and 6 cm/year less at Tornillo Flat. The data are from PRISM Climate Group (2023).

provided by the vegetation structure is fundamental to the ecosystem services that sustain the biodiversity. For instance, more complex and heterogeneous habitats provide greater diversity of niches and microclimates allowing for a community structure with many specialized species (Terborgh 1977). Most of this heterogeneity derives from the diversity and complexity of plant growth forms (Tews et al. 2004). Therefore, measurements of vegetation structure allow for both greater understanding of the overall characteristics of the ecosystem and how to manage it (Rhoades 1996, Pielke et al. 2002, Rutten et al. 2015). Thus, detailed information on the vegetation structure of the BBNP is crucial for the park management and the public to understand the vulnerability and resiliency of each of its ecosystems and therefore the management strategies required to protect and sustain them. In this study, we compare the changes in vegetation structure of 3 different study sites in BBNP between 2 time points approximately 60 years apart.

Beginning in 1955, the Texas Game and Fish Department contracted with the Texas Agricultural Experiment Station of the Agricultural and Mechanical College of Texas (now Texas A&M University) to conduct ecological studies of the flora and fauna of the Big Bend area. This research project (Project Number 965) entitled *Ecological Survey of the Big Bend Area* (ESBBA) included studies of birds (Dixon 1959), lizards (Degenhardt 1966), rodents (Porter 1962, 2011), mule deer (Davis et al. 1957, 1958), and plants (Davis et al. 1957, 1958, Wondzell 1984, Muldavin et al. 2010).

A total of 74 ESBBA vegetation plots were established in 1955 (Davis et al. 1957, 1958, Muldavin et al. 2010), and these plots have been reexamined at intervals in subsequent years (Wondzell 1984, Wondzell and Ludwig 1995, Muldavin et al. 2010). These plots form the basis of the primary ESBBA vegetation study which has extended through more than 6 decades.

In addition to the major ESBBA vegetation study, 2 additional aspects of the project included surveys of the plant community. Degenhardt (1966, 1977) investigated lizard communities of BBNP. As part of his ESBBA herpetological work, he surveyed vegetation at 6 locations representing different elevations and habitats in 1957, 1958, 1968, and 1969. Degenhardt's (1966) vegetation plots have been reexamined over several decades (Degenhardt 1977, Leavitt et al. 2010).

Porter's (1962, 2011) ESBBA rodent study also included plant surveys conducted in 1959 on plots throughout the park (see Appendixes I–III *in* Porter 2011). No follow-up studies have been done on the vegetation of these rodent plots. Our purpose was to evaluate long-term trends in the plant community on 3 of Porter's (1962, 2011) rodent study plots, as has been done for the plant and lizard plots.

METHODS

The 1959 Survey

In 1957–1959, Porter (1962, 2011) conducted a study of pocket mouse (*Chaetodipus* and *Perognathus*) ecology in BBNP. This ESBBA research included detailed surveys of vegetation conducted in 1959 on three 2.2-ha plots. Photographs of the plots as they appeared in 1959 can be seen in Porter (1962). Maps of the plots and recent photographs are shown in Porter (2011). The Nugent Mountain plot was laid out in rocky foothills of the Chisos mountains. The

Panther Junction plot was established in the gravelly desert pavement on an alluvial fan near the base of the mountains. Finally, the Tornillo Flat plot was laid out in sandy, sparsely vegetated habitat. The 3 plots are separated from each other by an approximately 10–16 km straight-line distance (Fig. 1) and by approximately 100–250 m of elevation.

Each of Porter's 2.2-ha plots was a square, 148.5 m on a side (Fig. 7 *in* Porter 2011). To survey the vegetation, Porter (2011) used a modification of the point-centered quarter method (Cottam and Curtis 1956, Mitchell 2015). The method involved identifying the nearest plant in each of 4 quadrants surrounding the sample point. The method used in this study differs from Cottam and Curtis (1956) and Mitchell (2015) in that the orientation of the quadrants was randomized using a spinning device placed at the sample point. Other long-term ESBBA vegetation studies in BBNP (Degenhardt 1966, 1977, Muldavin et al. 2010, Leavitt et al. 2010) have used a transect mapping method, rather than the point quarter method.

Porter's 1959 study (published as Porter 2011) sampled 49 points for vegetation on each plot. From each sample point, he measured the distance to the nearest annual herbaceous plant as well as the distances to the nearest perennial overstory and perennial understory plants. He recorded the species, height, and basal area of each sampled plant. Porter (2011) defined overstory plants as those that would not inhibit the movement of pocket mice, while understory plants are those that pose a barrier to the mice. Porter's (2011) 49 sample points were situated at rodent trap sites, marked by stakes 22 m apart in a 7 × 7 grid (see Fig. 7 *in* Porter 2011).

The Study Plots

The Nugent Mountain plot is located near the Nugent Mountain primitive campsite on the Glenn Spring Road, 1.6 km south of the junction with the Panther Junction–Boquillas highway (elevation 959–977 m). Turner et al. (2011) identified this location as a late-Cretaceous deposition (Black Peaks Formation) with some Pleistocene alluvium and adjoining igneous intrusions. Porter (2011) analyzed the physical properties of the plot in 1958–1959. He reported the Nugent Mountain plot to have a slope of 5% to 28% with abundant igneous boulders and cobbles. By weight, 71% of the substrate consisted of rock, the majority exceeding 5 cm in diameter, and some much larger. The remaining 29% of the substrate consisted of soil, mostly classified as a sandy loam. Porter (2011) reported 3 substrate types on the plot. The majority of the plot, including the more southerly and lower-elevation portions, consisted of shallow sandy loam (57%–71% sand) overlying igneous parent material. The northeastern portions of the plot had a deeper (15–76 cm) layer of sandy loam (58%–62% sand) with a thin layer of calcium carbonate caliche several centimeters below the surface with igneous parent material. The smaller western portion of the plot consisted of a silt loam (51% silt) overlying a shale parent material. All areas of the Nugent Mountain plot are abundantly covered with large (>5 cm) surface and subsurface cobbles and boulders. Outcrops of the parent material can be found in a few locations on the plot.

The Panther Junction plot is located on an alluvial fan of Pleistocene age (Turner et al. 2011) extending from the foothills of the Chisos Mountains. The plot is at Panther Junction west of the park highway leading to Marathon and north of the highway leading to Terlingua. The Panther Junction plot is <100 m directly north of the BBNP headquarters buildings and 9.5 km NNW of the Nugent Mountain plot (Fig. 1). The plot is relatively flat (4% gradient) with an elevation of 1127 m. Porter (2011) found the soil to be a fine, gravelly, sandy clay loam or sandy loam (53%–66% sand) about 35–45 cm deep. Fifty-six percent of the substrate consisted of gravel and cobbles, forming a desert pavement throughout the plot.

The Tornillo Flat plot is in level (1% gradient), sandy habitat about 150 m west of the Panther Junction–Marathon highway, 1.6 km south of the upper Tornillo bridge at an elevation of 864 m. Tornillo Flat is 10 km NNE of Panther Junction and 16 km north of Nugent Mountain (Fig. 1). Along the northern edge of the plot is a dry wash that continues about 1.8 km to the east and northeast, where it joins Tornillo Creek. The Tornillo Flat plot is primarily located on Holocene alluvial deposits but is surrounded by Eocene sandstone and shale outcrops of the Hannold Hill Formation (Maxwell 1968, Turner et al. 2011, Lehman et al. 2018). One outcrop extends a few meters into the plot from the south, and another small outcrop barely reaches the surface within the western edge. Most of the plot is sandy and nearly rock free (<1% rocks; Porter 2011), although scattered rocks can be found near outcrops. In addition, a narrow band of younger overlying gravelly colluvium is found along the north edge of the plot, where it was apparently deposited by mass wasting from the region of Avery Canyon. In contrast to the rest of the plot, this small region of colluvium consists of 61% gravel (Porter 2011). Most of the Tornillo Flat plot consists of calcareous sandy loam or loamy sand (67%–87% sand). One soil sample near the wash was a clay loam consisting of 38% clay and 40% silt (Porter 2011).

The 2019–2020 Survey

The study plots of Porter (1962) were precisely located (Porter 2011) based on remaining rebar stakes at plot corners. Using a GPS unit, we noted the exact UTM coordinates of Porter's (1962, 2011) remaining stakes and inferred the locations of missing corner stakes. In December of 2019 and 2020, we sampled the plant community of the 3 plots using the methods of Porter (1962, 2011). Porter's vegetation sampling grid included 49 points in a 7 × 7 grid evenly distributed across each plot, but the exact placement of his sample points is not known. On each plot, we established a 7 × 7 grid, 132 m on a side, centered within Porter's (1962) 148.5-m^2 rodent plots. The 49 grid points were placed 22 m apart, with each point centered in the likely area where Porter's (2011) 49 vegetation sample points would have been located. The precise location of our 49 grid points does not exactly correspond with the locations used in the 1959 survey, but in both instances, a 7 × 7 grid was evenly distributed across each plot. We therefore expect that the 2 surveys will give comparable results and that it would be unnecessary to attempt to locate the points more exactly with respect to the original vegetation survey.

In advance of fieldwork, we calculated UTM coordinates of the 49 grid points based on the known coordinates of the corner stakes of each plot. In the field, we used a hand-held GPS unit (Garmin Summit HC, precision ±3 m) to locate each grid point based on the previously calculated coordinates. A sample point was randomly selected within 4 m of each grid point. This procedure was followed to avoid conscious or unconscious bias in the precise positioning of the sample point relative to nearby vegetation. Upon arriving at the GPS-identified grid point, we randomly selected a direction with a 4-pointed spinning device (Supplementary Material 1) to determine a transect defined by a marked tine on the spinner. The sample point was established along that transect at a random distance from the grid point (Fig. 3). The distance was determined with a random number generator set to produce a distance ≥50 cm and ≤400 cm. The spinner was then relocated precisely to the randomized sample point. At the sample point, the whirled spinner was allowed to come to rest, and the tines locked in place to define the 4 quadrants around the point.

We followed Porter's (2011) classification of perennial overstory and understory species to provide continuity of methods between sampling periods. We did not survey annual herbaceous plants because the community of annual plants is likely to vary by season, so long-term studies of annuals would be less meaningful without more intensive sampling across seasons and years (Wondzell 1984). However, some species classified by Porter (2011) as annuals, are in fact perennials. We have included these species with our census of perennial plants.

For each quadrant, we identified and temporarily flagged the nearest understory and overstory perennial plant, measuring the distance from the sample point with a tape measure looped through the stake of the spinning device (Supplementary Material 1). We measured the height of each sampled plant as the perpendicular distance from the ground to the highest stem as the plant naturally stands. We also determined the basal perimeter of each plant at ground level and estimated basal area on the assumption that the perimeter was roughly circular. For prostrate shrubs (such as *Opuntia engelmannii*) the measured perimeter included the convex hull surrounding the stems in contact with the ground. All measurements were to the nearest centimeter.

We calculated overall plant density, relative species density, and dominance using the formulae of Cottam and Curtis (1956). Plant density is calculated as $D = 10^8/(\overline{d})^2$, where D = plant density per hectare and $\overline{d}$ = mean distance in centimeters from the sample point. The numerator, 10^8, is the number of square centimeters (cm^2) per hectare, necessary because distance was measured in centimeters, whereas density is expressed in plants per hectare.

Relative density was calculated as 100 × (number of individuals of a species/number of individuals of all species). Relative dominance was calculated as 100 × (total basal area of a species/total basal area of all species). Percentage ground cover was calculated from density

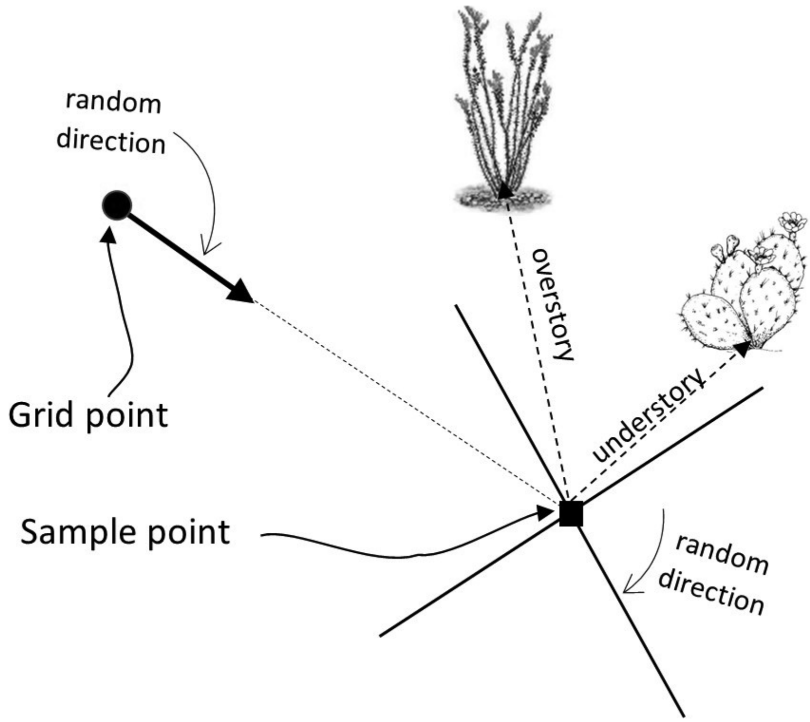

Fig. 3. Location of sample points relative to the 49 grid points. We located each grid point with a handheld GPS unit and positioned the spinner at the identified point. We established the sample point at a random direction and distance (≥50 cm and ≤400 cm) from the grid point using the spinner and a random number generator. The spinner was then repositioned at the sample point, whirled, and the tines locked into position to define the 4 quadrants of the sample point. Within each quadrant, we measured the distance to the nearest understory and overstory plant.

(plants/m^2) multiplied by average basal area (cm^2)/100. For the most abundant species, we also calculated absolute frequency and relative frequency (Mitchell 2015) of each species to test for uniform distribution on the plot. Absolute frequency is the proportion of sample points where one or more plants of a species were recorded. Relative frequency is the ratio of absolute frequency of a species to the total absolute frequencies of all species. The relative frequency is an indication of species clumping, as reflected by a species being commonly sampled in 2 or more quadrants of a single sample point (Mitchell 2015).

In addition to the separate overstory and understory analyses, we also analyzed the combined perennial data. In the combined analysis, we considered only the nearest perennial plant in each quadrant, regardless of overstory/understory classification. The sample is smaller in this analysis because it considers only 4 rather than 8 plants at each sample point. However, the analysis may give a better overall evaluation of the plant community since it avoids the somewhat arbitrary division between understory and overstory plants. For the combined analysis in 2019–2020, the plant density in plants per hectare is compared with the combined 1959 data (converted from plants/acre) presented in Table 7 of Porter (1962).

Plants were identified based on descriptions and keys in McDougall and Sperry (1951), Correll and Johnston (1979), Powell (2000), Morey (2008), and Shaw (2012). Botanical nomenclature follows Jones et al. (1997). The grass previously identified as gypsum grama (*Bouteloua breviseta*) by Porter (1962, 2011) is now recognized as a distinct species, chino grama (*Bouteloua ramosa*), being found in calcareous habitats (Reeder and Reeder 1980, Powell 2000) such as the plots examined in this study.

RESULTS AND DISCUSSION

For the combined analysis (disregarding the overstory/understory distinction), plant species sampled, relative dominance, percent composition, and density are shown in Tables 1–2 and in Supplementary Material 2. Supplementary Materials 3–11 show the results of the separate overstory and understory analyses, including percentage composition, density, relative dominance, basal area, and height. Densities of selected species are shown in Figs. 6–7.

Overstory species that have a relative dominance of >18% in one or more plots in at least one sampling period include green sotol, honey mesquite, giant dagger, cenizo, creosotebush, whitethorn acacia, and tarbush (Table 1). Relative dominance is calculated from abundance and basal area. It is worth noting that these species are among the tallest plants sampled, all having a mean height of 100 cm or more on at least one plot (Supplementary Materials 3, 6, 9). It is clear that these species constitute a substantial portion of the biomass on plots where they are found in abundance. Other species that average >100 cm in height include ocotillo, Anderson's desert thorn, and soaptree yucca (Supplementary Materials 3, 6, 9). However, these species are less dominant in terms of abundance and basal area (Table 1). Ocotillo is by far the tallest species sampled, averaging around 2 m in height (Supplementary Materials 3, 9), with one sampled plant reaching nearly 4 m. Due to its height, ocotillo can be considered more physiognomically prominent in Nugent Mountain and Tornillo Flat than might be presumed from its calculated dominance.

Understory species that are most dominant on one or more plots include lechuguilla, ground cholla, and 3 species of prickly pear (Table 2). Most of the understory species average <50 cm in height, with the exception of blind prickly pear, which we found to be uncommon (Supplementary Material 4) at Nugent Mountain, but unexpectedly dominant (Table 2) due to its large basal area (Supplementary Material 4). Blind prickly pear is also the only understory species to exceed 100 cm average height (Supplementary Material 4). Conversely, fluff grass is a common understory species on the 3 plots, but its small basal area makes it less dominant than suggested by its abundance (Supplementary Materials 4–5, 7–8, 10–11). However, basal area of fluff grass in both 1959 and 2019 was substantially larger at Tornillo Flat (Supplementary Material 10) than in the other 2 plots. Fluff grass on all plots averages around only 7–8 cm in height (Supplementary Materials 4, 7, 10), which is also a factor contributing to its relatively small biomass.

The basal area we observed for individual lechuguilla plants across all plots in 2019–2020 ranged from 6 to 945 cm^2. However, Porter (1962, 2011) reported an impossibly large mean basal area of 4594 cm^2 at Nugent Mountain (Supplementary Material 4), and 2333 cm^2 at Panther Junction (Supplementary Material 7) in 1959. It is not known whether these incorrect values for lechuguilla were used in calculation of total ground cover or species dominance in 1959, but that possibility must be considered in interpreting the results.

Nugent Mountain

Perennial plant density at the Nugent Mountain plot decreased overall from 51,256 plants/ha in 1959 (Porter 1962) to 33,870 plants/ha in 2020 (Fig. 4, Supplementary Material 2). As can be seen in Fig. 4, the overall decrease was due to a decrease in understory density rather than in overstory density, which slightly increased. The percent ground cover of understory plants at Nugent Mountain has also decreased dramatically (Fig. 5) since 1959. However, as noted above, the decrease in ground cover at Nugent Mountain (Fig. 5) may be partly an artifact of an incorrect value for basal area of lechuguilla in 1959.

Some changes in species composition can be noted at Nugent Mountain (Supplementary Materials 2–5). The most common species on the plot in 1959 (chino grama, lechuguilla, fluff grass, leatherstem, creosotebush, and ground cholla; Figs. 6–7, Supplementary Materials 2–5) are still present as of 2020. However, the density and percent composition of chino grama and lechuguilla have decreased substantially (Supplementary Materials 4–5). Feather dalea composed 16% (Supplementary Materials 3, 5) of the overstory in 1959 (though only 2% of the perennials; Supplementary Material 2) but was not observed in 2020. Several species have become more common at Nugent Mountain, notably skeleton-leaf goldeneye and three-awn (Supplementary Materials 3, 5). All of these species were reported in low density on the plot in 1959 (Porter 1962, 2011). Several species found in low frequency (≤2%) in 1959 were not sampled in 2020 and vice versa (Supplementary Materials 2–4). It is probable that many of these species were present but not reliably sampled in both study periods due to their scarcity. None

TABLE 1. Relative dominance (%) of overstory perennial species surveyed on 3 plots in 1959, 2019, and 2020, compared. An asterisk (*) means that Porter (1962, 2011) sampled the species in 1959 but did not report basal area or dominance. A dash (—) means that the species was not sampled.

		Nugent Mountain		Panther Junction		Tornillo Flat	
Common name	Scientific name	1959	2020	1959	2019	1959	2019
Green sotol	*Dasylirion leiophyllum*	70	8	6	<1	—	—
Honey mesquite	*Prosopis glandulosa*	<1	—	<1	5	57	4
Giant dagger	*Yucca torreyi*	—	—	48	6	—	27
Cenizo	*Leucophyllum* sp.	11	43	1	<1	—	—
Creosotebush	*Larrea tridentata*	2	15	—	2	26	39
Whitethorn acacia	*Acacia constricta*	*	2	*	27	*	9
Tarbush	*Flourensia cernua*	<1	—	19	17	<1	<1
Tasajillo	*Opuntia leptocaulis*	<1	—	18	6	<1	7
Anderson's desert thorn	*Lycium andersonii*	—	—	—	14	—	—
Mormon tea	*Ephedra* sp.	5	8	2	11	<1	—
Gregg coldenia	*Tiquilia greggii*	1	10	—	—	—	—
Cat claw acacia	*Acacia greggii*	—	7	—	—	—	—
Skeleton-leaf goldeneye	*Viguiera stenoloba*	*	6	*	5	—	1
Ocotillo	*Fouquieria splendens*	1	1	—	—	1	6
Mariola	*Parthenium incanum*	—	—	<1	<1	<1	4
Feather dalea	*Dalea formosa*	2	—	—	—	—	—
American threefold	*Trixis californica*	—	—	1	<1	—	—
Lignum vitae	*Guaiacum angustifolium*	—	—	—	1	—	—
Rough menodora	*Menodora* sp.	*	<1	—	—	*	—
Leatherweed	*Croton pottsii*	*[a]	<1	—	—	—	—
Bush croton	*Croton fruticulosus*	—	<1	—	—	—	—
False agave	*Hechtia texensis*	—	<1	—	—	—	—
Dealbata's bahia	*Bahia absinthifolia* var. *dealbata*	*[a]	<1	—	—	—	—
Vervain	*Verbena* sp.	—	—	*[a]	<1	—	—
Graythorn	*Ziziphus* sp.	—	—	—	—	*	<1
Soaptree yucca	*Yucca elata*	—	—	—	—	—	<1
Grassland croton	*Croton dioicus*	*	—	—	—	—	—
Poreleaf	*Porophyllum scoparium*	*	—	—	—	—	—
Guayacan	*Guaiacum angustifolium*	*	—	—	—	—	—
Slender janusia	*Janusia gracilis*	*	—	—	—	—	—
Parry's wild petunia	*Ruellia parryi*	*	—	—	—	—	—
Wrightwort	*Carlowrightia linearifolia*	*	—	—	—	—	—
Slim tridens	*Tridens muticus*	*	—	—	—	—	—
Swampprivet	*Forestiera* sp.	—	—	*	—	—	—
Littleleaf sumac	*Rhus microphylla*	—	—	*	—	—	—
Unidentified		8	<1	*	5	*	—
OVERSTORY TOTAL		100	100	100	100	100	100

[a]Porter (1962, 2011) misclassified these species as annuals and reported leatherweed as 6%, paperflower as 2%, vervain as 3%, and Dealbata's bahia as 0.5% of the annuals on the plot in 1959.

TABLE 2. Relative dominance (%) of understory perennial species surveyed on 3 plots in 1959, 2019, and 2020. An asterisk (*) means that Porter (1962, 2011) sampled the species in 1959 but did not report basal area or dominance. A dash (—) means that the species was not sampled.

		Nugent Mountain		Panther Junction		Tornillo Flat	
Common name	Scientific name	1959	2020	1959	2019	1959	2019
Lechuguilla	*Agave lechuguilla*	83	6	13	<1	2	2
Engelmann's prickly pear	*Opuntia engelmannii*	2	—	73	78	53	27
Blind prickly pear	*Opuntia rufida*	—	37	—	—	—	—
Ground cholla	*Opuntia schottii*	2	<1	—	—	32	28
Purple prickly pear	*Opuntia macrocentra*	—	17	—	—	—	32
Chino grama	*Bouteloua ramosa*	8	19	—	—	<1	—
Rhatany	*Krameria* sp.	1	4	10	9	—	9
Strawberry pitaya	*Echinocereus stramineus*	*	10	*	—	*	—
Fluff grass	*Dasyochloa pulchella*	<1	<1	<1	4	2	2
Three-awn	*Aristida* sp.	*	3	*	3	*	—
Lehmann lovegrass	*Eragrostis lehmanniana*	—	—	—	3	—	—
Leatherstem	*Jatropha dioica*	<1	2	—	—	—	—
Broom milkwort	*Polygala scoparioides*	—	—	*[a]	1	—	—
Red grama	*Bouteloua trifida*	*	<1	—	—	—	—
Euphorbia	*Euphorbia* sp.	*[a]	<1	—	—	—	—
Hedgehog cactus	*Echinocereus* sp.	—	<1	—	—	—	—
Black grama	*Bouteloua eriopoda*	—	—	<1	—	—	—
Twinleaf senna	*Senna bauhinioides*	—	—	—	<1	*	<1
Pincushion cactus	*Mammillaria* sp.	—	—	*	—	—	<1
Golden-spined prickly pear	*Opuntia aureispina*	*	—	*	—	—	—
Unidentified		4	1	*	2	*	—
UNDERSTORY TOTAL		100	100	100	100	100	100

[a]Porter (1962, 2011) misclassified broom milkwort and euphorbia as annuals, with broom milkwort representing 13% of the annuals on the Panther Junction plot in 1959 and euphorbia representing 41% of the annuals at Nugent Mountain in 1959.

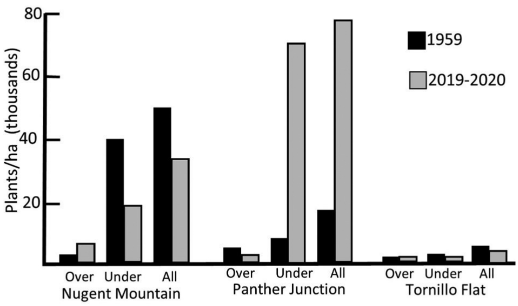

Fig. 4. Density of perennial plants on 3 plots in Big Bend National Park, Texas. The density of overstory (over), understory (under), and all perennials (all) are given. Surveys were made in 1959 (black bars) and 2019–2020 (gray bars).

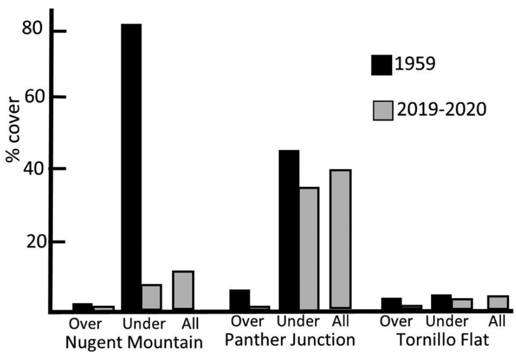

Fig. 5. Percentage of ground cover of perennial plants on 3 plots in Big Bend National Park, Texas. The percent cover of overstory (over), understory (under), and all perennials (all) are given. Surveys were made in 1959 (black bars) and 2019–2020 (gray bars).

of the species sampled at Nugent Mountain showed evidence of clumped distribution as determined by the relative frequency. The National Park Service (2005) mapped the locations of fire for the period 1946–2003 and did not report any fires on the Nugent Mountain plot during that time, and few fires within the larger vicinity.

Panther Junction

In contrast to Nugent Mountain, plant density (Fig. 4) and ground cover (Fig. 5) at Panther Junction increased dramatically as a result of the increased density of understory species. The increase in understory cover can be attributed to several perennial grass species, notably Lehmann lovegrass (*Eragrostis lehmanniana*; Fig 7), not reported in 1959 but composing 14% of the understory in 2019 (Supplementary Material 8). Fluff grass (*Dasyochloa pulchella*) was common in both 1959 and 2019, with the density (Fig. 7) and percent composition (Supplementary Material 8) increasing in 2019. However, owing to the small basal area ($\bar{x}$ = 36–45 cm^2, Supplementary Material 7), fluff grass was not a dominant contributor to ground cover in Panther Junction at either time. The mean height of this species at Panther Junction was 3.8 cm in 1959 and 7 cm in 2019 (Supplementary Material 7), so the total biomass is quite small considering the large number of plants on the plot. Fluff grass was the only species at Panther Junction that showed evidence of clumped distribution, with a relative frequency of 33%. This relative frequency was substantially lower than the relative density, indicating an increased tendency for the plant to be found in multiple quadrants of a sample point and suggesting a clumped distribution.

Leavitt et al. (2010) reported ongoing vegetation studies initiated by Degenhardt (1966). Those authors studied a plot at Burnham Flat, roughly 5 km (straight-line distance) NNW of Panther Junction in possibly similar habitat. Leavitt et al. (2010) reported a percentage ground cover at Burnham Flat of 32%, fluctuating in the range of 28% to 57% through 2006. The methods of Degenhardt (1966) and Leavitt et al. (2010) were different from ours, but we observed ground cover in a similar range at Panther Junction (Fig. 5).

The percent composition (Supplementary Materials 6–8) and density (Figs. 6–7) of lechuguilla, tasajillo, and tarbush decreased at Panther Junction between 1959 and 2019. Rhatany decreased in percent composition (Supplementary Material 8) but increased in density (Fig. 7). Species that increased in density and percent composition include fluff grass, three-awn, and whitethorn acacia (Figs. 6–7, Supplementary Materials 6–8). Engelmann's prickly pear increased in density on this plot (Fig. 7) but changed only slightly in percent composition (Supplementary Material 8).

Lehmann lovegrass (*Eragrostis lehmanniana*) has invaded the Panther Junction plot (Fig. 7), composing 14% of understory species (Supplementary Materials 7–8) and 13% of the perennials (Supplementary Materials 2, 8). Lehmann lovegrass is an exotic invasive also reported by Leavitt et al. (2010) in their study at several Big Bend locations in 2005–2006. According to Leavitt et al. (2010), lovegrass was not reported

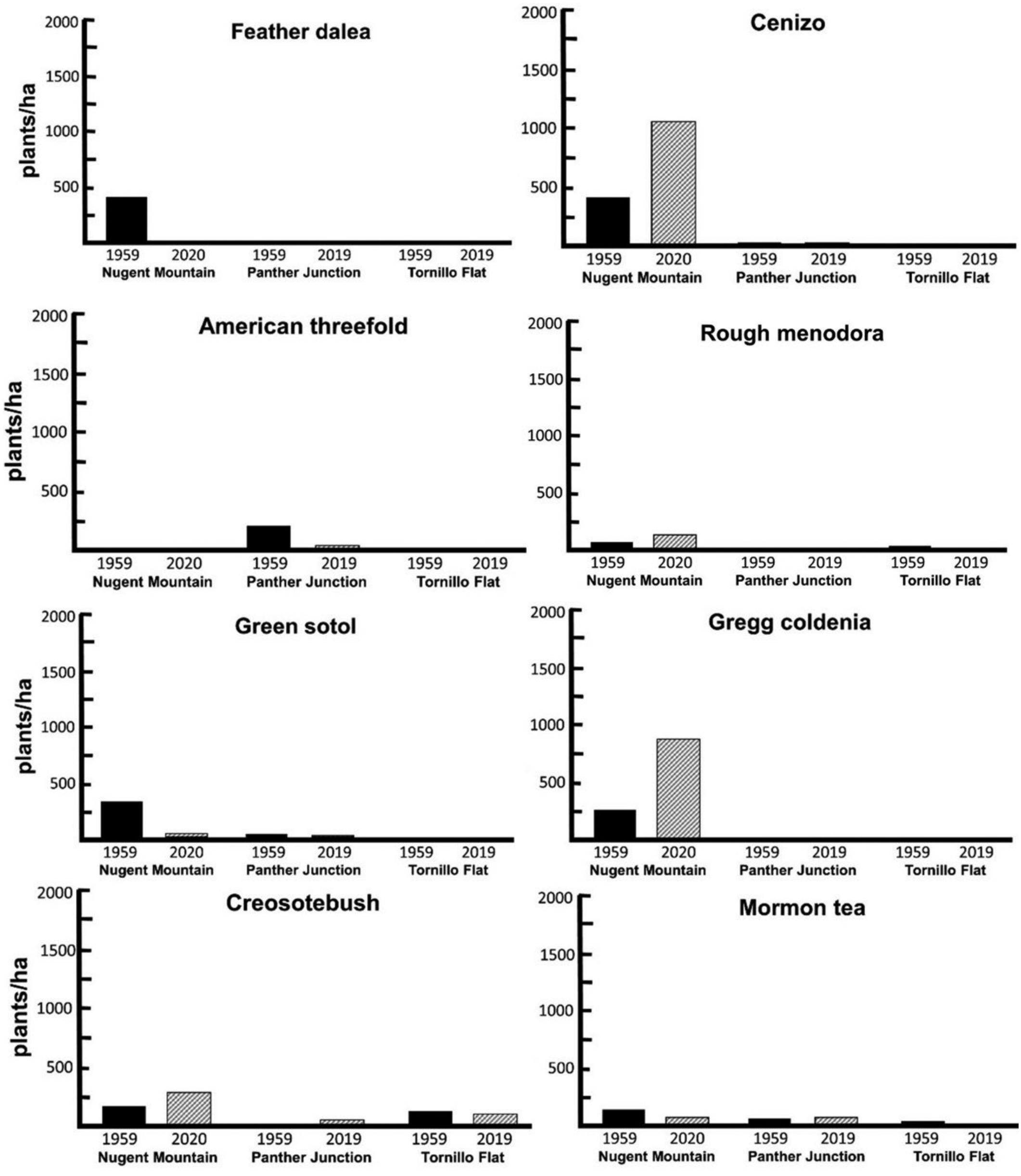

Fig. 6. Densities of 16 overstory species on 3 plots in Big Bend National Park, Texas. Scientific names of plant species are given in Table 1.

in the park in the 1950s and 1960s, and this invasive species is likely to increase the potential of unplanned fire and can reduce faunal diversity (Brooks and Pyke 2001). The Panther Junction site is located at the intersection of the major BBNP highways (Fig. 1) and is near the densest human population center in the park. Invasive species might be most expected in this area (Baccus 1971). The Panther Junction area has experienced numerous fires since 1946, including prescribed fires as well as natural and human-caused fires (NPS 2005). Fire has undoubtedly impacted the plant community on the Panther Junction plot. The potential effects of lovegrass and other invasives should be a consideration in management of park resources.

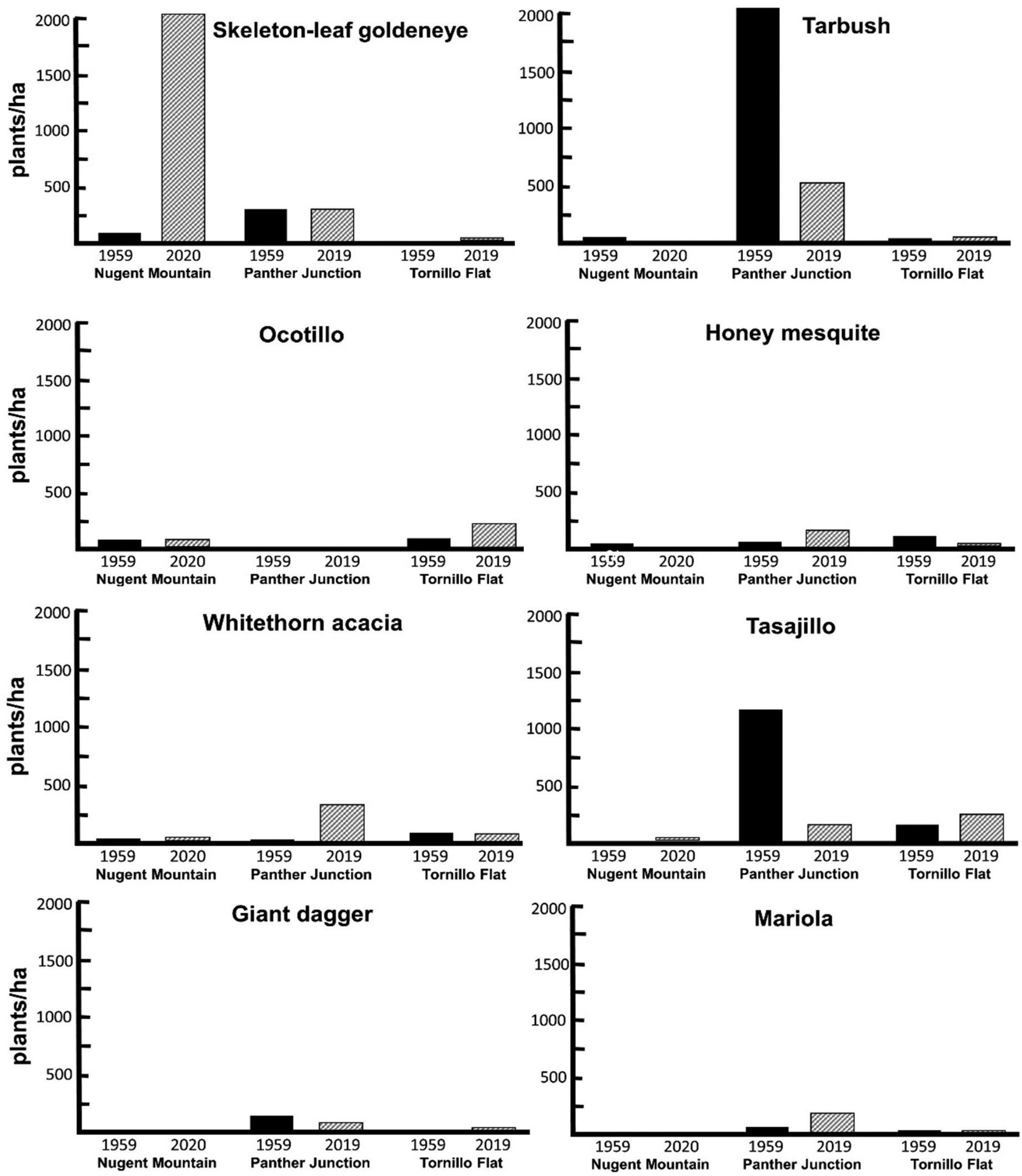

Fig. 6. Continued.

Tornillo Flat

Tornillo Flat did not have any notable change in vegetation density or ground cover between the 2 time periods (Figs. 4–5). Percent species composition was remarkably stable in Tornillo Flat over the period of 1959–2019 (Supplementary Materials 2, 9–11). Compared with the other study sites, plant density and diversity were low in this flat, sandy habitat near Tornillo Creek. The National Park Service (2005) did not report any fires at the location of the Tornillo Flat plot in the period of 1946–2003, so fire is unlikely to be a major factor affecting the plant community at this site.

Some species were sampled in only one study year (Supplementary Materials 2, 9–11), but these were more uncommon species (≤5% species

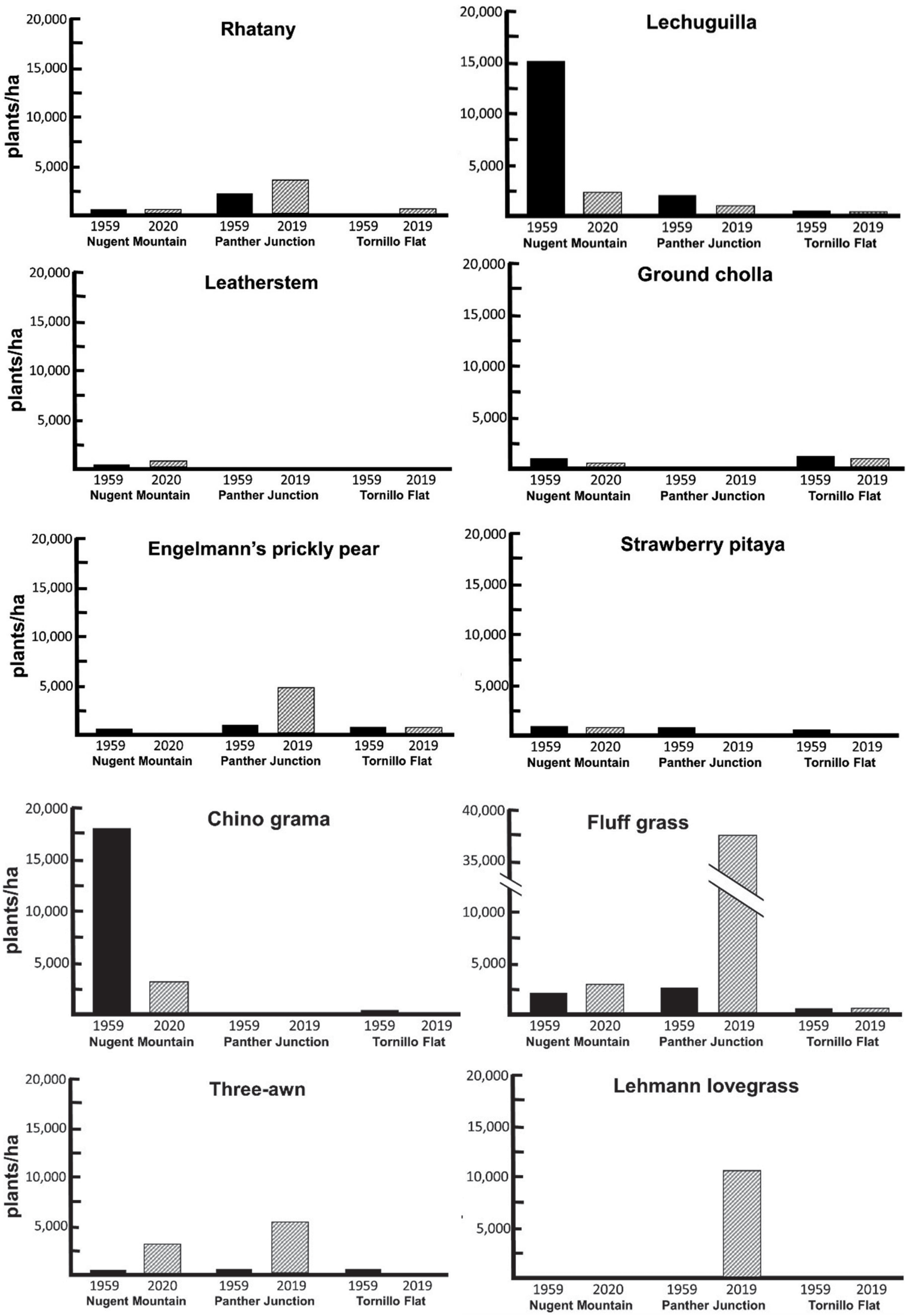

Fig. 7. Densities of 10 understory species on 3 plots in Big Bend National Park, Texas. Scientific names are in Table 2.

composition), plausibly present in both years but not reliably sampled due to their low density on the plot. Most species at Tornillo Flat did not show evidence of clumped distribution or were too sparse to make a determination. The exceptions were ground cholla (33% relative frequency) and creosotebush (43%), which both showed some tendency to cluster around a sample point.

Degenhardt (1966) and Leavitt et al. (2010) report a long-term study of vegetation at Tornillo Flat on a site 1.0 km northwest of our plot. The percent ground cover reported by Leavitt et al. (2010) at Tornillo Flat ranged from about 2% to 8% in the 1950s and 1960s and reached a peak of 15.6% in 2005 followed by 10% in 2006, the latter 2 measurements a little higher than our estimated ground cover at Tornillo Flat in 2019 (Fig. 5). Baccus (1971) reports unpublished data of B.H. Warnock for 2 sites in the Tornillo Flat area, calculating percent ground cover of grasses, cacti, and forbs. For one site, Warnock found 0.05% ground cover in 1956 and 0.10% in 1969. The other Tornillo Flat site had 0.2% ground cover in 1956 (Baccus 1971). This ground cover is not much different from the perennial ground cover at our Tornillo Flat site in either 1959 or 2019 (Fig. 5). The species composition at our Tornillo Flat site in 2019 was similar to the site of Leavitt et al. (2010) except that ground cholla and fluff grass were much more common at our plot, with the 2 species composing a combined 38% of the perennials (Supplementary Material 2). In addition, Leavitt et al. (2010) reported a notable population of exotic Lehmann lovegrass in 2005, but much less in 2006. We did not find lovegrass at Tornillo Flat in 2019, despite the site being near the same major highway as the Leavitt et al. (2010) plot.

Prior to 1918–1920, Tornillo Flat was covered with "stirrup high" tobosa grass (*Pleuraphis mutica*) in sufficient density that it was cut for hay and used as range for livestock (Maxwell 1968, 1985, Baccus 1971). Tobosa grass is particularly tolerant of desert conditions but was extirpated from Tornillo Flat due to a combination of drought and overgrazing (Maxwell 1968, Baccus 1971). Porter (1962, 2011) did not report tobosa grass on the Tornillo Flat plot in 1959, though he did identify the species at other locations in several different habitats (Appendix III *in* Porter 2011). Degenhardt (1966) did not observe tobosa grass at Tornillo Flat in 1957–1958, but Leavitt et al. (2010) did report it on the same plots in 2005–2006. We did not find tobosa grass at Tornillo Flat in 2019. The plant community of Tornillo Flat has not recovered to its pre-1918 condition of being dominated by tobosa grass as described by Maxwell (1968, 1985) and Baccus (1971).

Factors Influencing Changes in the Plant Community

Wondzell (1984) and Wondzell and Ludwig (1995) found a general increase in ground cover on the ESBBA vegetation plots in the time since grazing ended in BBNP. However, they found that other factors such as invasive plants, climate change, and fire have also impacted the plant community, making it difficult to distinguish these effects from the successional changes resulting from recovery from overgrazing (Wondzell and Ludwig 1995, Richardson 2003). Degenhardt's (1966, 1977) lizard plots were later studied by Leavitt et al. (2010). They reported a general increase in plant cover at most locations and some differences in species composition when they examined the plots in 2005 and 2006. Baccus (1971) cited unpublished results from B.H. Warnock also showing an increase in ground cover for several Big Bend habitats sampled in 1948, 1956, and 1969.

Much of the ecological analysis of Big Bend communities has focused on recovery from the overgrazing that occurred before the creation of the national park in 1944 (Maxwell 1968, Baccus 1971, Wondzell 1984, Leavitt et al. 2010). Baccus (1971) found that mountain grasslands in BBNP had recovered more from overgrazing than had the lower elevations in the park. Baccus (1971) also noted that in Tornillo Flat, grasslands had invaded the desert shrub community along the Panther Junction–Marathon highway. However, the grasses included invasive species rather than showing a return to native grasses such as the once-abundant tobosa grass. It is not necessarily clear to us what recovery from overgrazing would look like, or how it would be recognized, without having proper control plots with continued grazing.

The plant communities of BBNP have undergone secondary succession in the approximately 75 years following the protections afforded by national park status. This succession in many cases has resulted in increased density of vegetation and changes in species composition. However, it is more difficult to determine whether the community has or will return to the conditions that existed before the introduction of European settlers and their livestock, or even to the conditions before the intense overgrazing of 1944 (Wauer and Fleming 2002). These habitats likely do not follow a linear succession model in which a stable ecosystem is disturbed by overgrazing, and then "recovers" by moving backward along the reverse successional path to the original condition. The state-and-transition model of succession (Westoby et al. 1989, Laycock 1991) may provide a better explanation of community changes in these habitats. The biological communities of Big Bend may have settled into a relatively stable state that is unlikely to lead to a "recovery" to conditions that existed in the past.

The changes we observed, particularly at Nugent Mountain and Panther Junction, are likely due in part to continued succession following the end of livestock grazing. However, succession does not necessarily imply recovery or a return to previous communities. The initial 1959 study occurred when secondary succession would have been in its early stages, 15 years after the removal of livestock. In the 6 decades following the initial study, some form of succession from overgrazing would be expected, but other factors complicate analysis of the vegetational changes on the study plots, and the Tornillo Flat location appears little changed in plant density and species composition from 1959.

The effect of rainfall should be considered in evaluating changes in the plant communities. The Big Bend area experienced below-average rainfall during 1951–1957 (Fig. 2; Wondzell and Ludwig 1995, Muldavin 2010, Porter 2011). This period of drought coincided with some of the early years following the termination of livestock grazing. By 1959, the year of the original survey of our 3 plots, precipitation had rebounded above the long-term mean for the area (Fig. 2). Multiple factors were likely at play affecting conditions during the initial 1959 survey, including recovery from drought and continued recovery from overgrazing. Subsequent environmental events have also affected the area. A major freeze in 2011 was followed by a historically intense drought (Fig. 2). S.M. Wondzell (personal communication) surveyed in 2013 and reported the die-off of such species as grama grass, green sotol, lechuguilla, and prickly pear. However, these events had less impact on ocotillo, with most individuals surviving the drought (Scott 2021). Additional factors such as climate change, fires, fire suppression, introduction of invasive species, and other human impacts can be expected to affect community structure in coming decades. Continued periodic surveys of Porter's (1962, 2011) ESBBA study plots should provide a valuable supplement to other long-term studies (Degenhardt 1977, Wondzell 1984, Wondzell and Ludwig 1995, Muldavin et al. 2010, Leavitt et al. 2010) of vegetation in the park.

SUPPLEMENTARY MATERIAL

Eleven online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol83/iss4/8).

SUPPLEMENTARY MATERIAL 1. Spinner used for randomizing and defining the sample quadrants.

SUPPLEMENTARY MATERIAL 2. Frequency, density, and relative dominance of all perennial species surveyed on 3 plots in Big Bend National Park in December 2019 and 2020, compared with data from 1959.

SUPPLEMENTARY MATERIAL 3. Density, height, basal area, and relative dominance of overstory perennial species surveyed on the Nugent Mountain plot, December 2020, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 4. Density, height, basal area, and relative dominance of understory perennial species surveyed on the Nugent Mountain plot, December 2020, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 5. Percent species composition of perennial plants on the Nugent Mountain plot in 1959 and 2020.

SUPPLEMENTARY MATERIAL 6. Density, height, basal area, and relative dominance of overstory perennial species surveyed on the Panther Junction plot, December 2019, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 7. Density, height, basal area, and relative dominance of understory perennial species surveyed on the Panther Junction plot, December 2019, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 8. Percent species composition of perennial plants on the Panther Junction plot in 1959 and 2019.

SUPPLEMENTARY MATERIAL 9. Density, height, basal area, and relative dominance of overstory perennial species surveyed on the Tornillo Flat plot, December 2019, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 10. Density, height, basal area, and relative dominance of understory perennial species surveyed on the Tornillo Flat plot, December 2019, compared with data from 1959 (Porter 1962, 2011).

SUPPLEMENTARY MATERIAL 11. Percent species composition of perennial plants on the Tornillo Flat plot in 1959 and 2019.

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