

The Sandsage Prairie Ecological System: Biodiversity Hotspot for the Great Plains

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ABSTRACT

Sandsage prairie is a shrub-steppe ecological system of the Great Plains of North America in which sand sagebrush (*Artemisia filifolia*) is dominant and diagnostic. An estimated 5 million hectares of sandsage prairie occurs in discontinuous tracts across eight states in association with dune fields and other sandy habitat. This paper documents the biodiversity attributes of sandsage prairie, which is an ecological system of conservation concern due to range-wide declines in areal extent and ecological integrity. Sandsage prairie hosts many regional endemics, ecological specialists, and species of conservation concern at the state and global levels. It is particularly important to avian ecology in the Great Plains, with 14 species of endemic or obligate grassland birds utilizing sandsage prairie for breeding and/or foraging habitat. In many parts of its range, sandsage prairie is the only native vegetation of significant scale remaining on the landscape, providing islands of natural habitat critical to the support and persistence of biological diversity. These attributes make sandsage prairie a biodiversity hotspot for the central and southern Great Plains. Stewardship of sandsage prairie biodiversity requires preventing further loss, fragmentation, and degradation of existing occurrences as well as accommodating or restoring processes that drive the inherent heterogeneity of this unique ecological system.

Index terms: biological diversity; conservation; Great Plains; sandsage prairie

INTRODUCTION

Sandsage prairie is a shrub-steppe ecological system of the Great Plains of North America dominated by sand sagebrush (*Artemisia filifolia* Torr.) with a moderate to dense herbaceous layer dominated by perennial grasses. It is one of the three primary types of vegetation occupying areas of sandy habitat in the Great Plains (Figure 1), the others being Western Great Plains Sand Prairie and Harvard Oak Shrubland (NatureServe 2020), the latter commonly referred to as sand shinnery. Sandsage prairie and sand shinnery are distinguished from sand prairie by a strong shrub component, with *Artemisia filifolia* the dominant shrub of sandsage prairie and *Quercus havardii* Torr. the dominant of sand shinnery.

An estimated 5 million hectares (12 million acres) of sandsage prairie (Berg 1994) occurs in discontinuous tracts across the central and southern Great Plains in association with dune fields and other areas of sandy habitat (Figure 1). While the total areal extent of sandsage prairie is nearly equivalent to that of sand prairie in the well-known Nebraska Sandhills (Locklear 2019), discontinuous distribution across the more remote and thinly populated regions of eight different states may mask the significance of this ecological system. A relatively small percentage of sandsage prairie occurs on public and nonprofit conserved land, most of it being in private ownership and managed as rangeland for livestock production (Rondeau et al. 2011).

Sandsage prairie is recognized as an ecological system of conservation concern in most of the states in which it occurs, and is specifically identified as a conservation priority in the state wildlife action plans of Colorado, Kansas, Nebraska, and

Oklahoma. The primary threats, past and present, are loss and fragmentation of habitat and degradation of ecological integrity.

The introduction of center pivot irrigation technology into the Great Plains in the 1960s led to large-scale conversion of sandsage prairie rangeland to cropland in some regions (Opie et al. 2018). Speaking on the “Destruction of Sandsage Prairie in Southwest Kansas” at the North American Prairie Conference in 1980, wildlife biologist Mark Sexson (1983) described a 58% decline in sandsage prairie rangeland in the Arkansas River dune field in the 1970s due to expansion of center pivot irrigation in the region and noted comparable losses in the dune fields of the Cimarron River to the south. Other early warnings about the loss of sandsage prairie were raised by Daley (1972) for Colorado and Farrar (1993) for Nebraska. A more recent assessment for Colorado estimates about 20% of the historical acreage of sandsage prairie in the state has been lost due to conversion to agriculture (Rondeau et al. 2011). Expanding exurban development, particularly in eastern Colorado, has also contributed to the loss of sandsage prairie.

While conversion of sandsage prairie rangeland to cropland is not presently occurring on the same scale, construction of roads, pipelines, transmission lines, and other infrastructure associated with energy development (e.g., wind turbines and oil and gas wells) continues to fragment sandsage prairie occurrences and facilitate the introduction and spread of invasive species (Robel et al. 2004; Duquette et al. 2019). Encroachment of woody plants, primarily eastern red cedar (*Juniperus virginiana* L.) and honey mesquite (*Prosopis glandulosa* Torr.), also causes fragmentation of sandsage prairie rangelands, particularly in the southern Great Plains (Fuhlendorf et al. 2017b).

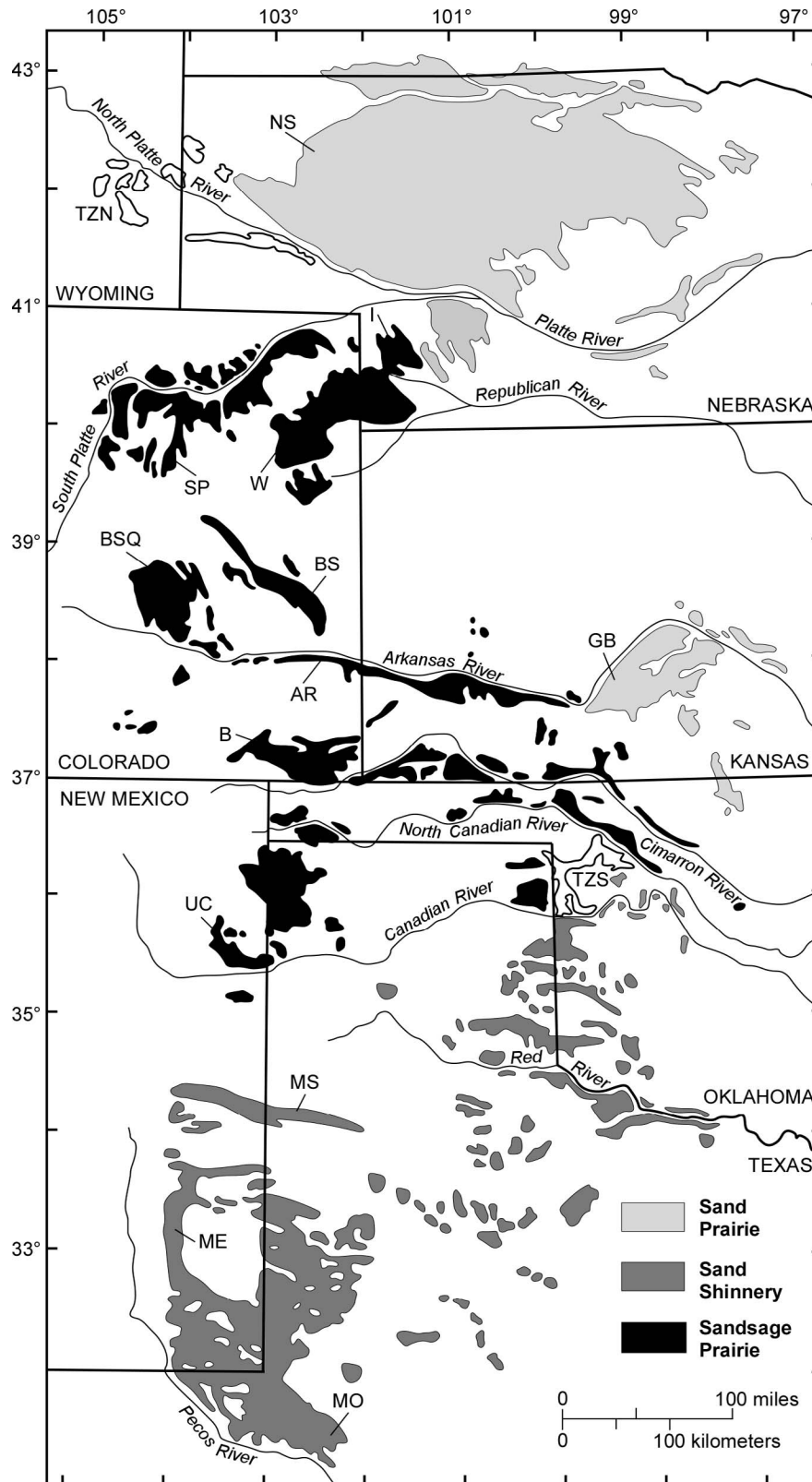


Figure 1.—Map showing the distribution of sandsage prairie in the Great Plains, USA (small tracts in southwestern South Dakota not mapped). Dune fields: AR, Arkansas River; B, Baca; BS, Big Sandy; BSQ, Black Squirrel Creek; GB, Great Bend; I, Imperial; ME, Mescalero; MO, Monahans; MS, Muleshoe; NS, Nebraska Sandhills; SP, South Platte; UC, Ute Creek; W, Wray. TZN = Transition Zone North. TZS = Transition Zone South. Used with permission from BRIT (Locklear 2019:255).

Table 1.—Literature documenting sandsage prairie biodiversity.

Taxon	References
Plants	Schantz 1911 (Colorado); Ramaley 1939 (Colorado); Sherwood and Riser 1980 (Oklahoma); Hulett et al. 1988 (Kansas); Dick-Peddie 1993 (New Mexico); Kelso et al. 2007 (Colorado); Locklear 2017b (Nebraska); Locklear 2019 (Great Plains)
Amphibians and reptiles	Ballinger et al. 1979 (Nebraska); Rush et al. 1982 (Kansas); Degenhardt et al. 1996 (New Mexico); Hammerson 2000 (Colorado); Montgomery and Mackesy 2003 (Colorado); Collins et al. 2010, 2011 (Kansas); Dixon 2013 (Texas)
Birds	Zimmerman and Patti 1988 (Kansas); Thompson and Ely 1989 (Kansas); Andrews and Righter 1992 (Colorado); Johnsgard 2001 (Great Plains); Seyffert 2001 (Texas); Sharp et al. 2001 (Nebraska); Cartron 2010 (New Mexico); Thompson et al. 2011 (Kansas)
Mammals	Maxwell and Brown 1968 (Wyoming); Moulton et al. 1981 (Colorado); Fleharty and Navo 1983 (Kansas); Dalquest et al. 1990 (New Mexico, Oklahoma, Texas); VanNimwegen et al. 2008 (Kansas); Armstrong et al. 2011 (Colorado); Schmidly and Bradley 2016 (Texas)

Where tracts of sandsage prairie are intact, the ecological integrity of this shrub-steppe ecological system has likely been altered or degraded by range management practices aimed at increasing the cover of forage-producing grasses by reducing the shrub component. Operating with the conviction that sandsage prairie was “sagebrush infested rangeland” (McIlvain and Savage 1949), sand sagebrush control research was initiated at the US Department of Agriculture Southern Plains Range Research Station in Oklahoma in the 1930s. Testing of herbicides began in the late 1940s with the “new chemical” 2,4-dichlorophenoxyacetic acid (2,4-D) proving to be highly effective in killing or suppressing sand sagebrush. Use of fixed-wing aircraft allowed aerial spraying of large tracts of rangeland with this herbicide (Vail 2018), a practice that spread from Oklahoma to other parts of sandsage country (Allred 1949; Bovey 1964; Rodgers and Sexon 1990) and has continued through recent years (Thacker et al. 2017). Other herbicides used to control sand sagebrush include picloram (trade name Tordon), silvex, and tebuthiuron (Bovey 1964; Wilson 1989).

Broad-spectrum herbicides like 2,4-D are also toxic to the annual and perennial forbs that are important constituents of sandsage prairie vegetation. Like sand sagebrush, these plants have been considered “range weeds” that compete with grasses. But they are key components of the structure and dynamics of sandsage prairie vegetation (Kelso et al. 2007; Locklear 2019) and foundational to community trophic structure (Jamison et al. 2002; Hagen et al. 2005). The residual effects of herbicide applications on the biodiversity of sandsage prairie are not known but research in Kansas (Rodgers and Sexon 1990) and Oklahoma (Thacker et al. 2012) suggest the impacts are significant and may persist for multiple (20+) years.

While habitat loss and deleterious management practices are recognized as threats to sandsage prairie vegetation, the significance of these losses to the larger Great Plains ecoregion has not been examined. Knowledge of the biological diversity supported by an ecological system is crucial to justifying,

prioritizing, and guiding conservation efforts. To that end, the aim of this paper is to enumerate the biodiversity attributes of sandsage prairie.

BIODIVERSITY SUPPORTED BY SANDSAGE PRAIRIE

Identification of plant and animal species associated with sandsage prairie was based on direct reconnaissance of sandsage prairie throughout the Great Plains coupled with review of relevant botanical, zoological, and ecological literature (Table 1). NatureServe Explorer (NatureServe 2020) was consulted to determine the conservation status of these species. A listing of the 45 sandsage prairie plants and animals of conservation concern is presented in Appendix 1.

Plants

A recent paper by Locklear (2019) describes the floristic composition, community structure, and vegetation dynamics of sandsage prairie throughout its range. Of the 119 plant taxa characteristic of sandsage prairie, 29 (24%) are endemic to the Central Grassland of North America (Locklear 2017a) and are ecological specialists of sand habitat. Kelso et al. (2007) identified a flora of 51 species associated with a sandsage prairie community in Colorado, of which they recognized 29 (57%) as “ecological specialists to sandy soils.” The high percentage of regional endemics and habitat specialists in the flora of sandsage prairie makes it a significant host of plant diversity for the Great Plains.

Of the 119 plants characteristic of sandsage prairie, 21 are of conservation concern (see Appendix 1). Four of these are considered globally vulnerable to extinction (G3)—*Chenopodium cycloides* A. Nelson, *Dalea cylindriceps* Barneby, *Euphorbia carunculata* Waterf., and *Euphorbia strictior* Holz. Two additional species might be added to this list. The recently described *Evolvulus arenarius* Harms (Harms 2014) is known from at least one occurrence in sandsage prairie (Hartley County, Texas) and is likely a species of conservation concern but has not yet been ranked. An obscure species of dodder, *Cuscuta plattensis* A. Nelson, is associated with sandhills in southeastern Wyoming (Handley and Fertig 2002) but direct association with sandsage prairie has not been documented.

Arthropods

Detailed studies of sandsage prairie arthropod communities are needed. Doxon et al. (2011) investigated the effects of patch-burn management on macroinvertebrate diversity and abundance in sandsage prairie in Oklahoma but identifications were not carried to the genus or species level. The potential of sandsage prairie to support at-risk arthropods is indicated by the association of nine endemic insects with sand shinnery in the Mesalero-Monahans Dunes of New Mexico and Texas (Longing et al. 2014).

Two insects found in association with sandsage prairie are of conservation concern at the global level (both G3). Ghost tiger beetle (*Cincidela lepida* Dejean) is an open-sand dwelling species with a large area of historical distribution in interior North America but has declined in abundance due to habitat degradation. Wiest’s sphinx moth (*Euproserpinus wiestii* Sperry)

is only known from dune fields in the western Great Plains where sandsage prairie is the dominant vegetation, and may be endemic to sandsage prairie. First collected in the South Platte Dune Field of northeastern Colorado (Sperry 1939), this poorly known and near-legendary species (Williams 1986) has been found in scattered sites in eastern Colorado, northeastern New Mexico, and the Texas Panhandle. The larva of Wiest's sphinx moth feeds on leaves of *Oenothera latifolia* (Rydb.) Munz, an associate of sandsage prairie from Nebraska into New Mexico and Texas. Previous taxonomic circumscriptions of *Euproserpinus wiestii* grouped populations from California, Arizona, and Utah with those from the Great Plains (Tuttle 2007), but recent phylogenetic analyses show the Great Plains populations to be a distinct species correctly treated as *Euproserpinus wiestii* (Rubinoff et al. 2015). While presently ranked G3 by NatureServe (2020), a more imperiled rank (G1 or G2) seems warranted.

The importance of sandsage prairie to arthropod biodiversity in general and pollinating insects in particular has yet to be documented, but it seems likely that this plant community plays a significant role within the context of the Great Plains. Compared to shortgrass prairie, sandsage prairie in good ecological condition has a strong component of floriferous forbs with many species representing genera (i.e., *Dalea*, *Mentzelia*, *Oenothera*, *Penstemon*) known to attract a diversity of insect pollen and nectar foragers, including oligolectic bees and other specialist pollinators.

An example is provided by *Oenothera cinerea* (Wootton & Standl.) W.L. Wagner & Hoch (formerly *Gaura villosa* Torr.), an important forb in southern stands of sandsage prairie as well as sand shinnery. In a pollination ecology study in sand shinnery in the Monahans Sandhills of Texas, *Oenothera cinerea* attracted 45 insect species with 32 of these carrying pollen of the plant (Clinebell et al. 2004). One of the major pollen carriers for this species was the “night-wandering” halictid bee *Lasiglossum noctivaga* Linsley & MacSwain, a specialist of *Oenothera* that the researchers also found associated with *Oenothera cinerea* in sandsage prairie in southwestern Kansas. Their study was the first to document the involvement of antlions (Neuroptera) in pollination, with the antlion *Scotoleon minusculus* (Banks) a major pollen carrier of *Oenothera cinerea* in the Monahans Sandhills.

Amphibians and Reptiles

Amphibians are not strongly represented in the herpetofauna of sandsage prairie except in areas adjacent to riparian or wetland habitat, which has been considerably diminished in extent due to groundwater depletion by agricultural irrigation. The amphibian most likely to be found in sandsage prairie is the plains spadefoot (*Spea bombifrons* (Cope)), a toad that tolerates xeric conditions by spending considerable time below ground in burrows of its own or those of small mammals.

Most of the reptiles associated with sandsage prairie are relatively widespread species that occur in other areas of sand habitat in the Great Plains including ornate box turtle (*Terrapene ornata ornata* (Agassiz)), six-lined racerunner (*Aspidoscelis sexlineatus* (Linnaeus)), lesser earless lizard (*Holbrookia maculata* Girard), southern prairie lizard (*Sceloporus*

consobrinus Baird and Girard), and plains hog-nosed snake (*Heterodon nasicus* Baird and Girard). Some are species of the arid Southwest that reach the northern limits of their range in Great Plains sandsage prairie, including Texas horned lizard (*Phrynosoma cornutum* (Harlan)), Kansas glossy snake (*Arizona elegans elegans* Kennicott), plains black-headed snake (*Tantilla nigriceps* Kennicott), long-nosed snake (*Rhinocheilus lecontei* Baird and Girard), and coachwhip (*Masticophis flagellum* (Shaw)).

Seven sandsage prairie reptiles of conservation concern are listed in Appendix 1. The only species of conservation concern at the global level (G3T3) is the desert massasauga (*Sistrurus caenatus edwardsii* (Baird and Girard)). The distribution of this rattlesnake is centered in southern New Mexico and adjacent parts of Arizona, Texas, and northern Mexico, with a significantly disjunct area of occurrence in southeastern Colorado (Hammerson 2000; Hobert et al. 2004). Research in Colorado has shown that the desert massasauga utilizes sandsage prairie for summer foraging, likely because it supports a higher abundance of prey (mammals and lizards) than surrounding shortgrass prairie (Wastell and Mackessy 2011).

Birds

The avifauna of sandsage prairie includes species that are relatively common and widespread in the Great Plains such as horned lark (*Eremophila alpestris* (Linnaeus)), lark sparrow (*Chondestes grammacus* (Say)), and western meadowlark (*Sturnella neglecta* Audubon). Yet 14 birds of conservation concern utilize sandsage prairie as breeding habitat and/or foraging habitat (see Appendix 1). Some are southwestern species at the northern limits of their distributions in Great Plains sandsage prairie, notably scaled quail (*Callipepla squamata* (Vigors)), greater roadrunner (*Geococcyx californianus* (Lesson)), and Chihuahuan raven (*Corvus cryptoleucus* Couch). Others are more widely distributed grassland specialists that have experienced precipitous declines in numbers (Brennan and Kuvlesky 2005; Correll et al. 2019).

Enumerations of endemic and/or obligate grasslands birds have been published by Mengel (1970) and Knopf (1994) and synthesized by Johnsgard (2001). Fourteen of these grassland-reliant birds are associated with sandsage prairie (Table 2). Of birds documented to breed in sandsage prairie, the life histories of lesser prairie-chicken (*Tympanuchus pallidicinctus* (Ridgeway)) and Cassin's sparrow (*Aimophila cassinii* (Woodhouse)) are the most strongly associated with this ecological system.

Ferruginous hawks (*Buteo regalis* (Gray)) and Swainson's hawks (*Buteo swainsoni* Bonaparte) are obligate grassland birds and species of conservation concern in several Great Plains states. Both raptors utilize sandsage prairie as foraging habitat. A study in Cimarron County, Oklahoma, found proximity to sandsage prairie was positively associated with breeding success for these two species in an otherwise agricultural landscape (Wiggins et al. 2014). The researchers concluded that loss of sandsage habitat in the southern Great Plains may have contributed to range declines in ferruginous hawks and decreased breeding success for Swainson's hawks.

A little-known avian association with sandsage prairie involves the spring migration of the long-billed curlew

Table 2.—Endemic or obligate grassland birds (after Johnsgard 2001) associated with sandsage prairie. Bird residency status abbreviations: M = migrant; PB = permanent resident, breeding in sandsage prairie documented; SB = summer resident, breeding in sandsage prairie documented; SV = summer visitant (foraging); WV = winter visitant (foraging); YRV = year-round visitant (foraging).

Species	Residency status
Long-billed curlew	M
Swainson's hawk	SV
Ferruginous hawk	YRV
Prairie falcon	WV
Greater prairie-chicken	PB
Lesser prairie-chicken	PB
Burrowing owl	SV
Short-eared owl	WV
Horned lark	PB
Cassin's sparrow	SB
Brewer's sparrow	SB
Lark sparrow	SB
Lark bunting	SB
Western meadowlark	PB

(*Numenius americanus* Bechstein), North America's largest shorebird and a species of conservation concern. The sandsage prairie region associated with the Arkansas River in Kansas appears to be a significant midcontinental stopover site for long-billed curlews migrating from the lower Gulf Coastal Plain of Texas to breeding areas in the northern Great Plains (Shane 2005; Thompson et al. 2011).

The only sandsage prairie bird of conservation concern at the global level (G3) is the lesser prairie-chicken. The historical range of this species stretched from the sand shinnery region of New Mexico and Texas north through areas of sandsage prairie in southeastern Colorado and southwestern Kansas. Studies aimed at understanding the ecology and management needs of the lesser prairie-chicken have contributed to better understanding of the structure and composition of sandsage prairie vegetation (Hagen et al. 2004; Pittman et al. 2006; Rondeau et al. 2013) and concern for the conservation of the lesser prairie-chicken has been a primary driving force behind the preservation and improved management of sandsage prairie in the southern Great Plains.

In addition to grassland specialists and birds of conservation concern, sandsage prairie is also utilized to some extent by the game species northern bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), and mourning dove (*Zenaidura macroura* (Linnaeus)).

The importance of sandsage prairie to avian ecology in the Great Plains has been underappreciated. Although 14 species of endemic or obligate grassland birds utilize sandsage prairie for breeding and/or foraging (Table 2), no mention is made of sandsage prairie in a recent assessment of grassland bird conservation published by the National Audubon Society (Wilsey et al. 2019). In certain instances sandsage prairie is subsumed under a broad interpretation of shortgrass prairie, as in the "Terrestrial Bird Conservation Regions" map published by the North American Bird Conservation International Committee (BSC and NABCI 2014).

Mammals

The mammals most strongly associated with sandsage prairie are relatively widespread rodents that occur in other areas of sand habitat in the Great Plains. Among the most frequently reported are granivores Ord's kangaroo rat (*Dipodomys ordii* Woodhouse), plains pocket mouse (*Perognathus flavescens* Merriam), and western harvest mouse (*Reithrodontomys megalotis* (Baird)), herbivores plains pocket gopher (*Geomys bursarius* (Shaw)), and prairie vole (*Microtus ochrogaster* (Wagner)), insectivore northern grasshopper mouse (*Onychomys leucogaster* (Wied-Neuwied)), and omnivore spotted ground squirrel (*Xerospermophilus spilosoma* (Bennet)). The only mammal of conservation concern documented from sandsage prairie is the spotted ground squirrel, a southwestern species that ranges into the southern Great Plains.

Sand sagebrush is seasonally important to the diets of several mammals. In studies in the Texas Panhandle, the shrub made up 12.9% of the annual diet of pronghorn (*Antilocapra americana* (Ord)), accounting for 15.1% in the spring and 20.3% in the winter (Koerth et al. 1984), and 8% of the annual diet of mule deer (*Odocoileus hemionus* (Rafinesque)), notably accounting for 24% in the spring (Sowell et al. 1985). Sand sagebrush is important to the diet of black-tailed jackrabbits (*Lepus californicus* Gray) during the late fall and winter, accounting for 34% of the food eaten in a February when snow covered most of the vegetation in a study area in northeastern Colorado (Sparks 1968).

SANDSAGE PRAIRIE AND AT-RISK SPECIES

Forty-five plants and animals associated with sandsage prairie are of conservation concern (see Appendix 1). Eight of these (four plants, two invertebrates, a reptile, and a bird) are vulnerable to extinction at the global scale (NatureServe G3/T3 ranking). As discussed above, two additional plants could be added to the list of globally rare sandsage prairie species and survey of sandsage prairie invertebrate communities would likely identify even more.

Rarity at the state level may reflect the global rarity of a species, but more often is a function of the species being at the limits of its overall range in a particular state. Many of these species have distributions centered in arid regions of the southwestern United States and northern Mexico and reach the northern limits of their range in the sandsage prairies of the Great Plains. Such peripheral populations have been shown to have conservation value even when the species is secure within the core of its range (Lepping and White 2006; Peterman et al. 2013).

SANDSAGE PRAIRIE AS A BIODIVERSITY REFUGE

Much of the geographical distribution of sandsage prairie coincides with that of the High Plains aquifer system (often referred to as the Ogallala aquifer), the largest body of groundwater in the United States (Opie et al. 2018). This relationship is illustrated in Figure 2. The High Plains aquifer has been tapped extensively to support irrigated agriculture in the Great Plains and large expanses of native grassland over the

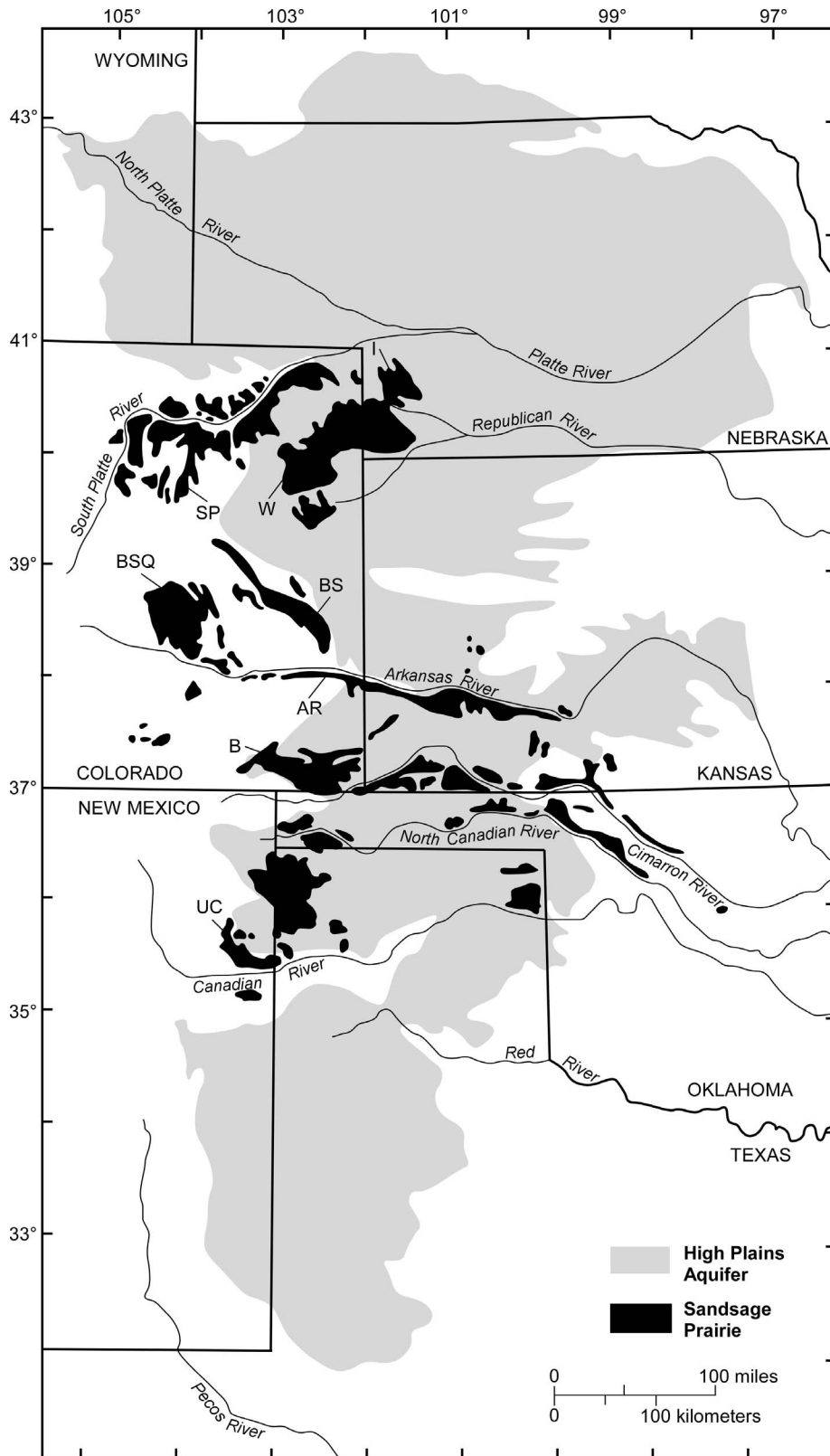


Figure 2.—Map showing the distribution of sand sage prairie in the Great Plains, USA, in relation to the distribution of the High Plains aquifer.

aquifer have been converted to cropland (World Wildlife Fund 2018). In some parts of the Great Plains, sandsage prairie is the only native vegetation of significant scale remaining on the landscape, providing islands of natural habitat critical to the support and persistence of biological diversity. In this regard, tracts of sandsage prairie have conservation values similar to playa wetlands on the southern Great Plains (Haukos and Smith 1994; Smith et al. 2011).

BIODIVERSITY AND HETEROGENEITY IN SANDSAGE PRAIRIE

The dune field habitat in which sandsage prairie occurs is highly dynamic and subject to a host of natural disturbance factors including fire, herbivory, and, most importantly, periodic and often severe drought. As a consequence, there is a high level of heterogeneity in the structure of sandsage prairie vegetation (Ramaley 1939; Collins et al. 1987; Kelso et al. 2007; Winter et al. 2011). Locklear (2019) delineated five sub-communities in sandsage prairie vegetation that intergrade to form a spatially complex, patchy, shifting mosaic of plant species tied to various degrees of disturbance and stabilization within the dune field.

The dynamic nature of sandsage prairie vegetation is evidenced in the life history traits of its constituent plant species, with 39% of the flora consisting of annuals, biennials, and short-lived perennials that are adapted to recurring cycles of vegetation disturbance and recovery (Locklear 2019). Three globally imperiled plants (G3) associated with sandsage prairie, *Chenopodium cycloides*, *Dalea cylindriceps*, and *Euphorbia carunculata*, occur in open sand or partially stabilized habitat and are not found in more densely vegetated areas. Conservation of such at-risk plants, and persistence of the crucial pioneer species of open habitat in sandsage prairie, requires the presence of disturbed areas. Based on research in Colorado sandsage prairie, Kelso et al. (2007) recommended allowing some open dune complexes to persist in the landscape for the benefit of narrowly adapted sand specialist plants and to strengthen ecological resilience by providing source material for the natural introduction of these stabilizing species in the event of drought-caused dune reactivation.

Animal diversity is influenced by heterogeneity in sandsage prairie vegetation structure. Research in Kansas sandsage prairie found habitat preferences among amphibians and reptiles ranged from more densely vegetated interdunal swales and flats to the open and sparsely vegetated slopes of “choppy” dunes (Rush et al. 1982). Vegetation structure has also been shown to influence the capacity of sandsage prairie to support bird species. Three permanent residents of sandsage prairie, lesser prairie-chicken (Jamison et al. 2002; Hagen et al. 2004, 2005), greater prairie-chicken (*Tympanuchus cupido*; Mohler 1952; Evans and Gilbert 1969) and scaled quail (Schemnitz 1961; Ault 1983), exhibit seasonal variation in how they interact with vegetation structure, particularly as it relates to courtship, nesting, and brood-rearing. These fine-scale connections between avian behavioral activities and vegetation structure need to be considered when developing management strategies for sandsage prairie.

The relationship between the inherent heterogeneity of sandsage prairie vegetation and the biodiversity it supports has significant implications for conservation actions. Managing sandsage prairie rangeland for the fullest expression of its biodiversity requires accommodating or restoring processes that drive this heterogeneity (Fuhlendorf et al. 2017a), particularly the interactive effects of prescribed fire and grazing (Winter et al. 2012).

CONCLUSION

Sandsage prairie is a significant host of biodiversity for the central and southern Great Plains. The dune fields that support sandsage prairie occur as regionally restricted physiographic islands or anomalies (Kelso et al. 2001) within the larger Great Plains landscape and have a biota distinct from that of surrounding habitats, including many regional endemics, ecological specialists, and species of conservation concern. In parts of its range, sandsage prairie is the only native vegetation of significant scale remaining on the landscape, providing islands of natural habitat critical to the support and persistence of biological diversity. These attributes make sandsage prairie a biodiversity hotspot for the Great Plains. Stewardship of sandsage prairie biodiversity requires preventing further loss, fragmentation, and degradation of existing tracts as well as accommodating or restoring processes that drive the inherent heterogeneity of this unique ecological system.

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Jim Locklear is Director of Conservation for Lauritzen Gardens, a botanical garden in Omaha, Nebraska. Research for this paper involved direct reconnaissance of sandsage prairie occurrences in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas, and Wyoming.

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Appendix 1.—Sandsage prairie plants and animals of conservation concern.

The following compilation enumerates plant and animal species that occur in association with sandsage prairie and are of conservation concern at the global and/or state level as indicated by the conservation status ranking system of NatureServe (2020). Listed below are the relevant NatureServe ranks and definitions.

G3—Vulnerable in the nation due to a restricted range, relatively few populations (often 80 or fewer populations), recent and widespread declines, or other factors making it vulnerable to extirpation. No sandsage prairie species were ranked G1 (critically imperiled) or G2 (imperiled) by NatureServe.

S1—Critically imperiled in the state because of extreme rarity (often 5 or fewer occurrences) or because some factor(s) such as very steep declines make it especially vulnerable to extirpation from the state.

S2—Imperiled in the state because of rarity due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors making it very vulnerable to extirpation from the state.

S3—Vulnerable in the state due to a restricted range, relatively few populations (often 80 or fewer populations), recent and widespread declines, or other factors making it vulnerable to extirpation.

Plants

- Poverty three-awn *Aristida divaricata* Humb. & Bonpl. ex Willd. KS (S1)
- Painted milkvetch *Astragalus ceramicus* Sheldon var. *filifolia* (A. Gray) F.J. Herm. KS (S1); OK (S1); WY (S3)
- Sandhill goosefoot *Chenopodium cycloides* A. Nelson **G3**; CO (S1); KS (S2); NE (S1); NM (S2); OK (SU); TX (S3)
- Sandsage prairie clover *Dalea cylindriceps* Barneby **G3**; CO (S3?); KS (S2); NE (S2); NM (SNR); OK (S1); SD (SNR); TX (S2); WY (S2)
- Spectacle-pod *Dimorphocarpa candicans* (Raf.) Rollins KS (S1)

- Red lovegrass *Eragrostis secundiflora* J. Presl. subsp. *oxylepis* (Torr.) S.D. Koch NE (S1)
- Sand-dune sandmat *Euphorbia carunculata* Waterf. **G3**; KS (S1); NM (SNR); OK (S1S2); TX (S3)
- Panhandle spurge *Euphorbia strictior* Holz. **G3**; NM (S3); TX (S3)
- Berlandier's flax *Linum berlandieri* Hook. NE (S1)
- Bailey's rabbitbrush *Lorandersonia baileyi* (Wootton & Standl.) Urbatsch, R.P. Roberts, & Neubig KS (S1)
- Eastern catclaw *Mimosa rupertiana* B.L. Turner KS (S1); OK (S1S2)
- Smooth four o'clock *Mirabilis glabra* (S. Watson) Standl. NE (S2)
- Engelmann's evening primrose *Oenothera engelmannii* (Small) Munz. CO (S1); KS (S2); OK (S1); TX (S2)
- Gilia penstemon *Penstemon ambiguus* Torr. NE (S1)
- Great Plains fameflower *Pemmeranthus calycinus* (Engelm.) Kiger NE (S1S2)
- Plains phlox *Phlox andicola* E.E. Nelson CO (S2?)
- Sand reverchonnia *Phyllanthus warnockii* G.L. Webster CO (S1); KS (S1)
- James' rushpea *Pomaria jamesii* (Torr. & A. Gray) Walp. NE (S1)
- Blowout grass *Redfieldia flexuosa* (Thurb.) Vasey KS (S2) TX (S1)
- Indian ricegrass *Stipa hymenoides* Roem. & Shult. KS (S2); OK (S1)
- Queen's delight *Stillingia sylvatica* L. CO (S1)

Invertebrates

- Ghost tiger beetle *Cincidela lepida* Dejean **G3**; CO (S3); NE (S2)
- Wiest's sphinx moth *Euproserpinus wiestii* Sperry **G3**

Amphibians and Reptiles

- Common lesser earless lizard *Holbrookia maculata* Girard KS (S3)
- Texas horned lizard *Phrynosoma cornutum* (Harlan) CO (S3); OK (S2)
- Kansas glossy snake *Arizona elegans elegans* Kennicott CO (S3S4), NE (S1), OK (S3)
- Coachwhip *Masticophis flagellum* (Shaw) NE (S3)
- Long-nosed snake *Rhinocheilus lecontei* Baird and Girard CO (S1?), KS (S3), OK (S3)
- Desert massasauga rattlesnake *Sistrurus catenatus edwardsii* (Baird and Girard) **G3T3**; CO (S2)
- Plains black-headed snake *Tantilla nigriceps* Kennicott NE (S1)

Birds

- NatureServe breeding status qualifiers: B = Breeding; N = Nonbreeding. Bird residency status abbreviations: **M** = migrant; **PB** = permanent resident, breeding in sandsage prairie documented; **SB** = summer resident, breeding in sandsage prairie documented; **SV** = summer visitant (foraging); **WV** = winter visitant (foraging); **YRV** = year-round visitant (foraging).
- Long-billed curlew *Numenius americanus* Bechstein KS (S1B, S2N) **M**

- Short-eared owl *Asio flammeus* (Pontoppidan) CO (S2B); KS (S2B, S3N); NE (S2); NM (S2N); OK (S3N) **WV**
- Burrowing owl *Athene cunicularia* (Molina) KS (S3B); NE (S3); OK (S2); TX (S3B) **SV**
- Ferruginous hawk *Buteo regalis* (Gray) CO (S3B); KS (S2B); NE (S2); NM (S2B); TX (S2B) **YRV**
- Swainson's hawk *Buteo swainsoni* Bonaparte NE (S3); OK (S3B) **SV**
- Prairie falcon *Falco mexicanus* Schlegel NE (S3); OK (S3); TX (S3B) **WV**
- Scaled quail *Callipepla squamata* (Vigors) KS (S2); NM (S3B, S4N); OK (S3) **PB** (Cable et al. 1996)
- Loggerhead shrike *Lanius ludovicianus* Linnaeus CO (S3S4B); KS (S4B, S2N); NE (S2S3); NM (S3B, SS4N) **SV**
- Brewer's sparrow *Spizella breweri* Cassin KS (S1B); NM (S3B, S4N); OK (S2N) **SB** (Ports 1980, 1981; Cable et al. 1996; Molhoff 2006)
- Cassin's sparrow *Peucaea cassini* (Woodhouse) KS (S3B), NE (S3), OK (S2S3) **SB** (Ports 1980, 1981; Herbert 1986)
- Greater prairie-chicken *Tympanuchus cupido* (Brewster) CO (S3), NE (S3S4), OK (S3) **PB** (Evans and Gilbert 1969)
- Lesser prairie-chicken *Tympanuchus pallidicinctus* (Ridgeway) **G3**; CO (S2), KS (S3), NM (S2B, S2N), OK (S1), TX (S2B) **PB** (Ports 1981; Pittman et al. 2006)
- Chihuahuan raven *Corvus cryptoleucus* Couch CO (S3S4); KS (S1); OK (S2B) **YRV**
- Greater roadrunner *Geococcyx californianus* (Lesson) KS (S3) **YRV**

Mammals

- Spotted ground squirrel *Xerospermophilus spilosoma* (Bennett) KS (S3); OK (S3)