

# Chapter 8

## Rangeland Biodiversity



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**Abstract** In its simplest form, biodiversity is defined as species richness (the number of species in a given area). More complex definitions include the variety of life on Earth, from genes to ecosystems, and include the ecological and evolutionary processes that sustain that life. As in other ecosystems, biological communities in rangelands are influenced by a number of different abiotic and biotic drivers or “filters” at both broad and fine scales, and an understanding of these processes is critical for maintaining ecosystem services as well as addressing widespread biodiversity declines. In rangeland ecosystems specifically, the primary threats to biodiversity are habitat loss, fragmentation, and degradation through mismanagement, which includes suppression or mis-application of historical disturbance regimes. Restoring heterogeneity to rangelands by mimicking historical disturbance regimes has been shown to benefit biodiversity, but the exact role of disturbance varies widely throughout North American rangelands. As such, careful consideration of the type, duration/periodicity, intensity, and spatial and temporal extent and configuration of these disturbances is necessary when managing for site-specific biodiversity outcomes. It is important to consider the effects of both inherent (i.e., either natural or historical) and human-caused variability on rangeland plant and wildlife communities. In the future, practitioners should promote management practices that maintain and enhance biodiversity to maximize ecosystem functions and services that improve the quality and quantity of economic (e.g., livestock production, carbon banking) and ecological (e.g., biodiversity, sustainability) outcomes in North American rangelands.

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## 8.1 Overview

In the broadest sense, biodiversity refers to the variety of life at each ecological scale from the genome to the biome (Gaggiotti et al. 2018). We use the term biodiversity to refer to the genetics of a population or the species within an ecological community; in both cases, greater biodiversity would indicate greater variation among the units of interest (genes or species, respectively). While biodiversity includes all taxa (e.g., plants, fungi, animals), in this chapter we focus primarily on animals, giving the bulk of our attention to vertebrate diversity but also discussing arthropod diversity and plant diversity as it relates to supporting animal diversity (see Chap. 26 for further treatment of rangeland insects). We also focus largely on species diversity; although genetic diversity is becoming increasingly important to consider, we do not expand on that here and we refer readers to other discussions of this topic (Allendorf and Luikart 2007; Costa and Delotelle 2008).

Animal biodiversity influences many different aspects of ecosystems. For example, the diversity of animal species within biological communities can affect ecological stability (Ives and Carpenter 2007), and communities can shift with the removal of one or a few species (Paine 1966). Genetic diversity is also important, and tracking this diversity is critical in endangered or reintroduced populations to ensure successful recruitment and to avoid inbreeding (Allendorf and Luikart 2007). From a management perspective, *biodiversity hotspots* provide high return on investment opportunities for conservation and management because focused efforts in these areas can protect a large suite of species (Marchese 2015).

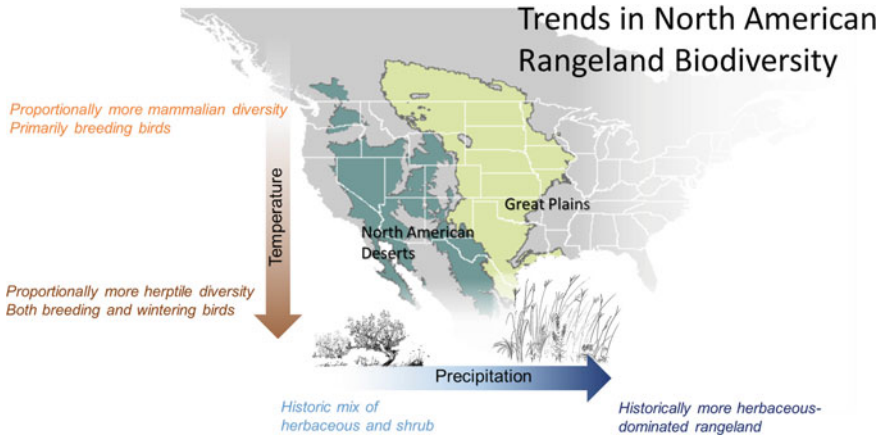
Across spatial and temporal scales, biodiversity conservation has become a major focus because species diversity is declining worldwide (WWF 2018; Fig. 8.1). As of 2021, current estimated extinction rates are 10–100 times higher than the average rate over the past 10 million years (IPBES 2019). It seems all but certain that these declines will become more ubiquitous under likely scenarios of global climate change and human population growth (WWF 2018). Understanding the drivers and consequences of these declines, and ameliorating them, will require an understanding of the natural processes that support biodiversity in rangelands, the success and failures of historical and current management strategies, and the best ways to evaluate conservation and measure success.

Rangeland biodiversity is largely determined by climate and *disturbance regimes*—the spatial and temporal characteristics of events that shape a system over time such as fire, grazing, and extreme weather events—and earlier chapters in this book highlight the central role of climatic variation and disturbance in shaping North American rangeland ecosystems (e.g., see Chaps. 2 and 6). Rangeland wildlife in North America co-evolved within the context of dynamic climate and disturbance regimes, leading to species adaptations that facilitate coping with



**Fig. 8.1** Rangeland biodiversity is a key conservation target worldwide. Clockwise from top left, examples of taxa native to North American rangelands that are of conservation concern include American bison (*Bison bison*), western meadowlark (*Sturnella neglecta*), regal fritillary (*Speyeria idalia*), Texas horned lizard (*Phrynosoma cornutum*), swift fox (*Vulpes velox*), and Great Plains toad (*Anaxyrus cognatus*). All taxa examples have undergone population declines and most are considered species of greatest conservation need in states where they occur

extreme changes in resource availability and vegetation structure over time (Knopf and Samson 1997). For example, as an adaptation to uncertain resource availability, many wildlife populations exhibit annual migrations across states and countries [e.g., mule deer (*Odocoileus hemionus*), see Chap. 17; pronghorn (*Antilocapra americana*), see Chap. 19], seasonally or in altitude [e.g., greater sage-grouse (*Centrocercus urophasianus*), see Chap. 10], or even across continents (e.g., rangeland songbirds, see Chap. 12; waterfowl, see Chap. 13). Other species evolved to be more nomadic, continuously following resources as they became available across the plains [e.g., American bison (*Bison bison*); see Chap. 23]. As such, rangeland wildlife species often exhibit lower levels of *site fidelity* relative to taxa in forested ecosystems in order to take advantage of an ever-shifting landscape (Jones et al. 2007; Jonzén et al. 2011). While climatic variability plays a central role in defining North American rangelands, other forms of disturbance also have important roles in maintaining the complexity of rangelands (Knopf and Samson 1997; Fig. 8.2). For example, fire, roaming bison herds, and burrowing mammals historically served to alter plant communities and landscape structure in multiple ways (e.g., increased bare ground, reduced vegetation structure, altered forage quality and soil nutrient content, greater structural heterogeneity) throughout North American rangelands. But, some of these same disturbances (fire, bison herbivory) were much less influential farther west within the sagebrush steppe because reduced herbaceous biomass in these systems (driven by different timing and frequency of precipitation) did not historically facilitate frequent fire or dense grazer populations (Innes and Zouhar 2018).



**Fig. 8.2** North American rangeland biodiversity is driven in large part by gradients in increasing moisture from west to east and increasing temperature from north to south as well as the seasonal distribution of these weather gradients. As a consequence, rangelands vary greatly in predominant herbaceous taxa and vegetation structure, which in turn influences community structure of flora and fauna and overall biodiversity

Although many North American wildlife species co-evolved in the context of frequent disturbance, the unpredictability of resources and heterogeneity inherent in these disturbance regimes has long been considered incompatible with livestock production goals (Fuhlendorf et al. 2017). As a result, the suppression of natural disturbances, especially fire, has occurred in disturbance-dependent rangelands (particularly, grasslands) of North America from European settlement to the recent past. Furthermore, suppression of disturbances for the perceived benefit of livestock has been linked to detrimental changes in rangeland wildlife communities, threatening biodiversity (Fuhlendorf et al. 2012; see Chap. 6). Conversely, climate change and invasive plants have increased disturbance frequency and intensity in western rangelands (particularly, shrubsteppe ecoregions), killing fire-intolerant big sagebrush (*Artemisia tridentata*) and reducing habitat availability for sagebrush *obligates* like sage-grouse (*Centrocercus spp.*, Chap. 10; Bagne et al. 2012; DiTomaso et al. 2017).

If we view biodiversity simply as species richness (i.e., the number of species present), rangelands often have lower richness compared to other biomes with most biodiversity hotspots found in parts of the tropics, and especially tropical forests. The broad-scale drivers of these relationships are discussed elsewhere (MacArthur 1958; Brown 1995), but include the relationship of increasing niche space with greater vertical structure provided within forested ecosystems (MacArthur and MacArthur 1961) as well as links between greater solar energy, increased vegetation productivity and resource availability (Clarke and Gaston 2006), all of which facilitate greater species richness. However, species richness is just one dimension of biodiversity. This metric does not capture the *evenness* (i.e., all species having similar abundance

versus a few highly abundant species and many rare) of species within the community, the conservation status of those species, the role they play in the community [e.g., *keystone species* (Paine 1969), *ecosystem engineers* (e.g., Chap. 15), whether they are components of a *mutualism*], or how genetically and/or functionally unique they are among regional and global taxa. Understanding rangeland biodiversity in North America requires considering all these aspects while keeping in mind the other services we utilize and expect from our rangeland systems, including livestock production.

Within this chapter, we take a broad view of rangeland biodiversity in North America, examining the mechanisms that shape and limit biodiversity (Sect. 8.2), how to measure and manage for biodiversity in rangelands (Sects. 8.3 and 8.4), and forces that threaten rangeland biodiversity (Sect. 8.5).

## 8.2 Processes that Influence Rangeland Biodiversity

One way to conceptualize the formation of ecological communities, and the diversity therein, is through the lens of abiotic and biotic filters (Götzenberger et al. 2012; Kraft et al. 2015). Put simply, this recognizes that the presence of a species in a given location is a function both of landscape and regional-scale drivers of species range [e.g., temperature gradients or drought (Choat et al. 2012; DeBello et al. 2013; Keddy and Laughlin 2022)], but also finer-scale drivers including species interactions like intraspecific or interspecific competition (Connell 1983; Chen et al. 2010), herbivory (Moolman and Cowling 1994), or predation (e.g., keystone species, Paine 1966). In rangelands, climatic gradients are major abiotic filters of species ranges. For example, we see much higher abundance of reptiles in southern rangelands as compared to northern (or high elevation) rangelands because of thermal limits of ectotherms (Fig. 8.2). The same north–south temperature gradient drives a transition in dominant photosynthetic pathway of grasses from C3 to C4 in hotter southern grasslands (Teeri and Stow 1976). Precipitation gradients east to west across North American rangelands also drive major shifts in vegetation, which in turn influence wildlife communities. For example, tall grasses transition to short grasses as average precipitation decreases and precipitation variability increases moving east to west (Anderson 2006). Moving further west, as precipitation regimes shift from spring/summer-dominated to winter-dominated, we observe a shift towards shrublands; sagebrush (*Artemisia* spp.) becomes more common where snowmelt is a dominant source of soil moisture (Schlaepfer et al. 2012), with desert shrublands occurring in the warmer parts of the southwest that experience extreme drought in late spring and summer (Gao and Reynolds 2003). Other abiotic filters include nutrient and hydrological cycling processes. Some important filters that influence species occurrence, like soils, are more difficult to categorize as biotic or abiotic because they are a combination of the two, but soil type plays a major role in vegetation communities, and thus can help in determining wildlife occupancy and community composition

(Evans et al. 2017). The natural and anthropogenic disturbances that shape rangelands are another major filter (Fuhlendorf et al. 2017), as some species benefit from disturbances while others are less disturbance tolerant. Finally, species interactions like predation, competition, and mutualisms all serve as fine-scale biotic filters that determine where certain species can occur. As an example in rangelands, researchers have noted that coyotes (*Canis latrans*) and swift fox (*Vulpes velox*; Fig. 8.1) rarely co-occur because the larger coyote behaviorally excludes, and sometimes even depredates, swift fox (Kitchen et al. 1999). Below we discuss some of the major drivers of biodiversity in rangelands, and how they impact rangeland wildlife.

### 8.2.1 Climate

Climate, or long-term weather patterns, can be characterized as average temperature and precipitation over time. However, in complex landscapes like the western United States, this simplistic description may be inadequate to describe the many factors influencing the climate. More appropriately, climate also includes factors like timing of precipitation, amount of sunshine, average wind speed and direction, number of days above freezing, weather extremes, and ocean currents. Climate is a major factor in determining biomes and critical for shaping overall species diversity (Begon et al. 2006) and macroecological theory suggests that patterns of diversity (i.e., species richness) are limited by ambient energy at high latitudes and moisture at low latitudes (Hawkins et al. 2003). Across North American rangelands, we see climate driving taxonomic composition of wildlife communities, with proportionally more mammals and migratory breeding birds in more northern rangelands, and more herpetofauna and resident or wintering birds in southern rangelands (Valentine-Darby 2010; Fig. 8.2).

Over broad spatial scales, regional climate is a determinant of biodiversity and plant-biomass productivity, and it is foundational in determining the *fundamental niche* of animal species (Hutchinson 1957). The fundamental niche is determined by the potential tolerances and requirements of individuals. How those interact with the conditions, resources, and individuals around them to shape actual occurrence determines an organism's *realized niche* (Hutchinson 1957). Niches have multiple dimensions that represent species tolerances of various biotic and abiotic factors, and the overall availability of niches or niche space plays a major role in determining the biodiversity in a system.

Temperature is one of the most important components of climate that influences biodiversity. In particular, the importance of extreme high-temperature events in influencing species distribution and fitness has long been acknowledged (Begon et al. 2006). Therefore, temperature regulation or amelioration of thermal extremes can be an important landscape function (Hovick et al. 2014a; Melin et al. 2014). For example, variation in vegetation composition can alter the variability in thermal environments (e.g., by providing shade) thereby allowing animals greater opportunity for selecting suitable thermal conditions (Carroll et al. 2015; Londe et al.

2020). This is increasingly important to understand in the face of climate change as temperature extremes become more frequent and organisms increasingly experience warmer temperatures (IPCC 2013a, b). Despite knowledge of how climate determines a species' distribution, survival, and reproduction, there are still relatively few studies focused on how temperature affects wildlife habitat selection and survival (Elmore et al. 2017). However, this field of research has been growing in recent years with more studies examining the influence of management on vegetation, and in turn, the influence on thermal environments and how that affects habitat selection of wildlife (Hovick et al. 2014a; Carroll et al. 2015; Raynor et al. 2018).

Precipitation is another major component determining a region's climate with the interannual variability, seasonal distribution, and annual total all impacting animal populations (Pearce-Higgins et al. 2015). In general, temperate species of the US have evolved in highly variable environments and are therefore highly adaptable to variation in precipitation and temperature (Bonebrake and Mastrandrea 2010). However, it is predicted that precipitation regimes are going to change in many regions of the world (IPCC 2013a, b), and overall there is limited understanding of how such alterations will affect biodiversity. Both extended drought and large rain events are expected to become more common throughout much of the US (IPCC 2013a, b), and these events will have varying impacts on biodiversity but are most likely to have a negative influence on shorter temporal scales (Albright et al. 2009).

## 8.2.2 Soils

Soils can be viewed as one of the underlying templates upon which rangeland biodiversity is structured. Soil properties (e.g., particle size, pH) serve as a filter for vegetation composition and structure, both of which have direct impacts on the species that can occupy an area. Soil type is also important for many species including burrowing organisms like prairie dogs (*Cynomys* spp.) (Reading and Matchett 1997; Chap. 15), and these burrowing organisms may in turn alter soil structure via soil mixing, or "bioturbation" (Barth et al. 2014). Not only are soils the foundation for above-ground biodiversity, they are alive with a wealth of below-ground biodiversity. Decaëns et al. (2006) predict that 25% of all species live in soil for some part of their lifecycle, including protists, nematodes, earthworms, and arthropods (Yarwood et al. 2020; Chap. 26). Some of these species, including arbuscular mycorrhiza (i.e., fungal associations in plant roots that form plant-fungal mutualisms), are critical for fixing nitrogen in rangeland plants, and are especially important to consider when trying to restore rangeland flora (Miller et al. 2012; Duell et al. 2022). In many ways, our rangeland soils remain a vast frontier on a microscopic scale. For example, we know very little about the capacity of rangeland soils to store carbon belowground (Fynn et al. 2010), but the USDA-Agricultural Research Service has estimated that rangelands in the United States have the capacity to store 19 million metric tonnes of carbon per year (Schuman and Derner 2004). Carbon storage is a major focus in efforts to reduce greenhouse gasses to mitigate climate change, and

thus, carbon storage potential in rangelands, which is driven both by abiotic and biotic factors in soil (Hungate et al. 2017), is important as we consider economic valuations in these systems and the bottom up influence of soils on rangeland biodiversity (Ritten et al. 2012).

### 8.2.3 *Herbivory*

Grazing is a dynamic process that interacts with other disturbances as well as topographic (i.e., soils and topography) and vegetation features across landscapes to form patterns that impact ecosystem functions and biodiversity (Collins et al. 1998; Tews et al. 2004). Historically, rangelands of North America were shaped by fire, herbivores, and their predators for nearly 10,000 years (Knapp et al. 1999; Anderson 2006). American bison, in particular, are considered keystone species that were critical in shaping the flora and fauna of North America's Great Plains (Knapp et al. 1999). Estimates on the number of bison inhabiting the Great Plains before the 1800s range from 30 to 60 million that roamed in herds large enough to span from horizon to horizon (Flores 1991). These nomadic herds followed fires created by lightning and Native Americans, feeding primarily on grasses and often leaving forbs ungrazed (Fahnestock and Knapp 1993; Damhoureyeh and Hartnett 1997). In addition to grazing patterns that can influence biodiversity, bison herds can alter nutrient cycling through fecal and urine inputs that can change plant species composition (Blair 1997). This is the result of the effects on nitrogen cycling which can be critical in grasslands because nitrogen availability often limits plant productivity in these landscapes (Seastedt et al. 1991; Turner et al. 1997). Another aspect of bison behavior that contributed to the diversity of grasslands is wallowing (discussed further below). Despite their abundance and influence on the landscape, bison numbers dwindled from tens of millions to just a few thousand near the end of the nineteenth century due to overexploitation by European settlers who were expanding westward (Flores 1991). Since their near extinction, the complex landscapes that contained roaming herds of bison have been replaced by highly parcelized and fragmented landscapes that resulted from early settlement and legislation such as the Homestead Act of 1862. This fragmentation has also had negative impacts on other extant native ungulate grazers or browsers that occur in North American rangelands including pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed (*O. virginianus*) deer (Chaps. 17–20). Non-native grazers on North American rangelands include feral equids (*Equus* spp.; Chap. 22) as well as domestic livestock (Chap. 4).

Globally, livestock grazing is the most widespread and pervasive anthropogenic land use on rangelands (Alkemade et al. 2013), occurring on approximately 60% of the world's agricultural lands (Alexandratos and Bruinsma 2012). Despite these large numbers, livestock consumption by humans has more than doubled over the last half century and is projected to increase by another 70% by 2050 (Thornton 2010; Alexandratos and Bruinsma 2012). Given the large amount of land that is used for



livestock production, it is not surprising that livestock herbivory has profound impacts on rangeland biodiversity. Grazing by domestic livestock can affect an ecosystem in many different ways, including altering plant community composition and diversity (Augustine and McNaughton 1998; Allred et al. 2012). Because grazed rangelands provide habitat for many wildlife species, livestock management decisions in these areas can have profound impacts on wildlife and biodiversity (Fuhlendorf et al. 2012; Alkemade et al. 2013). Some have suggested that livestock in rangeland ecosystems act as ecosystem engineers due to their direct and indirect influences on vegetation structure and the availability of resources to other organisms (Jones et al. 1997; Derner et al. 2009). Previous research investigating the influence of livestock grazing on wildlife has suggested a negative influence on some species (e.g., Tetraonidae spp.; Dettenmaier et al. 2017), whereas other studies have shown how restoring disturbance patterns, particularly grazing and burning, can have a positive influence on biodiversity (Fuhlendorf et al. 2006; Hovick et al. 2015; Duchardt et al. 2016; He et al. 2019). The influence of livestock grazing on wildlife is largely dependent upon the spatial and temporal distribution of the grazer and may also be influenced by livestock type, timing and frequency of grazing, grazing duration, livestock distribution across the landscape, seasonality, stocking rate, and the evolutionary history of grazing at a given site (Dettenmaier et al. 2017; see Chap. 4).

In addition to the influence of historical and contemporary grazing patterns by large herbivores, many native, smaller herbivores also play an important role in shaping rangeland ecosystems in North America. For example, prairie dogs and other rodents, rabbits and hares (*Leporidae*), and grasshoppers, locusts, and crickets (*Orthoptera*) have the ability to manipulate vegetation structure and composition in grasslands that influences biodiversity. These organisms are often thought of as pests in rangelands, but their importance as prey, ecosystem engineers, and nutrient cyclers should not be overlooked (Belovsky and Slade 2000; Augustine and Baker 2013; see Chaps. 15 and 26).

### 8.2.4 Fire

Fire as a disturbance process is critical in shaping world biomes and biodiversity patterns. Fire plays a large role in maintaining the structure and function of fire-prone ecosystems, which includes many rangelands (Bond and Keeley 2005). Moreover, fire influences global ecosystem patterns and processes, including vegetation distribution and structure, the carbon cycle, and climate (Bowman et al. 2009). The consequences of fire suppression can be significant for biological systems, and may result in a loss of biodiversity, alteration of ecosystem function, and changes in community structure and composition (Swetnam et al. 1999; Bond and Keeley 2005; Nowacki and Abrams 2008). In general, it is important to think of fire similarly to soils and climate in the sense that the biota in every region have evolved and are adapted to a particular regime (e.g., ranging from no fire to frequent fire) and alterations to those regimes can be detrimental. Fire regimes include important factors such

as fire-return intervals, seasonality, intensity, and severity. Variation in these factors, known as *pyrodiversity*, can have a strong influence on biodiversity (Beale et al. 2018; Fig. 8.3). Management of rangelands focused on maintaining or enhancing biodiversity may have limited success without restoring historical fire patterns, including variable fire season and fire intensity and combining these with other disturbances such as grazing across broad landscapes (Fuhlendorf et al. 2012).

Envisioning fire as an ecological process is important for its application in conservation and land managers should try to maintain historical fire regimes in native ecosystems that are fire-adapted. For example, this means targeting three to five-year fire-return-intervals in tallgrass prairies throughout the central United States (Allen and Palmer 2011; Ratajczak et al. 2016), which are made possible because of sufficient precipitation and the amount of biomass that creates adequate fuel loads to sustain fires at this interval. In these systems, cessation of fire for as little as ten years can lead to state shifts from tallgrass prairie to eastern red cedar (*Juniperus virginiana*)-dominated woodland (Briggs et al. 2002; Ratajczak et al. 2016). On the other end of the spectrum, too-frequent burning, as applied in much of the Flint Hills of the Great Plains in the form of annual burning, can lead to reduced litter accumulation and loss of native forb species as well as favoring a less diverse grassland breeding bird community (Hovick et al. 2015; McGranahan et al. 2018). Moving west from tallgrass prairie systems, precipitation declines and fire-return-intervals generally increase to 5–20 years in mixed and shortgrass prairie due to a reduction in annual biomass production that can act as fuels for fires (Zouhar 2021).



**Fig. 8.3** Fire is a major driver of rangeland biodiversity. Both wildfires and prescribed fires (top left) influence forage quality as well as vegetation structure. Recent burns provide foraging habitat for a number of bird species including Swainson's hawk (*Buteo swainsoni*, top right), American golden plover (*Pluvialis dominica*, bottom left), and upland sandpiper (*Bartramia longicauda*, bottom right)

Moving even further west into the sagebrush steppe, fire return intervals were extremely long historically (decades to centuries), as evidenced by extremely slow recovery of current sagebrush systems post-fire (Baker 2006). In these landscapes, invasions of nonnative annual grasses [e.g., cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*)] have created a positive feedback loop that has led to higher fire frequency than historically observed, through accumulation of high *fine fuel* loads (Balch et al. 2017). Collectively, this combination of annual grass invasion and alteration to fire regimes along with habitat loss and degradation associated with other factors such as agricultural, industrial, and urban development have reduced the extent of the sagebrush ecosystem by nearly 50% (Schroeder et al. 2004; Davies et al. 2011). These changes have led to decreased native plants and wildlife populations and reduced diversity in sagebrush systems (Crawford et al. 2004; Shipley et al. 2006; Davies et al. 2018; Mahood and Balch 2019). Many sagebrush obligate species including sage-grouse, pygmy rabbit (*Brachylagus idahoensis*), Brewer's sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), and sage thrasher (*Oreoscoptes montanus*) have declined because of changes in these historical disturbance patterns (Mutter et al. 2015; Oh et al. 2019; Smith et al. 2019). Sagebrush restoration is needed because these systems provide numerous *ecosystem services* and *functions* (Prevéy et al. 2010), including favorable microclimates for seed germination and establishment and habitat for wildlife of conservation concern. However, the success of sagebrush restoration is closely tied to the reinstatement of fire regimes that mimic historical intensities and return intervals to maximize the future conservation of biodiversity. Although we have highlighted threats of annual grass invasion and altered fire regimes to Wyoming big sagebrush (*A. t. wyomingensis*) habitat, which typically occurs in lower and drier elevations, we note that higher-elevation sagebrush species such as mountain big sagebrush (*A. t. vaseyana*) suffer from invasion by upslope coniferous species such as Juniper (*Juniperus* spp.) and pinyon pine (*Pinus monophylla* and *edulis*) due to long-term fire suppression (Davies et al. 2011). This change in woody species composition reduces herbaceous vegetation (Davies et al. 2011), which subsequently lowers biodiversity of higher trophic levels. As such, this is yet another example where managers must try to reinstate prescribed fire that replicates historical regimes to reduce juniper expansion.

### 8.2.5 Other Disturbances

In addition to the disturbances of herbivory and fire, many herbivorous species have secondary impacts on habitat structure and rangeland biodiversity through behaviors like wallowing, burrowing, and vegetation clipping. As mentioned above, bison wallowing, which involves individuals rolling on the ground, creates depressions with compacted soils that often collect water and provide habitat for amphibians (Gerlanc

and Kauffman 2003), and facilitate increased arthropod diversity at a landscape scale (Nickell et al. 2018). With the vast numbers of bison that once occupied the Great Plains, these soil depressions were probably abundant and widespread features of the landscape prior to European settlement (England and DeVos 1969).

Another suite of ecosystem engineers in North American rangelands are burrowing rodents that disturb soil and alter vegetation communities, providing unique habitats for a number of taxa [Fig. 8.4; see Chap. 15]. Beyond herbivory and burrowing, two species of prairie dog (the black-tailed (*C. ludovicianus*) and Mexican (*C. mexicanus*)] live at very high densities and are colonial, actively clipping vegetation on colonies to maintain visibility of predators (Hoogland 1995). This additional disturbance makes these colonies especially unique structurally, increasing avian diversity at a landscape scale where they occur (e.g., Duchardt et al. 2018), and leading to extreme community shifts in both birds and mammals when prairie dogs are removed from the landscape (Duchardt et al. 2023a, b).

Other potential disturbances in rangelands can include flooding or drought, which may occur over relatively short (e.g., a few days or weeks of flooding) to long (e.g., multiple decades of drought) intervals (Vose et al. 2015) and may be considered as a component either of climate or disturbance. Other events of discrete weather



**Fig. 8.4** Biodiversity associated with ecosystem engineering by the presence of black-tailed prairie dogs (*Cynomys ludovicianus*) within a biome. Clockwise from top: prairie rattlesnake (*Crotalus viridis*) and black widow (*Latrodectus hesperus*) occupying a prairie dog burrow, mountain plover (*Charadrius montanus*) reliant on short-structure grasslands created by prairie dogs, black-tailed prairie dog on burrow entrance, and pronghorn (*Antilocapra americana*) foraging on prairie dog colony

like hailstorms and tornadoes (e.g., Carver et al. 2017), as well as disease, can also lead to individual mortality or habitat alteration, shifting species interactions and influencing biodiversity in the impacted system.

### 8.2.6 Interactions Among Drivers

Climate, soils, herbivory, and fire all interact to shape rangeland wildlife biodiversity. Collectively, these factors have been acting over millennia to shape ecosystems that are now largely influenced by anthropogenic forces. Human action or inaction has a major influence on where and when disturbances occur. For example, fire is a pattern-driving process on rangelands that interacts with other disturbances to contribute to vegetation heterogeneity (Bond and keeley 2005; Fuhlendorf et al. 2009). In particular, the interaction of fire and grazing, or *pyric-herbivory*, is a critical process in rangelands that can affect patterns of wildlife colonization and influence site selection for many species throughout their life history, ultimately shaping biodiversity in many rangeland systems (Fuhlendorf et al. 2012). It has been argued that interacting grazing and fire may best be viewed as a single disturbance process in ecosystems that evolved with it, and that the resulting heterogeneity from this interaction is the foundation of biodiversity in grassland systems (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2009). Wildlife grazing, movement, and defecation also alter hydrologic and nutrient cycling, while nutrient and water availability inevitably shape wildlife habitat use. Some of these interactions, such as the fire-grazing interaction, have received attention in recent years, while others of these interactions are not yet understood, and require further study.

## 8.3 Methods for Evaluation and Monitoring Biodiversity

Whether we want to further evaluate the roles of abiotic and biotic filters in influencing diversity, or quantify the response of focal taxa to management, we must decide among many different methods of evaluating rangeland biodiversity. Biodiversity can be measured in a myriad of ways, depending on one's goals, and each method categorizes the value of communities differently. The simplest metric, species richness, is generated by counting the number of species within a site (Magurran 1988). This measure of diversity treats all species equally, regardless of their abundance, conservation needs, functional traits, relative abundance, or evenness, with respect to other species (Krebs 1999). Various diversity indices, such as the Simpson (1949) and Shannon (1948) indices, factor richness and evenness into a composite measure of site-level diversity (Buckland et al. 2005). In addition to types of diversity metrics, diversity can be viewed at multiple spatiotemporal scales. *Alpha diversity* quantifies species richness at a particular site and is likely the most familiar diversity metric

for ecologists (Sepkoski 1988). **Beta diversity** represents the differences in community composition between sites (also called “species turnover”, Sepkoski 1988), and **gamma diversity** summarizes diversity in a region and encompasses aspects of both alpha and beta diversity (Angeler and Drakare 2013).

Though the alpha diversity metric is commonly used to study biodiversity declines, doing so may neglect important components of biodiversity. For example, despite the low species richness in an advanced closed-canopy state, woody encroachment in rangelands often raises the site-level species richness of birds at low- to moderate levels of tree cover due to the addition of generalists and non-grassland species (Sirami et al. 2009; Andersen and Steidl 2019). From the perspective of alpha diversity, increasing woody cover in grasslands may enhance local biodiversity. However, if woody encroachment displaces some grassland species and replaces them with species more tolerant of woody vegetation over large scales, grassland specialists may become rare or absent and communities may become homogenized, which would reduce beta and gamma diversity. This highlights the importance of accounting for the level of specialization that a given species has on rangeland habitat: obligate grassland species require grasslands for most or all of their life history, whereas **facultative** species may use grasslands but are more generalist in their habitat preferences (Vickery et al. 1999). The importance of obligate versus facultative species becomes apparent when considering beta and gamma diversity in this example: the displacement of grassland specialists reduces regional diversity even while enhancing site-level species richness (Andersen and Steidl 2019). As climatic and land-use changes place new and varied extinction pressures on rangeland biota, a focus on regional and landscape-level biodiversity metrics (beta or gamma diversity) becomes more important so that the homogenization of biotic communities across large scales through the replacement of specialist species by generalists can be avoided.

Collecting data to measure biodiversity of just one taxa (e.g., birds, insects, mammals) can be time consuming, with multi-taxa surveys requiring even more time and effort. When possible, multi-species and multi-taxa surveys are desirable, but in some cases surveying for one or a few species can provide a surprising amount of information. Information about **umbrella species** is often a good indicator of the presence of other associated taxa. Species like sage-grouse and northern bobwhite (*Colinus virginianus*) require relatively large contiguous tracts of habitat, and often the presence of these species is correlated with that of many other grassland birds (Crosby et al. 2015; Carlisle et al. 2018). As such, protecting habitat of these umbrella species may also benefit a number of other species (often termed “background species”). Despite the fact that protections for umbrella species may benefit other species using the same habitat, researchers and managers should be cognizant that very specific habitat requirements of other target species may be overlooked, as sometimes these umbrellas can have unexpected “holes”. For example, umbrella reserves focusing on greater sage-grouse did not outperform randomly generated protected areas at providing habitat for 40 of 52 species considered (Carlisle et al. 2018). Broad area protections for sage-grouse failed to preserve habitat for species with specific requirements and species that are not associated with the larger habitat type (sagebrush) at fine spatial scales, such as the Wyoming pocket gopher (*Thomomys*

*clusius*; Carlisle et al. 2018). Consideration not only of spatial overlap but also niche overlap (e.g., similar nesting substrate; Duchardt et al. 2023b) will help managers in determining appropriate management for umbrella and background species.

Many evaluations of biodiversity use taxonomic groupings as the units of assessment; however, a simple tabulation of species in an environment ignores unique species identities and traits, and may not accurately quantify the level of ecosystem services and functions provided. **Functional traits**, which are physical characteristics of an organism with links to ecosystem processes and services (de Bello et al. 2010), can be used by scientists to quantify the effects of management on biodiversity and the ability of a landscape to provide ecosystem services (Garnier and Navas 2012; Keddy and Laughlin 2022). For example, bee (*Anthophila* spp.) researchers have used functional traits such as diet specificity and tongue length, sociality, body size, and nesting preferences to investigate the effects of cheatgrass invasion and livestock grazing on bee diversity (Thapa-Magar et al. 2020). Functional dispersion (i.e., variability in functional traits in a suite of biota) may be used as a biodiversity index instead of species richness or evenness due to asymmetrical taxonomic representation in the bee community; functional traits thus capture biodiversity in a way that is more directly relatable to provisioning ecosystem services and mechanistic drivers of diversity loss (Thapa-Magar et al. 2020). Researchers in forested systems have recently shown that structural diversity better predicts primary productivity than species diversity, making it a useful tool for inventorying ecological services and functioning (LaRue et al. 2019). Whether this relationship holds in rangelands is an open and promising research question. Despite the push towards using functional traits to measure diversity, these methods should be seen as companions to species identities. Above all, it is important to consider the purpose of categorizing diversity, and choosing the best classification method for the job.

## 8.4 Managing Rangelands for Biodiversity

### 8.4.1 Brief History

Conservation and management of rangelands began in the late 1800s and early 1900s in response to overexploitation of these resources. Initially, conserving soil and plant communities (especially in areas affected by the Dust Bowl) was the primary goal of rangeland management with more of a “habitat” focus than conservation of biodiversity. The Society for Range Management was founded in 1948 with the guiding principle of proper distribution of grazing animals to prevent negative impacts of overstocking and to determine the proper **carrying capacity** (Holecheck et al. 2004). The focus on even animal distribution and moderate use was successful at minimizing soil loss and degradation, but it largely ignored wildlife in rangeland systems and some even viewed managing for wildlife as antithetical to livestock production (Stoddart and Smith 1943; Sampson 1952; Fuhlendorf and Brown 2016). It was not until the

latter half of the twentieth century that grazing and conservation began to be viewed as compatible (Bakker and Londo 1998), but the intricacies of grazing management have still led to broad assessments that often label livestock grazing as bad for wildlife and biodiversity more generally (Fuhlendorf et al. 2012; Dettenmaier et al. 2017). Even as perspectives shift, much of grazing management still focuses on uniform grazing practices, which limits biodiversity and favors generalist species that can utilize areas that are moderately disturbed and have vegetation structure that reflects these practices (Fuhlendorf et al. 2006; Hovick et al. 2015; Duchardt et al. 2016).

Simultaneous to efforts being made to change grazing practices in the US, game management and consideration for an ecosystems approach to conservation was beginning to gain momentum (Leopold 1933). Eventually, this sportsman-guided movement led to the Pittman-Robertson Federal Aid in Wildlife Restoration Act, which has become one of the most instrumental pieces of legislation for the conservation of biodiversity. This act utilizes an 11% excise tax on all hunting weapons and ammunition. The resulting conservation funds are collected by the federal government and distributed to the states based on the number of hunting licenses sold, human population, and land area (Burger et al. 2006). While initially created with game species in mind, this act has also benefitted non-game species and biodiversity broadly across North American ecosystems, largely via the umbrella species concept as discussed above.

Most recently, rangeland management has been undergoing a paradigm shift, moving away from the early ideas of uniform distribution and moderate disturbance to a more nuanced approach focused on the conservation of disturbance processes. By restoring disturbance processes such as fire, grazing, and their interaction, complex patterns of vegetation structure are generated that can provide greater resources for the conservation of biodiversity (Fuhlendorf et al. 2012). However, many challenges still exist when attempting to unify profitable livestock production with biodiversity conservation (Samson et al. 2004). To describe these multi-objective management scenarios, Polasky et al. (2005) introduced the concept of '*working landscapes*'—rangelands simultaneously managed for livestock production and conservation—with the goal of achieving multiple stakeholder objectives on rangelands. This view of working landscapes has become central to biodiversity conservation on both public and private rangelands.

Many of the Great Plains states have  $\geq 90\%$  private ownership (NRCS 2021) with a focus on agricultural production, and while western rangeland occurs largely on public lands (managed by the U.S. Forest Service or Bureau of Land Management in the U.S., or by province-specific governments in Canada), even these are managed for “multiple uses” (including livestock grazing by permittees). In Mexico, though rangelands are largely composed of private parcels and communal lands, government efforts and collaborations with non-profits are also seeking to manage these rangelands to simultaneously benefit livestock and wildlife (PACP-Ch 2011; Villareal et al. 2019). While land ownership may vary, the paradigm that these landscapes serve the dual purposes of supporting livestock and wildlife is now shaping rangeland management across North America (NRCS 2021).



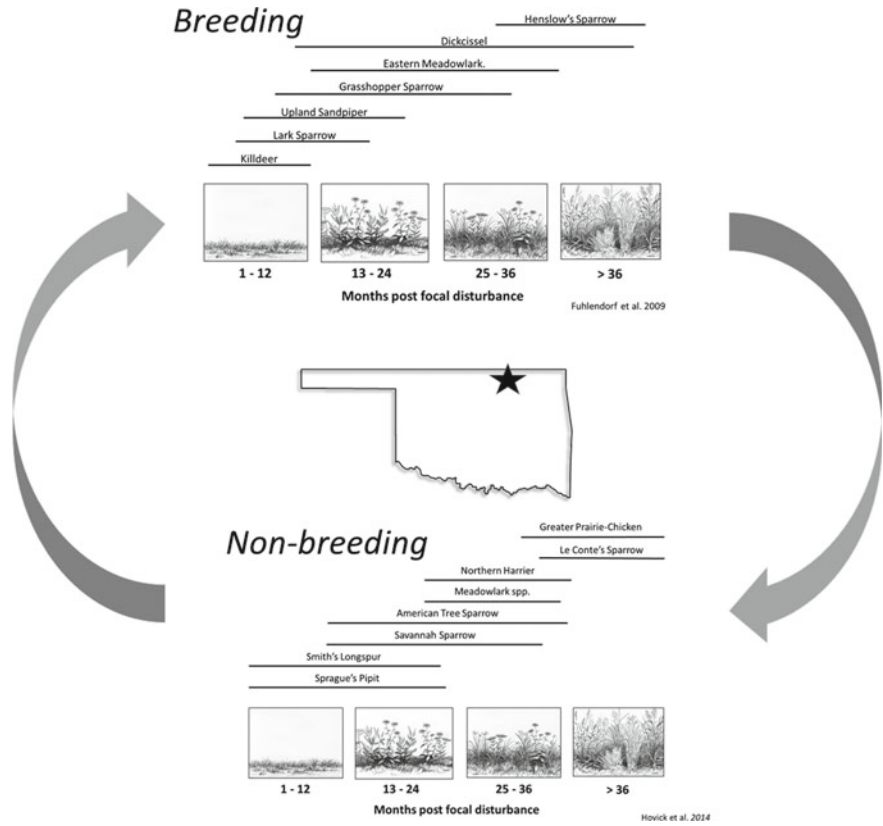
### 8.4.2 *Shifting Paradigms*

Modern approaches of landscape ecology and adaptive management suggest that embracing variability is important for promoting biodiversity and multi-functionality in rangeland working landscapes (Fuhlendorf and Brown 2016). However, mismanagement and overstocking of rangelands during the early twentieth century resulted in a focus on moderate and homogenous disturbance in rangelands that was largely detrimental to biodiversity conservation (Holechek et al 2004; Fuhlendorf et al. 2012). Such uniformity was achieved through techniques such as cross fencing to reduce pasture size, increasing livestock density, adding watering facilities to improve uniformity of use, and implementing supplemental feeding (Vallentine 1990; Bailey et al. 2008). Moreover, many rangeland managers adopted rotational grazing (see Chap. 4), with the goals of (1) improving plant species composition or productivity by allowing a rest period during the growing season, (2) reducing animal selectivity by increasing stock density, and (3) ensuring uniform animal distribution through water location and fencing (Savory 1978 but see Briske et al. 2008). Rotational systems have been regularly modified in attempts to attain livestock production and forage goals (Vallentine 1990) but all emphasize uniformity of livestock utilization with minimal thought given to biodiversity (Savory 1978; di Virgilio 2019). There are many factors (e.g., livestock density, duration of grazing period, precipitation) that can influence the impacts that rotational grazing has on rangeland biodiversity, but in general, the consequences have been negative for wildlife and livestock productivity alike (Briske et al. 2008; di Virgilio et al. 2019). Although management that achieves uniform grazing distribution and moderate forage utilization can benefit soil from erosion, protect water quality, and provide habitat for some generalist wildlife species, rotational management may not meet the objectives of an ever-diversifying pool of stakeholders, such as providing habitat requirements for organisms that rely on vegetation characteristics that result from highly disturbed (e.g., heavily grazed or burned) or undisturbed rangelands (Fuhlendorf et al. 2012).

Scientific research on rangelands has followed similar trends as agricultural research, in which the simplification and reduction of complex systems into homogenous units for the benefit of simplified analyses and understanding has been a goal (Fuhlendorf and Brown 2016). The focus has been on controlling variability rather than embracing or promoting inherent and imposed heterogeneity in rangelands that can benefit biodiversity (Fuhlendorf et al. 2017). However, a growing body of research suggests that vegetation structural heterogeneity enhances biodiversity in working landscapes (Benton et al. 2003; Fuhlendorf et al. 2012; Hovick et al. 2014b, 2015), and these findings support the earlier theoretical underpinnings of the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961). As further evidence, a meta-analysis of the relationship between animal species diversity and vegetation

heterogeneity found that over 80% of all studies surveyed found a positive relationship between heterogeneity in vegetation and faunal diversity (Tews et al. 2004). Therefore, management focused on conserving natural disturbance processes such as grazing and fire can create patterns of complex vegetation structure and composition that promote biodiversity (Tews et al. 2004; Fuhlendorf et al. 2012).

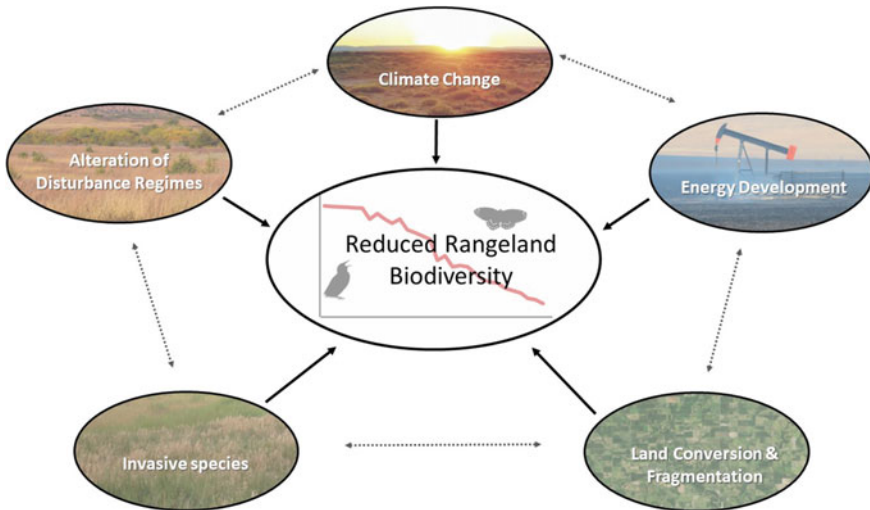
Benefits for biodiversity from managing for heterogeneity can be exemplified by the responses of grassland birds (see Chap. 12). Grassland birds evolved with dynamic disturbances, which created spatially and temporally distinct patterns in vegetation structure, sometimes referred to as a shifting grassland mosaic (Fuhlendorf and Engle 2001; Askins et al. 2007). Because of this, grassland bird species have very specific preferences in terms of breeding habitat structures (Cody 1985a, b). Efforts to conserve grassland bird populations have begun to focus on the maintenance or restoration of these spatiotemporal patterns to create heterogeneous vegetation structure that is beneficial to the suite of grassland bird species (Walk and Warner 2000; Fuhlendorf et al. 2006). Spatial heterogeneity of vegetation structure at appropriate scales (i.e., patches at the territory scale) provides greater breadth of niches and increases the variety of grassland bird communities that can occur across the landscape compared to traditional approaches that create minimal structural diversity (i.e., homogeneity; Fuhlendorf et al. 2006; Hovick et al. 2015). Moreover, interacting fire and grazing that promotes vegetation heterogeneity may also be beneficial for over-wintering, non-breeding birds (Hovick et al. 2014b; Fig. 8.5), and migrating grasslands birds (Hovick et al. 2017a, b). While the importance of disturbance regimes has received the greatest support in tallgrass prairie, evidence that mosaics of vegetation structure with differing disturbance histories and sources generates greater gamma diversity in birds has also been supported in northern mixed grass prairie (Duquette et al. 2023), southern sand-shinnery rangelands (Londe et al. 2021), shortgrass prairie (Skagen et al. 2018), and at the ecotone between the Great Plains and sagebrush steppe (Duchardt et al. 2018). Different sources of disturbance may be at play (native versus domestic herbivores, fire, burrowing rodents) and the proportion of disturbed and undisturbed landscapes may vary across North American rangelands, but the role of disturbance in creating a shifting structural mosaic of vegetation at appropriate scales seems nearly universal in supporting the conservation of biodiversity, especially rangeland birds. Collectively, this body of evidence is one of the most compelling cases for why the new paradigm of management in grasslands should focus on restoring disturbance processes to promote patterns of vegetation heterogeneity that can help conserve biodiversity (Fuhlendorf et al. 2012).



**Fig. 8.5** The interaction between fire and grazing creates a structural gradient of vegetation over time post-disturbance that influences the diversity of the breeding and non-breeding grassland bird community. Figure adapted from Fuhlendorf et al. (2009) and Hovick et al. (2014a, b)

### 8.5 Threats

Rangeland biodiversity faces a number of threats from emerging sources (Fig. 8.6). Many of these constitute an interaction between anthropogenic and natural drivers, and result in simplified or fragmented landscapes. Climate change, habitat loss/overexploitation, and invasive plants/woody encroachment are three of the main drivers of biodiversity declines in western rangelands, and each affect rangeland communities uniquely (Allred et al. 2015; Kreuter et al. 2016; Stephens et al. 2018).



**Fig. 8.6** Major threats to North American rangeland biodiversity include climate change, energy extraction and development, land fragmentation and conversion to row crop agriculture, invasive species including cheatgrass (*Bromus tectorum*) and eastern redcedar (*Juniperus virginiana*), and alteration of disturbance regimes such as fire suppression in the east or increasing fire severity and frequency in the west. Solid lines indicate direct effects on biodiversity, while dashed lines represent the potential for interactions among threats (e.g., fragmentation facilitates invasive species spread, while some invasive species alter disturbance regimes)

### 8.5.1 Climate Change

Climate change is defined as significant and persistent alterations to the mean or variability of climate regime components such as temperature, precipitation, and wind (Allen et al. 2019). Though climate change can refer to natural variation in trends, recent sharp deviations from long-term patterns are the result of anthropogenic greenhouse gas emissions (Allen et al. 2019). Increases in greenhouse gas concentrations in recent years have a broad range of impacts globally, including alterations to temperature and precipitation regimes, carbon sequestration rates, and photosynthetic capacity (Monzón et al. 2011; Staudinger et al. 2013). These sweeping changes have had broad impacts to species niches. If species cannot adapt, they must either shift their range along climatic gradients or risk extinction (Pecl et al. 2017; Roman-Palacios and Wiens 2020). Though often predictable at broad spatial and temporal scales, the effects of climate change are heterogeneous, even within discrete physiographic regions such as the North American Plains (Motha and Baier 2005).

Climate change has the potential to impact biodiversity on several levels. The widespread and variable shifting of species ranges has the potential to create novel species interactions (Gilman et al. 2010). Range shift theory states that biotic drivers (e.g., competition, predation, etc.) govern species ranges at the trailing edge of their

range, whereas abiotic factors (e.g., precipitation, frost-free days) restrict expansion at the leading edge of a species range (Anderegg and HilleRisLambers 2019). However, more interactions between biotic and abiotic drivers complicate this relationship, and abiotic stressors can predispose species to competitive disadvantage and vice versa (Sirén and Morelli 2020).

Though specific predicted effects of climate change on rangeland biota are lacking, climate change will likely negatively affect sagebrush, a keystone species in western US rangelands. Models of sagebrush cover under climate change scenarios generally predict declines at southern latitudes, with neutral or positive effects of warming temperatures at mid- to high latitudes (Rigge et al. 2021; Zimmer et al. 2021). However, increasing temperatures in sagebrush systems interact with invasive species to increase the risk of wildfire and associated mortality of sagebrush plants (Bishop et al. 2020; Schlaepfer et al. 2021). As such, sagebrush cover may increase in some areas while decreasing in others, with unknown impacts on associated wildlife species. More broadly, climate change may lead to other vegetation compositional shifts, such as between forbs and graminoids (Teyssonneyre et al. 2002) or C3 and C4 grasses (Morgan et al. 2011), which will influence habitat structure for wildlife.

Above we discussed climate as an abiotic filter not only in terms of averages but also as a function of timing and variation in temperature and precipitation. While increases in the mean value of climate variables like temperature and rainfall will be impactful to biodiversity, changes to the variability and intensity of climate weather events will also be impactful. For example, sagebrush sparrow nest survival has been shown to suffer under extreme wet and extreme dry conditions, indicating that future climate regimes with more variability would be detrimental to this species, even if average conditions were to stay the same (Schroeder et al. 2022). Similarly, predicted increases in the frequency and intensity of extreme weather events such as hail, flooding, and tornadoes, are projected to cause more wildlife mortality events (Carver et al. 2017). Inherent in this increased variability of climate is decreased predictability of seasonal events by people and wildlife. When timing of events like last frost, bud burst, and first significant rainfall of the year become more difficult to anticipate or track, this can create trophic mismatches (Post et al. 2008). Demonstrated examples include temporal gaps in flower blooming and pollinator emergence, caterpillar availability and breeding bird behavior, and ungulate migration and forage greenup (Post and Forchhammer 2008; Hindle et al. 2015; Burgess et al. 2018). Due to adaptation to inherently variable conditions, rangeland wildlife may be buffered from phenological mismatch somewhat compared to taxa from other biomes, but the extent to which rangeland taxa exhibit fitness consequences of mismatches is largely an open inquiry. In any case, landscape diversity and heterogeneity has been demonstrated to buffer the negative effects of phenological mismatch by increasing the spatial variability in event timing, further underscoring the consideration of heterogeneity in rangeland wildlife management (Hindle et al. 2015; Ohler et al. 2020).

### 8.5.2 *Habitat Loss and Overexploitation*

Habitat loss, here defined as the removal of lands that previously provided food, water, and cover for wildlife species (National Wildlife Federation) is occurring rapidly in North American rangelands. For example, rates of grassland conversion to crops in the Northern Great Plains are currently analogous to deforestation rates in tropical rainforests in Southeast Asia, Oceania, and South America (Wright and Wimberly 2013). Oil and gas development in North America directly removed an additional 3 million hectares of habitat between 2000 and 2012 (Allred et al. 2015). Past periods of intense row crop conversion in the southern and eastern Great Plains are currently being mirrored in new areas such as the prairie pothole region due to crop improvements, biofuel demand, and increases in commodity prices (Johnson 2013; Hendrickson et al. 2019). In addition to current and previous direct habitat loss, remaining rangelands are fragmented and experiencing declines in biodiversity as a result (Wimberly et al. 2018).

Contemporary cropland conversion often occurs on marginal land by necessity, as highly productive land has largely already been plowed (Lark et al. 2020). However, rangelands with low agricultural potential often serve as habitat for a high diversity of species, resulting in an uneven cost–benefit ratio of conversion (Lark et al. 2020). For example, in a study looking at cropland conversion in the Midwest, the initial stem densities of milkweed (*Asclepias* spp.) were 3.4-times greater on rangeland that was later chosen to be converted to agriculture compared to the average of unconverted land in the area, while high wetland densities in converted lands allowed potential access by twice as many breeding waterfowl pairs as the Midwest natural lands average (Lark et al. 2020). Once converted, these areas produced below average crop yields, suggesting that marginal croplands were often not marginal wildlife habitat before conversion, and that the value of remaining unconverted rangelands as wildlife habitat often exceeds its value as potential cropland.

The effects of grassland conversion to agriculture on biodiversity have been documented in numerous taxa. Steep declines in global avian diversity have been linked to agricultural intensification, including increased use of pesticides and land conversion (Rosenberg et al. 2019). This has also been linked to mortality of insects that grassland birds depend on as a food source (Rosenberg et al. 2019). Conversion to cropland and intensification of agricultural practices have resulted in documented declines in bees, butterflies and moths (*Lepidoptera*), and grasshoppers (*Orthoptera*; Raven and Wagner 2021).

In contrast to agricultural conversion in the central Great Plains, western rangelands are most vulnerable to habitat loss due to energy infrastructure. Western rangelands are key areas for the extraction of oil and natural gas and the development of “green” energy sources such as wind, solar, and biofuels (Kreuter et al. 2016). The infrastructure supporting these energy sources, including roads, pump jacks, pipelines, compressor stations, turbines, solar panels, power lines, and tanker trucks, have the potential to fragment, disturb, and deteriorate rangeland wildlife habitat.

Many rangeland species, such as mule deer, sage grouse, and rangeland songbirds are area-sensitive and experience declines or local extirpations in energy extraction landscapes (Hess and Beck 2012; Northrup et al. 2015; Shaffer and Buhl 2016).

Dissimilar to agricultural production, energy development impacts can partially be mitigated through flexibility in siting criteria. By factoring biodiversity metrics into energy infrastructure placement, developers can optimize tradeoffs between energy production goals and biodiversity conservation (Thomas et al. 2018). Mitigation tools are available that estimate the amount of grasslands and wetlands needed to support breeding pairs of grassland birds and waterfowl displaced by wind, oil, gas, or transportation infrastructure (Shaffer et al. 2019). New technologies allow site planning operations to minimize the surface footprint and fragmentary effect of energy capture activities. For example, horizontal well drilling allows for multidirectional oil and gas exploration from a single well pad, allowing for a smaller surface footprint on the landscape (Thompson et al. 2015). In addition, conservation plans for imperiled rangeland species such as sage- grouse reduce or prohibit the construction of new oil and gas wells during sensitive life stages such as lekking (Patricelli et al. 2013).

Regardless of cause, habitat loss requires a diversity of approaches to mitigate negative impacts. One method to protect rangeland diversity and preserve habitat is by restricting undesirable use. This can be accomplished in various ways, including enrolling in private conservation easements or purchase by private conservation organizations (Cameron et al. 2014). It is important to note that rangeland biodiversity conservation often does not benefit from “full protection”, as complete grazing cessation can have negative biodiversity outcomes (Toombs et al. 2010). That is, protection of rangelands should not necessarily be thought of as the removal of all disturbances. Rather, the preservation of rangeland biodiversity depends on informed, monitored, and responsible use. Whether at the programmatic level or via actions by private landowner, preventing rangeland habitat loss can be achieved through diverse stakeholder input and responsible working lands management.

### 8.5.3 *Invasive Plants*

By altering climate conditions, manipulating natural disturbance regimes, changing land use, and transporting propagules, humans have greatly increased the incidence of invasive plants in rangelands. In many cases, humans have also removed native vegetation from pastureland, replacing it with forage species that are perceived as higher in quality, and associated with greater weight gains in livestock (e.g. Svejcar and Vavra 1985). These homogenous “improved” pastures are typically poorer habitat for wildlife [e.g., Tall fescue (*Festuca arundinacea*), Washburn et al. 2000; Nelson et al.; crested wheatgrass (*Agropyron cristatum*), Rockwell et al. 2021], which is unsurprising given the importance of heterogeneity for rangeland biodiversity discussed above. In many cases these species do not readily spread without direct human assistance or outcompete native flora, and are thus not considered invasive, but some may become invasive in some locations.

Invasive plants are typically characterized as being both non-native and likely to cause environmental, economic, or medical harm (Barney et al. 2013). Invasive plants often proliferate in new systems due to high seeding rates, escape from competitors and pests that regulate them in native systems (Callaway and Aschehoug 2000; Mitchell and Power 2003; Gaskin et al. 2021). These factors often combine to allow invasive plants to achieve high densities in invaded areas, decreasing plant diversity as a result (Rout and Callaway 2009). Though hundreds of invasive species have been described in North American rangelands, here we focus on a few common and impactful examples.

Cheatgrass (*Bromus tectorum*) is a cool-season annual grass that was mostly accidentally introduced to western rangelands in the late 1800s, causing sweeping structural changes and becoming the dominant vegetation in large parts of its introduced range (Knapp 1996). Cheatgrass is uniquely impactful as an invasive species because it has a very different fuel structure from native perennial bunchgrass systems, increasing the size and frequency of fire beyond historic levels (D'antonio and Vitousek 1992). Though certain species seem to benefit from cheatgrass introduction, overall rodent abundance and diversity in cheatgrass-invaded systems decreases at high levels of invasion, likely due to reduced structural heterogeneity and loss of sagebrush cover (Freeman et al. 2014; Holbrook et al. 2016; Kleuver et al. 2019). In a similar fashion, grassland-associated bird species tended to decline in abundance as native perennial bunchgrasses were replaced by cheatgrass (Earnst and Holmes 2012). In that same study, shrubland-associated birds were less sensitive as long as adequate shrub cover remained (Earnst and Holmes 2012), but as discussed above, because cheatgrass facilitates reduced fire return intervals there is evidence that in the long-term cheatgrass also negatively impacts sagebrush birds (Knick et al. 2005). Similar declines have been reported in several sagebrush keystone species, including badger (*Taxidea taxus*, Holbrook et al. 2016) and greater sage grouse (Lockyer et al. 2015).

Many western rangelands are water limited, making riparian corridors both essential and sensitive landscape features. For this reason, the invasion of saltcedar (*Tamarisk* spp.) into western watercourses is viewed as particularly serious. Saltcedar is a salt-tolerant, deep-rooted deciduous shrub capable of forming dense stands along watercourses (DiTomaso et al. 2017). Replacement of native cottonwood/willow (*Populus/Salix*) riparian habitat reduces regional (gamma) avian diversity by displacing unique species (Brand et al. 2008), while effects on lizard and small mammal communities appear to be mixed (Bateman and Ostoja 2012). However, tamarisk is used extensively by the endangered southwestern willow flycatcher (*Empidonax traillii extimus*), possibly complicating control efforts (Owen et al. 2005).

Impacts of invasive species on rangelands including those above, as well as others (e.g., *Lespedeza cuneata*, *Festuca arundinacea*, *Pyrus calleryana*, *Taeniatherum caput-medusae*) could fill a whole book, but these examples highlight the multi-faceted issue. Invasive status on its own does not equate to uniform deleterious impacts to wildlife; there will usually be some 'winners' following invasive plant introduction. However, it is important to consider the traits or the invasive plant and



changes to native systems. When invasive plants displace natives, biodiversity often suffers as a result (Powell et al. 2013).

#### 8.5.4 *Woody Encroachment in Rangelands*

The potential for non-native plant introductions to have negative effects on diversity is easily understood. However, the proliferation of native plants beyond historic levels can be equally deleterious. Though many grasslands have a native and historic shrub or tree component, the extent of woody plant cover in southern and western rangelands has increased due to a variety of factors (Bestelmeyer et al. 2018). Periods of overgrazing, climate change, alterations to fire regimes, and soil erosion have increased woody cover in many rangelands beyond their historical levels (Staver et al. 2011; Bestelmeyer et al. 2018; Archer et al. 2017). Encroachment of woody species into rangelands has a variety of effects from both a livestock-production and ecological standpoint.

Eastern red-cedar and honey mesquite (*Prosopis glandulosa*) are two prominent woody encroaching species with profound effects on the central Great Plains and southwestern rangelands, respectively. Eastern red-cedar spread is thought to be primarily the results of alterations to historic fire return intervals (Ratajczak et al. 2016), and in the absence of fire, grasslands can be converted to closed-canopy woodlands in as little as 40 years (Zhou et al. 2015). Increases in honey mesquite dominance are thought to be due to increased dispersal by cattle and freedom of seedlings from fire mortality (Buffington and Herbel 1965). Once established, woody encroachers have varied and significant impacts on rangeland biodiversity; aside from the direct displacement of grasses by less palatable trees or shrubs, the proliferation of woody cover in rangelands can alter the spatial patterning of nutrients, causing positive feedback mechanisms that promote a state change to low diversity woodland ecosystems, particularly in arid environments (Zhou et al. 2018). In many rangeland systems, the number of encroaching woody species is low, which can have the effect of reducing plant species richness and associated niche diversity (Archer et al. 2017). Though in theory woody encroachment should add to structural complexity and increase diversity, in practice woody encroachment has caused widespread declines in the diversity of herbaceous vegetation through competition for water, light, and nutrients (Van Auken 2009; Ratajczak et al. 2016). Predictably, woody encroachment is broadly detrimental to grassland bird species, while benefitting some shrubland species, especially at low levels of encroachment (Coppedge et al. 2004). Similarly, most sagebrush small mammal species responded negatively to encroachment from upslope woody plants (pinyon-juniper encroachment), with negative effects outweighing those of simultaneous cheatgrass invasion (Hamilton et al. 2019).

Although woody encroachment can have extremely deleterious effects on rangeland biodiversity, it is important that we avoid a black-and-white approach that conducts woody plant removal without regard for historical woody distribution. Indeed, in some landscapes we are seeing the dangers of such a strategy—pinyon

juniper removal to improve greater sage-grouse habitat in the Great Basin has been linked to even steeper declines in the pinyon jay (*Gymnorhinus cyanocephalus*), an obligate species in pinyon-juniper systems currently (as of 2022) being petitioned for federal listing (Boone et al. 2018). In response to this emerging challenge, researchers are now rushing to identify target areas for conifer removal that do not negatively affect the pinyon jay.

In many of these systems, emerging evidence indicates that the reinstatement of historical abiotic and biotic filters may help slow woody spread or allow for a shift back to grasslands; as discussed above, Ratajczak et al. (2016) identified fire intervals that will likely prevent state-shift to woodlands, and other researchers have noted that prairie dogs reduce and sometimes eliminate mesquite from their colonies (Ponce-Guevara et al. 2016; Hale et al. 2020). Reinstatement of historical filters will also help to avoid removal of woody vegetation where it historically occurred, helping managers to avoid pitfalls such as those previously mentioned declines in pinyon jays.

## 8.6 Looking Ahead

Worldwide biodiversity is in decline and rangelands make up a large proportion of landcover (30–50%; Olson et al. 2001a, b; Briske 2012) across the globe (WWF 2018). As such, rangelands merit efforts towards biodiversity conservation, ensuring future provisioning of ecosystem services and maintenance of ecosystem functions. In rangelands, much of the variation in biodiversity is driven by climatic gradients and interacting disturbance processes. Managing for historic regimes that promote heterogeneity is paramount. North American rangelands are complex systems with large amounts of variation in species composition and richness, and this variation should be included in methods to evaluate diversity to ensure we can track changes in biodiversity trends. Despite the complexities and variation in North American rangelands, they all face a suite of threats including land conversion for energy development and agriculture, woody plant encroachment and plant invasions resulting from alterations in disturbance regimes, and climate change. To address these broad issues, research is shifting away from small, site-scale questions to larger gradient landscape-scale questions, but these findings need to be made available to managers in a way that is useful and actionable. Finally, if biodiversity conservation in rangelands is to be successful, land managers need to be adaptive and focus on the temporal and spatial scales of disturbance processes that resemble historic disturbance regimes to benefit native wildlife. These issues and a more in-depth discussion of the ecology and management of rangeland wildlife taxa are presented in the chapters that follow.

## Glossary of Terms BOX 8.7

**Abiotic filters**<sup>1,2</sup> Non-living components of community assembly, including precipitation, temperature, topography, disturbances (e.g., fire or severe weather), and soil structure.

**Biodiversity**<sup>3</sup> The variety of life at each ecological scale from the genome to the biome.

**Biodiversity hotspots**<sup>4</sup> Areas of diversity with particularly high species richness. In terms of conservation, these areas should be evaluated and ranked based on some level of uniqueness and endemism of the species or land features present.

**Biotic filters**<sup>5,6</sup> Living components of an ecosystem that drives community assembly, including herbivory, bioturbation, and species interactions like competition or predation.

**Carrying capacity**<sup>7</sup> Average number of livestock and/or wildlife that may be sustained on a management unit compatible with management objectives for the unit.

**Disturbance**<sup>8,9,10</sup> A temporary change to an ecological system that alters the ecosystem. Examples of disturbances in rangelands include fire, herbivory, bioturbation, and severe weather events. Disturbances may be natural/historical (e.g., fire and some herbivory) or novel and human-caused (e.g., energy extraction).

**Disturbance regime**<sup>11,12,13</sup> The spatial and temporal characteristics of events that shape a system over time. For example, the characteristics such as frequency, intensity, and seasonality that describe fire or grazing over longer time intervals such as decades or millennia.

**Driver**<sup>14</sup> Any natural or human-induced factor that directly or indirectly causes a change in an ecosystem.

**Ecosystem engineer**<sup>15</sup> A species that mechanically changes an ecological system in a way that influences other species. Examples of ecosystem engineers in rangelands include prairie dogs and bison.

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<sup>1</sup> Bedell (1998)

<sup>2</sup> Keddy and Laughlin (2022)

<sup>3</sup> Morin (2011)

<sup>4</sup> Myers (1988)

<sup>5</sup> Bedell (1998)

<sup>6</sup> Keddy and Laughlin (2022)

<sup>7</sup> Bedell (1998)

<sup>8</sup> Morin (2011)

<sup>9</sup> Briske (2012)

<sup>10</sup> Caro (2010)

<sup>11</sup> Morin (2011)

<sup>12</sup> Briske (2012)

<sup>13</sup> Caro (2010)

<sup>14</sup> Morin (2011)

<sup>15</sup> Morin (2011)

**Ecosystem function**<sup>16</sup> These are biological, geochemical, and physical processes that take place within an ecosystem. Examples may include soil retention, climate regulation, or nutrient cycling.

**Ecosystem services**<sup>17,18</sup> The components of nature that are directly consumed or enjoyed by humans and increase well-being. These are categorized into four groups: (1) provisioning (2) regulating (3) supporting and (4) cultural.

**Evenness**<sup>19</sup> This is generally reported as part of a diversity index (i.e., Shannon or Simpson, or separately as Pielou's evenness), and it quantifies the numerical value of each species represented in a system. Systems with higher evenness have similar representation of individuals, whereas systems with lower evenness have individuals with greatly varying abundances.

**Facultative**<sup>20</sup> Able to persist in multiple environmental conditions or habitats, but often with preference for one type.

**Fine fuels**<sup>21</sup> The herbaceous plants available for combustion in a system.

**Functional trait**<sup>22,23</sup> Component of an organism's phenotype that determines its effect on ecosystem processes and its response to environmental factors (de Bello et al. 2010). Examples of types of functional traits in rangeland wildlife include body size or sociality of pollinators, structural habitat preferences or diet requirements (e.g., granivores, insectivores, carnivores) of birds, or gut morphology of ungulates.

**Fundamental niche**<sup>24</sup> The full range of environmental conditions and resources an organism can possibly occupy and use in the absence of competition and geographic barriers.

**Heterogeneity**<sup>25,26</sup> Variability in a given trait at a specified scale. For rangeland wildlife, heterogeneity in structure of vegetation is a critical driver of species diversity.

**Keystone species**<sup>27,28,29</sup> A species with an outsized role in its community relative to biomass or population size. The removal of a keystone species typically results in major cascading changes in species abundance and community structure. Examples of keystone species in rangelands include bison, prairie dogs, top predators,

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<sup>16</sup> Morin (2011)

<sup>17</sup> Morin (2011)

<sup>18</sup> Briske (2012)

<sup>19</sup> Morin (2011)

<sup>20</sup> Morin (2011)

<sup>21</sup> Briske (2012)

<sup>22</sup> Keddy and Laughlin (2022)

<sup>23</sup> Morin (2011)

<sup>24</sup> Morin (2011)

<sup>25</sup> Morin (2011)

<sup>26</sup> Briske (2012)

<sup>27</sup> Morin (2011)

<sup>28</sup> Paine (1969)

<sup>29</sup> Caro (2010)

and some pollinators. Note this is different than the “Key species” described by Bedell (1998).

**Levels of diversity (Alpha, Beta, and Gamma)**<sup>30</sup> Alpha diversity, or site-level diversity, refers to any diversity metric calculated at the scale of a single site, whereas Gamma diversity refers to total diversity among all sites in a given study system and is often used to describe landscape-scale diversity. Beta diversity essentially refers to species turnover among sites and can be used as a metric of the community uniqueness of sites or strata within a landscape.

**Mutualism**<sup>31</sup> A type of species interaction wherein both species benefit from one another. Plant-pollinator relationships are an example of a mutualism.

**Obligate**<sup>32</sup> restricted to a specific environmental condition or habitat.

**Pyrodiversity**<sup>33</sup> The variation in the timing, spatial extent, and intensity of fire regimes.

**Pyric herbivory**<sup>34</sup> The interaction of fire and grazing where fire determines where grazing occurs and grazing patterns determine the extent and intensity of future fires.

**Realized niche**<sup>35</sup> The environment that a species occupies and lives in. This is the result of barriers and competition that constrain an organism into an area where they have access to resources to live and reproduce.

**Scale**<sup>36</sup> The dimensions used to study a phenomenon, often referring to temporal (days, weeks, years, centuries) or spatial (nest site, home range, landscape, region).

**Site Fidelity (also called “philopatry” or “site tenacity”)**<sup>37</sup> The tendency for an animal to return to the same place, generally in reference to breeding locations. For example, the tendency for some migrating bird species to return to the same location each year for nesting activities.

**Umbrella species**<sup>38</sup> A species that typically has specific and large-scale habitat requirements, where management for that species has the potential to benefit a suite of other species utilizing the same habitat resources. Examples of umbrella species in rangeland include *Galliformes* such as sage-grouse, and prairie chickens and sharp-tailed grouse (*Tympanuchus* spp.).

**Working landscapes**<sup>39</sup> These are rangelands simultaneously managed for multiple stakeholder objectives, including livestock production and conservation.

**Resources:** 8. Turner and Gardner (2001)

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<sup>30</sup> Morin (2011)

<sup>31</sup> Morin (2011)

<sup>32</sup> Morin (2011)

<sup>33</sup> Briske (2012)

<sup>34</sup> Briske (2012)

<sup>35</sup> Morin (2011)

<sup>36</sup> Morin (2011)

<sup>37</sup> Cody (1985a, b)

<sup>38</sup> Caro (2010)

<sup>39</sup> Polasky et al. (2005)

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