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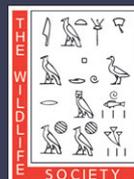
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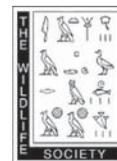


Invasive Plants and Wildlife Habitat



Conservation Planning in an Era of Change





Invasive Plants and Wildlife Habitat

Effects of Plant Invasions on Wildlife in Desert Grasslands

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ABSTRACT Like all grasslands across North America, the distribution of desert grasslands has been reduced markedly, and remnants have been altered extensively by humans. In Arizona, New Mexico, Texas, USA, and in Mexico, desert grasslands have been invaded by dozens of non-native plants, especially perennial grasses that evolved in arid systems with similar climate and disturbance regimes. In desert grasslands invaded by non-native plants, biomass, richness, and diversity of native plants typically decrease, whereas plant density, biomass, and litter typically increase. These changes in composition and structure of the plant community affect animals that inhabit grassland ecosystems, with the direction and magnitude of effects reflecting the resource needs of each species, the degree of plant invasion, and the contrast in structure between invading and native plants. When non-native plants present similar structural cues but provide different levels of resources than native plants, cues that trigger habitat selection by animals may be decoupled from the resources linked evolutionarily to that cue, creating the potential for an ecological trap. Plant invasions also influence the ecological drivers that maintain grasslands in an open condition, which will alter the long-term dynamics of plant and animal populations. Specifically, by increasing fuel load and continuity, fires in invaded grasslands increase in frequency and intensity relative to those in native grasslands. Although eradication is unlikely once a non-native plant has naturalized, retaining patches of native vegetation within a matrix of non-native plants may provide a strategy to reduce effects of plant invasions on wildlife in grasslands. © 2013 The Wildlife Society.

KEY WORDS desert grasslands, exotic species, grasslands, non-native species, semi-desert grasslands, species invasions.

Non-native grasses have invaded or been cultivated in nearly every grassland, shrubland, and savanna ecosystem in the world (D'Antonio and Vitousek 1992, Lonsdale 1994, Pivello et al. 1999, Richardson and van Wilgen 2004). Invasions by non-native grasses into these ecosystems can be especially consequential because the dominant native plants can be replaced entirely by non-native plants, which not only change composition and structure of the plant community, but also change rates of ecosystem processes relative to the native plant community, including primary production, decomposition, nutrient cycling, and carbon storage (e.g., Vitousek and Walker 1989). These changes in response to invasions by non-native grasses can interact to alter the primary ecological driver in grassland ecosystems—fire—that governs spatial and temporal patterns of biodiversity in these ecosystems (Wright and Bailey 1982, McPherson 1995, Steidl and Litt 2009).

Grasslands are among the most endangered ecosystems in North America, with most having been reduced to small remnants of their original distribution (Noss et al. 1995). For

example, <4% of the original distribution of tallgrass prairie remains intact (Samson and Knopf 1994). In the southwestern United States and Mexico, desert grasslands have been subjected to many of the same anthropogenic pressures that have affected the more widely distributed prairie grasslands of the Great Plains, which have been destroyed more rapidly and more completely than any other ecosystem in North America (Samson and Knopf 1994). Consequently, distribution and abundance of organisms that inhabit these ecosystems also have decreased alarmingly (e.g., Samson and Knopf 1994, Sauer et al. 2011). Because millions of hectares of grassland ecosystems have been invaded by dozens of species of non-native plants (Bahre 1995, McLaughlin 2002), the magnitude of the problem and breadth of potential impacts on organisms that inhabit grasslands is immense.

To develop effective yet practical conservation strategies to reduce adverse effects of invasions by non-native plants on native organisms, we must first understand the consequences of plant invasions on patterns and processes that affect biodiversity in grassland ecosystems. Our goal is to summarize research on effects of invasions by non-native plants on birds, mammals, reptiles, and arthropods that inhabit desert grasslands of southwestern North America, and to synthesize patterns resulting from these studies into a

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general framework that describes interactions between non-native plants and native animals in grassland ecosystems.

DESERT GRASSLANDS

Desert grasslands in southwestern North America are dominated by an array of perennial and annual grasses, and include light-to-moderate components of shrubs, stem-and-leaf succulents, cacti, and forbs, which are seasonally abundant (Brown 1994). Desert grasslands are physiognomically intermediate to desert scrub at lower elevations and Madrean evergreen woodlands, chaparral, or plains grasslands at higher elevations (Brown 1994). In North America, the distribution of desert grasslands is extensive but discontinuous, occurring between mountains and valleys at elevations from approximately 1,000–1,700 m, which reflects the basin-and-range topography that dominates much of the region (Brown 1994, McClaran 1995). Desert grasslands are distributed across southeastern Arizona, southern New Mexico, western Texas, and northern Mexico, where they extend southward until they transition into thornscrub (Brown 1994; Fig. 1). Given their proximity to and geographic and floristic overlap with Chihuahuan, Sonoran, and Mojave deserts, these plant communities often are described as semidesert grasslands (Brown 1994).

Desert grasslands are the most arid and least productive of all North American grasslands, with mean annual temperatures ranging between 13° C and 16° C and receiving only 200–400 mm of precipitation, which falls typically in a bimodal pattern of intense but infrequent monsoon rains during summer, and lighter but more frequent rains during winter (Brown 1994, Van Auken 2000). Compared with plains grasslands, which are true prairies, grasses in desert grasslands are shorter and less dense, woody shrubs and succulents are more common, and many plants have subtropical affinities (Whitford 1998). Nearly all grasses in desert grasslands employ a C₄ photosynthetic pathway that is more efficient in arid environments with high growing-season temperatures (McClaran 1995). Because C₄



Figure 1. Approximate distribution of desert grasslands in North America.

grasses are most efficient at low CO₂ concentrations, the distribution of these grasses is expected to change in response to increasing CO₂ concentrations predicted with climate change (Ehleringer et al. 1997).

During the past 150 years, anthropogenic activities have been the dominant forces affecting grassland plant communities in North America, especially wholesale conversion of grasslands to different land-use types (Bahre 1995). The overwhelming majority of North America grasslands have been converted to agriculture (Knopf 1994), a process that is accelerating throughout central Mexico (Macias-Duarte et al. 2011). Even where lands have not been converted in type, vegetation of desert grasslands has changed markedly due to the increase in distribution and density of native woody plants and invasion by non-native grasses (Archer 1989, Van Devender et al. 1997, Van Auken 2000). Only through intensive conservation and management efforts have some grassland remnants remained in relatively natural condition.

Desert grasslands often are labeled as rangelands to reflect the dominant land use since European settlement (Finch 2004). Although light grazing by livestock probably has only minor effects on structure and function of grassland ecosystems, intensive grazing can affect plants and animals that inhabit these ecosystems adversely by fostering growth of non-native plants that can reduce growth and richness of native plants in some circumstances (Kimball and Schiffman 2003, but see Milchunas et al. 1989) and by fostering increases in density and distribution of native woody shrubs (Van Auken 2000). Although many forces have contributed to encroachment by woody species, the dominant force has been intensive grazing by livestock, which removes fine fuels that carry fires that restrict establishment of woody species (Van Auken 2000). Fires are less frequent and of lower severity in areas grazed by livestock, allowing woody plants to reach sizes where they are less vulnerable to mortality from fire (McPherson 1995). Additionally, replacing large native herbivores once common in grassland ecosystems (including bison [*Bison bison*], pronghorn [*Antilocapra americana*], and prairie dogs [*Cynomys* spp.]) with cattle and sheep, has increased grazing pressure relative to historical rates and facilitated woody encroachment (Knopf 1994, Vickery et al. 1999, Van Auken 2000). Invasion of native woody plants into grasslands has affected the composition of animal communities that inhabit these areas (Samson and Knopf 1994, Lloyd et al. 1998, Vickery et al. 1999).

Management to increase production of livestock or to rehabilitate desert grasslands that were badly degraded from overgrazing and drought also have affected native plants and animals that inhabit desert grasslands (Finch 2005). Beginning in the 1930s, several species of non-native grasses were introduced to help achieve these goals; these species and others have invaded these grasslands, including Lehmann lovegrass (*Eragrostis lehmanniana*), Boer lovegrass (*E. curvula*), buffelgrass (*Cenchrus ciliaris* syn. *Pennisetum ciliare*), red brome (*Bromus madritensis*), filaree (*Erodium cicutarium*), Bermuda grass (*Cynodon dactylon*), Johnson grass (*Sorghum*

halepense), fountaingrass (*Cenchrus setaceus* syn. *Pennisetum setaceum*), and many others (Van Devender et al. 1997, Finch 2004, <http://www.invasivespeciesinfo.gov/>). We focus on Lehmann lovegrass and buffelgrass, both of which were introduced, have become widely distributed, and are a principal conservation and management concern across much of the southwestern United States and northern Mexico.

Lehmann lovegrass is a perennial bunchgrass native to southern Africa that was planted in Arizona, New Mexico, and Texas in the 1930s, and has since increased steadily in distribution and dominance (Cable 1971, Cox and Ruyle 1986, Anable et al. 1992, Schussman et al. 2006). By 1988, its distribution had increased from approximately 700–1,400 km² (Cox and Ruyle 1986), with potential for the distribution to reach 72,000 km² (Schussman et al. 2006).

Buffelgrass is a perennial bunchgrass native to Africa, India, and western Asia that was first established in Texas and Arizona in the 1940s and in Sonora, Mexico, in the 1970s (Marshall et al. 2012). Given its ability to withstand drought, buffelgrass was planted on >40,000 km² of Texas farmland and >4,000 km² of native desertscrub and thornscrub in Sonora, Mexico, where its establishment as a pasture crop continues (Arriaga et al. 2004, Franklin et al. 2006, Marshall et al. 2012). Seed from pastures in Mexico has provided the source for buffelgrass to naturalize across thousands of square kilometers of desert grasslands and true deserts in the southwestern United States (Marshall et al. 2012).

Buffelgrass is a threat to not only grasslands, but also to a variety of desert plant communities, which only rarely have sufficient fine fuel to carry fire (McLaughlin and Bowers 1982, Van Devender et al. 1997). When invaded by buffelgrass and other non-native grasses, however, areas of desertscrub and thornshrub are likely to burn more frequently and more intensely, which threatens iconic desert plants, such as saguaro cactus (*Carnegiea gigantea*), that are not adapted to fire (Marshall et al. 2012, Olsson et al. 2012).

EFFECTS OF NON-NATIVE GRASSES ON PLANTS IN DESERT GRASSLANDS

Effects of invasions on native plant communities vary in magnitude with the degree of invasion and the particular non-native plant species, although most invasions change structural and floristic complexity of the plant community relative to the native community. In desert grasslands of Arizona, for example, biomass, richness, and diversity of native plants decreased as dominance of Lehmann lovegrass increased (Geiger 2006); similarly, richness and cover of herbaceous plants and cover of shrubs decreased in areas invaded by non-native lovegrasses (Bock et al. 1986). In grasslands of southern Texas, canopy cover, species richness, and density of native forbs were lower on areas with buffelgrass and Lehmann lovegrass relative to areas dominated by native grasses (Flanders et al. 2006, Sands et al. 2009) and species richness of native plants and cover of forbs were lower in areas dominated by Kleberg bluestem (*Dichanthium annulatum*; a perennial bunchgrass native to

Africa, Asia, and Papua New Guinea) relative to areas dominated by native plants (Cord 2011). In Sonoran desertscrub, species richness, diversity, and cover of native shrubs, forbs, grasses, and succulents decreased as cover of buffelgrass increased (Olsson et al. 2012). In Sonora, pastures planted with buffelgrass had species richness of plants reduced by approximately 50% at local and regional scales, and cover of trees and shrubs reduced by 78% (Franklin and Molina-Freaner 2010).

Non-native grasses typically produce more litter and many times more biomass than the native grasses they replace (Cox et al. 1990, Geiger 2006, Esque et al. 2007). By increasing plant density and biomass relative to native plants, non-native plants not only alter composition and structure of the plant community, but also affect the ecological drivers that are integral to maintaining an open grassland condition (McPherson 1995). As plant densities and biomass increase, changes in fuel loads, fuel continuity, and soil moisture and temperature increase the frequency and intensity of fires in invaded areas relative to stands of native grasses (Brooks et al. 2004). Because most grass species that have invaded desert grasslands are adapted to fire, including Lehmann lovegrass and buffelgrass, germination rates, and dominance of non-native grasses sometimes increase after fire (Cable 1965, Ruyle et al. 1988, Sumrall et al. 1991, Bock and Bock 1992), which might facilitate a positive feedback grass-fire cycle (Anable et al. 1992, D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). These invasion-driven changes in plant composition and structure, and in the disturbance regime, affect the ways in which invaded areas function as habitat for organisms at higher trophic levels (Steidl and Litt 2009, Litt and Steidl 2011).

EFFECTS OF NON-NATIVE GRASSES ON ANIMALS IN DESERT GRASSLANDS

Structural characteristics of vegetation are among the most important features that determine which areas function as habitat for terrestrial vertebrates (Price and Waser 1984). The debate as to whether structure or floristic identity is more important in shaping animal communities has been ongoing for decades (e.g., Rotenberry 1985), although it seems plausible that both factors play a role in some circumstances (MacNally 1990). Because invasions by non-native plants alter both structure and composition of grassland plant communities, assessing effects of plant invasions on animal communities can provide insight into the relative roles of these factors in governing community structure.

Animals often rely on vegetation-based structural cues as an indicator of resource availability, especially for species that must decide where to settle before the level of resources they require becomes apparent. For example, some birds use leaf cover, flower cover, or leaf damage as cues to current or future abundance of insect prey (Heinrich and Collins 1983, Marshall and Cooper 2004, McGrath et al. 2009). Behaviors that trigger animals to settle in response to these cues have been honed by natural selection to ensure that individuals can

recognize quickly those areas that normally include the resources they need to fulfill all aspects of their life history (Jaenike and Holt 1991). When non-native plants provide similar structural cues but different levels of resources than native plants, the cues that trigger habitat selection are decoupled from the resources normally linked to that cue, which creates potential for an ecological trap (Schlaepfer et al. 2002, Battin 2004). Even when densities of animals are similar between areas dominated by native and non-native grasses, non-native grasses may create ecological traps if there is a significant reduction in fitness of animals in these areas. In these circumstances, individuals might be responding to structural cues rather than to levels of key resources when selecting areas to settle.

Structural and functional aspects of desert grasslands are important to native animals. Grasses provide cover for thermoregulation and predator avoidance, seeds or plant biomass for forage, and habitat for prey of predatory species (especially arthropod prey; Parmenter and Van Devender 1995, Whitford et al. 1995, Esque and Schwalbe 2002). Some changes caused by invasions of non-native plants, including grasses, can create a cascade of indirect effects in addition to more obvious direct effects (Jones et al. 1994, Crooks 2002), such as eliminating habitat for vertebrates that create burrows or other structures that are used secondarily by other animal species. Non-native grasses are unlikely to provide identical structural and functional elements to those provided by native vegetation, so research on these differences is critical to understanding the direct and indirect effects of invasions by non-native plants.

Birds

When non-native grasses are similar in structure to native grasses, species richness and population densities of breeding birds in invaded grasslands are often similar to areas dominated by native plants. In areas of Texas planted with native and non-native grasses, for example, overall abundance and richness of breeding birds were similar (Thompson et al. 2009), a pattern observed in grassland ecosystems across North America (e.g., King and Savidge 1995, Sutter et al. 1995, Delisle and Savidge 1997, Davis and Duncan 1999, Fletcher and Koford 2002, Scott et al. 2002, Lloyd and Martin 2005, Flanders et al. 2006, Kennedy et al. 2009). In desert grasslands of southern Arizona, however, density of breeding Botteri's sparrows (*Aimophila botterii*) was higher on uplands dominated by African lovegrasses (*Eragrostis* spp.) than on uplands dominated by native grasses (Jones and Bock 2005), reflecting sparrows responding to the increase in structure and biomass in areas invaded by lovegrasses (Cable 1971, Cox et al. 1990, Anable et al. 1992, Geiger 2006).

The similarity in densities of songbirds between areas of native grasses relative to areas invaded by non-native grasses with similar vegetation structure suggests that many grassland birds select areas for nesting based more on structural rather than floristic cues. Therefore, the effect of a non-native grass invasion on density of breeding birds and composition of the breeding bird community will largely reflect the degree to

which vegetation structure changes in response to a non-native plant invasion. Whether areas invaded by non-native grasses can provide all of the other resources generally associated with vegetation structure and necessary for species to complete their life cycles is a more complex issue that is best evaluated with demographic measures other than density (Sogge et al. 2008). For example, in southern Texas, species richness of breeding birds was similar between areas dominated by Lehmann lovegrass and buffelgrass relative to areas dominated by native grasses, although densities of birds in different foraging guilds varied, suggesting differences in forage resources between native and non-native plant communities (Flanders et al. 2006).

Results from studies that have contrasted reproductive success of grassland birds between areas dominated by native and non-native grasses have been mixed, indicating that resource levels in areas dominated by non-native grasses are sometimes, but not always, comparable to those in areas of native grasses. In southern Arizona, reproductive success of Botteri's sparrows was consistent across areas dominated by native and non-native grasses (Jones and Bock 2005). Similarly, in prairies of northeastern Oregon, no measure of reproductive success of songbirds varied with cover of non-native grasses, although diets of nestlings did; this suggests that composition of the invertebrate community varied with cover of non-native grasses, although total abundance of invertebrates did not (Kennedy et al. 2009). Nesting success of chestnut-collared longspurs (*Calcarius ornatus*) was marginally higher for birds nesting in areas of native versus non-native grass in eastern Montana, but brood sizes of successful nests were similar; nestlings grew at slower rate in non-native areas, suggesting that there was likely some reduction of forage resources in those areas (Lloyd and Martin 2005). In general, where the degree of invasion of non-native grasses was moderate, studies have reported no change in reproductive success of grassland birds (Wilson and Belcher 1989; Schneider 1998, Grant et al. 2004, 2006, Kennedy et al. 2009). Non-native grasses may increase nesting and escape cover important for some birds, including some species of quail (Kuvlesky et al. 2002) and sparrows (Jones and Bock 2005), yet may lack the abundance and diversity of arthropods and forbs that provide important food resources for breeding birds (Medina 1988).

Mammals

Mammals play strong functional roles in grassland ecosystems, including perturbing soil in ways that facilitate use by animals and promote germination in plants (Martin 2003). In grasslands of California, for example, burrowing, herbivory, and seed caching by giant kangaroo rats (*Dipodomys ingens*) disturbs soil and promotes dispersal and establishment of seeds (Schiffman 1994). Because kangaroo rats and many other mammalian granivores show clear preferences for particular seeds, rodents can promote establishment of non-native plants if they consume native plants preferentially (Brown and Heske 1990, Orrock et al. 2009, Pearson et al. 2011) or if seeds of non-native plants germinate in caches (Schiffman 1994). At the

transition between desert scrub and desert grassland plant communities, the increase in cover of perennial grasses observed in areas where kangaroo rats were removed was due almost entirely to increases in Lehmann lovegrass, a non-native species; cover of native perennial grasses changed little in response to removal of kangaroo rats (Brown and Heske 1990). Activities of kangaroo rats may have kept the non-native grass from establishing; however, when kangaroo rats were removed, the soils they disturbed may have facilitated establishment of this non-native grass that thrives in disturbed settings (Cable 1971). Grasslands in southern Arizona with highest dominance of Lehmann lovegrass also had the lowest densities of agaves (Lindsay et al. 2010), which could have implications for pollination by nectarivorous bats that preferentially forage in areas of high agave density (Ober et al. 2005). Therefore, invasions by non-native grasses that affect the distribution and richness of mammals are likely to have far-reaching effects on plants and animals that inhabit desert grasslands.

In grasslands of southern Arizona, composition of the small mammal community changed in response to the degree of dominance of Lehmann lovegrass, although total abundance of small mammals remained relatively constant (Litt and Steidl 2011). Abundance of many common species either increased or decreased in areas dominated by non-native plants relative to those dominated by native plants (Bock et al. 1986, Litt and Steidl 2011). In general, as dominance of Lehmann lovegrass increased, species that prefer dense vegetation increased, including Arizona cotton rats (*Sigmodon arizonae*) and fulvous harvest mice (*Reithrodontomys fulvescens*); and species that prefer sparse vegetation decreased, including northern grasshopper mice (*Onychomys leucogaster*) and silky pocket mice (*Perognathus flavus*; Litt and Steidl 2011). In grasslands of southern Texas, species richness, diversity, and biomass of small mammals were lower overall in areas dominated by kleingrass (*Panicum coloratum*), a warm-season perennial native to Africa, than in areas dominated by native grasses during most sampling periods; pygmy mice (*Baiomys taylori*), which prefer dense vegetation, were more abundant in areas dominated by kleingrass (Long 2005).

In general, information on effects of invasions by non-native plants on large, herbivorous mammals in grassland ecosystems is sparse; we expect, however, that some large herbivores could facilitate the spread of non-native grasses. Information on effects of invasions by non-native plants on reproductive responses of mammals also is similarly sparse. In southern Arizona, however, rates of reproductive activity of desert pocket mice (*Chaetodipus penicillatus*), silky pocket mice, deer mice (*Peromyscus maniculatus*), plains harvest mice (*Reithrodontomys montanus*), and Arizona cotton rats all decreased as the degree of dominance of non-native grasses increased (A. R. Litt and R. J. Steidl, unpublished data), perhaps in response to lower diversity and abundance of plant and arthropod foods in these areas (Geiger 2006, Litt and Steidl 2010).

Reptiles

Reptiles, like most vertebrates, respond strongly to structural features when selecting habitat. Therefore, areas that support

a variety of environmental conditions, including higher vegetation structural diversity, tend to support more species than do areas with less structural complexity (Bateman et al. 2008, Banville and Bateman 2012). Consequently, changes in vegetation that alter structural features of the environment are likely to affect use by reptiles. Removal of non-native trees, for example, favors reptiles that prefer open, sun-exposed sites (e.g., eastern fence lizards [*Sceloporus consobrinus*] Chihuahuan spotted whiptails [*Aspidoscelis exanguis*] and desert whiptails [*A. uniparens*]) and disfavors shade-tolerant and arboreal species (e.g., ornate tree lizard [*Urosaurus ornatus*] and desert spiny lizard [*S. magister*; Bateman et al. 2008, Pike et al. 2011]). Some reptiles rely, at least in part, on burrows created by other animals. Density of animal burrows was associated positively with abundance of desert spiny lizards in central Arizona (Banville and Bateman 2012), suggesting that if abundance and distribution of burrowing animals is reduced in areas dominated by non-native grasses, reptiles that rely on such burrows will likely be affected adversely.

Many reptiles native to desert grasslands evolved in areas of relatively sparse vegetation, with their foraging, locomotion, and predator-avoidance strategies adapted to these open conditions. These species are likely to be affected adversely when grasslands are invaded by non-native plants that increase biomass and plant density relative to historical conditions (Germano et al. 2001, Esque and Schwalbe 2002). For example, as cover of cheatgrass (*Bromus tectorum*) increased in sagebrush ecosystems of Utah, abundance of scat of desert horned lizard (*Phrynosoma platyrhinos*) decreased, indicating that horned lizards avoided areas of high cover (Newbold 2005). Cheatgrass also reduced sprint velocity of desert horned lizards and 3 other lizard species tested in field raceways (Newbold 2005, Rieder et al. 2010). Increases in non-native plants, such as buffelgrass, in semiarid regions also could reduce mobility of lizards, which may have negative consequences for foraging, predation risk, and social interactions (Rieder et al. 2010). In contrast, as density of non-native grasses in a Nebraska prairie increased, abundance of several lizard species increased (Ballinger and Watts 1995).

In the western Mojave Desert, desert tortoises (*Gopherus agassizii*) spent 95% of their time foraging on native plants, despite these plants being uncommon or rare (Jennings 1997). In the Sonoran Desert, body condition of adult desert tortoises (*G. morafkai*) was lower in areas invaded by buffelgrass relative to areas without buffelgrass (Gray 2012). A study contrasting nutritional quality of native and non-native grasses and forbs important to desert tortoises showed that forbs had higher nutritional value than did grasses, and that grasses provided little nitrogen and insufficient water to avoid a deficit during digestion (Nagy et al. 1998, Hazard et al. 2009). Therefore, areas where non-native grasses are dominant may offer lower quality forage for desert tortoises and other reptile grazers. Increases in non-native grasses also may affect abundance of other food resources for reptiles, especially arthropods, because non-native grasses generally support a different

complex of arthropods in lower abundances than do native grasslands (Samways et al. 1996, Herrera and Dudley 2003, McIntyre 2003, Yoshioka et al. 2010, Cord 2011, Litt and Steidl 2010).

Arthropods

Relative to vertebrates, many arthropods are less mobile, depend on a narrower range of plants for food, cover, and sites for reproduction, and can have specialized relationships with particular plant species (Kremen et al. 1993), which makes them especially vulnerable to changes in composition of the plant community resulting from invasions by non-native plants. Changes in vegetation structure from plant invasions could impede movements of arthropods in grasslands (Samways et al. 1996) and alter microclimatic conditions that affect diversity and abundance (Curry 1994). Changes in vegetation composition, especially where non-native plants establish monocultures, can decrease structural heterogeneity and reduce habitat quality for species that prefer mosaics of vegetation (Curry 1994). Changes in the arthropod community are likely to affect several ecological processes, including pollination, decomposition, and nutrient cycling, as well as food resources for insectivores, including breeding grassland birds, small mammals, and reptiles.

Richness and composition of the arthropod community and abundance of specific taxonomic groups have been observed to change frequently in response to invasions by non-native plants in grassland ecosystems. In southern Arizona, for example, as dominance of Lehmann lovegrass increased, richness of insect families and morphospecies, as well as overall abundance of 5 of 8 orders decreased, including Coleoptera, Diptera, Hemiptera, Homoptera, and Orthoptera (Litt and Steidl 2010); all groups that decreased in abundance consume plant material, reflecting either reduced availability of plant species that provide food for insect herbivores or reduced palatability of Lehmann lovegrass relative to native plants, especially as tissues become coarse and tough over the growing season (Crider 1945, Cable 1971). Similarly, 8 of 9 insect orders decreased in abundance in areas invaded by non-native lovegrasses (Bock et al. 1986). In grasslands of Texas invaded by kleingrass and Kleberg bluestem, richness and abundance of arthropods were lower than in areas dominated by native grasses (Long 2005, Cord 2011). Decreases in richness and abundance of arthropods also have been observed in other grassland ecosystems invaded by non-native plants (e.g., Collinge et al. 2003).

In studies specifically targeting pollinators, however, increased cover of Lehmann lovegrass did not affect abundance, richness, or diversity of bees (McDonald 2009) or arthropod pollinators important to agaves, including Hymenoptera, Diptera, Coleoptera, Lepidoptera, and Hemiptera (Lindsay et al. 2010). Richness and abundance of spiders did not vary with cover of Lehmann lovegrass in grasslands of New Mexico (Hu and Richman 2010). Similarly, abundance of small seed-harvesting ants (*Pheidole* spp.) also did not vary with cover of Lehmann lovegrass

(Whitford et al. 1997), which has a much smaller seed than do native grasses and forbs (Reichman 1975). In contrast, large seed-harvesting ants (*Pogonomyrmex* spp.) were more abundant in native grasslands, reflecting reduced availability of large seeds in areas invaded by small-seeded Lehmann lovegrass (Whitford et al. 1997). Therefore, arthropods with specialized diets may be affected more by changes in diversity and abundance of native plants.

DISCUSSION

Changes in the plant community resulting from invasions by non-native plants can vary widely, reflecting the degree to which non-native plants replace native plants or fill in open areas among existing native plants. Although plant invasions change both structure and composition of the plant community, we anticipate that the magnitude of effects on habitat quality of animals in grassland ecosystems will reflect primarily the contrast in structure between native and invaded plant communities, a pattern echoed in the majority of studies of plant invasions on birds, mammals, and reptiles (e.g., Wilson and Belcher 1989, Scheiman et al. 2003, Jones and Bock 2005, Litt and Steidl 2011). Ultimately, effects of invasions by non-native plants on animals will depend on the degree of invasion, characteristics of the invading plant species, the contrast in structure and function relative to native plants, and the needs of the particular animal species for various aspects of their life history (Steidl and Litt 2009). Some variation in results across studies evaluating effects of plant invasions on animals is surely an artifact of variation in the degree of invasion, which can range considerably across areas classified by researchers as “invaded.” To enhance the breadth and value of these studies, researchers need to quantify and report the degree of invasion of non-native plants in areas they survey rather than simply classify areas as invaded.

Effects of plant invasions on animal communities are likely to vary through time as invasions progress. When a non-native plant species first invades a grassland ecosystem, structural and compositional heterogeneity of the plant community increase (Litt and Steidl 2011), which may increase the types of resources available to animals. These changes increase the potential for an area to support novel animal species (Robinson and Holmes 1982, Maurer 1985). However, if the non-native plant becomes dominant as an invasion progresses, composition of the plant community will become simplified, heterogeneity in structure will decrease, and the number of animal species that can be supported will likely decrease. In grasslands of southern Arizona, species richness of small mammals was highest in areas where dominance of non-native grass was moderate (Litt and Steidl 2011).

Invasions by non-native plants in grassland ecosystems also can alter the fire regime, which will affect the long-term dynamics of animal communities compared with areas dominated by native plants. Invasions by non-native grasses reduce space among plants and increase biomass relative to native plant communities, which increases fuel loading and continuity (DeBano et al. 1998). These changes alter fire

behavior and increase fire frequency, intensity, and severity in many invaded systems (Rossiter et al. 2003, Brooks et al. 2004). In plant communities that evolved without a dominant grass component, such as Sonoran desertscrub, invasions by non-native grasses can support fires where they were once rare (Olsson et al. 2012). Consequently, fire in grasslands dominated by non-native grasses functions differently than fire in systems dominated by native plants, and is less likely to develop and maintain the highly heterogeneous conditions necessary to support the full diversity of animals that inhabit native grasslands (Steidl and Litt 2009, Litt and Steidl 2011).

MANAGEMENT IMPLICATIONS

Management alternatives thought to reduce abundance and distribution of non-native plants by shifting composition of the plant community back toward native plants include reintroducing fire at intervals designed to match the frequency and timing of the historical disturbance regime (McPherson 1995) and removing livestock (Geiger and McPherson 2005, Geiger 2006). Attempts to enact these alternatives have had little effect on richness, diversity, or biomass of native grasses, density of non-native grasses, or rates of encroachment by woody plants (McGlone and Huenneke 2004, Geiger and McPherson 2005, Geiger 2006). Alternatively, livestock grazing has been proposed as a mechanism for reducing dense cover created by non-native plants in some circumstances (Germano et al. 2001). Regardless of the strategy enacted, managers and conservationists must realize that a common outcome of vegetation control is that some native animal species will benefit from decreased density and distribution of non-native plants whereas other native species will be harmed (Crooks 2002).

An additional management alternative is direct suppression or eradication of non-native plants through application of herbicides and mechanical removal. Eradication programs for non-native plants have been most successful for species established on small areas (Rejmanek and Pitcairn 2002). Once a species has become well-established (i.e., >100 ha), the only practical alternative may be to initiate long-term suppression programs, because eradication efforts for well-established species are rarely successful (Rejmanek and Pitcairn 2002). Suppression efforts, although costly, may be practical only in relatively small, protected areas of the highest conservation value, such as National Parks, but are likely to fail unless maintained as a high priority and funded into perpetuity. Non-native plants that initiate complex sets of direct, indirect, and cascading effects should be high-priority targets for long-term suppression programs. Establishing monitoring programs to detect invasions early, such as those established in several National Park Service Networks (e.g., Vital Signs Monitoring, Sonoran Desert Inventory and Monitoring Network), will be less costly and may be more effective over the long term than efforts to eradicate plant species that are well established.

Although complete eradication of non-native grasses is unlikely in most circumstances, retaining patches of native

vegetation within a matrix of non-native plants may provide a viable and important management alternative. In southern Arizona, for example, ground-nesting birds placed their nests in clumps of native bunchgrass, even when surrounded by non-native grasses (E. Albrecht, University of Arizona, and R. J. Steidl, unpublished data). Birds and other species can benefit from even small patches of grassland to fulfill at least some aspects of their life history (Walk et al. 2010).

Effects of non-native plant invasions on animals are likely to interact with other physical and biological processes, including aspects of the fire regime and responses of plants to climate change, which can make predicting some effects of plant invasions on animals as well as the effectiveness of management manipulations challenging (D'Antonio and Vitousek 1992, Steidl and Litt 2009, Litt and Steidl 2011). Further, climate change and other aspects of global change will likely serve to further increase rates of establishment and spread of non-native species, alter effectiveness of control methods, and influence establishment of new species (Hellmann et al. 2008). Our ability to develop frameworks to predict and ameliorate effects of non-native plants on animals will require that we improve our understanding of mechanisms that underlie the novel interactions between animals and non-native plants.

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LITERATURE CITED

- Anable, M. E., M. P. McClaran, and G. B. Ruyle. 1992. Spread of introduced Lehmann lovegrass *Eragrostis lehmanniana* Nees in southern Arizona, USA. *Biological Conservation* 61:181-188.
- Archer, S. A. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545-561.
- Arriaga, L., A. E. Castellanos V., E. Moreno, and J. Alarcón. 2004. Potential ecological distribution of alien invasive species and risk management: a case study for buffel grass in arid regions of Mexico. *Conservation Biology* 18:1504-1514.
- Bahre, C. J. 1995. Human impacts on the grasslands of southeastern Arizona. Pages 230-264 in M. P. McClaran and T. R. Van Devender, editors. *The desert grassland*. The University of Arizona Press, Tucson, USA.
- Ballinger, R. E., and K. S. Watts. 1995. Path to extinction: impact of vegetational changes on lizard populations on Arapaho Prairie in the Nebraska sandhills. *American Midland Naturalist* 134:413-417.
- Banville, M. J., and H. L. Bateman. 2012. Urban and wildland herpetofauna communities and riparian microhabitats along the Salt River, Arizona. *Urban Ecosystems* 15:473-488.
- Bateman, H. L., A. Chung-MacCoubrey, and H. L. Snell. 2008. Impact of non-native plant removal on lizards in riparian habitats in the southwestern United States. *Restoration Ecology* 16:180-190.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482-1491.
- Bock, C. E., and J. H. Bock. 1992. Response of birds to wildfire in native versus exotic Arizona grassland. *Southwestern Naturalist* 37:73-81.

- Bock, C. E., J. H. Bock, K. L. Jepson, and J. C. Ortega. 1986. Ecological effects of planting African lovegrasses in Arizona. *National Geographic Research* 2:456–463.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Brown, D. E., editor. 1994. *Biotic communities: southwestern United States and northwestern Mexico*. Second edition. University of Utah Press, Salt Lake City, USA.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- Cable, D. R. 1965. Damage to mesquite, Lehmann lovegrass, and black grama by a hot June fire. *Journal of Range Management* 18:326–329.
- Cable, D. R. 1971. Lehmann lovegrass on the Santa Rita Experimental Range, 1937–1968. *Journal of Range Management* 24:17–21.
- Collinge, S. K., K. L. Prudic, and J. C. Oliver. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology* 17:178–187.
- Cord, E. E. 2011. *Changes in arthropod abundance and diversity with invasive grasses*. Thesis, Texas A&M University-Kingsville, USA.
- Cox, J. R., and G. B. Ruyle. 1986. Influence of climatic and edaphic factors on the distribution of *Eragrostis lehmanniana* Nees in Arizona, USA. *Journal of the Grassland Society of Southern Africa* 3:25–29.
- Cox, J. R., G. B. Ruyle, and B. A. Roundy. 1990. Lehmann lovegrass in southeastern Arizona: biomass production and disappearance. *Journal of Range Management* 43:367–372.
- Crider, F. J. 1945. Three introduced lovegrasses for soil conservation. U.S. Department of Agriculture Circular 730, Washington, D.C., USA.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.
- Curry, J. P. 1994. *Grassland invertebrates: ecology, influence on soil fertility, and effects on plant growth*. Chapman and Hall, New York, New York, USA.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Davis, S. K., and D. C. Duncan. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. *Studies in Avian Biology* 19:211–218.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. *Fire's effects on ecosystems*. John Wiley and Sons, New York, New York, USA.
- Delisle, J. M., and J. A. Savidge. 1997. Avian use and vegetation characteristics of Conservation Reserve Program fields. *Journal of Wildlife Management* 61:318–325.
- Ehleringer, J. R., T. E. Cerling, and B. R. Helliker. 1997. C_4 photosynthesis, atmospheric CO_2 , and climate. *Oecologia* 112:285–299.
- Esque, T. C., and C. R. Schwalbe. 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran desert scrub. Pages 165–194 in B. Tellman, editor. *Invasive exotic species in the Sonoran region*. The University of Arizona Press and Arizona-Sonora Desert Museum, Tucson, USA.
- Esque, T. C., C. R. Schwalbe, J. A. Lissow, D. F. Haines, D. Foster, and M. C. Garnett. 2007. Buffelgrass fuel loads in Saguaro National Park, Arizona, increase fire danger and threaten native species. *Park Science* 24:33–37.
- Finch, D. M. 2004. *Assessment of grassland ecosystem conditions in the southwestern United States Volume 1*. U.S. Forest Service General Technical Report RMRS-GTR-135, Rocky Mountain Research Station Fort Collins, Colorado, USA.
- Finch, D. M. 2005. *Assessment of grassland ecosystem conditions in the southwestern United States Volume 2*. U.S. Forest Service General Technical Report RMRS-GTR-135, Rocky Mountain Research Station Fort Collins, Colorado, USA.
- Flanders, A. A., W. P. Kuvlesky, Jr., D. C. Ruthven, III, R. E. Zaiglin, R. L. Bingham, T. E. Fulbright, F. Hernandez, and L. A. Brennan. 2006. Effects of invasive exotic grasses on South Texas rangeland breeding birds. *Auk* 123:171–182.
- Fletcher, R. J., and R. R. Koford. 2002. Habitat and landscape associations of breeding birds in native and restored prairie. *Journal of Wildlife Management* 66:1011–1022.
- Franklin, K. A., and F. Molina-Freaner. 2010. Consequences of buffelgrass pasture development for productivity and species richness of plants in the drylands of Sonora, Mexico. *Conservation Biology* 24:1664–1673.
- Franklin, K. A., K. Lyons, P. L. Nagler, D. Lampkin, E. P. Glenn, F. Molina-Freaner, T. Markow, and A. R. Huete. 2006. Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. *Biological Conservation* 127:62–71.
- Geiger, E. L. 2006. *The role of fire and a nonnative grass as disturbances in semi-desert grasslands*. Dissertation, University of Arizona, Tucson, USA.
- Geiger, E. L., and G. R. McPherson. 2005. Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes. *Journal of Biogeography* 32:895–902.
- Germano, D. J., G. B. Rathbun, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. *Wildlife Society Bulletin* 29: 551–559.
- Grant, T. A., E. M. Madden, and G. B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin* 32:807–818.
- Grant, T. A., E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmaz. 2006. Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies. *Journal of Wildlife Management* 70:691–701.
- Gray, K. M. 2012. *Effects of buffelgrass invasion on demography of Sonoran desert tortoises*. Thesis, University of Arizona, Tucson, USA.
- Hazard, L. C., D. R. Shemanski, and K. A. Nagy. 2009. Nutritional quality of natural foods of juvenile desert tortoise (*Gopherus agassizii*): energy, nitrogen, and fiber disutility. *Journal of Herpetology* 43:38–48.
- Heinrich B., and S. L. Collins. 1983. Caterpillar leaf damage and the game of hide-and-seek with birds. *Ecology* 64:592–602.
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* 22:534–543.
- Herrera, A. M., and T. L. Dudley. 2003. Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions* 5:167–177.
- Hu, D. H., and D. B. Richman. 2010. Effect of Lehmann lovegrass (*Eragrostis lehmanniana*) (Poaceae) on spider communities on upper bajada and basin grassland. *Southwestern Entomologist* 35:269–288.
- Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. *The American Naturalist* 137:S67–S90.
- Jennings, W. B. 1997. Habitat use and food preferences of the desert tortoise, *Gopherus agassizii*, in the western Mohave Desert and impacts of off-road vehicles. Pages 42–45 in J. Van Abbema, editor. *Proceedings: conservation, restoration, and management of tortoises and turtles—an international conference*. New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, Purchase, USA.
- Jones, Z. F., and C. E. Bock. 2005. The Botteri's sparrow and exotic Arizona grasslands: an ecological trap or habitat regained? *Condor* 107:731–741.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Kennedy, P. L., S. J. DeBano, A. M. Bartuszevige, and A. S. Lueders. 2009. Effects of native and exotic grassland plant communities on breeding passerine birds: implications for restoration of northwest bunchgrass prairie. *Restoration Ecology* 17:515–525.
- Kimball, S., and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* 17:1681–1693.
- King, J. W., and J. A. Savidge. 1995. Effects of Conservation Reserve Program on wildlife in southeast Nebraska. *Wildlife Society Bulletin* 23:377–385.
- Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247–257.
- Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7:796–808.
- Kuvlesky, W. P., Jr., T. E. Fulbright, and R. Engel-Wilson. 2002. The impact of invasive exotic grasses on quail in the southwestern United States. *Proceedings of the 5th National Quail Symposium* 5:118–128.
- Lindsay, D. L., P. Bailey, R. F. Lance, M. J. Clifford, R. Delph, and N. S. Cobb. 2010. Effects of a nonnative, invasive lovegrass on *Agave palmeri* distribution, abundance, and insect pollinator communities. U.S. Army

- Engineer Research and Development Center, ERDC/EL TN-10-1, Vicksburg, Mississippi, USA.
- Litt, A. R., and R. J. Steidl. 2010. Insect assemblages change along a gradient of invasion by a nonnative grass. *Biological Invasions* 12:3449–3463.
- Litt, A. R., and R. J. Steidl. 2011. Interactive effects of fire and nonnative plants on small mammals in grasslands. *Wildlife Monographs* 176.
- Lloyd, J. D., and T. E. Martin. 2005. Reproductive success of chestnut-collared longspurs in native and exotic grassland. *The Condor* 107: 363–374.
- Lloyd, J. D., R. W. Mannan, S. DeStefano, and C. Kirkpatrick. 1998. The effects of mesquite invasion on a southeastern Arizona grassland bird community. *Wilson Bulletin* 110:403–408.
- Long, D. B. 2005. Effects of exotic grasses on small mammals and invertebrates in southern Texas. Thesis, Texas A&M University—Kingsville, USA.
- Lonsdale, W. M. 1994. Inviting trouble: introduced pasture grasses in northern Australia. *Australian Journal of Ecology* 19:345–354.
- Macias-Duarte, A., A. O. Panjabi, D. Pool, E. Youngberg, and G. Levandoski. 2011. Wintering grassland bird density in Chihuahuan desert grassland priority conservation areas, 2007–2011. Rocky Mountain Bird Observatory Technical Report IMXPLAT-10-01, Brighton, Colorado, USA.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- MacNally, R. C. 1990. The roles of floristics and physiognomy in avian community composition. *Australian Journal of Ecology* 15:321–327.
- Marshall, M. R., and R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology* 85:432–445.
- Marshall, V. M., M. M. Lewis, and B. Ostendorf. 2012. Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. *Journal of Arid Environments* 78:1–12.
- Martin, B. G. 2003. The role of small ground-foraging mammals in topsoil health and biodiversity: implications to management and restoration. *Ecological Management and Restoration* 4:114–119.
- Maurer, B. A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. *Ecological Monographs* 55:295–312.
- McClaran, M. P. 1995. Desert grasslands and grasses. Pages 1–30 in M. P. McClaran and T. R. Van Devender, editors. *The desert grassland*. The University of Arizona Press, Tucson, USA.
- McDonald, C. J. 2009. Management of nonnative perennial grasses in southern Arizona: effects of prescribed fire and livestock grazing. Dissertation, University of Arizona, Tucson, USA.
- McGlone, C. M., and L. F. Huenneke. 2004. The impact of a prescribed burn on introduced Lehmann lovegrass versus native vegetation in the northern Chihuahuan Desert. *Journal of Arid Environments* 57:297–310.
- McGrath, L. J., C. van Riper, III, and J. J. Fontaine. 2009. Flower power: tree flowering phenology as a settlement cue for migrating birds. *Journal of Animal Ecology* 78:22–30.
- McIntyre, N. E. 2003. Effects of Conservation Reserve Program seeding regime on harvester ants (*Pogonomyrmex*) with implications for the threatened Texas horned lizard (*Phrynosoma cornutum*). *The Southwestern Naturalist* 48:274–313.
- McLaughlin, S. P. 2002. Exotic plant species in the western United States. Pages 47–62 in B. Tellman, editor. *Invasive exotic species in the Sonoran region*. The University of Arizona Press, Tucson, USA.
- McLaughlin, S. P., and J. E. Bowers. 1982. Effects of wildfire on a Sonoran desert plant community. *Ecology* 63:246–248.
- McPherson, G. R. 1995. The role of fire in the desert grasslands. Pages 130–151 in M. P. McClaran and T. R. Van Devender, editors. *The desert grassland*. The University of Arizona Press, Tucson, USA.
- Medina, A. L. 1988. Diets of scaled quail in southern Arizona. *Journal of Wildlife Management* 52:753–757.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11–23.
- Nagy, K. A., B. T. Henen, and D. B. Vyas. 1998. Nutritional quality of native and introduced food plants of wild desert tortoise. *Journal of Herpetology* 32:260–267.
- Newbold, T. A. S. 2005. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: the influence of cheatgrass (*Bromus tectorum*). *The Southwestern Naturalist* 50:17–23.
- Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States a preliminary assessment of loss and degradation. U.S. Department of Interior National Biological Service, Washington, D.C., USA.
- Ober, H. K., R. J. Steidl, and V. M. Dalton. 2005. Resource and spatial-use patterns of an endangered vertebrate pollinator, the lesser long-nosed bat. *Journal of Wildlife Management* 69:1615–1622.
- Olsson, A. D., J. Betancourt, M. P. McClaran, and S. E. Marsh. 2012. Sonoran desert ecosystem transformation by a C4 grass without the grass/fire cycle. *Diversity and Distributions* 18:10–21.
- Orrock, J. L., M. S. Witter, and O. J. Reichman. 2009. Native consumers and seed limitation constrain the restoration of a native perennial grass in exotic habitats. *Restoration Ecology* 17:148–157.
- Parmenter, R. R., and T. R. Van Devender. 1995. Diversity, spatial variability, and functional roles of vertebrates in the desert grassland. Pages 196–229 in M. P. McClaran and T. R. Van Devender, editors. *The desert grassland*. The University of Arizona Press, Tucson, USA.
- Pearson, D. E., R. M. Callaway, and J. L. Maron. 2011. Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. *Ecology* 92:1748–1757.
- Pike, D. A., J. K. Webb, and R. Shine. 2011. Removing forest canopy cover can restore a reptile assemblage. *Ecological Applications* 21:274–280.
- Pivello, V. R., C. N. Shida, and S. T. Meirelles. 1999. Alien grasses in Brazilian savannas: a threat to the biodiversity. *Biodiversity and Conservation* 8:1281–1294.
- Price, M. V., and N. M. Waser. 1984. On the relative abundance of species: postfire changes in a coastal sage scrub rodent community. *Ecology* 65:1161–1169.
- Reichman, O. J. 1975. Relationships between dimensions, weights, volumes, and calories of some Sonoran Desert seeds. *Southwestern Naturalist* 20:573–575.
- Rejmanek, M., and M. J. Pitcairn. 2002. When is eradication of exotic pest plants a realistic goal? Pages 249–253 in C. R. Veitch and M. N. Clout, editors. *Turning the tide: the eradication of invasive species*. International Union for Conservation of Nature Species Survival Commission Invasive Species, Specialist Group, Cambridge, England, United Kingdom.
- Richardson, D. M., and B. W. van Wilgen. 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? *South African Journal of Science* 100:45–52.
- Rieder, J. P., T. A. S. Newbold, and S. M. Ostoja. 2010. Structural changes in vegetation coincident with annual grass invasion negatively impacts sprint velocity of small vertebrates. *Biological Invasions* 12:2429–2439.
- Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* 9:169–176.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* 67:213–217.
- Ruyle, G. B., B. A. Roundy, and J. R. Cox. 1988. Effects of burning on germinability of Lehmann lovegrass. *Journal of Range Management* 41:404–406.
- Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418–421.
- Samways, M. J., P. M. Caldwell, and R. Osborn. 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment* 59:19–32.
- Sands, J. P., L. A. Brennan, F. Hernandez, W. P. Kuvlesky, Jr., J. F. Gallagher, D. C. Ruthven, III, and J. E. Pittman, III. 2009. Impacts of buffelgrass (*Pennisetum ciliare*) on a forb community in south Texas. *Invasive Plant Science and Management* 2:130–140.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American breeding bird survey, results and analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

- Scheiman, D. M., E. K. Bollinger, and D. H. Johnson. 2003. Effects of leafy spurge infestation on grassland birds. *Journal of Wildlife Management* 67:115–121.
- Schiffman, P. A. 1994. Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland. *Biodiversity and Conservation* 3:524–537.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Schneider, N. A. 1998. Passerine use of grasslands managed with two grazing regimes on the Missouri Coteau in North Dakota. Thesis, South Dakota State University Brookings, USA.
- Schussman, H., E. Geiger, T. Mau-Crimmins, and J. Ward. 2006. Spread and current potential distribution of an alien grass, *Eragrostis lehmanniana* Nees, in the southwestern USA: comparing historical data and ecological niche models. *Diversity and Distributions* 12:582–592.
- Scott, P. E., T. L. DeVault, R. A. Bajema, and S. L. Lima. 2002. Grassland vegetation and bird abundances on reclaimed coal Midwestern coal mines. *Wildlife Society Bulletin* 30:1006–1014.
- Sogge, M. K., S. J. Sferra, and E. H. Paxton. 2008. Tamarix as habitat for birds: implications to riparian restoration in the southwestern United States. *Restoration Ecology* 16:146–154.
- Steidl, R. J., and A. R. Litt. 2009. Do plant invasions change the effects of fire on animals? *Fire Ecology* 5:56–66.
- Sumrall, L. B., B. A. Roundy, J. R. Cox, and V. K. Winkel. 1991. Influence of canopy removal by burning or clipping on emergence of *Eragrostis lehmanniana* seedlings. *International Journal of Wildland Fire* 1:35–40.
- Sutter, G. C., T. Troupe, and M. Forbes. 1995. Abundance of Baird's sparrows, *Ammodramus bairdii*, in native prairie and introduced vegetation. *Ecoscience* 2:344–348.
- Thompson, T. R., C. W. Boal, and D. Lucia. 2009. Grassland bird associations with introduced and native grass Conservation Reserve Program fields in the Southern High Plains. *Western North American Naturalist* 69:481–490.
- Van Auken, O. W. 2000. Shrub invasions of North American semi-arid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.
- Van Devender, T. R., R. S. Felger, and A. Búrquez M. 1997. Exotic plants in the Sonoran Desert region, Arizona and Sonora. Pages 10–15 in M. Kelly, E. Wagner, and P. Wagner, editors. Proceedings of the California exotic pest plant council symposium. California Exotic Pest Plant Council, Trabuco Canyon, USA.
- Vickery, P. D., P. L. Tubaro, J. M. C. da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the Western Hemisphere. *Studies in Avian Biology* 19:2–26.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59:247–265.
- Walk, J. W., E. L. Kershner, T. J. Benson, and R. E. Warner. 2010. Nesting success of grassland birds in small patches in an agricultural landscape. *The Auk* 127:328–334.
- Whitford, W. G. 1998. The desert grasslands. Pages 313–323 in D. J. Rapport, R. Costanza, P. R. Epstein, F. C. Gaudet, and R. Levins, editors. *Ecosystem health*. Blackwell Science, Ames, Iowa, USA.
- Whitford, W. G., G. S. Forbes, and G. I. Kerley. 1995. Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. Pages 152–195 in M. P. McClaran and T. R. Van Devender, editors. *The desert grassland*. The University of Arizona Press, Tucson, USA.
- Whitford, W. G., J. Van Zee, M. S. Nash, W. E. Smith, and J. E. Herrick. 1997. Ants as indicators of exposure to environmental stressors in North American desert grasslands. *Environmental Monitoring and Assessment* 54:143–171.
- Wilson, S. D., and J. W. Belcher. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. *Conservation Biology* 3:39–44.
- Wright, H. A., and A. W. Bailey. 1982. *Fire ecology—United States and southern Canada*. John Wiley and Sons, New York, New York, USA.
- Yoshioka, A., T. Kadoya, S. Suda, and I. Washitani. 2010. Impacts of weeping lovegrass (*Eragrostis curvula*) invasion on native grasshoppers: responses of habitat generalist and specialist species. *Biological Invasions* 12:531–539.

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