Arizona Office
738 N 5th Ave, Suite 206
Tucson, AZ 85705
tel: (520) 623-1878
fax: (208) 475-4702
email: arizona@westernwatersheds.org
web site: www.westernwatersheds.org

Working to protect and restore Western Watersheds and Wildlife

November 2, 2020

Kerwin S. Newberry
Objections Reviewing Officer
U.S. Forest Service
Coronado National Forest
300 W. Congress Street
Tucson, AZ 85701

Submitted via email to: objections-southwestern-coronado@usda.gov

Cienega Creek FireScape Project EA Objection
Coronado National Forest

Dear Mr. Newberry,

The following Objection to the Cienega Creek FireScape Project Environmental Analysis (EA), Draft Decision Notice and Finding of No Significant Impact (DDN/FONSI) is being submitted on behalf of the members of Western Watersheds Project (WWP) who are concerned with the management of our public lands. WWP previously submitted comments for this project on May 10, 2019, and have included these comments as Appendix A. The legal notice for this decision was published on September 18, 2020 and this objection, filed November 2, 2020, is therefore timely.

This Objection is filed pursuant to, and in compliance with, 36 C.F.R. Part 218, Subparts A and B. All parties to this objection have filed timely, specific and substantive written comments in accordance with 36 C.F.R. 218(a).

As required by 36 C.F.R. § 218.8(d), Objectors provide the following information:

1. The name and contact information for the Objector is listed below.
2. This Objection was written on behalf of Objector by Cyndi Tuell whose signature and contact information are below.
3. Western Watersheds Project is the Objector. Cyndi Tuell is the Lead Objector for purposes of communication regarding the Objection.

Cyndi Tuell
Western Watersheds Project
738 N. 5th Ave, Suite 206
Tucson, AZ 85705

4. The project that is subject to this Objection is "Cienega Creek FireScape Project EA." The Responsible Official is Jim Copeland, District Ranger for the Nogales Ranger District.
5. Objector submitted, timely, specific, and substantive comments during the Public Comment Period on May 10, 2019. All points and issues raised in this objection refer to issues raised in that comment letter or new information.
6. In the following Statement of Reasons, Objector provides the specific reasons why the decision is being appealed and the specific changes or suggested remedies that he seeks, along with the related evidence and rationale on why the decision violates applicable laws and regulations.

NOTICE OF OBJECTION

Pursuant to 36 C.F.R. § 218, Western Watersheds Project is filing an Objection regarding the Draft DN/FONSI for the Cienega Creek FireScape Project EA in the Nogales Ranger District of the Coronado National Forest.

INTRODUCTION

This project covers more than 90,000 acres of federal public lands and includes designated Wilderness, an Inventoried Roadless Areas (IRA), sensitive wildlife habitat, and habitat for species listed as threatened and endangered. EA at 1. The failure of the Forest Service to adequately address our concerns, the geographic and temporal scope along with the special designations and species found in this area, and the proposal to use mechanized and motorized equipment in designated Wilderness and the long-term use of herbicides throughout the project area, require the development of an Environmental Impact Statement (EIS) and preclude a Finding of No Significant Impact (FONSI).

We describe our concerns more specifically below.

STATEMENT OF REASONS

I. Targeted livestock grazing is scientifically controversial and not scientifically proven as an effective treatment for invasive plants and will not meet the purpose and need for the project.

The stated purpose of the project is to: reduce fuel accumulations and uncharacteristic composition and structure that contribute to the risk of large, high intensity wildfire and associated negative effects; restore and sustain ecological processes in fire-dependent ecosystems, enhance overall health and resiliency of desired native plant and tree species and improve habitat for wildlife; facilitate fire management and ensure public and firefighter safety; and provide protection to values at risk within the project area. WWP 2020 comments at 1-2; USFS 2020 EA at 2. As we noted in our prior comments, targeted livestock grazing will not accomplish these goals and instead will further

exacerbate the spread of non-native invasive plants and increase the risk of high intensity wildfire. WWP 2020 at 3.

The Forest Service acknowledges that livestock grazing is a likely cause of unnatural fire regimes in the project area. USFS 2020 EA at 20. Targeted grazing will reduce fine fuels, which will preclude the use of natural fire and at the same time will continue to alter the plant composition, favoring invasive species over native species of grasses and other plants. *Id*. Additionally, the use of "targeted" livestock grazing, for the ostensible purpose of reducing invasive species of grasses, only worsens the problem. One recent peer-reviewed study found "no support" for the proposition that cattle reduce invasions by grazing on invasive grasses.[1] The study's findings raised serious concerns regarding proposals to use cattle grazing to control invasive grasses in systems where remnant bunchgrass communities persist. In fact, the findings support recent guidance for passively restoring resistance of these systems by reducing grazing levels

In our prior comments we provided the Forest Service with peer reviewed scientific literature regarding the impacts of targeted livestock grazing, including the likelihood that targeted grazing would prevent recovery of native vegetation and soil crusts, thwarting the stated purpose of this project. WWP 2020 at 4-5.

Unfortunately, the Forest Service has not conducted any on-the-ground analysis as it relates to the use of livestock for "targeted grazing" as a fuel reduction method. In our prior comments we asked the Forest Service to disclose whether or not the 45 percent utilization for targeted grazing would be implemented regularly or rarely. WWP 2020 at 2. The Forest Service response is that "utilization should be based on site-specific resource conditions and management objectives" and to repeat that utilization will be between 15 to 45 percent. The Forest Service fails to comply with NEPA by refusing to disclose to the public whether, based on its current information and analysis, it believes that the 45 percent utilization will be frequently or infrequently necessary. Certainly, the Forest Service has some idea of the conditions on the ground now and can base a discussion around the estimated frequency of need to use 45 percent of the forage on existing conditions. Yet, the Forest Service has refused to answer this direct question.

The Forest Service has not adequately responded to our concerns, has provided no information to refute our contention that targeted livestock grazing is scientifically controversial and therefore, cannot rely upon this Decision Notice and Finding of So Significant Impact to authorize targeted livestock grazing as a part of this project.

II. The Forest Service must consider new scientific information regarding vegetation treatments and livestock grazing impacts

The Forest Service bases its "targeted" livestock grazing program on the premise that livestock will remain where the Forest Service wants them to remain. Unfortunately, and as the Forest Service is well aware, this is rarely the case. Indeed, the U.S. Department of Agriculture has just today announced a

[1] Reisner, M. D., Grace, J. B., Pyke, D. A. and Doescher, P. S. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology, 50(4): 1039-1049. doi: 10.1111/1365-2664.12097

planned rule change regarding trespass livestock grazing on Forest Service lands.[2] *See* 85 Fed. Reg. 212, 69303-69307, Monday, November 2, 2020. This new rule proposes to amend existing regulations to remove fees charged for trespass livestock and cites as a rationale a 2016 Government Accountability Office report that details the lack of the ability of federal land managers to ensure livestock graze where they are supposed to. Any analysis based on the premise that livestock will remain where they are intended to remain as part of a "targeted" grazing program must be revisited.

As the Forest Service re-examine the relationship between livestock grazing and fire, it must consider this new information:

> "Grassland-to-shrubland state transitions in drylands are the result of changes in disturbance regimes amplified or mitigated by abiotic factors related to climate and soil (Archer and others 2017). For example, livestock grazing coupled with drought reduces fine fuel mass and continuity, thus reducing the probability of fire—a disturbance that historically kept woody plants in check (Higgins and others 2007). In the absence of fire, shrubs can establish and progress to more advanced life-history stages (Higgins and others 2000). At the same time, rates of erosion typically increase with declines in grass cover in arid grasslands, depleting soil resources and concentrating them below developing shrub canopies, as well as increasing disturbance to grasses by burial and abrasion, which constitutes a positive abiotic feedback that impedes future grass recovery while promoting shrub survival (Schlesinger and others 1996; Okin and others 2009)."

Pierce *et al*., 2019.[3]

New scientific studies more definitively link the presence of livestock grazing with cheatgrass. Time-series data and results in Williamson *et al*. (2019)[4] indicate that grazing corresponds with increased cheatgrass occurrence and prevalence regardless of variation in climate, topography, or community composition, and provide no support for the notion that contemporary grazing regimes or grazing in conjunction with fire can suppress cheatgrass. This concept is applicable to the project area and invasive species of grasses that are spread by livestock use, and the Forest Service must analyze these impacts with a critical eye towards protecting natural resources. The continued spread of invasive species of plants that are likely to alter the fire regime on project area present a clear risk to native plants and wildlife.

See also, Bradley and Colodner, 2019,[5] page 11:

> Livestock grazing is now permitted on 3.6 million hectares of the Sonoran Desert ecoregion and across 1 million square kilometers of public lands in the United States. Grazing has a far greater impact on ecosystem health than do all roads, timber harvest, and wildfires combined (Beschta et al., 2013)." Soil compaction from livestock grazing has severe effects on deserts soils and has been identified as an extensive problem on US public lands (FS and BLM, 1997). This is because the weight of a 450-kg cow will exert more than five times the compacting

[2] https://www.govinfo.gov/content/pkg/FR-2020-11-02/html/2020-24164.htm
[3] Attached as Appendix B.
[4] Attached as Appendix C.
[5] Attached as Appendix D.

pressure of a bulldozer and significantly reduce the soil's ability to store water (Cowley, 2002). When the soil cannot store as much water due to compaction and reduction of plant cover due to overgrazing, increased runoff will occur during high-intensity rainfall events of the summer monsoons (Branson et al., 1981). The increased runoff causes erosion, loss of topsoil and the downcutting of streambanks and washes commonly seen in western landscapes.

III. Alternatives

In our prior comments we asked the Forest Service to consider an alternative that prohibits the use of mechanized and motorized equipment in Wilderness and IRAs as well as an alternative that eliminates livestock grazing from the project area. WWP 2020 at 8. The Forest Service did not include these alternatives in its analysis for this project. This is a violation of the National Environmental Policy Act (NEPA).

This lack of alternatives renders the analysis in the EA inadequate, precludes a FONSI, and prevented adequate public review.

IV. Violations of the Wilderness Act

In our prior comments we noted that the use of motorized and mechanized equipment would result in a violation of the Wilderness Act. WWP 2020 at 7-8. While the Forest Service has finally provided the public with the Minimum Requirements Decision Guide (MRDG), the public has had no opportunity to review and comment upon that MRDG and our cursory review finds the analysis lacking.

There is no need for the use of chainsaws in designated Wilderness areas, nor does the Forest Service need to use motorized transportation for personnel engaged in planned wildland fire management actions taking place within designated Wilderness areas. The Forest Service attempts to justify the use of chainsaws and weed-eaters by stating that these tools are "necessary" because they will "reduce firefighter time and exposure to hazards." USFS 2020 MRDG at 21. The public must assume the "risk" the Forest Service is discussing in the MRDG is the risk associated with prescribed, unplanned, or natural fire ignitions because the Forest Service does not describe the risks. The Forest Service then admits that the exposure to hazards argument is not accurately described by stating that chainsaw and weed-eater use would be for line prep, prior to any fire ignitions. *Id*. The "need" to reduce time in the field is not a legitimate excuse to violate the Wilderness Act. Given that just 19 miles of trail are to be cleared within the designated Wilderness area, the amount of time saved via the use of chainsaws and weed-eaters does not outweigh the impacts to Wilderness. If personnel will be engaged in cutting of trees or other vegetation during ignition events, the Forest Service should require that personnel use only non-motorized cutting tools and do so only when it is safe to proceed without the use of motorized chainsaws. If trees need to be cut to ensure personnel safety this should be done as much as possible prior to any ignition events.

The MRDG indicates that with the use of chainsaws the crews in the Wilderness would be present for 1-3 weeks (depending on the alternative) and that without the use of chainsaws the crews would be present for "up to a month." USFS 2020 MRDG at 25 and 32. Given the very slight reduction in the amount of time personnel will be in the field if they use loud mechanized and motorized equipment such as chainsaws and weed-eaters, which carry their own risk of fire ignition (which is not disclosed

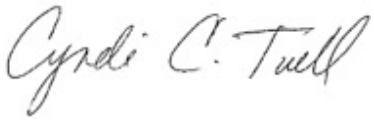
nor analyzed in the MRDG), the Forest Service should have selected Alternative 3, which authorizes fuels and vegetation treatments but prohibits the use of motorized or mechanized equipment.

Just because it would be easier or quicker does not make it legal. Therefore, the Forest Service should prohibit the use of chainsaws and weed-eaters within designated Wilderness areas as a part of this project.

Relief Requested: The Forest Service must withdraw the Draft FONSI/DN and prepare a supplemental analysis, including an EIS for this project. Alternatively, the Forest Service should modify the decision to preclude the use of livestock for "targeted grazing" and should prohibit the use of motorized and mechanized equipment in designated Wilderness areas.

Thank you for your consideration of this Objection. If you have any questions, or wish to discuss the issues raised in this objection letter in greater detail, please do not hesitate to contact me.

Sincerely,



Cyndi Tuell
Arizona and New Mexico Director
Western Watersheds Project

ATTACHMENTS
Appendix A
Comments of Western Watersheds Project submitted on May 10, 2019.

Appendix B
Pierce, N.A., Archer, S.R., Bestelmeyer, B.T., James, D.K. 2019. *Grass-Shrub Competition in Arid Lands: An Overlooked Driver in Grassland–Shrubland State Transition?* Ecosystems (2019) 22: 619–628 https://doi.org/10.1007/s10021-018-0290-9.

Appendix C
Williamson, M.A., Fleishman, E., Mac Nally, R.C., Chambers, J.C., Bradley, B.A., Dobkin, D.S., Fogarty, F.A., Horning, N., Leu, M., and Zillig, M.W., 2020. *Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass* (Bromus tectorum) *in the central Great Basin, USA*. *Biol Invasions* 22, 663–680 (2020). https://doi.org/10.1007/s10530-019-02120-8

Appendix D
Bradley, C.M., Colodner, D., 2019. *The Sonoran Desert*. Earth Systems and Environmental Sciences, Reference Module.

Appendix A

Arizona Office
738 N 5th Ave, Suite 200
Tucson, AZ 85705
tel: (520) 623-1878
fax: (208) 475-4702
email: arizona@westernwatersheds.org
web site: www.westernwatersheds.org

Working to protect and restore Western Watersheds and Wildlife

May 10, 2019

Nogales Ranger District
Attn: Jim Copeland
District Ranger
303 Old Tucson Road
Nogales, AZ 85621
Submitted this date via: https://cara.ecosystem-management.org/Public/CommentInput?project=51926

RE: Cienega Creek FireScape Project

The following comments on the Cienega Creek FiresScape Environmental Analysis (EA) are being submitted on behalf of the members of Western Watersheds Project (WWP) who are concerned with the management of our public lands. In addition to being an inappropriate level of National Environmental Policy Act (NEPA) analysis for a project this size and in this particular area, the EA here is insufficiently critical of the need to use livestock grazing in important habitat for wildlife species to "restore" wildlands or to reduce fire risk.

This project covers more than 90,000 acres of federal public lands and includes designated Wilderness, an Inventoried Roadless Areas (IRA), sensitive wildlife habitat, and habitat for species listed as threatened and endangered. EA at 1. The geographic and temporal scope along with the special designations and species found in this area, combined with the proposal to use mechanized and motorized equipment in designated Wilderness and the long-term use of herbicides throughout the project area, require the development of an Environmental Impact Statement (EIS) and preclude a Finding of No Significant Impact (FONSI).

The stated purpose of this project is to:

- Reduce fuel accumulations and uncharacteristic vegetation composition and structure in the Santa Rita Ecosystem Management Area that contribute to the risk of large, high intensity wildfire and the associated negative effects.
- Restore and sustain ecological processes in fire-dependent ecosystems, to enhance the overall health and resiliency of desired native plant and tree species to improve habitat for wildlife and forage for range and wildlife.

- Facilitate fire management within the project area to provide for public and firefighter safety and ability to manage natural ignitions to achieve desired Land and Resource Management Plan objectives and create conditions that enable naturally occurring fires to return to their historic role.

- Provide protection to values at risk within the project area, including, but not limited to, wildland-urban interface (WUI) communities and Forest Service (FS) infrastructure.

EA at 2. Unfortunately, the proposed action would not accomplish these goals, but would further exacerbate the spread of invasive non-native species of plants and the risk of fire.

Citing the Forest Plan, the EA for this project tries to justify the need for this project: "The Forest Plan objective for WUI is: 'treat 5,000 to 10,000 acres in the wildland-urban interface using wildland fire (planned and unplanned ignitions), prescribed cutting, and mastication every year to reduce fire hazard and risk to communities and the forest.' (Forest Plan, p. 23)." EA at 3. Notably, the Forest Plan does NOT call for livestock grazing as a WUI treatment. Yet this plan does call for the widespread use of livestock grazing to reduce fire risk. "Prescribed Grazing" (using targeted grazing in two treatment units to reduce fuel in WUI areas) would cover over 18,000 acres:

> Targeted grazing would be used as a management tool under specified conditions to remove fuel from predetermined WUI areas. Utilization standards and numbers would not be increased, and grazing permits would not change as part of this project. However, through range management practices in key locations with high fire risk and suppression difficulty at least one mile from the forest boundary, grazing utilization would increase but not pass the maximum 45% utilization standard due to improved livestock distribution in these target WUI areas.

EA at 4 and 6. And while "forage utilization should be based on site-specific resource conditions and management objectives" and "in general should be managed at a level corresponding to light to moderate intensity (15 to 45 percent of current year's growth)" according to the Forest Plan (at page 91), it appears that for this project the maximum end of the utilization (45 percent) is anticipated. Please clarify whether 45 percent utilization for targeted or prescribed grazing is expected to be implemented rarely, or regularly and disclose whether this would be in violation of the current Forest Plan.

As the Forest Service is aware, weather is a key part of this proposed project.

> Weather factors, limited operating periods, recent fire events, and available funding would dictate the amount and type of activities that might be applied in any given year. Anticipated treatments include wildland fire (planned and unplanned), hand thinning, mechanical treatments, and herbicide application, in addition to targeted fuels removal through grazing and fuelwood permits. Projects would be implemented incrementally over a period greater than 20 years.

EA at 4. However, the EA does not identify the weather conditions required for targeted grazing to be effective and safe.

Lack of NEPA Analysis in the Project Record

The analysis found in the EA is dependent on analysis supposedly located elsewhere, but that WWP cannot confirm the existence of:

> *The impacts* resulting from grazing not to exceed the maximum 45% utilization standard ***have already been analyzed*** for all of the proposed treatment units that include prescribed grazing. This **proposed action would not cause impacts that exceed the scope and range of effects analyzed *in these previous environmental assessments***.

EA at 30, emphasis added. And:

> Past disturbance could be fire, but the pervasive nature is more likely due to heavy grazing pressure. Currently, the entire project area is under grazing management. Grazing utilization standards and numbers would not be increased under the proposed action, ***but would instead be targeted within existing grazing permit specifications*** to remove fuel.

EA at 19, emphasis added. And:

> ***The impacts resulting from grazing*** not to exceed the maximum 45% utilization standard ***have already been analyzed for all of the proposed treatment units*** that include prescribed grazing. ***This proposed action would not cause impacts that exceed the scope and range of effects analyzed in these previous environmental assessments***:
>
> • Temporal Allotment Coordinated Ecosystem Restoration Project
> • Allotment Management Plan for Gardner Allotment[1]
> • Allotment Management Plan for Debaud, Greaterville, Rosemont Allotments
> • Santa Rita West Ecosystem Management Area Allotment Management Plan for Agua Caliente, Alto, Box Canyon, Proctor, and Stone Springs Allotments

EA at 22-23, emphasis added. WWP cannot find any information on the Forest Service website regarding any of these allotments, other than the Gardner Allotment, which does not have a signed final decision document available. The Forest Service should have included information from the EAs for all of these allotments in the EA for this project. Additionally, there are no AOIs available for this ranger district on the Forest Service website.

The Forest Service has not in any way analyzed the impacts of targeted or prescribed grazing ***in this EA*** and has not provided the public with information on where to find the existing grazing management documents. There is no clear indication of what the current AUM allocation is now, how those AUMs will change, or whether any grazing infrastructure will be modified or added. These oversights must be corrected and precludes a FONSI at this time.

This leaves unanswered questions, including:

> Who is/are the permittee/permittees?

[1] Note that this AMP was located but is in a draft form from 2018 and there is no signed final decision document for this allotment.

Would the permittee have to pay AUM rates and what would those AUM rates be? Is the permittee/are the permittees in good standing?

Does the permittee hold the requisite base property for the allotment?

Best Available Science

A study conducted in Arizona found that fire-control benefits from targeted grazing occur only when wind speeds are 5 m.p.h. or less. Bruegger, *et al*. 2016. Such conditions generally do not lead to large, out-of-control wildfires. The level of grazing needed to affect fire behavior would, in all likelihood, prevent recovery of native vegetation and soil crusts. Launchbaugh et al. (2008) found that the level of grazing required to influence fire behavior causes unacceptable impacts to habitat.

In general, researchers have found that "[r]educing fuel loads" in forests "has little, if any, benefit for protecting structures and communities from wildfires." Bracmort 2013. Fuels treatments "can leave slash on the ground, [and] increase[e] fire hazards at least in the short-run." *Id*. In one study, "rate of spread and flame length" in forest fires "were positively correlated with the proportion of area logged in the sample watersheds." Gedalof *et al*. 2005.

Additionally, the analysis of impacts from targeted or prescribed grazing on recreation are incomplete. There is no description of how year-round livestock grazing impacts forest recreational users and the impacts on "visitors who prefer to camp away from livestock and their effects (e.g. feces, concentration at water sources)" are artificially minimized with the statement "the presence of animals could have a negative effect[.]" EA at 37. Furthermore, the analysis of the impacts of targeted or prescribed grazing are inconsistent. They are described in one area of the EA as the same as current grazing impacts (which are not disclosed in this EA), but at page 37 the impacts appear to be more targeted or site and time specific. The Forest Service must clarify exactly how the targeted or prescribed grazing proposal differs from the existing grazing program. Similarly, just because "visitors are generally used to seeing some form of livestock grazing" does not mean that the impacts are minimal or unimportant. EA at 37.

Please explain why the Forest Service believes this project will be successful in light of the 2003 McClaren report indicating that "burroweed cycles appear to be more closely related to winter precipitation patterns and maximum plant longevity than land management activities. Similarly, the increase of Lehmann lovegrass is largely independent of livestock grazing management. McClaran *et al*. 2003. Mesquite density seems unchanged as a result of fire regimes as well and is spread via livestock grazing. *Ibid.* And, "[s]imilar to burroweed, the eruption of cholla and recent increases of prickly pear appear to be largely independent of livestock grazing and fire manipulations." *Id*. at 26. Declines of cholla and increase of prickly pear between 1972 and 1984 were no different in areas with yearlong versus seasonal rotation of grazing. *Ibid*. Fire produced only a short-lived decline of cactus density and within 10 to 13 years after fire the cactus density exceeded that which existed prior to the fires. *Ibid*.

Livestock grazing promotes the spread and colonization of alien plants, which can increase fire frequencies. Billings 1990, Billings 1994, Rosentreter 1994, Belsky and Gelbard 2000, Kimball and

Schiffman 1993. Disturbance is a reliable indicator of alien dominance in vegetation composition, and livestock grazing is a significant disturbance. Brooks and Berry 2006. Further, weed invasions are strongly associated with livestock watering sites. Brooks et al 2006. The Forest Service has not adequately addressed this issue and, in addition, must analyze the cause and effect relationship of livestock grazing with the woody vegetation. See, e.g. Bahre and Shelton 1993.

Disturbed soils with fewer intact soil crusts favor invasive annual plants like cheatgrass and medusahead over native perennial grasses and forbs. Reisner *et al*. (2013) found "strong evidence" that livestock grazing indirectly increases cheatgrass dominance by: increasing native bunchgrass abundance, shifting bunchgrass composition, increasing gaps between perennial plants, and damaging biological crusts. Cheatgrass invasion has in turn been found to increase fire frequency and severity.

WWP is concerned that the Forest Service may be forging ahead with a project that is designed to increase non-native invasive species instead of reaching the stated goal of the project, which is to reduce non-natives and therefore the risk of fire. However, the effects of fire as reported in McClaran et al 2003 indicate that native grass abundance decreases following fire, and the recovery is dependent on subsequent growing conditions while seed germination of the non- native lovegrass increases after fire. *Id*. at 30.

The Analysis is Generally Inadequate

The impacts of livestock grazing on cultural resources is not described at all. The impacts of livestock on cultural resources is well known[2] and the Forest Service must amend this EA, or preferably prepare an EIS, to include the identification, disclosure and analysis of the impacts of livestock grazing – both ongoing and as modified for targeted and prescribed grazing – throughout the project area. Appendix A of the EA does not include any design features to reduce the impacts of livestock grazing on cultural resources. EA at 42-44.

The use of targeted or prescribed grazing is not adequately analyzed in the EA. There is no information regarding AUMs, season of possible use, pasture rotation, if any, or the need for water developments or supplemental feeding.

Why is this project necessary given that for the Gardner allotment (and presumably other allotments) the purpose of that grazing authorization was to correct the effects of historic grazing? Why does the Forest Service believe that continued livestock grazing is the solution to the problems caused by livestock grazing?

There is insufficient analysis of the impacts of prescribed grazing on the hydrology of the project area. EA at 19. The Forest Service must identify how livestock grazing and related infrastructure and any water pumping will impact hydrology.

There is insufficient analysis of the impacts of this project on butterflies and bees. This analysis must be included and expanded.

[2] See, for example, page 15 of the Gardner Allotment Draft EA. These impacts include trampling, breaking, knocking down standing features.

General Questions

What model was used to determine the potential fire behavior for the existing condition?

What percent of large diameter trees, snags, and shrubs will remain following fuel treatments in the project area? Are large paniculate agaves present and if so, how many (by percent) will remain on the landscape post-treatments?

Why is the Gardner allotment being proposed as part of this project given that the Draft EA for this allotment indicates that 60% of the allotment is in high ecological condition and the remaining 40% is in mid ecological condition? Gardner Allotment DEA at 5. How will implementation of this project affect ecological condition?

For the Gardner allotment, given that the EA for this allotment is not signed, please explain the status of all livestock improvements and explain whether waters and/or pipelines would need to be constructed/installed for this project or whether they have already been constructed/installed (despite no signed decision for this allotment). Because WWP can find no information on the other nine allotments that are a part of this project, please also provide that same information for each of the 9 allotments. How does targeted or prescribed livestock grazing differ for this project as compared to the signed decisions for each of the allotment.

What level of utilization would be necessary to make targeted grazing an effective tool for fire reduction

What is chance you will be able to repeat/retreat the area to ensure fuel reduction?

Who is paying for this "treatment" – the Forest Service? The permittee/permittees? Another entity?

How is grazing infrastructure a part of this project? Who pays for it? What is it exactly and where? Who will maintain it? Is it permanent?

Is the true impetus for this project to improve the project area as a livestock feedlot?

How will converting the project area from a shrub and woody species dominated area to a grassland affect soil storage of CO2?

Please explain why there is no alternative that excludes livestock grazing for entire area.

How did the Forest Service make a fire history determination?

Please identify areas where prescribed fire is "not feasible." EA at 8.

This Project Requires the Development of an EIS

The use of an EA for this project fails to comply with National Environmental Policy Act requirements. The proximity to and overlap with specially designated areas require a higher level of analysis in light of the intensity and context of this specific project. Similarly, the presence of federally

listed species and their habitat covering vast swaths of the project area raise the level of analysis necessary to ensure compliance with federal regulations. *See* 40 C.F.R. §§ 1508.27(a) (context), b (intensity)).

In addition to the scientific and political controversy surrounding fuel reduction/treatment projects, prescriptive or targeted grazing, this area is home to threatened and endangered species and designated Wilderness which prohibits the use of motorized and mechanized equipment, which is planned for this project (hand thinning of 688 acres using chainsaws and weed-eaters in the Mt. Wrightson Wilderness for "prescribed fire"). EA at 7.

Wilderness and Inventoried Roadless Areas

In 1964, Congress passed the Wilderness Act "to secure for the American people of present and future generations the benefits of an enduring resource of wilderness." The law provided statutory protections for wilderness areas and established the National Wilderness Preservation System. The Act, among other things, mandated that wilderness areas be administered in a manner that will leave them "unimpaired for future use and enjoyment as wilderness" and that will provide for "the protection of these areas" and "the preservation of their wilderness character."

The Wilderness Act defines "wilderness" in part: "A wilderness, in contrast with those areas where man and his works dominate the landscape, is hereby recognized as an area where the earth and its community of life are *untrammeled by man*, where man himself is a visitor who does not remain." Wilderness is "land retaining its *primeval character and influence*, without permanent improvements or human habitation, which is protected and managed so as to *preserve its natural conditions*…"[3] In addition, wilderness should be "*affected primarily by the forces of nature, with the imprint of man's work substantially unnoticeable*."

Grazing is recognized as a nonconforming use. The language in the Wilderness Act and the subsequent grazing guidelines do not mean livestock grazing must occur at any cost, rather, decisions about livestock grazing won't rest *solely* on whether an area is designated as Wilderness. For example, a decision to close sheep allotments to protect bighorn sheep, as was done on the Payette National Forest, was made regardless of whether the allotments in question were Wilderness or not (most, if not all, were not).

At this stage of the project, no Minimum Requirements Decision Guide or Minimum Requirements Analysis has been done, but at some point "will be" done. EA at 7:

> Treatments within the 25,121-acre Mount Wrightson Wilderness include approximately 13,253 acres of wildland (planned and unplanned) fire. Treatment is needed in this portion of the wilderness, and boundaries have been identified to allow treatment unit boundaries to follow existing trails and natural control features, such as ridgelines, which best provide for firefighter safety during prescribed burning activities. In the long term, fire would transition from prescribed fire treatments to unplanned ignitions to restore natural fire across the landscape.
>
> Prescribed fire within the Mount Wrightson Wilderness would be conducted using tools prohibited under Section 4(c) of the Wilderness Act. Therefore, a Forest Service Minimum

[3] 16 U.S.C. 1131(c) (emphasis added).

> Requirements Decision Guide would be used to plan treatments on NFS lands in wilderness. The guide provides the information for the Regional Forester to determine whether or not action is necessary to meet the minimum requirements for administration of the wilderness area and, if so, which actions are the minimum necessary.
>
> Prohibited tools, including chainsaws and weed-eaters, would be used to reduce firefighter time and exposure to hazards in extremely rugged terrain. Chainsaws and weed-eaters would be used for fire control line preparation and as a safety precaution during ignition and holding efforts. Due to the number of snags and other down woody debris that would need to be cut beneath snags, it is critical, for the safety of firefighters, to minimize the length of time preparing or holding lines. Chainsaw and weed-eater use for line prep would be limited to improving existing trails and natural control features, with a 150 foot buffer on each side of the control features, totaling about 688 acres in the Hopkins, Wrightson, and Josephine- Temporal units, or less than 3% of the Mount Wrightson Wilderness.

This EA fails to analyze the impacts to Wilderness and IRAs individually and, as such, the analysis of and impacts to Wilderness and IRAs is not fully disclosed. This lack of analysis in a specially designated area precludes a FONSI.

Additional NEPA Violations

The range of alternatives is insufficient. The Forest Service should have considered: 1) an alternative that prohibits use of mechanized and motorized equipment in Wilderness and IRAs; and 2) an alternative that would have eliminated livestock grazing in the project area to facilitate analysis regarding livestock grazing's impacts on fire susceptibility, especially the continued proliferation of non-native invasive plants. The single most effective thing the Forest Service could do to stop the spread of non-native invasive plants and reduce fire risk is to eliminate livestock grazing throughout the forest.

WWP strongly recommends the Forest Service select the No Action Alternative for fuel treatment in Wilderness and Inventoried Roadless Areas. Especially in Wilderness areas, natural processes should be allowed to play out and the use of mechanized or motorized equipment to unnaturally modify the environment should be prohibited.

WWP's final question for the Forest Service is whether this project will impact the ongoing research on the Santa Rita Experimental Range? If so, are the uncertain and probably temporary effects of this project worth the potential losses to the scientific community?

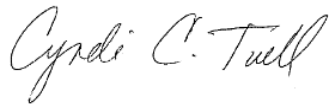
> The most incontestable conclusion from this century of vegetation change is that future changes cannot be perceived and understood if there are no records of previous conditions. An equally important conclusion is that the response of vegetation to management practices will be contingent on past and future precipitation patterns, elevation and soils at the location, and the current mix and vigor of plant species.

McCalan 2003, at 31. With this in mind, it is imperative that the Forest Service act cautiously and responsibly and acknowledge that livestock grazing played a large role in the current conditions of this

project area and it is unlikely that continued, more intense, or more frequent livestock grazing will restore this area. We simply cannot graze our way out of these problems.

As we note above, the sheer scope of this project clearly precludes the use of an EA and there are many reasons that a Finding of No Significant Impact is inappropriate. Therefore, Western Watersheds Project encourages the Forest Service to revise the existing environmental analysis to correct the deficiencies we have identified above. We look forward to reviewing the next step in this NEPA process for this project.

Sincerely,



Cyndi Tuell
Arizona and New Mexico Director
Western Watersheds Project

REFERENCES

Bahre, C.J. and M.L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* 20(5): 489-504.

Belsky, A.J., and J.L. Gelbard. 2000. Livestock Grazing and Weed Invasions in the Arid West. Oregon Natural Desert Association: Portland, OR. April. 31 pp.

Billings, W. D. 1990. Bromus tectorum, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301-322 in G. M. Woodwell, editor. The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press New York.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Pp. 170-175 in Monsen, S. B. and S. G. Kitchen (compilers), Proceedings – Ecology and Management of Annual Rangelands. General Technical Report INT-GTR-313. US Department of Agriculture, Forest Services, Intermountain Research Station, Ogden, UT.

Bracmort, Kelsi. Wildfire Fuels and Fuel Reduction, Congressional Research Service (Dec. 17, 2013).

Brooks, M. L. and K. H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, U.S.A. Journal of Arid Environments 67 (2006) 100-124.

Brooks, M. L., J. R. Matchett, K. H. Berry, 2006. Effects of livestock watering sites on alien and native plants of the Mojave Desert, U.S.A. Journal of Arid Environments 67 (2006) 125-147.

Bruegger, Retta A. et al., 2016. Targeted Grazing in Southern Arizona: Using Cattle to Reduce Fine Fuel Loads, 69.1 Rangeland Ecology & Management 43 (2016).

Gedalof, Ze'ev, D.L. Peterson, N.J. Mantua, Atmospheric, Climactic, and Ecological Controls on Extreme Wildfire Years in the Northwestern United States, 15(1) Ecological Applications 154 (2005).

Kimball, S. and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. Conservation Biology: 17(6): 1681-1693.

Launchbaugh, K., B. Brammer, M.L. Brooks, S. Bunting, P. Clark, J. Davison, M. Fleming, R. Kay, M. Pellant, D.A. Pyke, and B. Wylie. 2008. Interactions Among Livestock Grazing, Vegetation Type, and Fire Behavior in the Murphy Wildland Fire Complex in Idaho and Nevada, U.S. Geological Survey Open-File Report 2008-1214 (July 2007), available at: http://pubs.usgs.gov/of/2008/1214/pdf/ofr20081214.pdf.

McClaran, Mitchel P.; Ffolliott, Peter F.; Edminster, Carleton B., tech. coords. Santa Rita Experimental Range: 100 years (1903 to 2003) of accomplishments and contributions; conference proceedings; 2003 October 30–November 1; Tucson, AZ. Proc. RMRS-P-30. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Reisner, Michael D. et al., Conditions Favouring Bromus Tectorum Dominance of Endangered Sagebrush Steppe Ecosystems, 50.4 J. Applied Ecology 1039 (2013).

Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. Pp. 170-175 in Monsen, S. B. and S. G. Kitchen (compilers), Proceedings – Ecology and Management of Annual Rangelands. General Technical Report INT-GTR-313. US Department of Agriculture, Forest Services, Intermountain Research Station, Ogden, UT.

Appendix B

Ecosystems (2019) 22: 619–628
https://doi.org/10.1007/s10021-018-0290-9

Grass-Shrub Competition in Arid Lands: An Overlooked Driver in Grassland–Shrubland State Transition?

Nathan A. Pierce,[1]* Steven R. Archer,[1] Brandon T. Bestelmeyer,[2] and Darren K. James[2]

[1]*School of Natural Resources and the Environment, University of Arizona, ENR2 - N325, 1064 E Lowell St, Tucson, Arizona 85721, USA;* [2]*United States Department of Agriculture-Agricultural Research Service Jornada Experimental Range, Jornada Basin Long Term Ecological Research Program, New Mexico State University, Las Cruces, New Mexico 88003, USA*

Abstract

Traditional models of state transition in arid lands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland, whereas biotic interactions like competition and facilitation are often overlooked. Here, we conducted an experiment to determine whether shrubs have a positive, neutral, or negative effect on grasses and if these interactions may play a role in grassland–shrubland state transition. *Prosopis glandulosa* shrub neighbors within 5 m of *Bouteloua eriopoda* grass patches were left intact (controls) or killed with foliar herbicide, and metrics of grass performance were evaluated over 5 years. We saw no evidence of shrub facilitation of grasses. Instead, grass ANPP responded positively to shrub removal in all years, but more so in years with above-average rainfall. Grass allocation to vegetative reproduction and grass patch size also increased when shrub neighbors were removed. These results demonstrate that biotic interference by shrubs upon grasses reinforce and magnify grazing- and drought-induced abiotic feedbacks during grassland–shrubland transitions. Shrub effects on grass should therefore be considered a key process in desert grassland state transitions.

Key words: *Bouteloua eriopoda*; Chihuahuan desert; Competition; Grassland; *Prosopis glandulosa*; Shrubland; State transition; Woody plant encroachment.

Highlights

- Grasses with shrub neighbors have lower productivity than grasses without shrub neighbors.
- The competitive effect of shrubs on grasses was also evident in allocation to reproductive structures and grass patch size/continuity.

Received 6 April 2018; accepted 29 July 2018;
published online 21 August 2018
Author Contributions NAP, SRA and BTB conceived of the study and designed the research; NAP conducted the research; DKJ and NAP analyzed the data; NAP and SRA wrote the manuscript; NAP, SRA and BTB edited the manuscript.

**Corresponding author; e-mail:* npierce@email.arizona.edu

- Shrub-on-grass competition can reinforce and amplify abiotic feedbacks during grassland–shrubland state transition.

Introduction

Arid and semiarid grasslands worldwide have undergone state transitions from grassland to shrubland dominated by xerophytic, unpalatable shrubs and bare ground. This transition can represent landscape degradation with regard to primary production (Knapp and others 2008), erosion and nutrient loss (Li and others 2008), biodiversity (Ratajczak and others 2012), and forage production (Fredrickson and others 1998), although specific patterns and interpretations vary globally (Eldridge and others 2011). Grassland-to-shrubland state transitions in drylands are the result of changes in disturbance regimes amplified or mitigated by abiotic factors related to climate and soil (Archer and others 2017). For example, livestock grazing coupled with drought reduces fine fuel mass and continuity, thus reducing the probability of fire—a disturbance that historically kept woody plants in check (Higgins and others 2007). In the absence of fire, shrubs can establish and progress to more advanced life-history stages (Higgins and others 2000). At the same time, rates of erosion typically increase with declines in grass cover in arid grasslands, depleting soil resources and concentrating them below developing shrub canopies, as well as increasing disturbance to grasses by burial and abrasion, which constitutes a positive abiotic feedback that impedes future grass recovery while promoting shrub survival (Schlesinger and others 1996; Okin and others 2009). Inherent in these scenarios is the implicit assumption that grass-shrub interactions in arid grasslands are of little or no significance after shrubs have established. However, this assumption has not been widely tested or rigorously evaluated.

Grass-shrub interactions may be dismissed as a driver of state change in arid lands under the presumption that selection pressures favor adaptations for stress tolerance over competitive ability (Grime 1977; Brooker and Callaghan 1998). Accordingly, a growing body of research supports the notion that facilitation takes precedence over competition with increasing environmental stress (Maestre and others 2009; Dohn and others 2013). This framework helps explain the coexistence of grasses and woody plants in some systems, whereby woody plants facilitate understory grasses via ameliorating harsh environmental conditions (Ludwig and others 2004b) or by providing refugia from grazers (Howard and others 2012). However, in grassland–shrubland transitions, shrub-on-grass facilitation must be eclipsed by other factors detrimental to grass survival, including shrub-on-grass competition. The predominance of facilitation versus competition might also change along a continuum of woody plant abundance, that is, competition increases with increasing shrub size and density (Scholes 2003; Vander-Yacht and others 2017).

The predominance of competition versus facilitation in grass-shrub interactions may also vary at fine spatial scales. Certain xerophytic shrub species have extensive shallow lateral roots (Gibbens and Lenz 2001) and may therefore interact with grasses occurring well beyond their canopies. Such shrubs could facilitate grasses via hydraulic redistribution (Priyadarshini and others 2016). However, shrub lateral roots could also have a negative effect on grasses by utilizing soil resources that grasses would otherwise obtain (Ludwig and others 2004a). In situations where grass and shrub rooting niches are segregated spatially (Walker and others 1981; Ward and others 2013), or where phenology separates their activity patterns temporally, shrubs may have no influence on neighboring grasses (Golluscio and others 1998; Ludwig and others 2001). Net neutral interactions could also occur if competitive and facilitative processes are in balance (Maestre and others 2009). Neutral interactions would support the prevailing assumption that grass loss and shrub proliferation in the course of grassland–shrubland transition are driven primarily by interrelationships among climate, disturbance (grazing, fire), and soil erosion.

Here, we report the outcome of a 6-year field experiment aimed at quantifying grass-shrub interactions to ascertain if shrubs have a positive (facilitation), neutral, or negative (competition) effect on grass production beyond their canopies. We hypothesized that the production of grasses occurring in the vicinity of shrubs with extensive, shallow lateral root systems would be reduced owing to the predominance of competitive interactions. Knowledge of the direction and strength of the influences of shrubs on grasses growing beyond their canopies would help us predict grass patch capacity to recover from disturbance and the extent to which shrub interactions with grasses might either dampen or reinforce abiotic feedbacks during grassland–shrubland state transitions. Support of the hypothesis that shrubs have no discernible effect or a positive effect on grasses would corroborate the prevailing view that competitive grass-shrub interactions are of little consequence compared to facilitation or abiotic drivers. We offer three alternative predictions in testing these

hypotheses regarding shrub effects on grasses: (1) no effect, which would suggest abiotic processes triggered by grazing-induced grass losses and subsequent soil erosion are responsible for grassland–shrubland transitions (Okin and others 2006); (2) a positive effect due to hydraulic lift, from which we would infer grasses might be more persistent in the face of grazing and drought stress; and (3) competition, wherein the presence of shrubs would amplify stresses on grasses imposed by grazing and drought.

Methods

Study Area

The field experiment was conducted on the USDA Agricultural Research Service Jornada Experimental Range (JER), which hosts the Jornada Basin Long-Term Ecological Research (LTER) site, approximately 37 km north of Las Cruces, NM, in the northern Chihuahuan Desert (UTM 13S 336659 3610160; 1325 m a.s.l.; https://jornada.nmsu.edu/lter). The climate is arid (Köppen Climate Classification BWk), with long-term (1926–2015) mean annual precipitation (PPT) of 241 mm (SE ± 9.6, CV = 36%), approximately 65% of which occurs in July–October. June is the warmest month (mean minimum of 17°C and mean maximum 36°C); January is the coldest month (mean minimum and maximum of − 6 and 4°C, respectively).

The study was conducted along a grassland-to-shrubland gradient, reflecting the ongoing spread of shrubs and consequent spatial variations in the rate of state transitions (Bestelmeyer and others 2011). One end of the 3 km × 1 km study area (UTM 13S 334878, 3601198) was grassland dominated by the C_4 perennial grass *Bouteloua eriopoda* (Torr.) Torr. (26% foliar cover), which is a stoloniferous bunchgrass that proliferates via axillary tillers from the genet, as well as stoloniferous ramets. The grassland end was also populated with small, scattered C_3 *Prosopis glandulosa* (Torr.) shrubs (2% canopy cover). The opposing end (UTM 13S 333764, 3604817) was shrubland, with *B. eriopoda* foliar cover of 4% and *P. glandulosa* canopy cover of 18%. Soils are fine-loamy, mixed, thermic Typic Haplargids and Typic Petrocalcids underlain by a petrocalcic horizon 64 to 76 cm beneath the surface (Havstad and Schlesinger 2006).

Experimental Design

Ninety plots were established in 2010 in a stratified random fashion at locations along the grassland–shrubland continuum, ensuring 30 plots within the grassland, the ecotone, and the shrubland portions of the gradient. Plots with a fixed radius of 5 m were centered upon 1 × 1 m subplots containing a *B. eriopoda* patch. Only grass patches with at least one *P. glandulosa* shrub within the 5 m plot radius were chosen. Target grass patches therefore had a broad range of shrub neighborhood configurations, that is, few, small shrub neighbors in the grass-dominated segments of the transect and numerous, larger shrub neighbors in the shrub-dominated segment. Grass patch size and shape was quantified within a grid of 25–20 × 20 cm cells in the 1 × 1 m subplots at the end of the 2010 growing season (October, near peak production) by counting the number of cells occupied by *B. eriopoda*. Clonal reproductive output (number of ramets) was also quantified at this time. Grasses in the entire subplot were then clipped to a height of 10 cm, and current year's biomass was dried and weighed to estimate aboveground annual net primary productivity (ANPP). These measurements were repeated in October of 2011–2013 and 2015 (measurements were not taken in 2014).

The volume of all *P. glandulosa* shrubs within the 5 m radius of each plot was determined in the spring of 2011 by measuring canopy diameter along the longest axis and the diameter perpendicular to the midpoint of the longest axis, as well as plant height. Aboveground ANPP was then determined using a site- and species-specific allometric regression (R^2 = 0.89, Gherardi and Sala 2015).

All *P. glandulosa* shrubs located within 45 randomly selected plots were killed in June 2011, prior to the summer rainy season, using a foliar herbicide solution (0.5% triclopyr, 0.5% clopyralid, and 5% diesel fuel) applied in a fine mist. The herbicide mixture was effective at defoliating shrubs within 2 weeks of spraying, and no new growth was observed for the remainder of the growing season. Targeted spot-spraying was conducted as needed to suppress new basal shoots (which typically emerged from only the largest of shrubs) in 2012 and 2013, after which no regrowth occurred.

Data Analysis

Overall treatment effects on *B. eriopoda* aboveground ANPP were analyzed using repeated-measures linear-mixed effects models (PROC MIXED; SAS V9.4; SAS Institute, Cary, NC, USA). Shrub removal, year, and their interaction were fixed effects; year was also a repeated effect with plot as the subject. A heterogeneous Topelitz temporal covariance model was used based on Akaike's

Information Criterion (AIC_c). The Kenward–Roger method was used to adjust denominator degrees of freedom to account for bias associated with estimating the fixed effects after the repeated effect. All fixed effects were highly significant; because of the highly significant shrub removal × year interaction, interpretations of the main effects are qualified by year.

We also examined the relationship between *B. eriopoda* ANPP and PPT by regressing annual, growing season (July–October) and dormant season (November–June) PPT (independent variable) against *B. eriopoda* ANPP (dependent variable) and calculating the treatment × PPT interaction coefficients (JMP, Version 13. SAS Institute, Cary, NC, USA). As antecedent precipitation can be a better predictor of current year's ANPP (Sala and others 2012), we also conducted this analysis for previous year's PPT.

ANOVA was used to compare the number of non-stoloniferous and un-rooted stoloniferous ramets on plots with intact and killed shrubs; Tukey's HSD was used to test for significant differences among treatments and years.

Finally, we sought to determine if differences in ramet production translated into changes in grass patch size and continuity over the course of the experiment. We approached this using repeated-measures linear-mixed effects models as described above, but using a heterogeneous compound symmetry covariance structure, which was the best fit based on AIC_c. The response variable was the number of 20 cm × 20 cm cells within the 1 m^2 subplot that was occupied by *B. eriopoda*. An increase in the number of cells occupied over time would reflect net ramet recruitment and genet patch infilling and/or expansion; a decrease in cell occupation would be indicative of patch fragmentation and/or contraction.

Results

Precipitation patterns varied considerably over the course of the experiment (Figure 1). Drought occurred during the first 2 years of the study with annual PPT 54% (2011) and 50% (2012) below the long-term (1926–2015) mean. Similarly, growing season (July–October) PPT was 33% below average in 2011 and 55% below average in 2012. Annual PPT in 2013 and 2014 approximated the long-term average, but growing season PPT was 41 and 37% higher than the long-term mean, respectively. Annual PPT in 2015 was 15% higher than the long-term average, while growing season PPT was near average.

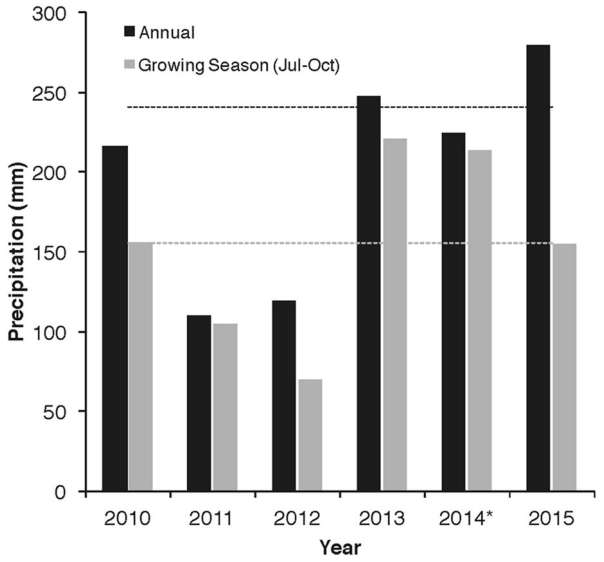


Figure 1. Annual (*black*) and growing season (July–October, *gray*) precipitation (PPT) over the course of the experiment. The *dashed black* and *gray* lines represent long-term (1926–2015) annual and growing season mean PPT, respectively. (*Plot data was not collected in 2014).

B. eriopoda aboveground ANPP in 2010 on control plots and plots slated for shrub removal was nearly identical (Figure 2). Subsequent to shrub

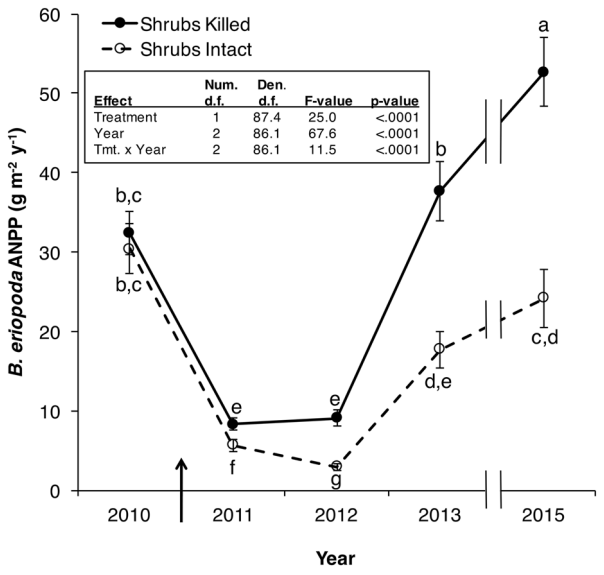


Figure 2. *Bouteloua eriopoda* aboveground ANPP in plots with neighboring shrubs intact (*open circles*) or killed (*closed circles*). Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects. The arrow between 2010 and 2011 designates when shrub neighbors were killed in treatment plots. Data were not collected in 2014.

removal, grass ANPP varied by an order of magnitude in both control and treated plots over the course of the 6-year experiment in response to inter-annual variation in PPT (Figure 1). For example, mean (± SE; g m^{-2} y^{-1}) ANPP in control plots was 2.9 (0.7) during the dry year of 2012 and increased to 24.2 (3.9) in the above-average PPT year of 2015.

The presence of shrub neighbors mediated grass ANPP response to precipitation (Figure 2). During the dry period (2011–2012), control plots with shrub neighbors intact had significantly reduced *B. eriopoda* ANPP compared to treatment plots with shrub neighbors killed. Upon return to average and to above-average PPT conditions in 2013 and 2015, differences in grass ANPP between treatment and control plots were amplified: mean *B. eriopoda* (± SE; g m^{-2} y^{-1}) ANPP was 19.9 (4.4) and 28.1 (5.6) higher in plots with shrubs killed than in plots with shrubs intact in 2013 and 2015, respectively.

B. eriopoda ANPP was directly related to PPT in both control and treatment plots. However, *B. eriopoda* ANPP was more responsive to PPT in plots with shrub neighbors killed than in control plots with shrub neighbors intact. This was true for annual PPT, growing season PPT, and dormant season PPT (Figure 3). There was no significant relationship between *B. eriopoda* ANPP and previous year's annual PPT in either the control or treatment plots ($F = 2.07$; $df = 1$; $P = 0.152$; data not shown).

Allocation to clonal reproduction, measured by the number of ramets produced per plot, was near zero in the dry years of 2011–2012 on control and treated plots. During the wet years of 2013 and 2015 ramet production increased, but more so on plots where shrubs had been killed than on plots where shrubs were intact (Figure 4). Vegetative production of axillary tillers also differed in 2013, where the mean number of tillers was significantly higher in plots with shrub neighbors killed than in plots with shrub neighbors intact (Table 1). Despite this difference in tiller number, average ANPP per tiller did not differ between control and treatment plots ($P = 0.37$).

Ramet production, in concert with axillary tiller proliferation, translated into changes in grass patch size over the course of the experiment (Figure 5). Where shrubs were present, the mean number of 20 cm × 20 cm cells within the 1 m^2 subplot occupied by *B. eriopoda* decreased from 2011 to 2012, was stable through 2013 and then returned to 2011 levels by 2015. Conversely, where shrubs had been killed, *B. eriopoda* cell occupancy was maintained through the 2011–2012 dry period and subsequently increased to reach levels 65% higher in 2015.

Discussion

Our results support the hypothesis that competitive effects of shrubs on perennial grasses play an important role in the progression of grassland–shrubland transitions. Shrubs in this Chihuahuan Desert system were relatively short-statured (mean height = 0.6 m, mean canopy diameter = 1.5 m), and focal grass patches occurred well beyond their canopies. Consequently, aboveground interactions related to light competition or temperature amelioration were not likely to have been important. Rather, competitive interactions between grasses and shrubs must have occurred for belowground resources. The presumption of competition for soil water is reflected in the fact that the presence of shrubs significantly reduced grass production during dry periods (2011, 2012) and moderately (2013) to substantially (2015) constrained grass responses to increased rainfall (Figure 2).

Further evidence of belowground competition is demonstrated in the relationship between grass ANPP and PPT. The grass ANPP response to precipitation was positive on plots with and without shrubs; however, this trend was more pronounced for grasses without shrub neighbors than for grasses with shrub neighbors (Figure 3). The contrasting slopes of the ANPP versus PPT lines suggest the competitive influence of *P. glandulosa* shrubs on *B. eriopoda* grasses strengthens with increasing PPT over the rainfall ranges encountered in this study. We hypothesize that intensification of shrub competition with increased PPT may reflect the plastic response of shrub roots to variations in soil moisture availability. *P. glandulosa* plants at the study site have dimorphic root systems, with deep tap roots and lateral roots that extend many times their canopy diameters at depths overlapping grass root systems (Gibbens and Lenz 2001). These shallow coarse lateral roots may opportunistically proliferate fine roots when soil moisture is abundant and curtail this fine root production and lose fine root mass under dry conditions. Competition between grasses and shrubs could thus be more intense when water and other soil resources are more abundant. Such trait-mediated interactions (Callaway and others 2003) have been observed for other dryland plant species (Schwinning and others 2002).

Collectively, the vegetation in our 6-year experiment experienced a dry year with average antecedent conditions (2011); a dry year with dry

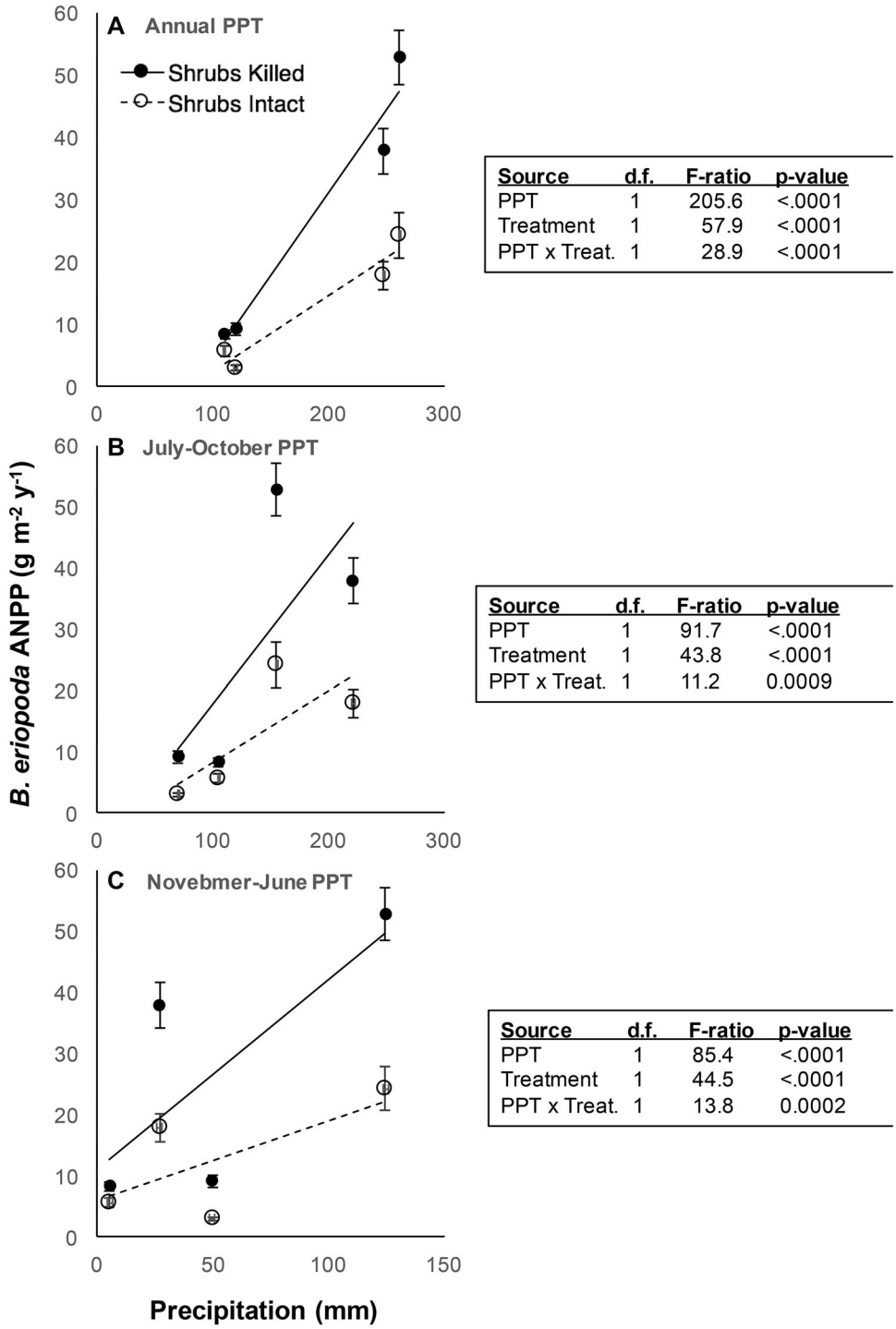


Figure 3. Relationship between precipitation (PPT) and *Bouteloua eriopoda* aboveground ANPP on plots where neighboring shrubs were intact (*open circles*) or killed (*filled circles*). **A** Annual PPT; **B** growing season (July–October) PPT; **C** dormant season (November–June) PPT. Analysis of variance summaries are shown beside each panel.

antecedent conditions (2012); a wet year with dry antecedent conditions (2013); and wet years with wet antecedent conditions (2014–2015). Strong seasonality signals also occurred: growing season PPT predominated 2013–2014, whereas rainfall in 2015 was mostly during the cool season when grasses were largely dormant. Our results support those of other research that shows how the intensity of grass-shrub interactions fluctuates as a function of variability in PPT quantity and season-

ality. Grasses tend to respond to precipitation more quickly than shrubs (Jobaggy and Sala 2000), which may portend a competitive advantage for grasses under the highly variable precipitation regimes characteristic of drylands (Soriano and Sala 1984). However, recent studies demonstrate the importance of previous years' precipitation in determining current year's grass productivity, wherein wet antecedent conditions lead to higher production than expected based on current year's precipitation alone, and antecedent dry conditions have the opposite effect (Sala and others 2012). Although consecutive wet years are thus a boon for grass productivity, this timescale would also allow for a positive shrub response to the wet conditions. Our data suggest that shrub competition intensifies in multiple, consecutive wet years to constrain increases in grass ANPP that might otherwise occur. Accordingly, we saw no effect of previous year's PPT on current year's grass ANPP. Winter/spring PPT could amplify this effect if a significant proportion of rain falls while grasses are dormant, allowing moisture to percolate to deeper soil layers where it is ostensibly less accessible to grasses when their growth resumes and more accessible to shrubs (Walker and Noy-Meir 1982; Ward and others 2013). Moreover, leaf-level carbon and water relations indicate that *P. glandulosa*, a deciduous shrub, physiologically outperforms *B. eriopoda* under conditions of both low and high soil moisture availability, and for a longer portion of the year (Throop and others 2012), providing a possible mechanism by which shrubs outcompete grasses in this study. This is in direct contrast to interactions between *B. eriopoda* and *Larrea tridentata,* an evergreen shrub species featured in studies of grass-shrub interactions in the Chihuahuan Desert. In these studies, *B. eriopoda* had higher leaf-level photosynthetic rates than the shrub following small rainfall events that characterize dryland systems (Pockman and Small 2010), yet *B. eriopoda* cover declines under long-term drought while *L. tridentata* cover remains consistent (Baez and others 2013). Furthermore, precipitation variability along with changes in aridity can favor one grass species over another (Rudgers and others 2018). This suggests that the relative importance of stress tolerance versus competitive ability as a driver of grassland-to-shrubland transitions may vary with grass and shrub species or functional types.

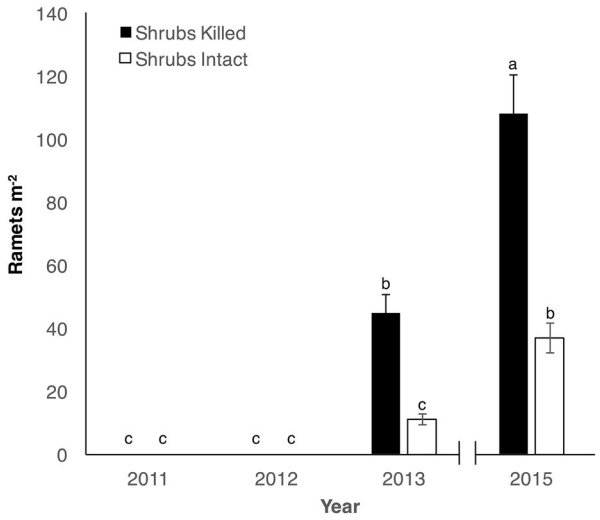


Figure 4. Number of ramets per m^2 in plots with neighboring shrubs intact (*open bars*) or killed (*filled bars*); different letters indicate significant ($P < 0.05$) differences among treatments and years (Tukey's HSD). Years with below-average PPT (2011, 2012) had zero ramet production, but were included in the analysis.

The competitive influence of shrubs on grasses was also apparent via changes in grass patch structural attributes. When shrub neighbors were present, grass patches contracted and became fragmented, and did not rebound to their initial configuration until after three consecutive years of above-average PPT (Figure 5). Plots without shrub neighbors, on the other hand, did not contract/fragment during the dry period, and dramatically expanded/infilled during the wet period. Grass patch size and bare soil connectivity can be used as leading indicators of state transitions in arid systems (Kefi and others 2007; Dakos and others

Table 1. Mean (± SE) Values for *B. eriopoda* Patch-Scale Aboveground ANPP (g m^{-2} y^{-1}), Number of Tillers per m^{-2}, and One-Way ANOVA Results for Differences Between Control and Treatment Plots in 2013

Variable	Treatment		*F* ratio	*P* value
	Shrubs intact	Shrubs killed		
ANPP	17.3 (3.1)	37.7 (3.1)	21.4	< 0.0001
Number tillers	145.0 (19.2)	268.1 (19.0)	20.7	< 0.0001

Tiller production was near zero in the dry years of 2011–2012.

2011), and abiotic soil erosion processes are considered the primary drivers of grass patch contraction (Okin and others 2009). Our results demonstrate that biotic interference can also influence grass patch size and level of fragmentation and hence bare soil connectivity and susceptibility to erosion forces.

Grass ANPP is a combined function of the total number of tillers and the mass per tiller, that is, similar productivity could be achieved with fewer large tillers or with a greater number of small tillers. Our results suggest that grass ANPP at the Jornada site was more dependent on the number of tillers. Although the number of 20 cm × 20 cm cells occupied by *B. eriopoda* was similar between control and treatment plots in 2013 (Figure 5), axillary tiller number was higher in plots with shrubs removed than in plots with shrub neighbors intact (Table 1). This could help explain the increasing ANPP difference between control and treatment plots following consecutive years of wet conditions, as current year ANPP is related to previous year tiller density (Reichmann and others 2013).

Some evidence suggests shrub effects on grasses shift from net negative to net positive along gradients of increasing environmental stress (Maestre and others 2009). Annual precipitation at our site during this experiment (216–279 mm) was well below the threshold (479 mm) that has been proposed for this shift (Dohn and others 2013), so our findings of competitive suppression in this arid grass-shrub system do not support this idea. Instead, our results are more in line with predictions that have been reported for grass-woody plant interactions in mesic savanna systems. Shrubs do, however, appear to facilitate some grass species at this Chihuahuan Desert site. Whereas our study focused on *B. eriopoda* patches in areas beyond shrub canopies, *Muhlenbergia porteri* has been observed growing within and seemingly confined to *P. glandulosa* and *Larrea tridentata* canopies (Welsh and Beck 1976). It is unclear if this is because shrubs ameliorate microclimate conditions, enhance nutrient availability, or provide refugia from grazers. This study supported the stress gradient hypothesis in that shrub-on-grass competition intensified with increasing precipitation. However, we detected no facilitative influence of shrubs on grasses. Due to the small stature of *P. glandulosa* shrubs and the occurrence of *B. eriopoda* grass patches beyond their canopies, aboveground shrub facilitation of grasses via environmental amelioration is irrelevant between these species. If *P. glandulosa* at our site carried out beyond-canopy hydraulic redistribution (Bleby and others 2010) as has been shown in other systems (Zou and others 2005), the redistributed water was not utilized by grasses to a degree that overcame soil water competition with shrubs (Barron-Gafford and others 2017).

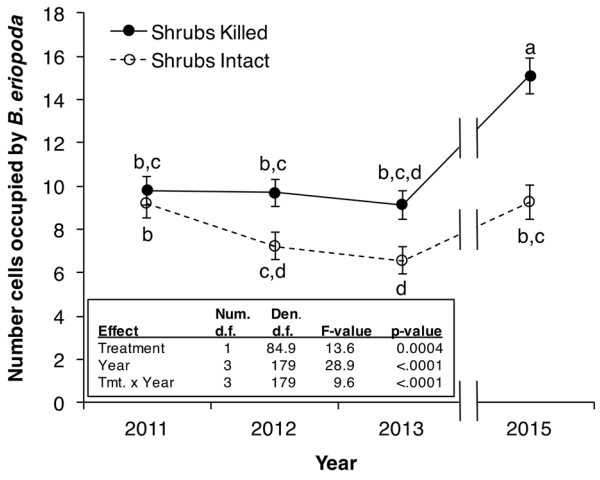


Figure 5. Number of 20 × 20 cm cells per 1 m^2 plot containing rooted *Bouteloua eriopoda* genets or ramets in control (*open circles*) and treatment (*closed circles*) plots; an increase in number of cells occupied represents grass patch expansion/infilling, whereas a decrease represents grass patch size constriction/fragmentation. Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects.

Land-management practices have long sought to restore herbaceous cover and production in shrub-invaded grasslands using herbicides, mechanical treatments, or prescribed fire. Such treatments often do not produce the expected results, however, and reasons for this are not clear (Archer and Predick 2014). Under the assumption that abiotic factors are largely driving system dynamics, shrub removal at broad scales could be expected to exacerbate grass loss because of increased erosion potential. Similarly, if hydraulic lift was important, removing shrubs could render grasses more susceptible to stresses imposed by grazing and drought. Our results, however, confirm that shrub removal in this Chihuahuan Desert system has the potential to be an effective restoration tool in that grass patches expanded in size, connectivity, and productivity when shrub neighbors were removed. Although not addressed in this study, reducing shrub cover could also reduce the density and/or activity of mammalian herbivores to the benefit of grasses, particularly in dry years when C_3 forbs with large seeds are less available (Daniel and

others 1993; Whitford 1993; Kerley and Whitford 2009).

Traditional models of grassland–shrubland transition in drylands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland (Schlesinger and others 1990, 1996). In this study, we demonstrate that shrub-on-grass biotic interference has the potential to reinforce grazing- and drought-induced stresses on mesophytic grasses that would amplify positive abiotic feedbacks driving grassland–shrubland transition. Accordingly, competitive ability may be as, or more, important than stress tolerance in shaping community structure and function in this arid grassland. Shrub-driven declines in grass cover and production also help explain observations of shrub encroachment into arid grasslands where disturbances related to livestock grazing (Browning and Archer 2011) and fire (O'Connor and others 2014) have been eliminated. Further development of dryland state-and-transition models (for example, Bestelmeyer and others 2011) should incorporate biotic interactions as a mechanistic driver of state change.

ACKNOWLEDGEMENTS

Support was provided, in part, by USDA-NRI Grant 2008-35320-18684, NSF-LTER Grant DEB-1235828, Arizona Agricultural Experiment Station Project ARZT-1360540-H12-199; and by fellowships from Science Foundation Arizona and the University of Arizona School of Natural Resources and the Environment. The constructive input of two anonymous reviewers is appreciated. Thanks also to John Anderson, JER HQ staff, the numerous USDA-ARS Jornada staff and students who assisted with field work, and the summertime residents of Jornada Acres.

REFERENCES

Archer SR, Predick KI. 2014. An ecosystem services perspective on brush management: research priorities for competing land-use objectives. J Ecol 102:1394–407.

Archer SR, Andersen EM, Predick KI, Schwinning S, Steidl RJ, Woods SR. 2017. Woody plant encroachment: causes and consequences. In: Briske DD, Ed. Rangeland systems: processes, management and challenges. New York: Springer. pp 25–48.

Baez S, Collins SL, Pockman WT, Johnson JE, Small EE. 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. Oecologia 172:1117–27.

Barron-Gafford GA, Sanchez-Canete EP, Minor RL, Hendryx SM, Lee E, Sutter LF, Tran N, Parra E, Colella T, Murphy PC, Hamerlynck EP, Kumar P, Scott RL. 2017. Impacts of hydraulic redistribution on grass-tree competition vs facilitation in a semi-arid savanna. New Phytol 215:1451–61.

Bestelmeyer BT, Goolsby DP, Archer SR. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? J Appl Ecol 48:746–57.

Bleby TM, McElrone AJ, Jackson RB. 2010. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant Cell Environ 33:2132–48.

Brooker RW, Callaghan TV. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81:196–207.

Browning DM, Archer SR. 2011. Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. Ecol Appl 21:1629–42.

Callaway RM, Pennings SC, Richards CL. 2003. Phenotypic plasticity and interactions among plants. Ecology 84:1115–28.

Dakos V, Kefi S, Rietkerk M, van Nes EH, Scheffer M. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. Am Nat 177:E153–66.

Daniel A, Holechek J, Valdez R, Tembo A, Saiwana L, Fusco M, Cardenas M. 1993. Jackrabbit densities on fair and good condition Chihuahuan Desert range. J Range Manag 46: 524–8.

Dohn J, Dembele F, Karembe M, Moustakas A, Amevor KA, Hanan NP. 2013. Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. J Ecol 101:202–9.

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–22.

Fredrickson E, Havstad KM, Estell R. 1998. Perspectives on desertification: south-western United States. J Arid Environ 39:191–207.

Gherardi LA, Sala OE. 2015. Enhanced precipitation variability decreases grass- and increases shrub-productivity. Proc Natl Acad Sci U S A 112:12735–40.

Gibbens RP, Lenz JM. 2001. Root systems of some Chihuahuan Desert plants. J Arid Environ 49:221–63.

Golluscio RA, Sala OE, Lauenroth WK. 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. Oecologia 115:17–25.

Grime JP. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–94.

Havstad KM, Schlesinger WH. 2006. Introduction. In: Havstad KM, Huenneke LF, Schlesinger WH, Eds. Structure and function of a Chihuahuan Desert ecosystem. New York, NY, USA: Oxford University Press, pp 3–14.

Higgins SI, Bond WJ, Trollope WSW. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J Ecol 88:213–29.

Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DIW, Enslin B, Govender N, Rademan L, O'Regan S, Potgieter ALF, Scheiter S, Sowry R, Trollope L, Trollope WSW. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology 88:1119–25.

Howard KSC, Eldridge DJ, Soliveres S. 2012. Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. Basic Appl Ecol 13:159–68.

Jobaggy EG, Sala OE. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. Ecol Appl 10:541–9.

Kefi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, de Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:U213–15.

Kerley GIH, Whitford WG. 2009. Can kangaroo rat graminivory contribute to the persistence of desertified shrublands? J Arid Environ 73:651–7.

Knapp AK, Briggs JM, Collins SL, Archer SR, Bret-Harte MS, Ewers BE, Peters DP, Young DR, Shaver GR, Pendall E, Cleary MB. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Glob Change Biol 14:615–23.

Li J, Okin GS, Alvarez L, Epstein H. 2008. Effects of wind erosion on the spatial heterogeneity of soil nutrients in two desert grassland communities. Biogeochemistry 88:73–88.

Ludwig F, de Kroon H, Prins HHT, Berendse F. 2001. Effects of nutrients and shade on tree-grass interactions in an East African savanna. J Veg Sci 12:579–88.

Ludwig F, Dawson TE, Prins HHT, Berendse F, de Kroon H. 2004a. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. Ecol Lett 7:623–31.

Ludwig F, de Kroon H, Berendse F, Prins HHT. 2004b. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecol 170:93–105.

Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J Ecol 97:199–205.

O'Connor TG, Puttick JR, Hoffman MT. 2014. Bush encroachment in southern Africa: changes and causes. Afr J Range Forage Sci 31:67–88.

Okin GS, Gillette DA, Herrick JE. 2006. Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. J Arid Environ 65:253–75.

Okin GS, D'Odorico P, Archer SR. 2009. Impact of feedbacks on Chihuahuan Desert grasslands: transience and metastability. J Geophys Res Biogeosci 114:G01004.

Pockman WT, Small EE. 2010. The influence of spatial patterns of soil moisture on the grass and shrub responses to a summer rainstorm in a Chihuahuan Desert ecotone. Ecosystems 13:511–25.

Priyadarshini KVR, Prins HHT, de Bie S, Heitkonig IMA, Woodborne S, Gort G, Kirkman K, Ludwig F, Dawson TE, de Kroon H. 2016. Seasonality of hydraulic redistribution by trees to grasses and changes in their water-source use that change tree-grass interactions. Ecohydrology 9:218–28.

Ratajczak Z, Nippert JB, Collins SL. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703.

Reichmann LG, Sala OE, Peters DPC. 2013. Precipitation legacies in desert grassland primary production occur through previous-year tiller density. Ecology 94:435–43.

Rudgers JA, Chung YA, Maurer GE, Moore DI, Muldavin EH, Litvak ME, Collins SL. 2018. Climate sensitivity functions and net primary production: a framework for incorporating climate mean and variability. Ecology 99:576–82.

Sala OE, Gherardi LA, Reichmann L, Jobbagy E, Peters D. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philos Trans R Soc B-Biol Sci 367:3135–44.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science 247:1043–8.

Schlesinger WH, Raikes JA, Hartley AE, Cross AE. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–74.

Scholes RJ. 2003. Convex relationships in ecosystems containing mixtures of trees and grass. Environ Resour Econ 26:559–74.

Schwinning S, Davis K, Richardson L, Ehleringer JR. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130:345–55.

Soriano A, Sala O. 1984. Ecological strategies in a Patagonian arid steppe. Vegetatio 56:9–15.

Throop HL, Reichmann LG, Sala OE, Archer SR. 2012. Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. Oecologia 169:373–83.

Vander-Yacht AL, Barrioz SA, Keyser PD, Harper CA, Buckley DS, Buehler DA, Applegate RD. 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For Ecol Manag 390:187–202.

Walker BH, Ludwig D, Holling CS, Peterman RM. 1981. Stability of semi-arid savanna grazing systems. J Ecol 69:473–98.

Walker BH, Noy-Meir I. 1982. Aspects of the stability and resilience of savanna ecosystems. Ecol Stud 42:556–90.

Ward D, Wiegand K, Getzin S. 2013. Walter's two-layer hypothesis revisited: back to the roots!. Oecologia 172:617–30.

Welsh RG, Beck RF. 1976. Some ecological relationships between creosotebush and bush muhly. J Range Manag 29: 472–5.

Whitford WG. 1993. Animal feedbacks in desertification - an overview. Rev Chil Hist Nat 66:243–51.

Zou CB, Barnes PW, Archer S, McMurtry CR. 2005. Soil moisture redistribution as a mechanism of facilitation in savanna tree-shrub clusters. Oecologia 145:32–40.

Biol Invasions
https://doi.org/10.1007/s10530-019-02120-8

Appendix C

ORIGINAL PAPER

Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass (*Bromus tectorum*) in the central Great Basin, USA

Matthew A. Williamson · Erica Fleishman · Ralph C. Mac Nally · Jeanne C. Chambers · Bethany A. Bradley · David S. Dobkin · David I. Board · Frank A. Fogarty · Ned Horning · Matthias Leu · Martha Wohlfeil Zillig

Received: 27 December 2018 / Accepted: 1 November 2019

Abstract Cheatgrass (*Bromus tectorum*) has increased the extent and frequency of fire and negatively affected native plant and animal species across the Intermountain West (USA). However, the strengths of association between cheatgrass occurrence or abundance and fire, livestock grazing, and precipitation are not well understood. We used 14 years of data from 417 sites across 10,000 km^2 in the central Great Basin to assess the effects of the foregoing predictors on cheatgrass occurrence and prevalence (i.e., given occurrence, the proportion of measurements in which the species was detected). We implemented hierarchical Bayesian models and considered covariates for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 as strongly associated with the response variable. Similar to previous research, our models indicated that fire is a strong, positive predictor of cheatgrass occurrence and prevalence. Models fitted to all sample points and to only unburned points indicated that grazing and the proportion of years grazed were strong positive predictors of occurrence and prevalence. In contrast, in models restricted to burned points, prevalence was high, but decreased slightly as the proportion of years grazed increased (relative to other burned points). Prevalence of cheatgrass also decreased as the prevalence of perennial grasses increased. Cheatgrass occurrence decreased as elevation increased, but

M. A. Williamson (✉)
Boise State University, Boise, ID 83725, USA
e-mail: mattwilliamson@boisestate.edu

M. A. Williamson · E. Fleishman · F. A. Fogarty · M. Wohlfeil Zillig
University of California, Davis, CA 95616, USA

E. Fleishman
Colorado State University, Fort Collins, CO 80523, USA

R. C. Mac Nally
Institute for Applied Ecology, University of Canberra, Bruce, ACT 2617, Australia

R. C. Mac Nally
School of BioSciences, The University of Melbourne, Parkville, VIC 3052, Australia

J. C. Chambers · D. I. Board
Rocky Mountain Research Station, USDA Forest Service, Reno, NV 89512, USA

B. A. Bradley
University of Massachusetts, Amherst, MA 01003, USA

D. S. Dobkin
High Desert Ecological Research Institute, Bend, OR 97702, USA

N. Horning
American Museum of Natural History, New York, NY 10024, USA

M. Leu
College of William and Mary, Williamsburg, VA 23185, USA

Published online: 08 November 2019

prevalence within the elevational range of cheatgrass increased as median winter precipitation, elevation, and solar exposure increased. Our novel time-series data and results indicate that grazing corresponds with increased cheatgrass occurrence and prevalence regardless of variation in climate, topography, or community composition, and provide no support for the notion that contemporary grazing regimes or grazing in conjunction with fire can suppress cheatgrass.

Keywords *Bromus tectorum* · Hierarchical models · Fire · Great Basin · Livestock grazing · Resilience

Introduction

Increases in the distribution and abundance of non-native grasses have modified fire dynamics worldwide, often leading to loss of human life and property and to substantial financial costs (D'Antonio and Vitousek 1992; Brooks et al. 2004). Cheatgrass (*Bromus tectorum*), an annual grass native to Eurasia, has increased in abundance and geographic distribution across the Intermountain West (USA) in recent decades. For example, the cover of cheatgrass is estimated to be at least 15% across about 210,000 km^2 of the Great Basin, a $>$ 425,000 km^2 desert within the Intermountain West (Bradley et al. 2018). As cheatgrass expands, it drives a cycle of increases in the frequency and extent of fire and further expansion of cheatgrass (Bradley et al. 2018). The area burned has increased by as much as 200% since 1980, accompanied by over US$1 billion in fire-suppression costs (Balch et al. 2013; NCEI 2018). Cheatgrass-induced changes in fire patterns are associated with loss of sagebrush (*Artemisia* spp.), perennial grasses, and forbs that provide habitat for hundreds of plant and animal species. These species include Greater Sage-Grouse (*Centrocercus urophasianus*), which repeatedly has been considered for listing under the U.S. Endangered Species Act (Freeman et al. 2014; USFWS 2015; Germino et al. 2016).

Although the effects of cheatgrass on fire dynamics are well known, the effects of some potential predictors of cheatgrass distribution and abundance at large spatial extents, such as livestock grazing, abundance of native perennial grasses, precipitation, elevation, and solar exposure, are less clear. For example, it has been suggested that livestock grazing, a major land use in the region, directly and indirectly (e.g., through reductions in the abundance of native perennials) increases the likelihood of invasion (e.g., Reisner et al. 2013). Moreover, the strength of response of both cheatgrass occurrence and prevalence (the proportion of binary occurrence measurements in a given area in which a species is present, and a critical component of the species' effects; Parker et al. 1999) to fire, grazing, and precipitation are unknown. We aimed to clarify these relations.

Several studies assessed environmental correlates of cheatgrass cover, density, or abundance in the Intermountain West (e.g., Gelbard and Belnap 2003; Bradley and Mustard 2006; Compagnoni and Adler 2014; Pilliod et al. 2017). These correlates vary across the range of cheatgrass (e.g., Bradley et al. 2016; Brooks et al. 2016), in relation to fire, and potentially over time. The cover, density, or abundance of cheatgrass can increase rapidly in areas that recently have burned or been disturbed by land uses such as road construction, maintenance, or use; agricultural activities; or grazing by domestic livestock (Mack 1981; Bradley and Mustard 2006; Banks and Baker 2011; Reisner et al. 2013; Pyke et al. 2016; Svejcar et al. 2017).

Previous field research rarely quantified the links between cheatgrass and livestock grazing due to the difficulty of obtaining reliable, quantitative data regarding this land use. Yet management of livestock grazing on the public lands that cover more than half of the Intermountain West, and about 75% of the Great Basin, may have a substantial effect on the expansion and ecological effects of cheatgrass. Livestock trample soil crusts, which can increase potential colonization by cheatgrass; feed on native perennial grasses that can compete with cheatgrass (see below); and disperse cheatgrass seeds (Reisner et al. 2013). In many cases, the US Forest Service (USFS) and US Bureau of Land Management (BLM)—the agencies with jurisdiction over the majority of public lands in the western United States—defer continuation of livestock grazing on active allotments for 2 years following fire (BLM 2007). Although there are advocates for both shorter and longer exclusion periods, there are few empirical data to inform management decisions, especially in areas where cheatgrass has become widespread.

The abundance and cover of native perennial grasses that compete with cheatgrass independent of land use also are directly and negatively associated with the intensity of livestock grazing (Adler et al. 2005; Reisner et al. 2013). These grasses did not coevolve with high abundances of large ungulates (Mack and Thompson 1982). Although fires in Great Basin ecosystems typically remove fire-intolerant shrubs such as sagebrush, most native perennial grasses survive. The cover of cheatgrass and other non-native annual, invasive grasses is negatively related to the cover of perennial native grasses following prescribed fire and other management actions (Davies 2008; Chambers et al. 2014; Roundy et al. 2018). For example, in areas dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), about 20% cover of perennial, native forbs and grasses is necessary to prevent increases in the cover of annual, invasive grasses after prescribed fire treatments (Chambers et al. 2014; Roundy et al. 2018). Therefore, livestock-grazing history and the abundance of perennial native grasses are likely to be associated with cheatgrass presence and abundance, and to interact with fire.

Establishment of cheatgrass is associated with relatively high levels of precipitation during autumn or spring, which facilitate the species' germination and growth (Bradley et al. 2016). Percent cover and biomass of cheatgrass also are highly responsive to heavy winter and spring precipitation (Knapp 1998). Cheatgrass biomass can increase tenfold following wet winters (Garton et al. 2011), substantially increasing fine-fuel loads and the probability of fire (Balch et al. 2013; Pilliod et al. 2017). Biomass of cheatgrass may remain high during the year following a wet winter, especially when competition from perennial grasses is low (Bradley et al. 2016). There is some evidence that the abundance of cheatgrass is less likely to increase in areas with relatively high summer precipitation and cool annual temperatures (Taylor et al. 2014; Brummer et al. 2016). Therefore, precipitation is likely to be associated with the presence and abundance of cheatgrass.

Cheatgrass occurs over extensive topographic gradients (Brooks et al. 2016), but the likelihood of presence or the abundance of cheatgrass generally decreases as elevation increases (Compagnoni and Adler 2014; Chambers et al. 2016). For example, in both 1973 and 2001, probability of cheatgrass presence in the central Great Basin was highest at elevations from 1200 to 1400 m (Bradley and Mustard 2006). Between those years, cheatgrass expanded into lower elevations, but did not expand at elevations above 1700 m, and the probability of cheatgrass presence above 2500 m was almost zero (Bradley and Mustard 2006). The mechanisms underlying the relation between cheatgrass presence or abundance and elevation are fairly well understood. Germination, growth, and reproduction of cheatgrass generally are highest at intermediate elevations with moderate temperatures and water availability, limited at low elevations by relatively high temperatures and low precipitation, and limited at high elevations by low soil temperatures (Meyer et al. 2001; Chambers et al. 2007, 2017; Compagnoni and Adler 2014). Strong competitive interactions between perennial grasses and cheatgrass affect density and cover of cheatgrass across elevational gradients (Chambers et al. 2007; Reisner et al. 2013; Larson et al. 2017). Soil moisture and nutrient levels generally increase as elevation increases, leading to an increase in primary productivity and higher levels of competition between cheatgrass and other species (Chambers et al. 2007; Compagnoni and Adler 2014).

Some work has suggested that cheatgrass is more likely to be present and abundant on certain topographic aspects, although relations with aspect may vary across the Great Basin and among assessment methods. On the basis of Landsat data for the central Great Basin, Bradley and Mustard (2006) found that likelihood of cheatgrass presence was greatest on west- and northwest-facing slopes. However, fine-resolution empirical analyses in the northern Great Basin and in the Rocky Mountains suggested that cheatgrass abundance was greatest on south-facing slopes (Banks and Baker 2011; Svejcar et al. 2017), especially at relatively high elevations (Brooks et al. 2016).

Here, we use a 14-year time-series of data collected within a bounding area of $\sim$ 10,000 km^2 of the central Great Basin (Fig. 1) to assess empirically the relative strengths of association of cheatgrass occurrence and prevalence with fire, livestock grazing, precipitation, and other abiotic environmental conditions. Our selection of predictor variables was motivated by the ecological theories and previous research summarized above, and facilitated by the unusually extensive topographic gradients and duration covered

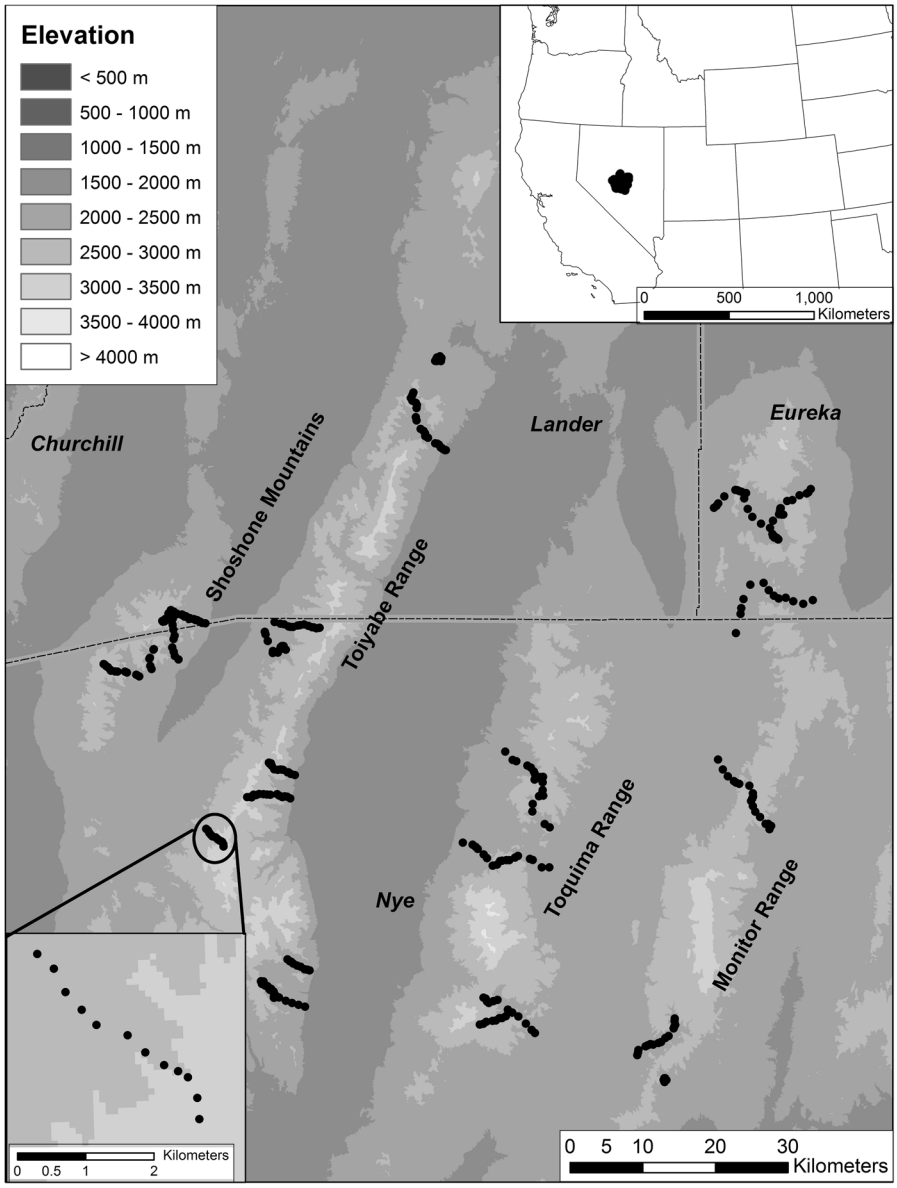


Fig. 1 Locations of the 417 sample points that were distributed among 29 canyons in four mountain ranges in the central Great Basin (Lander, Eureka, and Nye Counties, Nevada, USA). We sampled cheatgrass at each point for a minimum of three years and a maximum of eight years

by our data. Our ultimate aim is to inform policy and management actions that may minimize the further expansion and undesirable direct and indirect effects of cheatgrass on species and ecosystem function across the Intermountain West. Our results also may inform research priorities or sampling designs to more thoroughly examine interactive effects of drivers of cheatgrass colonization and dominance.

Methods

Data collection and development

We used two sets of data collected from 2001 through 2015 in 29 canyons in four mountain ranges (Shoshone, Toiyabe, Toquima, and Monitor) in Lander, Nye, and Eureka Counties, Nevada (Fleishman 2015) (Fig. 1). Within those canyons, we sampled cheatgrass at elevations from 1886 through 3219 m over a range of disturbance histories. Complete

vegetation data and metadata are in Chambers et al. (2010) and Fleishman (2015). Detailed information about data collection methods also is in Urza et al. (2017).

First, we collected data on cheatgrass and other elements of vegetation structure and composition from 30 to 50 m point-intercept transects (10–31 locations per transect per year) along elevational gradients of the 29 canyons. We refer to each transect as a *sample point*. We collected data from each sample point for 3–8 years from 2001 to 2015.

Second, we collected vegetation data in three pairs of adjacent alluvial fans on burned and unburned sites at elevations of 2073, 2225, and 2347 m on a north-facing slope within one watershed in the Shoshone Mountains. We established three sampling plots of ca 0.1 ha within burned and unburned plots at each elevation. We measured areal cover of herbaceous species and shrubs within 50, 2-m^2 quadrats per plot in 2001, prior to a prescribed fire. We remeasured the same plots in 2002, 2004, and 2006, after the fire. We measured areal cover of herbaceous species within 25–30, 0.25-m^2 quadrats. We converted these quadrats to presence–absence estimates for a sample point assigned to the geographic center of the plots to allow combination with the transect data (i.e., the number of the 50 quadrats in which cheatgrass was detected).

We assessed cheatgrass occurrence by considering sample points at which cheatgrass was not recorded during the study period as absences, and sample points at which cheatgrass was recorded present in $\geq$ 1 year during the study period as presences. For each sample point at which cheatgrass was recorded present, we estimated local prevalence of cheatgrass by summing the number of point intercepts (or quadrats) where cheatgrass was recorded present and comparing that to the total number of point intercepts (or quadrats) taken at each point in a given year.

We characterized the grazing and fire history of each sample point for each year during the period in which we collected vegetation data. Each year from 2001 through 2015, EF or JC made multiple visits (generally 3–6) to each point at which data were collected and recorded whether it was grazed by domestic cattle and whether a fire occurred during the growing season or between the previous and current growing season. We augmented these observations with information on whether grazing by domestic cattle was permitted on each allotment (i.e., whether the allotment was active) from 2006 through 2015 (M. West, USFS, personal communication). We assigned a binary value to indicate whether the allotment in which a given sample point was embedded was grazed during each year. Because data on realized (as opposed to permitted) grazing intensity are not maintained by the USFS, which manages virtually all of the land on which our sample points were located, we assumed that all active allotments were grazed. Although permitees may use a portion of an allotment rather than an entire allotment, or engage in short-term non-use of an allotment, it is reasonable to assume that active allotments were grazed recently or during the years in which data were collected. We calculated the proportion of years during which each sample point was grazed (years grazed/years during the study period prior to collection of data in a given year) to estimate levels of livestock use. We classified sampled points as burned if a fire occurred at the sample point from 2000 through 2015.

For burned points, we calculated the number of growing seasons between the fire and a given field sample. We included both linear and quadratic terms for number of growing seasons between the fire and the sampling event because Miller et al. (2013) suggested that cheatgrass could decrease in abundance after about 12 years if the abundance of other grasses, forbs, and shrubs increases. To examine the potential effect on cheatgrass of competition from perennial native grasses, we also estimated the prevalence of perennial native grasses at each sample point by summing the number of points along transects or within quadrats at which perennial native grass was recorded present and dividing by the total number of points.

We derived the elevation of each sample point from the 10-m National Elevation Dataset (lta.cr.usgs.gov/NED). We calculated a hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded) in ArcGIS 10.4 (Esri, www.esri.com/en-us/home) for each sample point (at the geographic center of transects or quadrats) on the basis of the sun angle and azimuth at the center of study area on 21 June at 15:00. The date and time represent maximum solar exposure on summer solstice (Blackard and Dean 1999). Values of the hillshade index ranged from 0 to 254, with higher values indicating greater solar exposure on southwest-facing slopes. We estimated solar radiation on the basis of a hillshade index

Table 1 Predictors included in models of the probability of presence (occurrence) of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Model	Level	Predictor
Occurrence		
All sample points	Point	Elevation
		Hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded)
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no) (whether a fire occurred during the growing season or between the previous and current growing season)
		Grazed (yes/no) (whether grazing by domestic cattle was permitted on the allotment within which the point was located)
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Grazed (yes/no)
Prevalence		
All points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no)
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Burned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual spring precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Time since fire
		Time since fire^2
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling

rather than aspect because it is difficult to differentiate between opposite aspects (e.g., north vs. south or east vs. west) within a statistical model. We estimated precipitation at each sample point with data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM). We calculated both cumulative precipitation in the winter (1 October–31 March) and spring (1 April–30 June) preceding sampling and the proportion of precipitation in those two seasons that fell in winter. We included the latter variable to distinguish associations with precipitation seasonality from those with cumulative precipitation.

We restricted the data to years for which data on cheatgrass and predictors were available for each sample point. In some cases, the bivariate correlation between winter and spring precipitation was > 0.7. We retained the precipitation estimate that had the lowest correlation with all other predictors in the model. We scaled all predictors to a mean of zero and unit variance to facilitate model convergence and to represent the predictors on a common scale.

Statistical modeling

We modeled associations between predictors and occurrence across the 14-year study period, and between predictors and annual variation in prevalence throughout the 14-year study period. To evaluate associations with predictors in the presence and in the absence of fire, we applied these models to (1) all of the data ($N_{occurrence} = 417, N_{prevalence} = 624$), (2) only those points that had not been burned ($N_{occurrence} = 326, N_{prevalence} = 314$), and (3) only those points that had been burned ($N_{occurrence} = 91, N_{prevalence} = 310$). We did not fit occurrence models to burned points because cheatgrass was recorded present in 88 of those 91 points, preventing the model from discriminating between the determinants of presence and absence.

We classified sample points as *recorded present* if cheatgrass was detected at any time during the study period (occurrence = 1) and *recorded absent* if cheatgrass was not observed during the study period (occurrence = 0). We used a Bernoulli response model to link occurrence with candidate predictors (Table 1). We then used a binomial response model to identify predictors that were associated strongly with the prevalence of cheatgrass in the sample points at which cheatgrass was recorded. We used separate response models rather than zero-inflated models (e.g., hurdle models sensu Mullahy 1986) because the spatial–temporal processes almost certainly are not statistically stationary. Hurdle models assume that occurrence is stationary, but cheatgrass is still spreading throughout our study area.

Cheatgrass occurrence

For each sample point, we calculated winter and spring precipitation as the median annual value across the study period. We assigned binary values for fire and grazing that reflected whether the point had been burned or grazed in any year of the study period prior to the year in which cheatgrass first was recorded present or, if cheatgrass consistently was recorded absent, the final year of sampling.

We modeled whether cheatgrass was recorded present ($\Phi_{i,j,k,s}$) during a given year (i) at sample point j within canyon k within mountain range s as the outcome of a Bernoulli trial with probability $p_{i,j,k,s}$. We modeled probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{j,k,s}$) and the product of observation-level regression parameters (β_{obs}) and observation-level standardized predictors (some predictors vary among years; $\boldsymbol{X}_{obs}$, Table 1).

$$\Phi_{i,j,k,s} \sim Bernoulli\left(p_{i,j,k,s}\right), \tag{1}$$

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{2}$$

We modeled the point-level intercepts as the outcome of a canyon- and range-specific, point-level intercept ($\alpha_{k,s}$) and the sample point-level regression parameters (β_{point}) and sample point-level predictors (i.e., predictors with values that were constant throughout the study period, $\boldsymbol{X}_{point}$, Table 1).

$$\alpha_{j,k,s} \sim Normal\left(\mu_{j,k,s}, \sigma_{k,s}\right), \tag{3}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}\boldsymbol{X}_{point}, \tag{4}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{5}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal\left(\mu_{k,s}, \sigma_{s}\right), \tag{6}$$

$$\mu_{k,s} = \alpha_s, \tag{7}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{8}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{9}$$

$$\mu_0 \sim Normal(0, 2), \tag{10}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{11}$$

This hierarchical structure accounted for potential systematic variation among points within the same canyon and among canyons within the same mountain range, and for potential spatial organization in the data.

Cheatgrass prevalence

For sample points at which cheatgrass was recorded present, we modeled cheatgrass prevalence as functions of topographic, climatic, and land-use variables (Table 1). We attributed observation-level predictor values to each point for the corresponding year of sampling. We included the annual estimate of each precipitation variable as an observation-level predictor and the median of the annual values of each precipitation variable throughout the study period as a point-level predictor. We used the proportion of years grazed as the grazing predictor in these analyses.

We modeled the prevalence of cheatgrass ($y_{i,j,k,s}$) in a given year (i) at sample point j within canyon k within mountain range s as the binomial outcome of the number of detections, which in turn was a function of the number of samples taken at that point in that year ($n_{i,j,k,s}$), where cheatgrass is present with probability $p_{i,j,k,s}$. We modeled the probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{i,j,k,s}$) and the product of an array of observation-level slope parameters (β_{obs}) and observation-level predictors ($\boldsymbol{X}_{obs}$, Table 1).

$$y_{i,j,k,s} \sim Binomial\left(n_{i,j,k,s}, p_{i,j,k,s}\right), \tag{12}$$

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{13}$$

We modeled the point-level intercepts as the outcome of a point-specific, canyon-level intercept ($\alpha_{k,s}$) and the product of an array of point-level slope parameters (β_{point}) and point-level predictors ($\boldsymbol{X}_{point}$, Table 1).

$$\alpha_{j,k,s} \sim Normal\left(\mu_{j,k,s}, \sigma_{k,s}\right), \tag{14}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}\boldsymbol{X}_{point}, \tag{15}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{16}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal\left(\mu_{k,s}, \sigma_s\right), \tag{17}$$

$$\mu_{k,s} = \alpha_s, \tag{18}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{19}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{20}$$

$$\mu_0 \sim Normal(0, 2), \tag{21}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{22}$$

Model fitting

We fitted models in R (v3.4.1, R Core Team 2017; Williamson 2019) with the rstan package (Stan Development Team 2018), a wrapper to the Hamiltonian Monte Carlo program Stan (Stan Development Team 2017). We used four sampling chains, each with 2000 iterations (1000 iterations for warmup), and set the adaptation parameter (adapt delta) to 0.95. The latter reduces the step-size of the sampler to allow sampling of complex posterior geometries of model parameters and reduces the potential that bias will result from chains that do not sample the posterior distribution effectively (Stan Development Team 2017).

Assessing model fit

We assessed goodness-of-fit of the occurrence model by evaluating the area under the receiver-operating curve [AUC; implemented in package pROC (Robin et al. 2011)]. AUC > 0.75 is regarded as a good model fit and AUC $\sim$ 1 as an excellent fit to the data. We evaluated the AUC for the lower quartile, median, and

upper quartile values for posterior predictions of p (the posterior estimate of the probability of occurrence) to evaluate the sensitivity of our AUC calculations across the posterior distribution of p.

For the binomial models, we sampled values from the posterior of the parameterized model ($y_{i,jk,s}^{sampled}$) and calculated the Freeman-Tukey measure of discrepancy for the observed ($y_{i,j,k,s}^{obs}$) or sampled data, given their fitted values ($\mu_{j,k,s}$):

$$D_{obs} = \sum_i \sqrt{\left(y_{i,j,k,s}^{obs} - \mu_{j,k,s}\right)^2}; \quad (23)$$

$$D_{sampled} = \sum_i \sqrt{\left(y_{i,j,k,s}^{sampled} - \mu_{j,k,s}\right)^2} \quad (24)$$

Any number of samples from the posterior can be drawn and corresponding discrepancies calculated. The posterior predictive fit is the proportion of sampled discrepancies that exceed the observed discrepancy. Values of posterior predictive fit near 0.5 indicate excellent model fits, but values from 0.05 through 0.95 are regarded as plausible fits of the parameterized model to the data (Gelman et al. 2013).

Strength of association of individual predictors

We assessed the strength of evidence that a predictor was strongly associated with the probability of occurrence (Bernoulli model) or with the prevalence (binomial model) of cheatgrass by calculating the proportion of the posterior probability distribution that exceeded zero for each predictor's regression coefficient. Predictors for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 were regarded, respectively, as strongly and positively or strongly and negatively associated with the response variable. Given our use of uninformative priors (i.e., half of the posterior predictive mass ≥ 0), posterior proportions > 0.90 correspond to odds ratios of > 10, which are strong positive associations (Jeffreys 1961). Similarly, posterior proportions < 0.10 equate to odds ratios of < 0.1, which are evidence of strong negative associations.

We did not interpret the strength of associations of predictors on the basis of the magnitudes of the regression coefficients for two reasons. First, only the continuous predictors were scaled given that the mean of a binary predictor is not relevant, making comparisons with the binary predictors inappropriate. Second, although expressing the continuous predictors on a common scale facilitates model fitting, it results in regression coefficients that indicate the predicted change in outcome associated with a unit standard deviation change in the predictor value. As such, the regression coefficients provide an estimate of the relative effect of the predictor subject to its measured variation and conditional on all other predictors in the model. Given that our continuous predictors had different standard deviations, use of the magnitude of the regression coefficients to compare the relative strength of the predictors in our models would be inappropriate. Instead, we provide marginal effects plots to illustrate the effect of multiple standard deviation changes in the predictor on the response while all other predictors are held at their mean.

Results

Occurrence models for all sample points and unburned points fitted the data well (AUC > 0.98 for the median, lower, and upper quartile posterior estimates of p). Posterior predictive checks indicated that the prevalence models also fitted the data well, with posterior predictive fits of 0.25, 0.32, and 0.26 for models that included all sample points, unburned points only, and burned points only, respectively.

The probabilities of cheatgrass occurrence and prevalence were associated strongly with fire. Results of the model that included all sample points (Fig. 2A) indicated that fire occurrence was associated with an increase in the probability of cheatgrass occurrence (Table 2, Fig. 2B) and an increase in prevalence (conditional on cheatgrass presence; Table 3, Fig. 2C). In models restricted to burned points, cheatgrass prevalence increased as time since fire increased. However, the strength and sign of the quadratic term suggested that this relation may peak at intermediate values of time since fire.

Grazing and prevalence of native perennial grasses were associated with the probability of cheatgrass occurrence and prevalence. Models that included either all sample points or only unburned points (Fig. 3A) indicated that grazing occurrence and an increase in the proportion of years grazed were associated positively with an increase in the

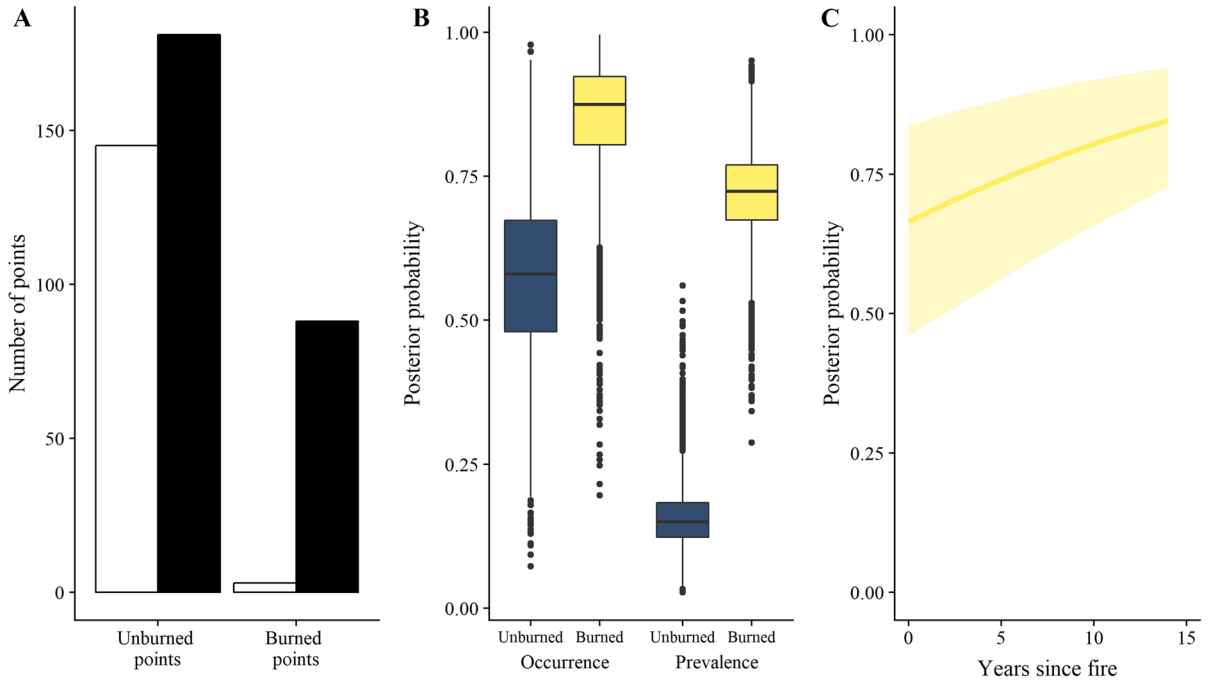


Fig. 2 Relations between fire and the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year). Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of sample points in which cheatgrass was recorded present (black) was much greater than the number of sample points in which it was recorded absent (white); cheatgrass was recorded present in 97% of burned points. **B** Probability of occurence of cheatgrass and of prevalence of cheatgrass were higher in models that included only burned points (yellow) than in models that included only unburned points (blue). **C** In the model restricted to burned points, the marginal effect of time since fire on cheatgrass prevalence (conditional on cheatgrass presence) was strongly positive. SD, standard deviation from the mean value of time since fire

Table 2 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of cheatgrass occurrence

Variable	All sample points Mean (SD)	Unburned points Mean (SD)
Elevation	− 0.46 (0.23)*	− 0.43 (0.24)*
Hillshade index	0.17 (0.15)	0.14 (0.17)
Median winter precipitation	− 0.07 (0.23)	− 0.02 (0.25)
Median proportion of precipitation falling in winter	− 0.47 (0.23)*	− 0.42 (0.25)*
Burned (yes/no)	1.64 (0.56)*	NA
Grazed (yes/no)	0.64 (0.44)*	0.25 (0.45)

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with occurrence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)

probability of cheatgrass occurrence (Table 2, Fig. 3B) and in the prevalence of cheatgrass (Table 3, Fig. 3C). However, in models restricted to burned points, prevalence of cheatgrass remained quite high, but decreased slightly as the proportion of years grazed increased (Table 3, Fig. 3D). Few burned points (8 of 91) were not grazed. In models that included all sample points or only unburned points,

Table 3 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Variable	All sample points Mean (SD)	Unburned points Mean (SD)	Burned points Mean (SD)
Elevation	0.03 (0.04)	0.09 (0.06)*	0.41 (0.10)*
Hillshade index	− 0.08 (0.02)*	− 0.13 (0.03)*	− 0.31 (0.03)*
Median spring precipitation over the study period	NA	NA	− 0.53 (0.09)*
Median winter precipitation over the study period	0.15 (0.03)*	0.04 (0.06)	0.25 (0.06)*
Median proportion of precipitation falling in winter over the study period	− 0.18 (0.04)*	0.01 (0.06)	0.04 (0.04)
Burned (yes/no)	2.69 (0.06)*	NA	NA
Time since fire	NA	NA	1.03 (0.05)*
Time since fire^2	NA	NA	− 0.73 (0.03)*
Proportion of years grazed	0.47 (0.03)*	0.13 (0.06)*	− 0.13 (0.04)*
Prevalence of perennial grasses	− 0.08 (0.03)*	− 0.18 (0.04)*	− 0.01 (0.03)
Spring precipitation in the year of observation	− 0.31 (0.08)*	0.00 (0.04)	− 0.22 (0.11)*
Winter precipitation in the year of observation	0.27 (0.07)*	NA	0.26 (0.09)*
Proportion of precipitation falling in winter in the year of observation	− 0.27 (0.07)*	− 0.16 (0.04)*	− 0.27 (0.11)*

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with prevalence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)

prevalence of cheatgrass decreased as prevalence of perennial grasses increased (Table 3). We did not estimate relations between prevalence of perennial grasses and probability of cheatgrass occurrence because we did not have a complete record of perennial grass prevalence and, therefore, could not estimate the median prevalence of perennial grasses across the study period.

The response of cheatgrass to longer-term precipitation (median winter and spring precipitation and the median proportion of precipitation falling in winter) was inconsistent. Median winter precipitation was not strongly associated with probability of cheatgrass occurrence (Table 2) but was associated positively with cheatgrass prevalence in models that included all sample points or only burned points (Fig. 4A). The median proportion of precipitation falling in winter was negatively associated with the probability of cheatgrass occurrence in models that included all sample points or only unburned points (Table 2, Fig. 4B). Similarly, the proportion of precipitation falling in winter in the year of observation was negatively associated with cheatgrass prevalence in all three models (Table 3, Fig. 4C). We did not include median spring precipitation as a predictor because it was highly correlated with median winter precipitation. However, regardless of the amount or proportion of winter precipitation, prevalence of cheatgrass in models restricted to burned points increased as median spring precipitation decreased.

Precipitation in the year of observation was associated strongly with the prevalence of cheatgrass. In models that included all sample points or only burned points, cheatgrass prevalence increased as winter precipitation increased (Table 3, Fig. 4C). The effect could not be estimated in the model restricted to unburned points, in which winter precipitation was excluded given its high correlation with other variables.

Elevation was associated strongly with cheatgrass occurrence in all models and with prevalence of cheatgrass in models restricted to unburned or burned points (Tables 2, 3; Fig. 5A). Probability of cheatgrass occurrence increased as elevation decreased, and prevalence increased as elevation increased when controlling for fire (i.e., restricting the data to either burned or unburned points, Tables 2, 3; Fig. 5B, C). This may be due to the occurrence of most fires at the lower end of the range of elevations occupied by cheatgrass. Solar exposure was not strongly associated with probability of cheatgrass occurrence (Table 2),

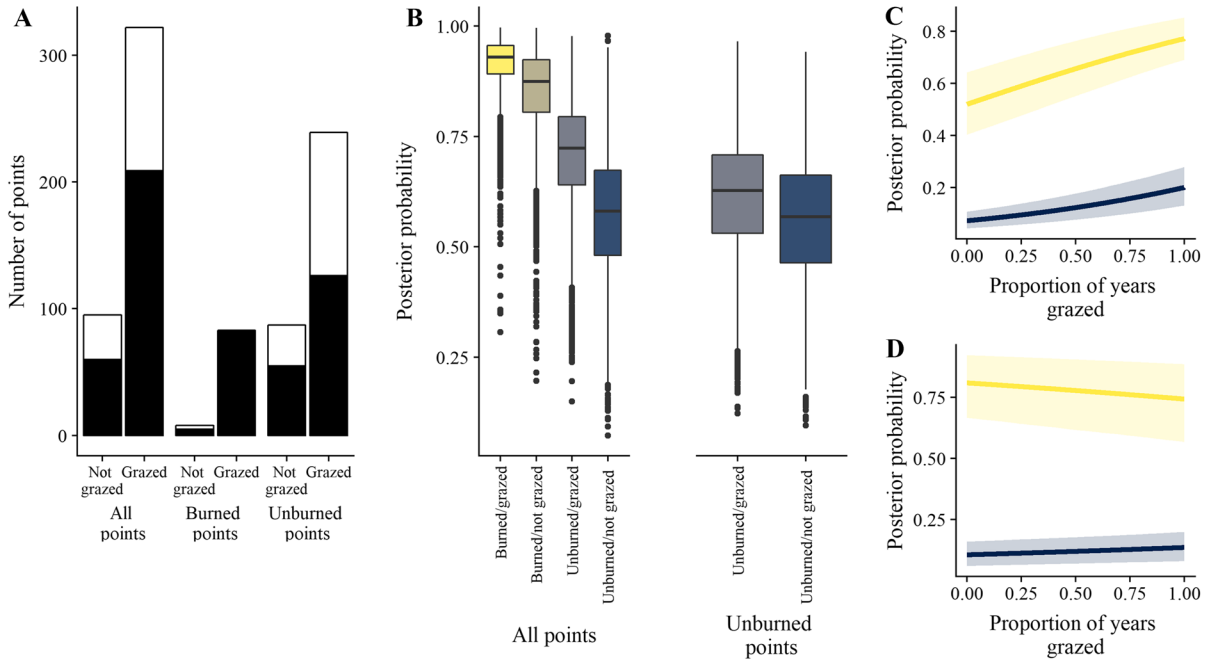


Fig. 3 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to the interaction between livestock grazing and fire. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Livestock grazing and fire both increased the probability of cheatgrass occurrence. Yellow, grazed and burned; tan, burned only; gray, grazed only; blue, neither grazed nor burned. Values derived from models that included either all sample points or unburned points. **C** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that included all sample points. Yellow, burned points; blue, unburned points. SD, standard deviation from the mean value of proportion of years grazed. **D** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that were restricted to either burned points (yellow) or unburned points (blue)

but prevalence increased as exposure decreased (Table 3).

Discussion

We capitalized on spatially and temporally extensive data on cheatgrass in both burned and unburned areas to evaluate explicitly the associations of fire, livestock grazing, precipitation, elevation, and solar exposure with probability of occurrence and with prevalence of cheatgrass across a large area and extensive topographic gradients. Our results generally were consistent with expectations that fire and a history of livestock grazing are associated positively with probability of cheatgrass presence and prevalence, and that ongoing disturbance is likely to induce expansion and increases in cover, density, abundance, or similar measures. Moreover, our work highlights that the potential response of cheatgrass to any one predictor, regardless of whether that predictor can be managed, is affected by other biotic and abiotic environmental attributes and feedbacks.

Regardless of fire history, cheatgrass was more likely to be recorded present at lower elevations. However, given presence, cheatgrass prevalence was greater at higher elevations and in areas with lower solar exposure. These areas likely have relatively high soil water availability while meeting the thermal requirements of cheatgrass for establishment, growth, and seed production (Chambers et al. 2007, 2016). Many of these areas are in canyons and occur in association with pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*, *J. occidentalis*) trees, which may reduce the exposure of cheatgrass to sunlight and heat stress. Higher prevalence of

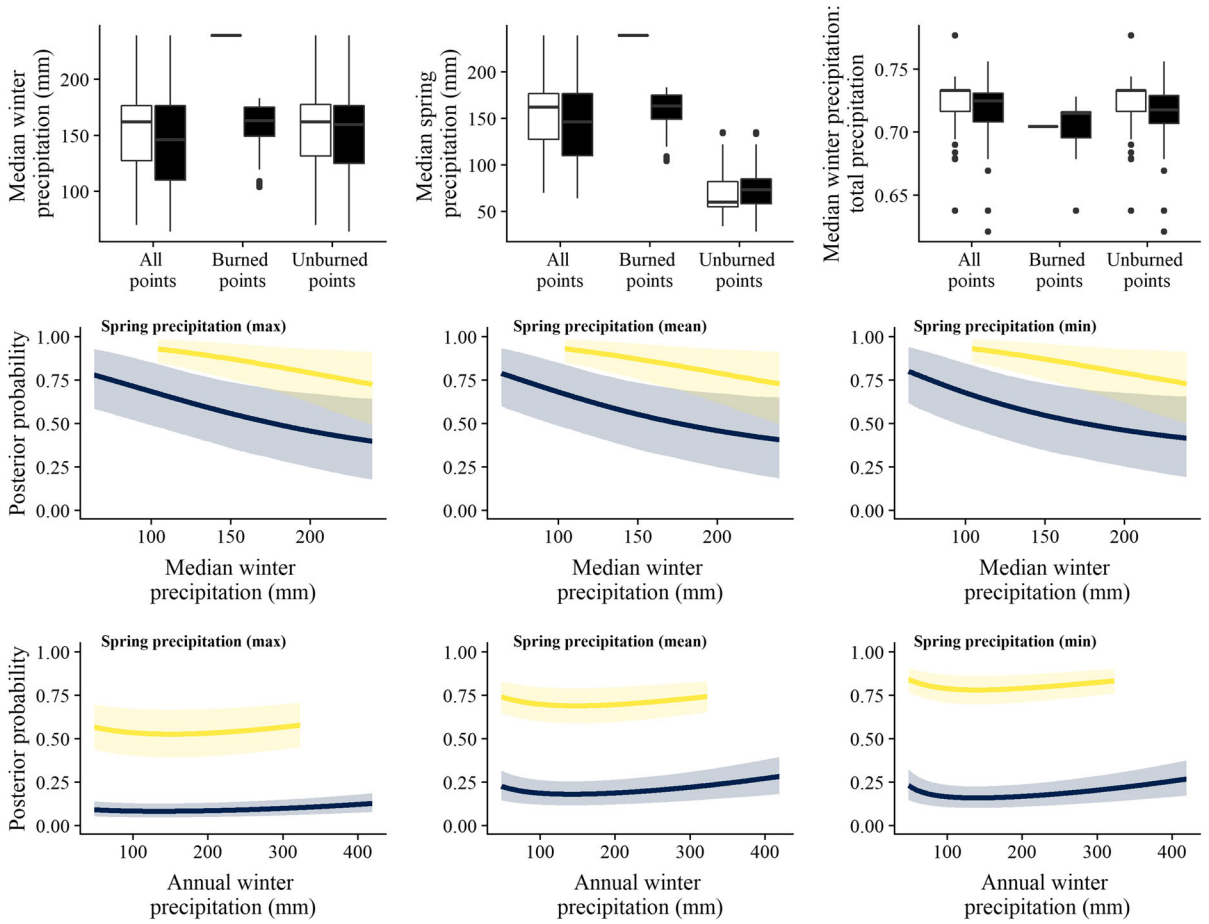


Fig. 4 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to precipitation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. Top row: Median winter precipitation, spring precipitation, or proportion of precipitation falling in winter at sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. Middle row: The probability of cheatgrass occurrence decreased as median winter precipitation (or the median proportion of precipitation falling in winter) increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. Yellow, burned points; blue; unburned points. SD, standard deviation from the mean value of median winter precipitation. Bottom row: The probability of cheatgrass prevalence increased as median winter precipitation (or the median proportion of precipitation falling in winter) over the study period increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. SD, standard deviation from the mean value of winter precipitation in the year of sampling

cheatgrass at relatively high elevations at the edges of unoccupied areas suggests that cheatgrass is likely to expand to higher elevations if thermal conditions are consistent with its requirements and if ground disturbances continue.

Consistent with previous studies on the cheatgrass-fire cycle (Balch et al. 2013; Germino et al. 2016; Bradley et al. 2018), the presence of fire was the predictor most strongly associated with probability of cheatgrass presence and was positively related to prevalence. In models restricted to burned points, prevalence of cheatgrass increased as time since burn increased. A lag in increases in cheatgrass density and cover of one to three years after fire is common (Chambers et al. 2016). Subsequent increases in cover and density can occur over time as the abundance of cheatgrass in the seed bank increases (Chambers et al. 2016).

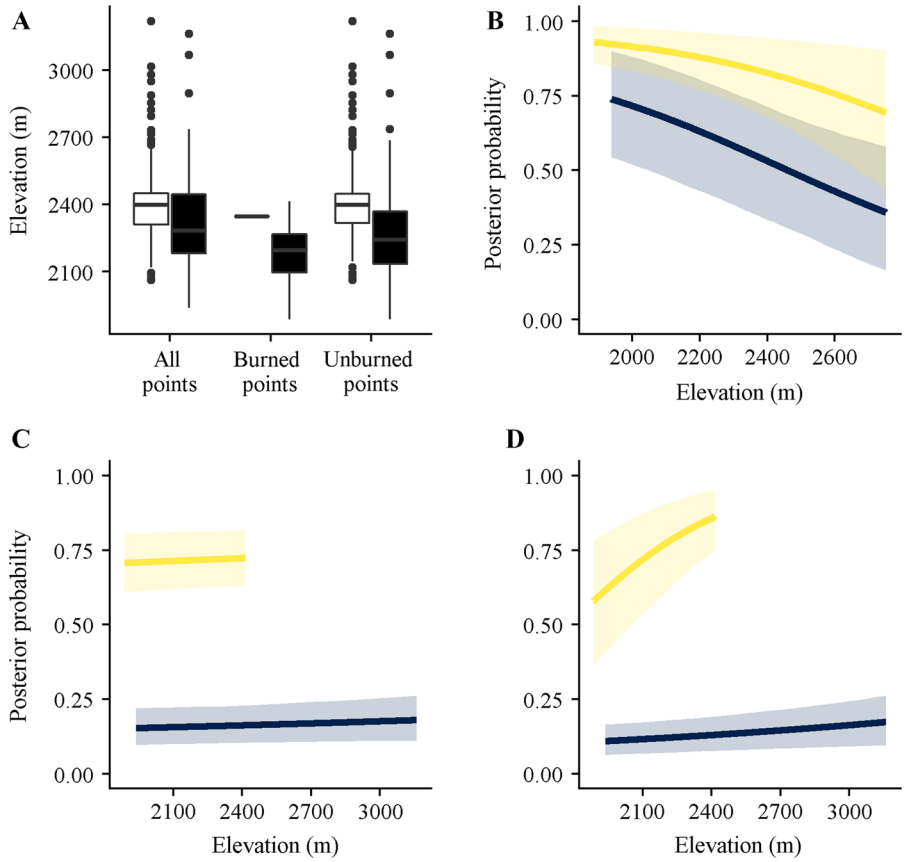


Fig. 5 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to elevation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** Elevational distribution of sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Probability of cheatgrass occurrrence decreased as elevation increased in a model that included all sample points (yellow, burned; blue, unburned). SD, standard deviation from the mean value of elevation. **C** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in a model that included all sample points. **D** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in models that were restricted to either burned points (yellow) or unburned points (blue). Differences in line lengths reflect different elevational ranges covered by the points included in the three models

Abundance of perennial native herbaceous species often is associated negatively with the abundance of cheatgrass or other non-native invasive annual grasses following prescribed fire and other management treatments (Davies 2008; Chambers et al. 2014). We found negative associations between prevalence of native perennial grasses and prevalence of cheatgrass in models that included all sample points or only unburned points, but not in models restricted to burned points. Following fire, loss of sagebrush and other fire-intolerant woody species increases the area of habitat for cheatgrass, soil water content, and nutrient content, and typically leads to increases in cheatgrass presence and abundance (Roundy et al. 2014, 2018). Cheatgrass likely will persist on these burned sites. However, maintaining or increasing the abundance of native perennial grasses can increase resistance to cheatgrass (Chambers et al. 2016; Pyke et al. 2016). The longer-term trajectories of these systems are unknown, but the strength and sign of the quadratic form of time-since-fire suggests that prevalence may stabilize or even decrease slightly at some point beyond the 14-year period we examined.

Consistent with Reisner et al. (2013), our analyses of all sample points and of only unburned points support the inference that, over an extensive area, both the presence of livestock grazing and the proportion of years in which a location is grazed are associated with an increase in the probability of presence and prevalence of cheatgrass. However, the negative association between the proportion of years grazed and prevalence of cheatgrass in models restricted to burned points may reflect a modest reduction in cheatgrass growth and seed production. This decrease in cheatgrass prevalence was accompanied by a decrease in the incidence of perennial grasses, suggesting that grazing on burned sites may lead to an overall decrease in herbaceous cover or biomass rather than selectively suppressing cheatgrass per se. Regardless, that the probability of encountering cheatgrass at any observation around a sample point (i.e., probability of prevalence) was > 0.5 on burned sites suggests that cheatgrass is likely to remain fairly dense on sites that are both burned and grazed, even if prevalence decreases modestly from its absolute peak.

It has been suggested that livestock grazing can reduce fuel loads and the likelihood of severe fires in sagebrush ecosystems (Davies et al. 2010). In the Owyhee Front in southern Idaho, the BLM has begun implementing intensive grazing in an effort to create fuel breaks, although evidence that fuel breaks reduce the spread and undesirable effects of fire is lacking (Shinneman et al. 2019). Grazing often reduces the abundance of perennial native grasses, which can facilitate increases in the presence and relative abundance of cheatgrass (Reisner et al. 2013, 2015); as our work suggests, these increases can occur over large areas, especially after fire. Widespread increases in cheatgrass presence and abundance, in turn, can increase fine-fuel loads and the likelihood of more frequent and extensive wildfires (Balch et al. 2013). We acknowledge that our characterization of grazing history includes some uncertainty. Grazing by cattle and sheep has occurred throughout our study region for well over a century, and likely for at least 75 years on allotments that were active during the study period, but reliable records are limited. Although we do not have precise information on number of livestock per unit area, duration of grazing, or intensity of grazing, livestock grazing long has been the single most widespread land use across the Intermountain West. Our results suggest a strong positive relation between the probability of presence and prevalence of cheatgrass and livestock grazing, particularly in unburned locations, where resistance to cheatgrass is greater than in burned locations.

Cheatgrass prevalence tended to be lower in years in which precipitation at a given point was high relative to that point's long-term median, but higher when regional winter precipitation was high and regional spring precipitation was at or below the median for the study period. This result is consistent with observations that growth and reproduction of cheatgrass occur earlier than that of many native shrubs and grasses (Peterson 2005). As a result, cheatgrass abundance may respond more strongly than abundance of native species to precipitation early in the water year. For example, at relatively low elevations, autumn precipitation may lead to germination and establishment of cheatgrass, provided the thermal requirements of cheatgrass are met (Roundy et al. 2018). By contrast, native species that compete with cheatgrass may respond more strongly than cheatgrass to precipitation later in the water year. Many of our observations of high prevalence of cheatgrass that coincided with relatively high proportions of precipitation in winter were associated with water-years in which precipitation was low. Thus, the amount of precipitation falling during periods favorable for cheatgrass establishment and growth may be more important than the total precipitation for the year (Bradley and Mustard 2006; Chambers et al. 2014; Jones et al. 2015).

The frequency of wet days in the Intermountain West is projected to decrease during the 21st century, whereas the amount of precipitation on wet days (Polade et al. 2014) and variability in precipitation are projected to increase (Dettinger et al. 2011; Gershunov et al. 2013; Kunkel et al. 2013). It is unclear how these projected changes will affect water availability, and how water availability may affect land uses, such as livestock grazing. Our results suggest that both the timing and amount of precipitation may affect the abundance of cheatgrass. Moreover, increases in temperature may lead to expansion of cheatgrass at higher elevations. We believe that interactions between land use and climate change will continue to affect the composition, structure, and function of ecosystems throughout the arid western United States and globally. Our work may inform prioritization of management actions to minimize anthropogenic

drivers of climate change that independently and cumulatively drive expansion of cheatgrass, changes in fire cycles, and the status of species and ecosystems across the Intermountain West. Our results, which derive from a novel time-series of data on cheatgrass and covariates from within an extensive area, do not support the use of livestock grazing to suppress cheatgrass and its undesirable effects on the habitats of native species or regional fire dynamics. Livestock grazing with the aim of suppressing cheatgrass may be especially counterproductive in unburned areas in which native perennial grasses may remain viable.

Acknowledgements This research was supported by the Joint Fire Science Program (05-2-1-94, 09-1-08-4, and 15-1-03-6), the US National Science Foundation Graduate Research Fellowship Program (1650042), the US Geological Survey's Northwest and Southwest Climate Science Centers (F16AC00025), and the Strategic Environmental Research and Development Program of the US Department of Defense (RC-2202).

References

Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK (2005) Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. Ecol Appl 15:774–792

Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biol 19:173–183

Banks ER, Baker WL (2011) Scale and pattern of cheatgrass (*Bromus tectorum*) invasion in Rocky Mountain National Park. Nat Area J 31:377–390

Blackard JA, Dean DJ (1999) Comparative accuracies of artificial neural networks and discriminant analysis in predicting forest cover types from cartographic variables. Comput Electron Agric 24:131–151

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecol Appl 16:1132–1147

Bradley BA, Curtis CA, Chambers JC (2016) *Bromus* response to climate and projected changes with climate change. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zürich, pp 257–274

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu MN (2018) Cheatgrass (*Bromus tectorum*) distribution in the Intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biol Invasions 20:1493–1506

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM et al (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brooks ML, Brown CS, Chambers JC, D'Antonio CM, Keeley JE, Belnap J (2016) Exotic annual *Bromus* invasions: comparisons among species and ecoregions in the western United States. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zürich, pp 11–60

Brummer TJ, Taylor KT, Rotella JJ, Maxwell BD, Rew LJ, Lavin M (2016) Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. Ecosystems 19:986–1000

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

Chambers JC, Board D, Dhaemers J, Reiner A (2010) Vegetation response to prescribed fire in the Shoshone mountains of Nevada. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2010-0016

Chambers JC, Miller RF, Board DI, Grace JB, Pyke DA, Roundy BA, Schupp EW, Tausch RJ (2014) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangel Ecol Manag 67:440–454

Chambers JC, Germino MJ, Belnap J, Brown CS, Schupp EW, St. Clair SB (2016) Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zurich, pp 275–306

Chambers JC, Maestas JD, Pyke DA, Boyd C, Pellant M, Wuenschel A (2017) Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and Greater sage-grouse. Rangel Ecol Manag 70:149–164

Compagnoni A, Adler PB (2014) Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. Ecosphere 5(9):121. https://doi.org/10.1890/ES14-00047.1

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Davies KW (2008) Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangel Ecol Manag 61:110–115

Davies KW, Bates JD, Svejcar TJ, Boyd CS (2010) Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. Rangel Ecol Manag 63:662–669

Davies GM, Bakker JD, Dettweiler-Robinson E, Dunwiddie P, Hall SA, Downs J, Evans J (2012) Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. Ecol Appl 22:1562–1577

Dettinger MD, Ralph FM, Das T, Neiman PJ, Cayan DR (2011) Atmospheric rivers, floods and the water resources of California. Water 3:445–478

Fleishman E (2015) Vegetation structure and composition in the Shoshone Mountains and Toiyabe, Toquima, and Monitor ranges, Nevada, 2nd edn. Forest Service Research Data Archive, Fort Collins. https://doi.org/10.2737/RDS-2013-0007-2

Freeman ED, Sharp TR, Larsen RT, Knight RN, Slater SJ, McMillan BR (2014) Negative effects of an exotic grass invasion on small-mammal communities. PLoS ONE 9(9):e108843. https://doi.org/10.1371/journal.pone.0108843

Garton EO, Connelly JW, Horne JS, Hagen CA, Moser A, Schroeder MA (2011) Greater Sage-Grouse population dynamics and probability of persistence. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, vol 38. University of California Press, Berkeley, pp 293–381

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv Biol 17:420–432

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis, 3rd edn. CRC Press, Boca Raton

Germino MJ, Belnap J, Stark JM, Allen EB, Rau BM (2016) Ecosystem impacts of exotic annual invaders in the genus *Bromus*. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, New York, pp 11–60

Gershunov A et al (2013) Future climate: projected extremes. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds) Assessment of climate change in the southwest United States: a report prepared for the National Climate Assessment. Island Press, Washington, DC, pp 126–147

Jeffreys H (1961) Theory of probability, 3rd edn. Clarendon Press, Oxford

Jones RO, Chambers JC, Board DI, Johnson DW, Blank RR (2015) The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (*Bromus tectorum*). Ecosphere 6(7):107. https://doi.org/10.1890/ES14-00285.1

Knapp PA (1998) Spatio-temporal patterns of large grassland fires in the Intermountain West, USA. Global Ecol Biogeogr 7:259–272

Kunkel KE, Karl TR, Easterling DR, Redmond K, Young J, Yin X, Hennon P (2013) Probable maximum precipitation and climate change. Geophys Res Lett 40:1402–1408

Larson CD, Lenhoff EA, Rew LJ (2017) A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. Oecologia 185:763–774

Mack RN (1981) Invasions of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hooved mammals. Am Nat 119:757–773

Meyer SE, Garvin SC, Beckstead J (2001) Factors mediating cheatgrass invasion of intact salt desert shrubland. In: McArthur ED, Fairbanks DJ (compilers) Proceedings—Shrubland Ecosystem Genetics and Biodiversity; 13–15 June 2000. RMRS-P-21, US Department of Agriculture Forest Service, Rocky Mountain Research Station, Provo, Utah

Miller RF, Chambers JC, Pyke DA, Pierson FB, Williams CJ (2013) A review of fire effects on vegetation and soils in the Great Basin region: response and ecological site characteristics. General Technical Report RMRS-GTR-308, US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado

Mullahy J (1986) Specification and testing of some modified count data models. J Econom 33:341–365

NOAA National Centers for Environmental Information (NCEI) (2018) U.S. billion-dollar weather and climate disasters. https://www.ncdc.noaa.gov/billions/

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Karieva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Peterson EB (2005) Estimating cover of an invasive grass (*Bromus tectorum*) using tobit regression and phenology derived from two dates of Landsat ETM plus data. Int J Remote Sens 26:2491–2507

Pilliod DS, Welty JL, Arkle RS (2017) Refining the cheatgrass-fire cycle in the Great Basin: precipitation and fine fuel composition predict wildfire trends. Ecol Evol 7:8126–8151

Polade SD, Pierce DW, Cayan DR, Gershunov A, Dettinger MD (2014) The key role of dry days in changing regional climate and precipitation regimes. Nat Sci Rep 4:4364. https://doi.org/10.1038/srep04364

Pyke DA, Chambers JC, Beck JL, Brooks ML, Mealor BA (2016) Land uses, fire and invasion: exotic annual *Bromus* and human dimensions. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zurich, pp 307–337

Reisner MD, Grace JB, Pyke DA, Doescher PS (2013) Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. J Appl Ecol 50:1039–1049

Reisner MD, Doescher PS, Pyke DA (2015) Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. J Veg Sci 26:1212–1224

Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez J, Müller M (2011) pROC: an open-source package for R and S + to analyze and compare ROC curves. BMC Bioinform 12:77. https://doi.org/10.1186/1471-2105-12-77

Roundy BA, Young K, Cline N, Hulet A, Miller RR, Tausch RJ, Chambers JC, Rau B (2014) Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangel Ecol Manag 67:495–505

Roundy BA, Chambers JC, Pyke DA, Miller RF, Tausch RJ, Schupp EW et al (2018) Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. Ecosphere 9:02417

Shinneman DJ, Germino MJ, Piliod DS, Aldridge CL, Vaillant NM, Coates PS (2019) The ecological uncertainty of wildfire fuel breaks: examples from the sagebrush steppe. Front Ecol Environ. https://doi.org/10.1002/fee.2045

Stan Development Team (2017) Stan modeling language: user's guide and reference manual. Version 2.17.0

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3. http://mc-stan.org/

Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L (2017) Challenges and limitations to native species restoration in the Great Basin, USA. Plant Ecol 218:81–94

Taylor K, Brummer T, Rew LJ, Lavin M, Maxwell BD (2014) *Bromus tectorum* response to fire varies with climate conditions. Ecosystems 17:960–973

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Urza A, Weisberg PJ, Chambers JC, Board DI, Dhaemers J, Flake S (2017) Post-fire vegetation response at the woodland-shrubland interface is mediated by the pre-fire community. Ecosphere 8(6):e01851. https://doi.org/10.1002/ecs2.1851

US Department of the Interior Bureau of Land Management (BLM) (2007) Burned area emergency stabilization and rehabilitation handbook. BLM Handbook H-1742-1. https://www.blm.gov/sites/blm.gov/files/uploads/Media_Library_BLM_Policy_Handbook_h1742-1.pdf

U.S. Fish and Wildlife Service (USFWS) (2015) Endangered and threatened wildlife and plants; 12-month finding on a petition to list the greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species; proposed rule. Fed. Register 80, 59858–59942. http://www.gpo.gov/fdsys/pkg/FR-2015-10-02/pdf/2015-24292.pdf. Accessed 9 Jan 2016

Williamson, MA (2019) Code for Williamson et al. 2019. https://doi.org/10.5281/zenodo.3237935. Available at https://github.com/mattwilliamson13/GBbrte

Appendix D

The Sonoran Desert

Chapter · January 2019

DOI: 10.1016/B978-0-12-409548-9.11939-6

2 authors:

Curtis Bradley
Center for Biological Diversity
12 PUBLICATIONS **90** CITATIONS
SEE PROFILE

Debra Colodner
Arizona-Sonora Desert Museum
25 PUBLICATIONS **1,423** CITATIONS
SEE PROFILE

The Sonoran Desert

Curtis M Bradley, Center for Biological Diversity, Tucson, AZ, United States
Debra Colodner, Arizona-Sonora Desert Museum, Tucson, AZ, United States

A Unique Ecoregion 1
Geologic History 2
Defining the Ecoregion 2
Vegetative Subdivisions of the Sonoran Desert 2
Lower Colorado River Valley 2
Arizona Upland 3
Central Gulf Coast 4
Plains of Sonora 4
Climate 4
Representative Sonoran Desert Animals 5
Arthropods 5
Birds 6
Mammals 7
Fishes and Amphibians 7
Reptiles 8
Indigenous Peoples and Colonization 9
Threats to Biodiversity 10
Climate Change 10
Invasive Species 10
Livestock Grazing 11
Border Wall 12
Land Conversion and Loss of Riparian Habitat 13
Conservation Status and Planning 13
Mexico 13
United States 14
The future of the Sonoran Desert 15
References 15

Abstract

The Sonoran Desert has been identified as one of the most distinctive ecoregions in the world, recognized for its columnar cacti such as the saguaro and cardón. It is home to 130 mammal, 400+ bird, 100 endemic reptile, 750 bee, and nearly 2500 endemic plant species. This great variety of species and habitats is due to the desert's subtropical climate, wide-ranging topography, bimodal rainfall pattern, and location at the crossroads of several different ecoregions. Geologic processes shaped the landscape and created the Gulf of California, a biologically rich body of water that influences the region's climate. The desert's biota faces numerous challenges including increasing temperatures and changing rainfall patterns, loss of native vegetation from invasive species and livestock grazing, habitat fragmentation from transportation and border wall infrastructure, and loss of habitat and riparian areas due to human expansion and groundwater pumping. In the US, nearly 3.88 million hectares (9.58 million acres) is protected from development or other incursions, although other threats to the ecoregion are ongoing. In Mexico, nearly 1.5 million hectares (3.7 million acres) have been set aside as biosphere reserves and other protected areas. A large marine biosphere reserve in the northern Gulf of California has been unsuccessful at preventing the alarming population decline of the vaquita porpoise, which hovers on the brink of extinction.

A Unique Ecoregion

Spanning over 224,000 km^2 across two countries and four Mexican and US states, the Sonoran Desert encompasses a great variety of species and habitats. The area has been identified as one of the most distinctive ecoregions in the world based on analyses of species richness, species endemism, and global rarity of major habitat types (Olson and Dinerstein, 2002). The species list includes 130 mammals, 400+ birds, 100 endemic reptiles, 750 bees, and over 4000 plants, nearly 2500 of which are endemic to the Sonoran Desert (Nabhan, 2015a). This great biodiversity is due to the subtropical climate, varied geology, wide-ranging topography, and most importantly, rainfall that occurs in both the summer and winter, which supports a broad array of both warm and cool season flora. In fact, this desert has the greatest diversity of plant growth forms, or adaptive strategies evolved to survive high temperatures and drought, of any desert in the world (Nabhan, 2015b).

Geologic History

The contemporary desert Southwest landscape was formed by two main geological events that occurred over millions of years and involved the movement of tectonic plates. The first event occurred from approximately 200 to 50 million years ago, when the Farallon plate was subducted beneath the lighter North American Plate. This action compressed the North American plate, like pushing a rug up against a wall, forming the Rocky Mountains and the Sierra Madre Occidental, and causing much of the volcanic activity in the region.

The second event, starting at about 35 million years ago, occurred as the spreading center between the Pacific plate and the Farallon plate was also subducted beneath the North American plate. Because the Pacific plate was moving in a generally westerly direction, it pulled and stretched this portion of the North American plate along with it. This stretching caused the earth's crust to crack like the surface of a cooling pumpkin pie and formed huge valleys as sections dropped downward in what is called block faulting. The high ground between the valleys remains as today's mountain ranges, creating what is known as the Basin and Range province and the hundreds of isolated mountain ranges that extend from southern Oregon to central Mexico. At about 5.5 million years ago, this motion began pulling the Baja California peninsula away from the mainland of Mexico, eventually creating the Gulf of California. This motion continues today as the peninsula and areas in California west of the San Andreas fault continue moving northwest at a rate of about 5 cm a year (Scarborough and Brusca, 2015).

Defining the Ecoregion

The Sonoran Desert (Fig. 1) is at the crossroads of several different ecoregions and biotic communities that contribute to its incredible biodiversity. To the north, interior chaparral leads to the higher-elevation montane conifer forests of the Mogollon Rim. The west and east edges are bookended by the peninsular ranges of southern California and the grasslands and woodlands of the Sky Islands. Sinaloan thornscrub, the ancestral biome from which many Sonoran Desert plants and animals evolved, transitions into tropical deciduous forests further south (Van Devender and Brusca, 2015).

The Sonoran Desert is visually distinguished from other North American deserts by two life forms: legume trees such as the acacia, and large columnar cacti (Dimmitt, 2015). These cacti include the saguaro (*Carnegiea gigantea*) and the cardón (*Pachycereus pringlei*), the largest cactus in the world. Forrest Shreve first described and mapped the boundary of the desert in 1942 while working at the Carnegie Institution's Desert Laboratory in Tucson (Shreve, 1942). Being a botanist, he differentiated the deserts based on their floristic composition, physical appearance, and community structure of the dominant plant species. He subsequently refined his description of the Sonoran Desert and defined seven subregions that included the deserts of the Baja California peninsula (Shreve, 1951).

More recently, scientists have used a different approach to define the boundaries of the Sonoran Desert (Riddle et al., 2000). They used DNA to reconstruct the historic processes that are responsible for the contemporary geographic distribution of species in the desert. They found that the desert biota of the Baja California peninsula has a unique evolutionary history, as distinct as the other regional deserts, and proposed that it should be considered a separate desert, the Peninsular Desert, instead of a subdivision of the Sonoran Desert. This additional classification has not been met with wide acceptance (Hafner and Riddle, 2011), but for the purposes of this chapter we will discuss the Sonoran Desert and Baja Peninsular Desert as separate entities.

Vegetative Subdivisions of the Sonoran Desert

Desert plants are supremely adapted to their arid environment. To people from wetter parts of the planet, it may appear that they are just eking out an existence, but in fact, these plants could not survive in wetter places. They thrive in the desert. Their adaptations to aridity include succulence (the ability to store water in fleshy leaves, stems, and roots), extensive shallow root systems designed to absorb water from any rainfall, waxy coatings to prevent water loss from stems and leaves, small leaves to prevent overheating and limit water loss, and green stems which provide photosynthesis even when leaves are small or absent. Another strategy is drought-avoidance, as displayed by annual plants which complete their life cycles during brief wet seasons and then die after channeling all their energy into producing seeds (Dimmitt, 2015).

Lower Colorado River Valley

The largest, hottest and driest subdivision is found along the Lower Colorado River, and is second only to the Mohave Desert's Death Valley as the hottest and driest place in North America. Summer highs can exceed 120 F (48.5C), and humidity is often less than 10%. Annual rainfall in the driest areas is generally less than 75 mm, and it is not uncommon for some locations to go two or 3 years without rain. Even so, life exists here, and is abundant in the rare wet years (Dimmitt, 2015).

The landscape in this subdivision is dominated by broad flat basins interrupted by small rocky ranges. It includes the Gran Desierto de Altar, a 5700 km^2 sand sea, the only area one might recognize as stereotypical desert. The spectacular Pinacate volcanic field lies within this sub-region as well. The valleys are dominated by low shrubs, primarily creosote bush (*Larrea tridentate)* and

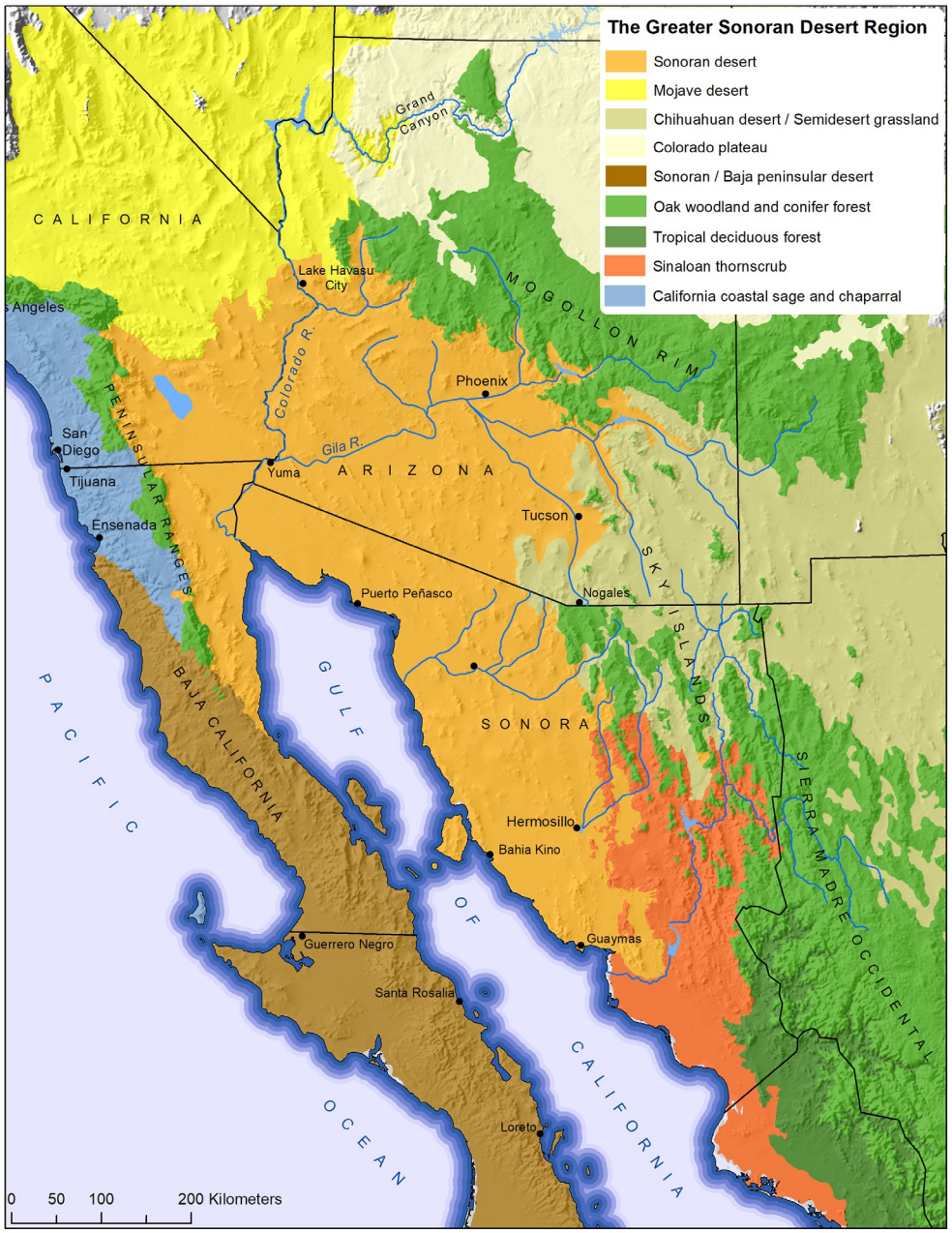


Fig. 1 Map of the Sonoran Desert and surrounding ecoregions by Curtis Bradley. Data Source: Ecoregions 2017 © Resolve.

white bursage (*Ambrosia dumosa*). These are the two most drought-tolerant plants in North America, but in the driest areas of this subdivision even they are restricted to drainages. Trees are found only in the larger washes. The mountains support a wider variety of shrubs and cacti, but the density is sparse. Columnar cacti are rare and restricted to drainages. Annual plants comprise well over half the flora (90% at the driest sites), and are abundant only in wet years (Dimmitt, 2015).

Arizona Upland

This northeastern section, mostly in south-central Arizona and northern Sonora, is the highest and coldest subdivision of the Sonoran Desert (Fig. 2). The terrain contains numerous mountain ranges, and the valleys are narrower than in the Lower Colorado River Valley subdivision. Trees are common on rocky slopes as well as drainages, and saguaros are found everywhere except the valley floors. This community is also called the saguaro-palo verde forest. It is the only subdivision that experiences frequent hard winter frosts, so many species of the lower elevation and more southerly subdivisions cannot survive here.

Fig. 2 Arizona Upland in the Tucson Mountains. Photo by Dug Schoellkopf.

The Arizona Upland is home to a great variety of cacti, ranging from saguaros that can reach heights of 12 m to several tiny species less than 10 cm. There are tall columnar cacti, round cacti (barrels), jointed stick-like cacti (chollas), and cacti with flat pads (prickly pears). Other common plants found here are agaves (*Agave spp.)*, yuccas (*Yucca spp.)*, and legumes such as mesquite (*Prosopis* spp.*)*, palo verde (*Parkinsonia* spp.*)*, ironwood (*Olneya tesota*), and acacia *(Acacia* spp.*)*. Low shrubs include white bursage, brittlebush (*Encelia farinosa)*, jojoba (*Simmondsia chinensis)*, ocotillos (*Fouquieria splendens)*, and a variety of desert grasses.

Central Gulf Coast

The Central Gulf Coast subdivision occupies strips along both sides of the Gulf of California, and desert vegetation grows right to the seashore. Small shrubs are nearly absent; their shallow root systems and lack of water storage cannot sustain them through the extreme aridity here. Dominating the vegetation are large stem-succulents, particularly the massive cardón (Fig. 3) and trees such as palo verde, ocotillo, ironwood, elephant trees (*Bursera* spp.), and limberbush (*Jatropha* spp.), which are leafless most of the time. The average annual rainfall of less than 5 in (125 mm) occurs mostly in summer, though not dependably enough to call it a rainy season (Dimmitt, 2015).

Plains of Sonora

The Plains of Sonora, a small region of central Sonora, is similar to the Arizona Upland with denser vegetation (due to more rain and deeper, finer soils) and additional tropical species. Most of the subdivision has been converted to agriculture (Dimmitt, 2015).

Climate

Annual precipitation in the Sonoran Desert ranges from 50 to 400 mm (2–16″) a year with substantial inter- and intra-annual variability in timing and quantity. Lower elevations near the Colorado River and Gulf of California receive the least amount of rain and higher elevations near the Sierra Madre Occidental receive the most. The desert is situated at 28–34° latitude which, combined with its location at the western edge of a large land mass, is in an area dominated by sinking, dry equatorial air and high pressure that serves to reroute incoming frontal storms. During the cooler winter months, from December to March, this high pressure breaks down and moisture from the Pacific Ocean arrives on the back of strong westerly winds. Much of this moisture is lost on the windward side of the peninsular mountain ranges of Southern California and Baja California, and never makes it to the desert. This rain shadow effect is caused when an air mass is forced up and over a mountain range, cooling it, and thus causing the moisture to precipitate out as rain or snow.

There are five seasons in the Sonoran Desert: fall, winter, spring, and two summer seasons. Fore-summer occurs in May and June and is characterized by cloudless, dry, sunny days with temperatures commonly exceeding 40 °C (104 °F). Monsoon season typically arrives in early July and is characterized by a shift in the wind patterns, increasing humidity, and chances for rain. The North American monsoon shares the basic characteristics of the Indian counterpart but lacks its duration and intensity. The event is created by several factors working in concert. A thermal low-pressure system forms near the Arizona and California border created by

Fig. 3 Organ pipe cactus (*Stenocereus thurberi)* in foreground, cardón, and saguaro in background. Photo by Sky Jacobs.

rising air from the intense solar heating of the Earth's surface. This pulls in low level moisture from the nearby warm waters of the Gulf of California. Secondly, a high pressure system develops over the Four Corners area where the US states of Arizona, New Mexico, Colorado, and Utah meet. The air cools over this higher elevation area, falling, and creating a counter clockwise air flow that draws in higher-level moisture from the Gulf of Mexico. These conditions can combine to produce intense but localized afternoon thunderstorms.

Representative Sonoran Desert Animals

Arthropods

Just as elsewhere in the world, arthropods comprise over 85% of the described animal species in the Sonoran Desert. They are the most important pollinators, and they aerate the soil, and decompose dead plants and animals. Arthropods are also some of the most important herbivores and prey in terrestrial food webs. The Sonoran Desert is a biodiversity hotspot for arthropods. Their great variety of adaptations to desert life, interesting behaviors, and critical ecological functions are fascinating. Each summer during monsoon season, two-legged entomologists swarm the region to study its six- and eight- legged residents.

The most famous/infamous arthropods in the Sonoran Desert are probably its black widow spiders (*Latrodectus hesperus*), tarantulas (*Aphonopelma* spp., Fig. 4), and scorpions. Most spiders are venomous, but only the black widow and brown recluse (*Loxosceles* spp.) have venom dangerous to people. The female black widow will sometimes eat the male after mating, thus the name "widow," although this behavior is actually seen in many types of spiders. Tarantulas are 3 to 4 in. long and commonly seen during the summer rainy season when males leave their burrows to seek out females. They have an unusual defense mechanism: irritating barbed hairs that they can brush onto the mouth, nose or paws of a predator.

There are more than 30 species of scorpion in the region. They occur in a great variety of habitats, spending much of their time underground, under rocks or, as with bark scorpions, high above ground in trees or in rock crevices. Scorpions give birth to live young which quickly clamber on to their mother's back to hitch a ride until their first molt. One of the most unusual traits of scorpions is that they fluoresce under ultraviolet light (Lizotte, 2015).

Fig. 4 Arizona-Sonora Desert Museum. Photograph of tarantula by Howard Byrne III.

Many other arthropods are keystone ecological players in the Sonoran Desert. The region is home to more than 750 species of bees. They range in size from the world's smallest bee, *Perdita minima*, measuring less than 2 mm, to carpenter bees (*Xylocopa* spp.), which are up to 40 mm long. Unlike most other groups of animals, bee diversity peaks in deserts and savannahs, rather than in rainforests. Most native Sonoran Desert bees are solitary, creating nests inside perfectly circular holes dug in the ground, although some make their nesting holes in dried stems or wood (Buchmann, 2015).

Birds

People flock from all over the world to catch a glimpse of both the diversity and distinctiveness of the Sonoran Desert's more than 400 bird species (Fig. 5). Some of the greatest stars are the dozen or so hummingbird species that live in or pass through the region.

Fig. 5 The cactus ferruginous pygmy-owl (*Glaucidium brasilianum*) was formerly common in the Arizona Upland subdivision but is now considered endangered in the United States due to habitat loss. Photograph by Sky Jacobs.

They include the smallest birds in the world and range from 7 to 13 cm. They have the most brilliant iridescent colors, the fastest wingbeats, and the most amazing flying acrobatics, with the ability to fly up, down, sideways, and backward.

The greater roadrunner (*Geococcyx californianus*) is probably the most iconic desert bird. These birds can fly, but usually walk or run instead. In the open, they can reach speeds of 30 km per hour. A fierce predator, the roadrunner can catch snakes, lizards, rodents, small birds and insects. They prefer the open habitat of desert or pinyon/juniper.

Gambel's quail (*Callipepla gambelii*) are some of the most visible and audible birds in the Sonoran Desert. They spend most of their time on the ground and are commonly seen scurrying in groups from the cover of one sprawling mesquite to another. During spring and summer, one often sees young quail following their parents in a single file line of 10 or more brown fluff balls. They are common in desertscrub, thornscrub and riparian areas (Kaufman, 2015).

Of the many hawks and eagles that inhabit the Sonoran Desert, Harris's hawks (*Parabuteo unicinctus)* are the only ones that live and hunt in social groups. They cooperate in defending their nest, and in flushing out prey during a hunt. Other common hawks are Cooper's hawks (*Accipiter cooperii*) and red-tailed hawks (*Buteo jamaicensis*). The American kestrel (*Falco sparverius*) is a familiar sight as well. This small falcon can reach great speeds chasing the large insects that make up most of its diet. Another bird in the falcon family, the crested caracara (*Caracara cheriway*), is a large, majestic, slow-flying bird that will catch live prey or eat carrion. It is mainly a tropical bird, common in the southern part of the Sonoran Desert, however its range is expanding northward into Arizona (Jennes, 2015). Many other birds inhabit the diverse landscape and soundscape of the Sonoran Desert, much too numerous to list here.

Mammals

Over 40 species of bat live in the Sonoran Desert Region. Bats are one of the most diverse groups of mammals and one of the most threatened. White nose syndrome, which has devastated bat populations in the northeast US, has not yet reached the Sonoran Desert. Bats keep insect populations in check and are important pollinators of many Sonoran Desert plants, including the iconic columnar cacti (Tyburec, 2015).

Sonoran Desert canids include coyotes (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and kit fox (*Vulpes macrotis*). Coyotes are found in all habitats, while gray foxes prefer rocky canyons and kit foxes like more open flats, with deeper soils for digging their dens. Coyotes appear prominently in the stories people have told about this region throughout time. All three desert dogs are omnivores, eating whatever they can find. Coyotes are mostly social animals, living in small family groups and filling the desert with their yips and howls whenever there is news to share, but especially at dusk. Gray foxes can climb, forage and sleep in trees, safe from many of their predators. Kit foxes are nocturnal and use their underground dens year-round. They can survive without free water, getting all the water they need from their food. The endangered Mexican gray wolf (*Canis lupus baileyi*) also lives in the region, in the mountains at the desert's edges.

Four wild cats make their homes in the Sonoran Desert region. The largest two, the jaguar (*Felis onca*) and mountain lion (*Felis concolor*), live mostly in the sky islands. Bobcats (*Felis rufus)* are common in many habitats, including people's back yards. Ocelots (*Felis pardalis*) are found in thornscrub, oak woodland and riparian areas in Sonora, Mexico, and are rarely seen in the northern part of the Sonoran Desert.

Two distinctive, but rarely seen Sonoran Desert mammals are the ringtail (*Bassariscus astutus;* Fig. 6) and coati (*Nasua narica*). Both are related to raccoons in the procyonid family. Ringtails are squirrel-sized, with large eyes and a long fluffy ringed tail. They have excellent climbing abilities and are solitary and nocturnal. Coatis are social animals, living in large bands of up to 30 individuals in riparian areas or oak-sycamore canyons. They are longer and thinner than a raccoon with a longer snout ringed tails. They often walk with their tails erect. Both of these animals, like raccoons, are omnivores.

Other Sonoran Desert mammals are: desert bighorn sheep (*Ovis canadensis nelson*), Sonoran pronghorn (*Antilocapra americana sonoriensis*) and multiple species of skunks, badgers, deer, rabbits, and a variety of rodents, many with fascinating adaptations to the heat and aridity of the desert.

Fishes and Amphibians

"Desert fish" may sound an oxymoron, but fish are also found in the Sonoran Desert. Many washes that are dry today were once streams that ran at least intermittently. There are dozens of freshwater species native to the region, and even more that have been introduced. Native species include the small (5 cm) Gila topminnow (*Poeciliopsis occidentalis*) and the largest minnow in the region—the 1.8 m Colorado pikeminnow (*Ptychocheilus lucius*). At least two thirds of the native species are threatened or endangered due to loss of habitat and competition from nonnative species (Ivanyi and Marsh, 2015) including the Sonoyta or Quitobaquito pupfish (*Cyprinodon eremus*), which is found in one location on the Rio Sonoya in Sonoran and at Quitiobaquito Springs in Organ Pipe National Monument.

Sonoran Desert amphibians have evolved some ingenious methods to get and keep the water they need. For example, Couch's spadefoots (*Scaphiopus couchii*) burrow into moist soil and emerge to feed and breed only on rainy nights. They lay their eggs in temporary ponds, and they hatch and metamorphose in less than 2 weeks, hopefully before the pond has dried up. Similarly, the large (18 cm) Sonoran Desert toad (*Incilius alvarius*) spends most of the year in rodent or other underground burrows, emerging in the rainy season to mate and feed. Their tadpoles take longer to mature – 6 to 10 weeks, requiring larger or longer-lived ponds to complete the life cycle. Both types of amphibian are generally nocturnal (Ivanyi et al., 2015).

Fig. 6 Ringtail Photo by Paul and Joyce Berquist.

Reptiles

Sonoran Desert tortoises (*Gopherus morafkai*) are widespread throughout the region. They survive the heat of summer days and the cold of winter in a hibernation-like state in burrows, which they dig with strong, flattened, front legs. They extract water from the plants they eat and will drink free water if it's available. Their bladder has the capacity to store 40% of their body weight in water to get them through long dry spells. Gila monsters (*Heloderma suspectum*, Fig. 7) are one of only two medically significant venomous lizards in the world, the other being the beaded lizard found along the Pacific slopes of Mexico from Southern Sonora into

Fig. 7 Gila monster. Photograph by Alex Kerstitch.

Guatemala. The Gila monster is a large wide-bodied lizard, reaching about 45 cm in length and brightly bedecked in bands or a network of pink, red, or orange, contrasted with black—which is considered warning (aposematic) coloration (Ivanyi et al., 2015).

There is a great diversity of other lizards and snakes in the Sonoran Desert, reflecting not only the diversity of habitats, but the region's position adjacent to grasslands of the mid-continent and the tropics to the south. A species that is adapted to the Sonoran Desert is the Tucson shovel-nosed snake (*Chionactis annulata klauberi*), a non-venomous mimic of the Sonoran coral snake (Fig. 8). It has a specially adapted spade like snout that allows it to burrow or "swim" through sandy soils and preys on everything from beetle larvae to scorpions.

Arizona is home to at least 18 different varieties of rattlesnake and, if you add in those found in the state of Sonora and the Baja California peninsula, as well as species found on islands in the Gulf of California, this region easily rivals any other in rattlesnake diversity. Rattlesnake venom is a highly specialized mixture of enzymes that attacks blood, tissue, heart and nerves. They are most active in the warmer seasons, and mostly nocturnal in the summer. To aid seeing in the dark, they have a pair of unusual infrared-sensing organs that help them find prey, avoid predators, and navigate the challenging thermal landscape in which they live (Ivanyi et al., 2015).

Indigenous Peoples and Colonization

Humans have been living in Sonoran Desert for at least 13,000 years, shaping its ecosystems and biodiversity, just as the environment has shaped human cultures through time. Some scientists believe that Paleo-Indians contributed to the extinction of large megafauna that roamed North America during the Ice Age. Archeologists have documented changes in the abundance of various mammal species near early human settlements due to human consumption patterns. Hohokam people built extensive irrigation networks and cleared desert vegetation for fields and firewood. The Seri people on the Sonoran coast helped to expand the range of several species of reptiles during their travels. For at least 4000 years, Sonoran Desert peoples such as the O'odham, Cocopas, Yoemem, and Mayos (and their ancestral cultures) cultivated maize, tepary and pinto beans, gourds, squash, cotton, amaranth, devil's claw, agaves, and many other plants, changing their abundance and distribution on the landscape (Sheridan, 2015).

With the arrival of Europeans in the 16th century, came the devastating dispersal of new diseases, which are estimated to have killed up to 95% of the indigenous population. Europeans also brought new plants and animals including winter wheat, fruit trees, mules, oxen, cattle, sheep, goats, and horses, which further changed the landscape and biodiversity. The discovery of silver and gold deposits in the late 17th century accelerated this trend. Ranching and mining settlements were developed. The railroad arrived in the 1880s, followed by cattle, copper, and cotton. Each did their part to remake portions of the Sonoran Desert. The widespread availability of air conditioners starting in the 1940s led to rapid urban growth in Arizona. Each successive wave of human settlement left its mark on the biome we call the Sonoran Desert, a process that continues today (Sheridan, 2015).

Fig. 8 The venomous Sonoran coral snake (*Micruroides euryxanthus*) is distinguished from its non-venomous shovel-nosed mimics by its black snout and thicker bands. Photograph by Sky Jacobs.

Threats to Biodiversity

Climate Change

Nearly all the world's biomes have experienced temperature increases over the last 50 years, and the Sonoran Desert is no exception. According to the Fourth National Climate Change assessment, the region has already seen a 0.89 °C (1.61 °F) increase in average annual temperature since the beginning of the 20th century. This is predicted to increase by an additional 2.7 to 4.8 °C (4.9–8.7 °F) by the end of this century under the lower (RCP4.5) and higher (RCP8.5) emissions scenarios, respectively (Wuebbles et al., 2017).

Changes in rainfall patterns have been equally significant (Fig. 9). Regions of the Sonoran Desert have experienced a 15% reduction in precipitation (USGCRP 2017), and a 19% reduction of flows has been observed on the Colorado River (Udall and Overpeck, 2017). Most models forecast less winter and spring rain and lower overall precipitation in the future. At the same time, rainfall intensity, or the amount of rain in a given period of time, is predicted to increase during summer thunderstorms because warmer air can hold more moisture. Summer rains typically produce localized precipitation that does not percolate into the soil as deeply as winter rains that originate from large Pacific Ocean frontal systems (MacMahon and Wagner, 1985).

These changes in climate are predicted to affect the distribution and abundance of many Sonoran Desert species. The hotter temperatures will mean a decrease in available soil moisture due to increased evapotranspiration. Plants with root systems that can tolerate water stress and can utilize summer versus winter precipitation will be favored. This change is being observed with the reduction of foothill paloverde (*Parkinsonia microphyllum*) and ocotillo (*Fouquieria splendens*) on south and west facing slopes (Munson et al., 2011). It is also predicted that many of the desert's plant species ranges will move up in elevation in response to climate change. A study on the Santa Catalina Mountains near Tucson found that 15 of 27 plant species already had shifted higher in elevation over a 49-year period (Brusca et al., 2013).

Invasive Species

An invasive species is defined by the U.S. Department of Agriculture as a species that is non-native to that ecosystem and whose introduction will cause economic or environmental harm. There are several invasive plants that pose a threat to the native plants of the Sonoran Desert either through competition or by changing the fire regime. Fast growing annuals such as red brome (*Bromus*

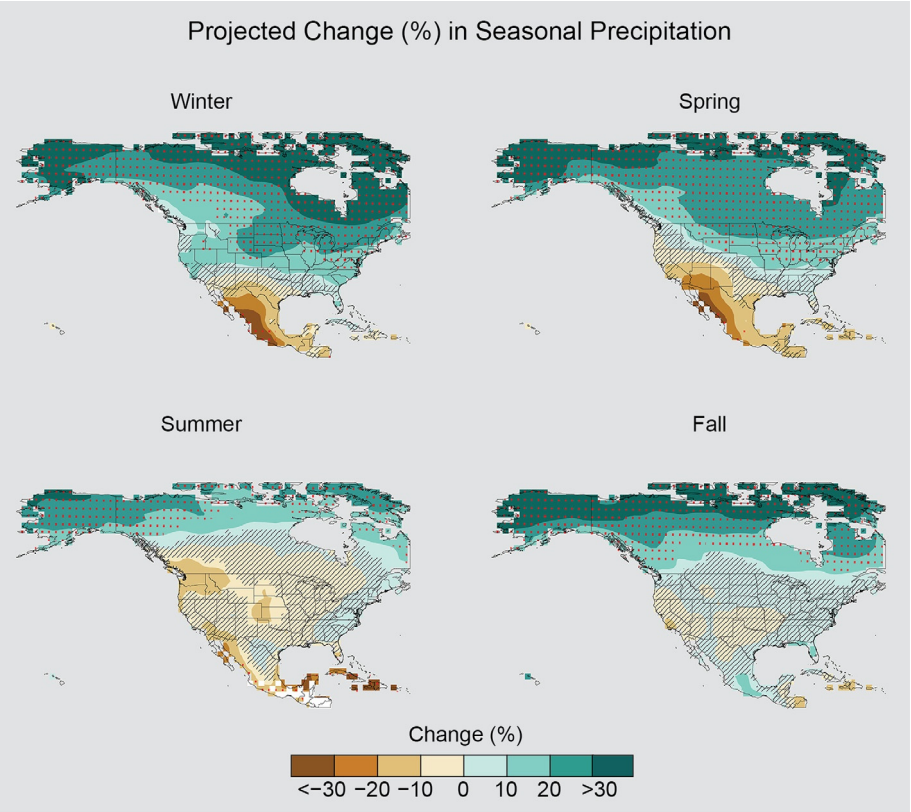


Fig. 9 Projected change (%) in total seasonal precipitation from CMIP5 simulations for 2070–99 relative to the 1976–2005 average. These are results for the higher scenario (RCP8.5). Stippling indicates large changes and hatching indicates small changes as compared to natural variations. Data source: World Climate Research Program's (WCRP's) Coupled Model Intercomparison Project. Figure source: NOAA NCEI - National Oceanic and Atmosheric Administration National Center for Environmental Information.

rubens), Arabian grass (*Schismus arabicus*), Sahara mustard (*Brassica tournefortii*), and cheatgrass (*Bromus tectorum*) outcompete native annuals. Perennials such as buffelgrass (*Pennisetum ciliare*), and fountain grass (*Pennisetum setaceum*) can grow large and dense enough to compete with native shrubs for light and nutrients (Dimmit and Fusari, 2015). Saltcedar (*Tamarix* spp.) is an invasive tree that displaces native trees in riparian areas that are habitat for many birds.

Buffelgrass, native to the savannas of Africa and India, has been planted in Sonora and Arizona since the 1950s to increase forage for cattle production (Brenner, 2011). In Sonora, buffelgrass cultivation boomed from government-subsidized programs to support the ranching industry. By 2002, nearly 1.6 million hectares of land in Sonora had been cleared and seeded with buffelgrass (Búrquez et al., 2002). In Arizona, its planting was promoted by the US department of Agriculture as a soil stabilizer and is now a common sight in disturbed areas, along roads, or in desert scrub covered slopes. It produces large amounts of seed in response to rain but its ability to withstand fire is what makes it a threat to the desert.

Native vegetation is not dense enough to support fires larger than a few hectares and plants such as the giant saguaro have not evolved with fire. Whereas a single fire can kill significant numbers of cacti and succulents, buffelgrass will quickly colonize these disturbed areas, repeat the fire cycle, and expand to form dense, single species stands. Once buffelgrass is established in an area it is extremely difficult to eradicate (Fig. 10).

Livestock Grazing

Domestic cattle are another invasive species that arrived in 1540 with the Spanish explorer Coronado and were subsequently promoted by the numerous missions in the region (Fleischner, 2010). By the late nineteenth century, large numbers of livestock roamed the Southwest and their overgrazing, combined with a severe drought, converted the majority of the desert grasslands into desert-like scrublands that persist today (Dimmit and Fusari, 2015) (Fig. 11). Livestock grazing is now permitted on 3.6 million hectares of the Sonoran Desert ecoregion and across 1 million square kilometers of public lands in the United States. Grazing has a far greater impact on ecosystem health than do all roads, timber harvest, and wildfires combined (Beschta et al., 2013).

Soil compaction from livestock grazing has severe effects on deserts soils and has been identified as an extensive problem on US public lands (FS and BLM, 1997). This is because the weight of a 450-kg cow will exert more than five times the compacting pressure of a bulldozer and significantly reduce the soil's ability to store water (Cowley, 2002). When the soil cannot store as much water due to compaction and reduction of plant cover due to overgrazing, increased runoff will occur during high-intensity rainfall events of the summer monsoons (Branson et al., 1981). The increased runoff causes erosion, loss of topsoil and the downcutting of streambanks and washes commonly seen in western landscapes.

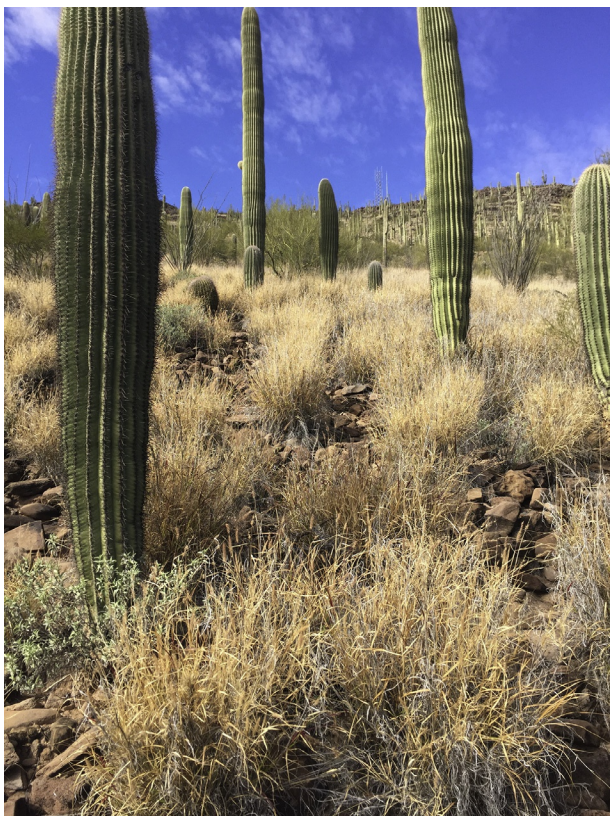


Fig. 10 Buffelgrass and saguaros on Tumamoc Hill in Tucson, Arizona. Photo by Curtis Bradley.

Fig. 11 Soil loss from cattle grazing in a mesquite bosque that once supported sacaton grass. Photo by Sky Jacobs.

Border Wall

Since the early 1990s, the U.S. government's border control efforts have been driven by a "prevention through deterrence" strategy—the concept that increased personnel and infrastructure will discourage undocumented immigration. This strategy was first implemented in heavily populated border areas such as San Diego and El Paso and shifted immigration, drug trafficking and other activities to more remote areas of the Sonoran Desert, causing extensive environmental damage and social disruption.

Border wall construction accelerated with the passage of the 2006 Secure Fence Act, which mandated more than 1287 km (800 miles) of border wall construction, and the REAL ID Act of 2005, which gave the secretary of Homeland Security the power to waive US environmental laws to expedite construction (Fig. 12). In total, Homeland Security has installed 570 km (354 miles) of primary border wall ("pedestrian fencing") as well as 482 km (300 miles) of vehicle fencing (United States, 2017).

Fig. 12 Border pedestrian fencing along Organ Pipe National Monument. Photo by National Park Service.

Border walls threaten the biological integrity of the borderlands through direct habitat destruction, fragmentation, and creation of barriers between wildlife populations. These barriers prevent essential movement and gene flow while facilitating increased vehicular traffic and human disturbance in previously undisturbed areas (ACE, 2001).

One of the species that would be affected by additional proposed border wall infrastructure is the Sonoran pronghorn, whose population has declined to fewer than 1000 animals. Pronghorn require immense open areas and must travel long distances in search of food and water. They are also particularly sensitive to disturbance from human activities. The proposed border wall would limit their ability to travel freely in search of food and water and would permanently separate the species' northern and southern populations, preventing dispersal and gene flow that are essential to their survival and recovery.

Several scientific studies demonstrate the impact the wall is having on animals of the Sonoran Desert. Flesch et al. (2010) examined two species, the cactus ferruginous pygmy owl and desert bighorn sheep, and found that these species along with others with similar movement abilities and spatial distributions may be affected by border development. McCallum et al. (2014) used camera traps to compare movements of people and wildlife between areas with and without border walls and found that both pumas and coatis were recorded in higher numbers in areas without walls. The authors found no difference in number of people detected between the two, suggesting that intermittent fencing in this area was not effective at deterring human migrants, but did affect wildlife populations.

Land Conversion and Loss of Riparian Habitat

Historically, the southwest deserts of North America were less populated, and less disturbed, than the rest of the continent due to the lack of water and extreme heat. This changed in the mid-20th century with the construction of large-scale irrigation projects bringing water from the Colorado River and the introduction of air conditioning. Since then cities and agricultural lands have grown rapidly and, as of 2014, over 2.9 million hectares (7.16 million acres) of Sonoran Desert in the United States had been converted to urban environments, agriculture, roads, or non-native scrublands.

Damming, diversion of rivers, and ground water pumping to satisfy the booming population have strongly altered riparian areas in the Sonoran Desert and much of the riparian forests have been lost due to changes in land usage (Zaimes, 2007). Persistent drought through the early 2000s has further dried riparian habitats, and climate change models predict continued drying. Riparian areas support more diverse plant and animal communities than the surrounding drier uplands. The impacts of disappearing rivers are most severe for aquatic species—fish, amphibians and some reptiles and arthropods, but many other animals rely on these waters for some part of their life cycle, or for a source of drinking water. Even intermittent streams support denser ribbons of vegetation through the desert, providing more diverse habitat for animals.

Conservation Status and Planning (Fig. 13)

Mexico

Land tenure in Mexico radically changed after the Mexican Revolution and with the land reforms of the Cárdenas presidency of 1934–40. The land reforms redistributed nearly 18 million hectares of expropriated private land into ejidos, or common property used for agriculture (Stoleson et al., 2005). In Sonora, most of the desert ejidos were barely able to produce a subsistence crop and were used for cattle grazing, where it is now the default land use. A 1992 amendment to the Mexican Constitution allowed these lands to be sold and has accelerated the pace of privatization. As of 2007, a majority of municipalities in Sonora were under private land tenure while the majority of Baja California lands remain in ejidos. Public land tenure only covers 4% of the entire nation (Bonilla-Moheno et al., 2013).

In 1993 two large biosphere reserves were established in northern Mexico, the Alto Golfo de California y Delta del Río Colorado and the El Pinacate y Gran Desierto de Altar. These reserves were created to protect endangered species both from the Gulf of California and the Colorado River estuary including the vaquita (*Phocoena sinus*), the totoaba (*Totoaba macdonaldi*), the desert pupfish (*Cyprinodon macularius*), and the Yuma clapper rail (*Rallus longirostris yumanensis*).

The vaquita is a small and elusive porpoise that occupies a limited range in the northernmost reaches of the Gulf of California and is considered the most endangered marine mammal in the world. Its population has plummeted due to entanglement in fishing gear, including in nets set for the totoaba, a large and endangered fish endemic to the Gulf. Totoaba swim bladders are illegally exported to Asia to make soup perceived to have medicinal properties. In 2011, a single bladder could reportedly sell for between $2500 and $10,000.

The high demand for totoaba has meant more vaquita drowning as bycatch and the population has plummeted from 567 individuals in 1997 to less than 20 in 2018. In response to international pressure, in 2015 Mexico announced a ban on gillnets, with exemptions for two fish species (curvina and sierra), in the Gulf to protect the vaquita. But the remoteness of the Gulf—ringed by high cliffs and dotted with hundreds of desolate islands—has made it challenging to police, particularly given the involvement of drug cartels in the illegal totoaba trade. Attempts to capture vaquita to establish a captive breeding program have so far failed. If drastic action is not taken soon this species will disappear forever.

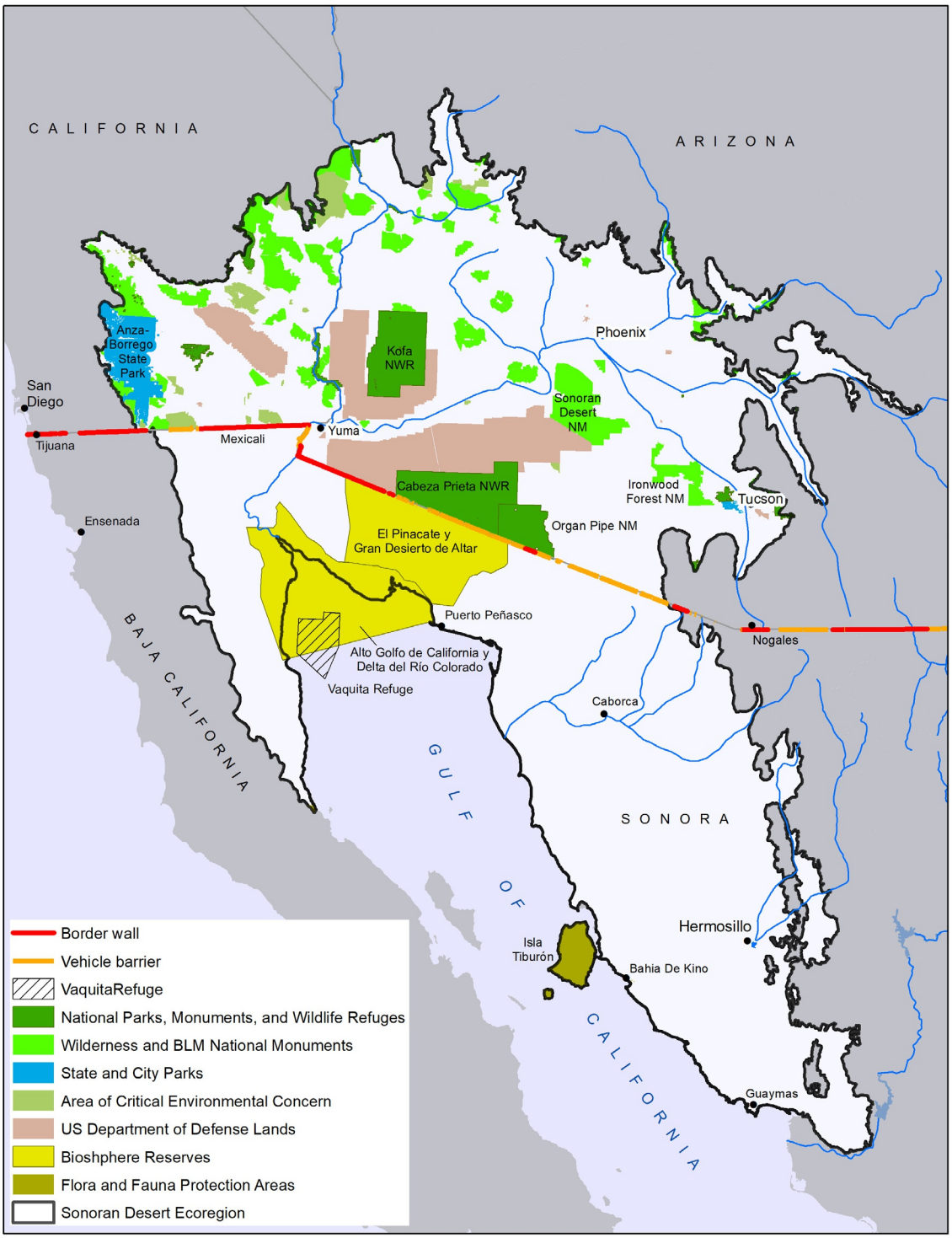


Fig. 13 Map of protected areas of the Sonoran Desert by Curtis Bradley. Data Sources: Ecoregions 2017 © Resolve (Sonoran Desert Ecoregion), Reveal from the Center for Investigative Reporting (Border Wall), World Database on Protected Areas, Protected Areas Database of the US (Protected Areas).

United States

Despite the significant population pressures in the United States, large tracts of Sonoran Desert are protected from human development because they are managed by the US federal government as either public lands: Bureau of Land Management, National Park Service, US Fish and Wildlife Service or military lands (Department of Defense).

Various US federal government agencies manage lands under different protocols to conserve resources. Congressionally designated wilderness areas are managed to minimize human imprint and prevent activities such as land conversion, road construction, power lines, pipelines, and off-road vehicle use. Wilderness areas and national monuments administered by the Bureau of Land Management typically allow cattle grazing within the desert. US Department of Defense lands are typically not thought of as protected areas but do provide valuable restrictions on human development, off-road vehicle use, and cattle grazing. National parks, monuments administered by the National Park Service, national wildlife refuges, and some state parks are managed to protect the flora and fauna of the Sonoran Desert and don't allow cattle grazing or other desert harming activities. Organ Pipe National Monument, Saguaro National Park, Anza-Borrego Desert State Park, and Tucson Mountain Park are excellent places to see the desert preserved in a relatively untouched state.

The future of the Sonoran Desert

The most critical threat to the flora and fauna of the Sonoran Desert is climate change, which is predicted to bring with it increasing temperatures and a shift in the timing and amounts of rainfall to the region. Although there is evidence that similar changes may have happened in the past and the desert has adapted accordingly, the rate of change was over millennia, not decades as is predicted under our current climate trajectory.

Unlike climate change, which needs to be addressed at a global scale, habitat destruction can be prevented if local governments and private citizens organize to protect the desert they love. An example of this can be found in southern Arizona with the Sonoran Desert Conservation Plan. This multispecies conservation plan has a goal of ensuring the long-term survival of Pima County's native biota through maintaining the habitat conditions and ecosystem functions necessary for their survival. It was developed over a 20-year process among diverse stakeholders that balanced the conservation and protection of cultural and natural resources with efforts to maintain an economically vigorous and fiscally responsible community. The plan requires continued citizen involvement to make sure it is implemented in a region that is experiencing some of the fastest population growth in the country. And while threats to the desert's biodiversity such as invasive species, the border wall, livestock grazing, and groundwater pumping are challenging, the result of inaction is equally severe with the vaquita serving as an example of when self-centered economic interests are allowed to rule our future.

References

ACE (US Army Corps of Engineers). (2001). Supplemental Programmatic Environmental Impact Statement for INS and JTF6 Activities. Fort Worth District.

Beschta RL, Donahue DL, DellaSala DA, et al. (2013) Adapting to climate change on Western public lands: Addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management* 51: 474–491.

Bonilla-Moheno M, Redo D, Aide M, Clark M, and Grau R (2013) Vegetation change and land tenure in Mexico: A country-wide analysis. *Land Use Policy* 39: 355–364.

Branson FA, Gifford GF, Renard KG, and Hadley RF (1981) *Rangeland hydrology*. Dubuque: Kendall/Hunt Publishing.

Brenner JC (2011) Pasture conversion, private ranchers, and the invasive exotic buffelgrass (Pennisetum ciliare) in Mexico's Sonoran Desert. *Annals of the Association of American Geographers* 101: 84–106.

Brusca RC, Wiens JF, Meyer WM, et al. (2013) Dramatic response to climate change in the southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution* 3: 3307–3319.

Buchmann SL (2015) Bees. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran desert*, 2nd edn., pp. 310–316. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Búrquez A, Miller A, and Martinez-Yrizar A (2002) Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). In: Tellman B (ed.) *Invasive exotic species in the Sonora region*, pp. 126–146. Tucson, Arizona: University of Arizona Press, University of California Press.

Cowley ER (2002) *Monitoring current year streambank alteration*. Boise: US Bureau of Land Management.

Dimmit MA and Fusari MH (2015) Conservation issues in the Sonoran Desert region. In: Phillips SJ and Dimmitt MA (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 113–123. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Dimmitt MA (2015) Biomes and communities of the Sonoran Desert region. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 5–19. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Fleischner TL (2010) Livestock grazing and wildlife conservation in the American West: Historical, policy and conservation biology perspectives. In: du Toit JT, Kock R, and Deutsch JC (eds.) *Wild rangelands: Conserving wildlife while maintaining livestock in semi-arid ecosystems*, pp. 235–265. Boston, Massachusetts: Blackwell Publishing.

Flesch AD, Epps CW, Cain JW III, et al. (2010) Potential effects of the United States-Mexico border fence on wildlife. *Conservation Biology* 24: 171–181.

FS and BLM (Forest Service and Bureau of Land Management) (1997) *The assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and great basins, vol I–IV. PNW-GTR-405*. Portland, Oregon: US Forest Service and US Bureau of Land Management.

Hafner DJ and Riddle BR (2011) Boundaries and barriers of north American warm deserts: An evolutionary perspective. In: Upchurch P, McGowan AJ, and Slater CSC (eds.) *Palaeogeography and Palaeobiogeography: Biodiversity in space and time*, 1st edn., pp. 75–114. Boca Raton, Florida: CRC press.

Ivanyi CI and Marsh PC (2015) Sonoran Desert fishes. In: Phillips SJ and Dimmitt MA (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 438–452. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Ivanyi CI, Johnson J, Van Devender T, and Lawler H (2015) Sonoran Desert reptiles and amphibians. In: Phillips SJ and Dimmitt MA (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 454–489. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Jennes D (2015) Arizona birds. *Journal of Arizona Field Ornithologists* 2015: 1–10.

Kaufman K (2015) Quail. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran desert*, 2nd edn., pp. 275–285. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Lizotte R (2015) Spiders. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 275–285. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

MacMahon JA and Wagner FH (1985) The Mojave, Sonoran and Chihuahuan deserts of North America. In: Evenari M, Noy-Meir I, and Goodall DW (eds.) *Hot deserts and arid Shrublands. Ecosystems of the world*, vol. 12A, pp. 105–202. Amsterdam: Elsevier.

McCallum JW, Rowcliffe JM, and Cuthill IC (2014) Conservation on international boundaries: The impact of security barriers on selected terrestrial mammals in four protected areas in Arizona, USA. *PLoS One* 9: e93679.

Munson SM, Webb RH, Belnap J, et al. (2011) Forecasting climate change impacts to plant community composition in the Sonoran Desert region. *Global Change Biology* 18: 1083–1095.

Nabhan GP (2015a) Welcome to the Sonoran Desert. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 1–2. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Nabhan GP (2015b) Biodiversity. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 130–135. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Olson DM and Dinerstein E (2002) The global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* 89: 199–224.

Riddle BR, Hafner DJ, Alexander LF, and Jaeger JR (2000) Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *PNAS* 97: 14438–14443.

Scarborough R and Brusca RC (2015) Geologic origin of the Sonoran Desert. In: Phillips SJ and Dimmitt MA (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 71–84. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Sheridan T (2015) Human ecology of the Sonoran Desert. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 101–111. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Shreve F (1942) The desert vegetation of North America. *The Botanical Review* 8: 195–246.

Shreve F (1951) *Vegetation of the Sonoran Desert*. Washington, D.C: Carnegie Institution of Washington Publication no. 591.

Stoleson SH, Felger RS, Ceballos G, et al. (2005) Recent history of natural resource use and population growth in northern Mexico. In: Cartron J, Ceballos G, and Felger RS (eds.) *Biodiversity, ecosystems, and conservation in Northern Mexico*, pp. 52–86. New York, New York: Oxford University Press.

Tyburec J (2015) Bats. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 401–410. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Udall B and Overpeck JT (2017) The twenty-first century Colorado River hot drought and implications for the future. *Water Resources Research* 53: 2404–2418.

United States (2017) Southwest border security, additional actions needed to better assess fencing's contributions to operations and provide guidance for identifying capability gaps: Report to congressional requesters. http://purl.fdlp.gov/GPO/gpo77780.

Van Devender TR and Brusca RC (2015) Deep history of the Sonoran Desert. In: Dimmitt MA, Comus PW, and Brewer LM (eds.) *A natural history of the Sonoran Desert*, 2nd edn., pp. 63–84. Tucson, Arizona: Arizona-Sonora Desert Museum Press, University of California Press.

Wuebbles DJ, Fahey DW, Hibbard KA, et al. (2017) *Climate science special report: Fourth National Climate Assessment, Volume I*. Washington, DC: U.S. Global Change Research Program.

Zaimes G (2007) Human alterations to riparian areas. In: Zaimes GN (ed.) *Understanding Arizona's riparian areas*. Tucson, Arizona: University of Arizona.