

DISTURBANCE, VEGETATION CO-OCCURRENCE, AND HUMAN
INTERVENTION AS DRIVERS OF PLANT SPECIES DISTRIBUTIONS IN THE
SAGEBRUSH STEPPE

by

Fiona Claire Schaus Noonan



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DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Fiona Claire Schaus Noonan

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The following individuals read and discussed the thesis submitted by student Fiona Noonan, and they evaluated the student's presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

Megan E. Cattau, Ph.D.	Chair, Supervisory Committee
Brittany D. Brand, Ph.D.	Member, Supervisory Committee
Jodi S. Brandt, Ph.D.	Member, Supervisory Committee
T. Trevor Caughlin, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by Megan E. Cattau, Ph.D., Chair of the Supervisory Committee. The thesis was approved by the Graduate College.

DEDICATION

To the people and places who have taught me—and continue to teach me—what it means to mālama ‘āina.

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ABSTRACT

Changes in fire regimes, invasive species dynamics, human land use, and drought conditions have shifted important plant species in the Northern Great Basin (NGB)—including big sagebrush (*Artemisia tridentata* ssp.), conifers (e.g., *Juniperus* spp.) and invasive annual grasses (e.g., *Bromus tectorum*). Characterizing how these overlapping disturbances influence species distributions is critical for land management decision-making. Previous research has explored the individual effects of drought, wildfire, restoration, and invasive species on sagebrush steppe communities, but the specific effects of these disturbances in context with one another remain poorly understood at a landscape scale. To address this gap, I constructed multilevel conditional autoregressive (CAR) species distribution models (SDMs) to map the distributions of big sagebrush, juniper, and cheatgrass on lands managed for grazing in the NGB, both with and without a history of fire. These models illuminate the concurrent influences of species co-occurrences, drought, wildfire characteristics (e.g., fire size, time since fire, and number of fires), and restoration treatments. For all SDMs, results indicate that species co-occurrence exhibits the strongest effect—between 1.23 and 19.2 times greater than the next strongest predictor—on all species' probability of occurrence, suggesting that vegetation co-occurrence meaningfully influences landscape-scale species distributions. In portions of the NGB both with and without historical fire, number of fires and maximum vapor pressure deficit (VPD) also exert substantial influence on the likelihood of species presence, and results indicate that restoration treatments have broadly met desired outcomes for both sagebrush and juniper.

Narrowing down to only areas that have previously burned, however, models do not support the efficacy of post-fire restoration. All versions of the SDMs, which rely on Bureau of Land Management-administered grazing allotments as a spatial varying intercept, also explicitly point to the differential influence of long-term management regimes on species distributions. These model predictions capture post-disturbance vegetation outcomes under changing fire, climate, and invasive species regimes and in the context of human decision-making, in turn defining a plausible ecological space as these disturbance and management processes play out into the future.

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LIST OF ABBREVIATIONS

AIM	Assessment, Inventory, and Monitoring
BLM	Bureau of Land Management
CAR	Conditional autoregressive
DOI	United States Department of the Interior
EPA	United States Environmental Protection Agency
ESR	Emergency Stabilization and Rehabilitation
GLMM	Generalized linear mixed model
HES	Human-Environment Systems
JSDM	Joint species distribution model
LANDFIRE	Landscape Fire and Resource Management Planning Tools
LFDRDB	LANDFIRE Reference Database
LTDL	Land Treatment Digital Library
NGB	Northern Great Basin
NLCD	National Land Cover Database
PRISM	Parameter-elevation Regressions on Independent Slopes Model
RCMAP	Rangeland Condition Monitoring Assessment and Projection
SDM	Species distribution model
SES	Social-ecological systems
TerrADat	Terrestrial AIM Database
USFS	United States Forest Service

USGS United States Geological Survey

VPD Vapor pressure deficit

INTRODUCTION

Positionality Statement

By necessity, all science carries with it a lens or paradigm that shapes the questions, data, interpretations, and conclusions of the work in complex, multifaceted ways (Scotland, 2012; Secules et al., 2021). My research on plant species distributions in the NGB is no different, and is strongly informed by a background in private land protection and management in the inland Northwest. I come to this work with a distinctly Western lens, but one that also places primacy on systems thinking, social-ecological interactions, and a belief that people can, have, and should steward the land.

Background

Artemisia tridentata ssp., or big sagebrush (hereafter, sagebrush), is a foundation plant species throughout the Great Basin that has undergone substantial, ongoing decline in abundance and area of distribution due to development, grazing, shifting fire regimes, climate change, woody plant encroachment, and invasive species (Balch et al., 2013; Bradley, 2010; Coates et al., 2017; Davies et al., 2021; Falkowski et al., 2017; Prev y et al., 2010). It now occupies just 56% of its historical range, leaving the remaining sagebrush highly fragmented and less able to support the wildlife and soils that have made sagebrush so vital to the landscapes of the American West (Davies & Bates, 2020; Meinke et al., 2009). Although a multitude of known disturbances—including climate change, wildfire, grazing, and human land-use—influence the composition and configuration of sagebrush landscapes, the drivers and outcomes of simultaneously shifting vegetation, climate, and

fire regimes remain especially unclear (M. L. Brooks et al., 2015; Copeland et al., 2021; Requena-Mullor et al., 2019). In this research, I examine these simultaneous dynamics in the context of the Northern Great Basin (NGB), a portion of the Great Basin ecoregion covering southeastern Oregon, southern Idaho, and parts of northern Utah, Nevada, and California (Map 1).

Fundamentally, sagebrush ecosystems respond to disturbances, including wildfire and drought, both of which are exacerbated by climate change, based on their capacity for resilience or resistance, which varies based on subspecies and life histories (Chambers et al., 2019). Chambers, Miller, et al. (2014) define resilience as “the capacity of an ecosystem to *regain* its fundamental structure, processes, and functioning when altered by stressors like drought and disturbances like...altered fire regimes” (emphasis theirs). They define resistance as “the capacity of an ecosystem to *retain* its fundamental structure, processes, and functioning despite stresses, disturbances, or invasive species” (Chambers, Miller, et al., 2014; emphasis theirs). Big sagebrush subspecies, for example, have adapted to a historically low-severity fire regime which they have minimal capacity to resist, but to which they are ultimately resilient. As fire regimes and other disturbances change, species and ecosystems may not have adequate resistance and resilience capacity, which may induce state transitions (Chambers, Miller, et al., 2014; Ellsworth et al., 2016; Johnstone et al., 2016).

In addition to resistance and resilience, understanding landscape-scale disturbance ecology processes relies on accounting for ecological memory, or “the degree to which an ecological process is shaped by its past modifications of a landscape” (Peterson, 2002). This phenomenon guides how ecosystems respond to disturbances, and encompasses the

informational—long-term—and material—physical abiotic and biotic responses to disturbance events—legacies of landscape processes and patterns on the current state of a landscape’s function (Johnstone et al., 2016; Newman et al., 2019). These legacy effects are particularly relevant in post-fire vegetation recovery and dynamics, as well as in vegetation-fire cycles (Peterson, 2002; *sensu* Pickett et al., 2009; van Mantgem et al., 2018). Informational legacies may confer ecosystem resilience; conversely, changing disturbance regimes can degrade ecological memory, triggering potential shifts in landscape pattern, process, and function (Johnstone et al., 2016). More generally, ecological memory relies on the idea that species have adapted to a particular set of disturbance regimes, and these past disturbances will dictate how species respond to current and future disturbances. The ability for NGB sagebrush systems to regain and/or retain their structure and function dictates abundance and distributions of species under shifting disturbance regimes, which may include novel disturbances, novel disturbance interactions, or disturbance characteristics outside of the historical range of variability.

The NGB—here defined as the Northern Basin and Range EPA Level III Ecoregion—comprises plant functional groups typical of the entire Great Basin. Sagebrush shrublands and sagebrush steppe dominate the region, including plant species such as big sagebrush, Western juniper, Utah juniper, Rocky Mountain juniper, and various other conifers (*e.g.*, *Pinus monophylla*, *Pinus ponderosa*) at higher elevations (R. F. Miller et al., 2008). Grasslands, which historically have contained native bunchgrasses but are increasingly dominated by annual invasive grasses (*e.g.*, *Bromus tectorum*, *Taeniatherum caput-medusae* [L.] Nevski) characterize the NGB at some lower elevations (Pilliod et al., 2017). These plant functional groups have distinct dynamics with one another and varied

responses to abiotic disturbances such as climate change and wildfire. While these species do not represent the NGB's full range of biotic diversity, they do collectively and individually represent key management challenges across the region that this research seeks to redress.

Invasive Annual Grasses

The first of these challenges is species invasions, and particularly the influx of cheatgrass—among other invasive annual grasses—into arid and semiarid ecosystems since its introduction alongside cattle and sheep grazing in the West in the mid-late 19th century (D'Antonio & Vitousek, 1992; Novak & Mack, 2001). *Bromus tectorum* (hereafter, cheatgrass) currently occupies nearly a third of the Great Basin (210,000km²), and outcompetes other native forbs, grasses, and shrubs through earlier germination, greater seed production, and faster growth (Bradley et al., 2018; Pilliod et al., 2017). This adds fine, arid fuels to otherwise more fuel-limited systems (Abatzoglou & Williams, 2016; M. L. Brooks et al., 2004; Pilliod et al., 2017). At the same time, cheatgrass also exhibits more resilience to fire than native species, with a far greater ability to re-establish post-fire than many native species, especially at lower elevations (Chambers, Miller, et al., 2014; Reisner et al., 2013). This positive feedback induces an invasive grass-fire cycle that has been explored at length in the Great Basin ecoregion (Balch et al., 2013; Bradley et al., 2018; M. L. Brooks et al., 2004; D'Antonio & Vitousek, 1992). Successful cheatgrass invasions occur particularly in years with higher than average winter precipitation, and are often exacerbated by human land-use activities, including grazing and development (Chambers, Bradley, et al., 2014; Pilliod et al., 2017). Cheatgrass also thrives in hotter, drier regions, both of which contribute to the grass-fire cycle and displacement of sagebrush species,

which are far less resilient to fires in the short term (Chambers, Miller, et al., 2014; Ellsworth et al., 2016; Pilliod et al., 2017).

Conifer Expansion

The second of these challenges is conifer expansion, which primarily includes Western juniper (*Juniperus occidentalis*) in southeastern Oregon and Rocky Mountain (*Juniperus scopulorum*) and Utah juniper (*Juniperus osteosperma*; hereafter, collectively referred to as “juniper”) in southern Idaho, northern Nevada, and northeastern Utah. Juniper species often exist in association with pinyon pine (e.g., *Pinus edulis*, *Pinus monophylla*), particularly in the more southern and eastern portions of the NGB, as well as further south in the Great Basin (Romme et al., 2009). This expansion, often characterized as encroachment by both researchers and managers, results in reduced productivity and diversity, as well as increased soil erosion and resource competition that can displace sagebrush and other associated species, including the imperiled greater sage-grouse (*Centrocercus urophasianus*; Bates et al., 2005; Coates et al., 2017; Olsen et al., 2021; C. J. Williams et al., 2014). There is also evidence that juniper removal may increase opportunities for cheatgrass invasion (Coultrap et al., 2008).

Unlike cheatgrass, juniper species are native to the NGB, but the abundance and density of juniper and pinyon pine have increased substantially due to fire suppression and livestock grazing since settlers began colonizing the Great Basin in the mid-19th century (R. F. Miller & Rose, 1999; Shinneman & Baker, 2009b). In the central and northern parts of the Great Basin, studies indicate that pinyon and juniper have increased between 125 and 625% since the 1860s, largely through infilling and ecotonal shifts (R. F. Miller et al., 2008, 2014; Weisberg et al., 2007). Pinyon-juniper is also the third-largest vegetation type

in the US, covering 40 million hectares (Filippelli et al., 2020). As a result, decades of land management and research in the Great Basin have focused on limiting or even eliminating juniper (*e.g.*, Bates et al., 2005; Fick et al., 2022; R. F. Miller et al., 2014; Olsen et al., 2021), despite their being native to the region, having cultural and ecological significance, and the fact that they are sharply declining in some areas due to persistent modern drought conditions (Filippelli et al., 2020).

Studies of pinyon-juniper in the Great Basin have largely focused on rangeland management concerns, generally explicating the behavior of pinyon-juniper woodlands as a form of biotic disturbance itself, and often at relatively small scales (J. E. D. Miller & Safford, 2020). Rarely, though, does the literature address landscape-scale patterns of conifer responses to fire without the subtext of woodland eradication, nor do studies often examine the long-term legacies of disturbance on pinyon-juniper vegetation dynamics (Baker & Shinneman, 2004; Shinneman & Baker, 2009b) and ecological memory (*sensu* Johnstone et al., 2016; Pickett et al., 2009). While Miller and Safford (2020) explicitly suggest that plant responses to wildfire depend on adaptations to historical fire regimes (*i.e.*, informational legacies; *sensu* Johnstone et al., 2016) the effects of specific fire attributes on pinyon-juniper woodlands remain understudied at landscape scales.

Wildfire

The third major management challenge, which builds from the first two, is wildfire. Fire has always characterized the NGB, contributing to the heterogeneity, regulation, and regeneration of the ecosystem's various landscapes through pyrodiversity (*e.g.*, McLauchlan et al., 2020), which can itself spur biodiversity (see Jones & Tingley, 2022). Indigenous populations also shaped historical fire regimes in the Great Basin through land

use and cultural burning, contributing to a fire regime of frequent low-severity fires (Carter et al., 2021). On a global scale, it is becoming increasingly clear that interactions among fire and anthropogenic drivers like climate change, land use, and invasive species are shifting both fire regimes and biodiversity toward greater extremes and, in some cases, homogeneity (Kelly et al., 2020).

Recent studies indicate that fire severity, frequency, anthropogenic ignitions, and size, in addition to fine fuels and aridity, have all increased across the American West due to climate change and land use (Abatzoglou et al., 2019; Abatzoglou & Williams, 2016; Balch et al., 2017; M. L. Brooks et al., 2015; Cattau et al., 2020; Dennison et al., 2014). Fire seasonality, including timing and length of fire season, have also changed in the past several decades (M. L. Brooks et al., 2015; Westerling et al., 2006). In other words, not only are average fire attributes experiencing increases, but the most extreme attributes of fires are also becoming more extreme, largely as the result of interacting biophysical and social factors (Balch et al., 2020). These pattern changes have borne successional consequences for the sagebrush biome, which is not adapted to the more frequent, higher-intensity fires that increasingly characterize the NGB's fire regime (Brooks et al., 2015; Ellsworth et al., 2020; Mahood & Balch, 2019).

This holds true in the NGB, where the invasive annual grass-fire cycle is a well-known threat, especially in sagebrush-dominated areas (Coates et al., 2016; D'Antonio & Vitousek, 1992; Shinneman & Baker, 2009a). Recently, researchers have suggested that the "human-grass-fire cycle" more accurately captures the role of anthropogenic influences on how invasive grasses alter fire regimes (Fusco et al., 2021). The threats posed by this cycle have been exacerbated by climate change, which has in turn increased fire

occurrence, frequency, ignitions, and season lengths in the NGB (Balch et al., 2013; Bradley et al., 2018; M. L. Brooks et al., 2004; Fusco et al., 2019). Meanwhile, a combination of historical grazing, fire suppression, and climate change has driven decades of conifer expansion (Falkowski et al., 2017; Romme et al., 2009). This not only reduced biodiversity, but has also increased canopy biomass, resulting in larger, more intense fires than those that historically characterized sagebrush steppe (R. F. Miller & Tausch, 2002; C. J. Williams et al., 2014). Conifer woodlands exhibit slow post-fire recovery, often on the order of decades, and this is particularly true in the wake of severe wildfires (Baker & Shinneman, 2004). Fire return interval approximations for pinyon-juniper woodlands range from 50 to 200 years, although there is evidence that increasing invasions of annual grasses, such as cheatgrass, may simultaneously alter fire frequency in pinyon-juniper and other Great Basin plant functional groups (Balch et al., 2013).

Meanwhile, fire regimes themselves are changing in response to human influences (*e.g.* human ignitions, land use; Balch et al., 2017; Cattau et al., 2020), vegetation dynamics (Balch et al., 2013) and climate change (Abatzoglou & Williams, 2016), creating a set of interwoven fire-vegetation-climate feedbacks (Figure 1) whose impacts are difficult to predict yet critical for managers to understand (McLauchlan et al., 2020).

Previous studies have generally addressed only single-species components of these fire-vegetation-climate dynamics, such as the respective relationships between wildfire and sagebrush, pinyon-juniper, and cheatgrass. Spatially-explicit, management-oriented data on these species' interactions with each other, and with fire, remain sparse. Further, most studies on vegetation responses to wildfire have been conducted on the scale of a single

fire, rather than at a regional level that might have broader management implications (J. E. D. Miller & Safford, 2020).

Climate Change

Climate projections for the NGB depict a future that has hotter temperatures, more precipitation, and much greater variability in precipitation timing. While climate change underlies the dynamics in each of the preceding interlinked challenges in the NGB, it also directly impacts sagebrush steppe ecosystems. In the Great Basin, increased atmospheric warming may induce particular adaptive mismatches for those subspecies that occupy basin sub-regions (*e.g.*, *A. tridentata* ssp. *wyomingensis*), survive at higher elevations (*e.g.*, *A. tridentata* ssp. *vaseyana*), or are better suited for either more xeric or more mesic conditions (Brabec et al., 2017; Kleinhesselink & Adler, 2018; Schlaepfer et al., 2012; Still & Richardson, 2015). Some studies suggest that sagebrush in cooler, wetter areas may actually be more resilient to the impacts of climate change since they respond positively to increased warming, while the inverse is true for sagebrush in warmer, drier areas (Rigge et al., 2019). Meanwhile, the impacts of climate change are projected to benefit cheatgrass, with populations expected to either remain steady or expand their land area in the NGB by as much as 18% (Boyte et al., 2016; Zimmer et al., 2020). Most studies agree that juniper (and the pinyon-juniper association more broadly) will face declines under climate change, particularly in the NGB (Zimmer et al., 2020).

Here, I use maximum vapor pressure deficit (VPD) as the primary predictor related to climate, which represents the conditions of greatest aridity in a given location and serves as a proxy for drought. Increased warming has directly increased VPD, and will continue

to do so under climate change (A. P. Williams et al., 2019). In turn, this propels each of the aforementioned cycles of increased wildfire, cheatgrass invasion, and plant stress.

Management and Restoration

Collectively, the interlinked, climate-exacerbated challenges of species invasions, conifer expansion, and wildfire point to a broader ecological possibility: the diminution or possible displacement of big sagebrush and associated shrubs, forbs, and bunchgrasses. (Bowman-Prideaux et al., 2021; M. L. Brooks et al., 2015; Davies et al., 2021; Davies & Bates, 2017). This interplay among ecosystem disturbances and broader vegetation dynamics requires management responses, including restoration actions, in the face of increasing climatic uncertainty. In the NGB, management decision-making falls primarily to the Bureau of Land Management (BLM), which manages 63.6% of the total land mass of the ecoregion. This includes the state-level BLM administration of grazing allotments that account for an even greater proportion—roughly 74%—of the NGB. The BLM leases these allotments to private individuals for grazing livestock such as cattle and sheep at relatively low costs and with management plans overseen by the agency, a system that dates back to the federal 1934 Taylor Grazing Act (Wilkinson, 1992).

Management actions in sagebrush systems can alter species' resilience to disturbance and ability to withstand biotic invasions, contingent on historical community composition and disturbance regimes (Chambers, Miller, et al., 2014). Certain restoration treatments, particularly of expanding pinyon-juniper woodlands, have exhibited success, mostly at site-specific scales (*e.g.*, Freund et al., 2021). However, regional-scale management requires a better understanding of how concurrent shifts in biotic and abiotic disturbances influence common rangeland species distributions at the scale of the NGB.

Specifying distributional responses to disturbance regimes is a critical step toward more effective conservation-decision making as climate change-induced fire activity expansion continues to accelerate (Abatzoglou et al., 2021).

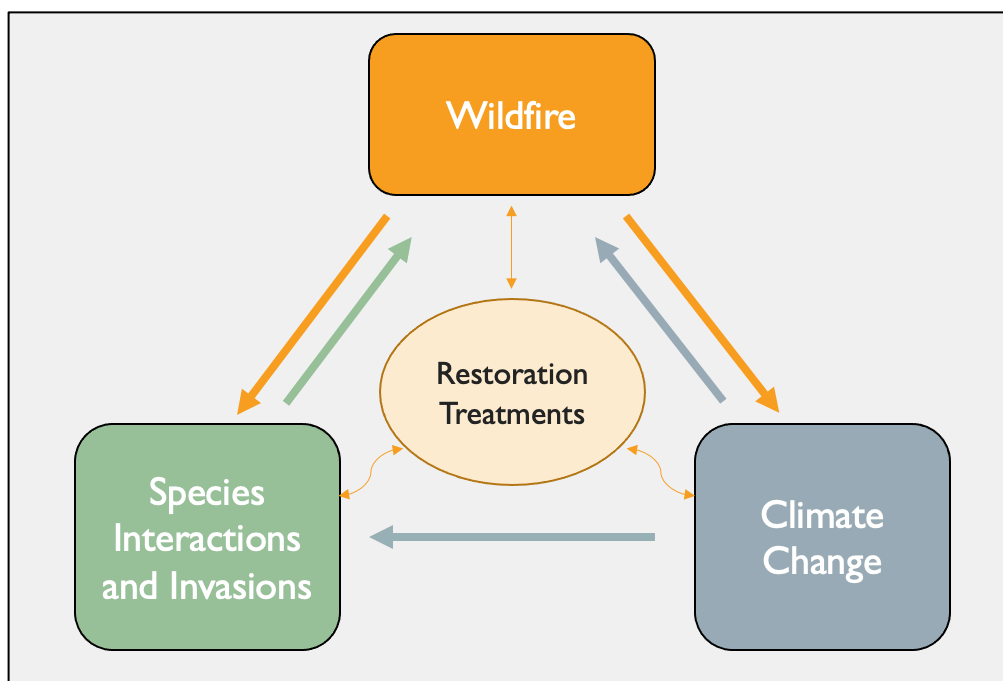


Figure 1. Conceptual framework for the social-ecological underpinnings of and feedbacks captured by sagebrush, juniper, and cheatgrass SDMs in the NGB.

Although historical disturbance regimes tend to dictate species' responses to wildfires in the present (Johnstone et al., 2016; J. E. D. Miller & Safford, 2020; Stevens et al., 2020), little is known about how recent changes in fire regimes influence shrubland vegetation dynamics. Many models implicitly assume that species respond to disturbances in isolation, rather than capturing the ways in which species jointly respond to shifting disturbance regimes based on their interactions with one another (Pollock et al., 2014). Here, I address these gaps by exploring how wildfire, vegetation co-occurrence, and restoration activities influence the distributions of sagebrush, juniper, and cheatgrass in the NGB. Clarifying disturbance-distribution dynamics for these three important sagebrush ecosystem species, particularly with the inclusion of anthropogenic factors like wildfire

and restoration, can highlight the outcomes of the disturbance-management interface at a landscape scale. In turn, these results point to considerations for sagebrush steppe management decisions, particularly as climate change continues to alter disturbance regimes.

This work additionally addresses the issue of spatial autocorrelation—a lack of independence across spatially proximate points or features—to which species distribution models (SDMs) are inherently sensitive (Beguin et al., 2012). To do so, I used multilevel Bayesian conditional autoregressive (CAR) models with NGB grazing allotments as the spatial unit. While examples of using a multilevel CAR model implementation exist in fields such as epidemiology (*e.g.*, Bivand et al., 2017; Djeudeu et al., 2022), this appears to be the first implementation of the multilevel areal unit approach in an ecological context. The use of grazing allotments, which are a management-relevant areal unit, offers more useful management insights as compared to an arbitrary spatial unit, such as a grid.

Objectives and Relevance

Given the context of wildfires, vegetation co-occurrences and interactions, climate, and restoration in grazing allotments in the NGB, my research aims to answer the question: *How do vegetation co-occurrence, wildfire histories, and human interventions influence the distributions of sagebrush, juniper, and cheatgrass in the NGB?* In the context of previously burned areas, I also address the question: *How do wildfire characteristics such as size, frequency, and time since fire influence plant species distributions in the NGB in the context of other abiotic and biotic drivers?*

Within these two questions, I have three main objectives:

1. Capture the relative effects of wildfire, restoration, and vegetation co-occurrences—which may represent biological invasions—as well as climate and topography, on sagebrush, juniper, and cheatgrass distributions.
2. Delineate spatially-explicit predicted distributions of sagebrush, juniper, and cheatgrass.
3. Identify areas of management success and/or concern based on the outcomes of wildfire-restoration-species invasion dynamics across grazing allotments, while also clarifying the role of allotments themselves in determining species occurrence.

This research serves to clarify the recent ecological past of the NGB and illuminate plausible ecological futures in sagebrush ecosystems. My results are particularly relevant to public land managers seeking to address complex fire-vegetation-climate dynamics in the NGB.

METHODS

To meet the above objectives, I constructed multilevel Bayesian conditional autoregressive (CAR) SDMs to predict the distributions of sagebrush, juniper, and cheatgrass as a function of wildfire, climate, restoration, topography, and species co-occurrences in NGB grazing allotments. These models, constructed and analyzed in the R environment (R Core Team, 2021), build on previous research that examines the roles of fire and management in sagebrush distributions (Requena-Mullor et al., 2019). The models also pull from the insights of prior work that has examined the effects of species co-occurrence on species distributions (*e.g.*, Mod et al., 2020; O'Reilly-Nugent et al., 2020; Pollock et al., 2014).

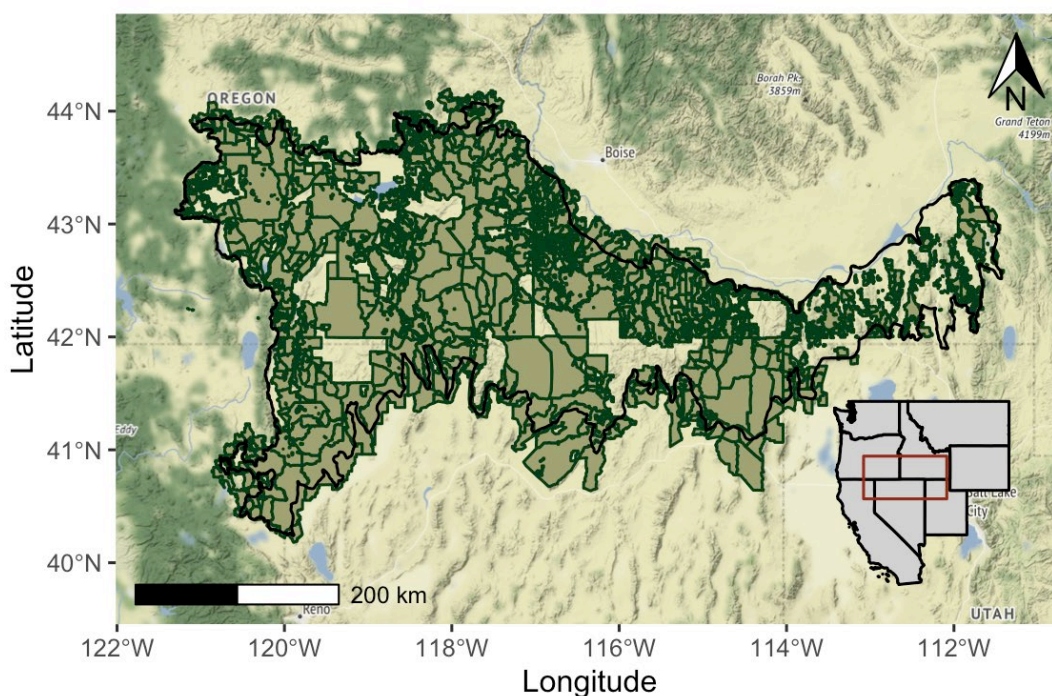
Study Area

Northern Great Basin

The Great Basin, which spans the arid portions of the Western U.S. between the Sierra Nevada and the Rocky Mountains, comprises roughly half of the historical sagebrush biome in North America (Requena-Mullor et al., 2019). This location and composition make the Great Basin an appropriate area for studying the effects of fire and vegetation dynamics on sagebrush ecosystems in a variety of topographic contexts. Although the Great Basin has numerous hydrographic, ecological, and cultural definitions, I selected the Northern Basin and Range EPA Level III Ecoregion (referred to here as the NGB) for my study area based on discussions with Bureau of Land Management (BLM) personnel, many

of whom frequently work with these ecoregional boundaries (Map 1; Don Major, personal communication, Feb. 23, 2021).

The NGB covers 140,200 km² in the northern portion of the broader Great Basin, including parts of Oregon, Idaho, Utah, Nevada, and California (Map 1). The region also contains some or all of 1415 unique grazing allotments administered by the Department of the Interior (DOI) via the Bureau of Land Management (BLM). Collectively, these allotments comprise 74.25% of the total land area of the NGB, and are managed by a variety of stakeholders, primarily for livestock grazing. Complex dynamics among sagebrush, juniper, cheatgrass, wildfire, restoration, and increasing drought also manifest across the NGB.



Map 1. BLM-allocated grazing allotments in the study area, the Northern Great Basin, in the context of BLM-managed lands. Black outline indicates the boundary of the Northern Basin & Range Level III Ecoregion. N.B. Not all grazing allotments are fully within BLM (public) lands; some extend across multiple management jurisdictions. (Data: EPA, BLM, US Census Bureau).

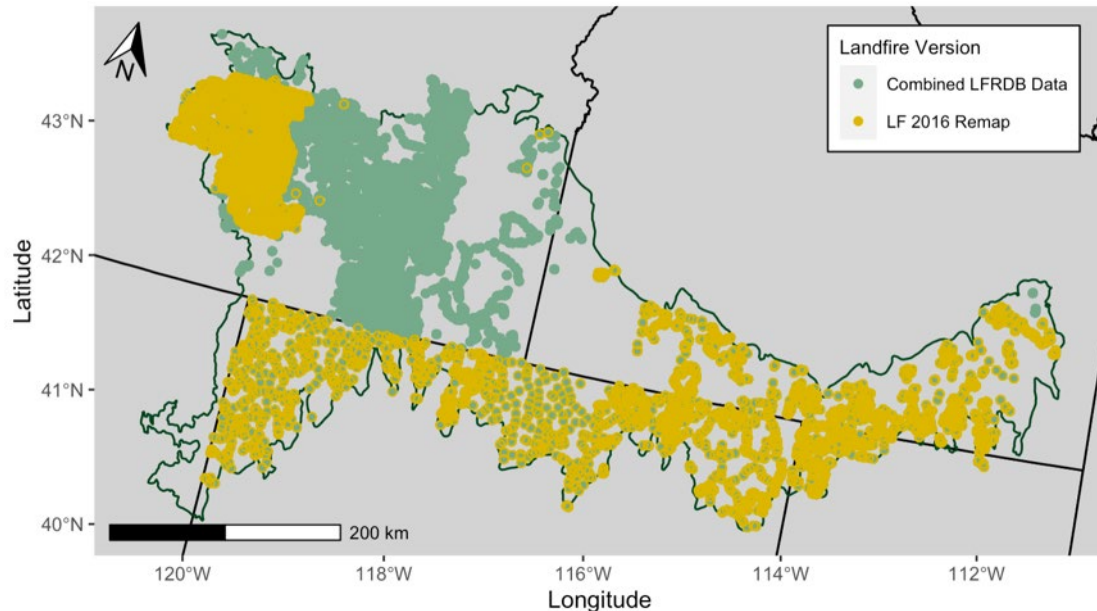
Data Selection

Species distribution models rely on a combination of environmental variables and observations of species presence to predict where species are likely to occur across space (Elith & Leathwick, 2009). Typically, this involves identifying climatic and topographic predictor variables likely to influence a species' broader environmental niche. Here, I expand beyond geophysical and climatic covariates to also include the influences of abiotic disturbance and biotic interaction factors.

Species Occurrence Data

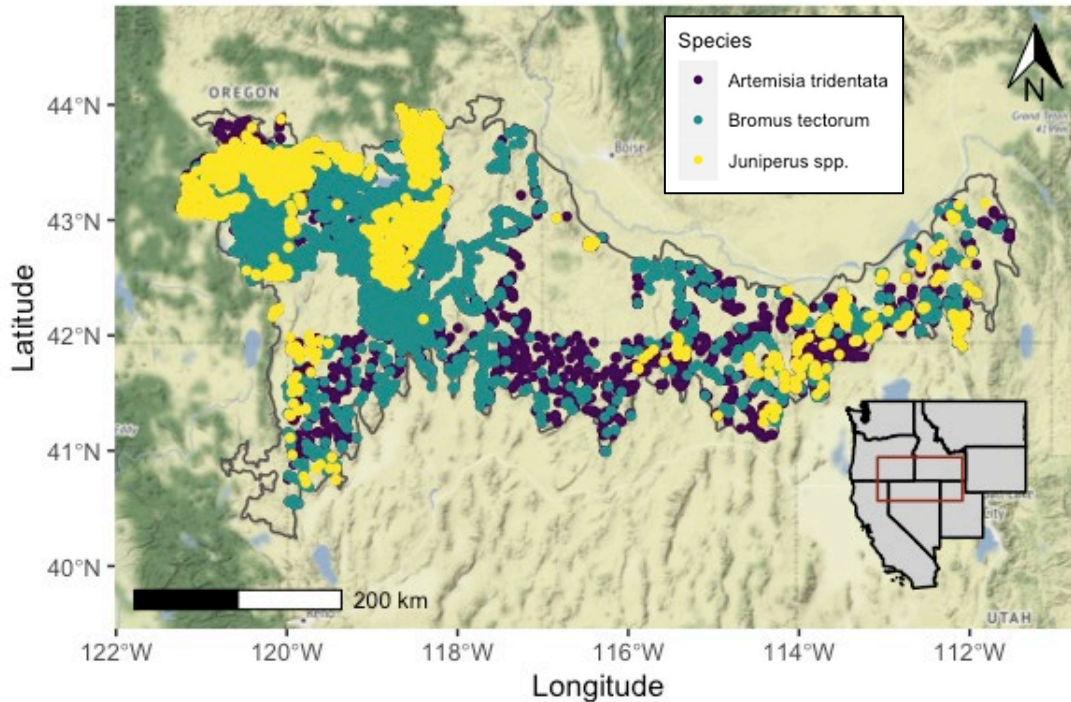
My SDMs use both presence and absence points from confirmed field observations in the LANDFIRE Reference Database (LFRDB), where presence points are any of the three species or species groups, respectively, and absence points are any other plant species observation in the NGB. The LFRDB is a multi-agency effort that includes geolocated observations of plant species, including those of management concern, across the entire United States. These data come from a variety of sources, including the USFS Forest Inventory Analysis, USFS National Gap Analysis Program, and National Park Service Inventory and Monitoring (LANDFIRE, 2016). This includes observations from as far back as the mid-1950s for some species, and a data release in 2021 known as the LF 2016 Remap added species observations up to 2016, from a previous endpoint of 2006. Most point data, however, including for sagebrush, juniper, and cheatgrass, span a shorter temporal subset. The LF 2016 Remap process also substantially altered the available data, not only adding many more years of georeferenced observations to the LFRDB, but also removing previous submissions by federal agencies without noting their removal. This resulted in large gaps

in point data in the NGB and necessitated merging the initial LFRDB and the 2016 Remap version to retain a more complete dataset for the study area (Map 2).



Map 2. Map of both merged datasets in the NGB with an overlay of the LF 2016 Remap LFRDB data for comparison. All points in this map were incorporated in species distribution modeling as presence or absence points.

The merge process added five additional years of data, updating the LFRDB points from 2004 to 2009 in the NGB. In total, this merge process resulted in 111,179 species points in the NGB. After subsequently limiting points only to BLM grazing allotments with spatial adjacencies to other allotments in the NGB, there were 13,827 combined instances of the species of interest (presence points) and 6398 true absence points from the LFRDB to use for the response variables in modeling, for a total of 20,225 points.



Map 3. Map of presence points for sagebrush, cheatgrass, and juniper in the NGB, collected between 1974 and 2009. Data: EPA, LFRDB, US Census Bureau, Stamen.

Of the 13,827 presence points for the three species types of interest, 7334 were sagebrush, 2038 were juniper, and 4455 were cheatgrass (Map 3). Although the NGB contains four subspecies of sagebrush with unique traits and niches—ssp. *tridentata* (basin big sagebrush), ssp. *vaseyana* (mountain big sagebrush), ssp. *spiciformis* (snowfield big sagebrush), and ssp. *wyomingensis* (Wyoming big sagebrush)—I grouped them for purposes of this model as a unified sagebrush category, per previous sagebrush distribution modeling research (Requena-Mullor et al., 2019). Known difficulties distinguishing among sagebrush subspecies, particularly in-field, further substantiated this grouping approach (McArthur et al., 1988; Richardson et al., 2012), as did similarities in subspecies' responses to elevation and site exposure gradients (Appendix A). Similar in-field identification issues, as well as evidence for interspecific gene flow and hybridization among Great Basin juniper species, led to a similar decision to use one grouped juniper

category, rather than tracking Western juniper, Utah juniper, and Rocky Mountain juniper as separate response variables (Terry, 2010; Terry et al., 2000). Plotting group means and standard errors for juniper species' responses to elevation and exposure indicated, as with sagebrush subspecies, some differences in elevational distributions, but very similar exposure distributions across species (Appendix A). This data exploration conveyed adequate similarities across species to use one juniper category as the juniper response variable.

I further subset presence and absence data based on whether or not they fell within a grazing allotment. I eliminated any species presence/absence points not located in an allotment, and in turn eliminated any allotments without points in order to later build a neighbor adjacency matrix in order to account for the spatial effects of grazing units via conditional autoregressive models.

Biotic Predictor Variables

The models also included presence of the two non-focal species as predictor variables to represent co-occurrence. For example, the sagebrush distribution model included cheatgrass and juniper as predictor variables, and so on. Here, co-occurrence serves as a proxy for species interactions, whether competitive or symbiotic, that many correlative SDMs do not capture (Pollock et al., 2014). Past studies indicate that including biotic predictor variables in SDMs has improved their predictive performance (Araújo & Luoto, 2007; Leathwick, 2002; Pollock et al., 2014). In this case, since juniper, sagebrush, and cheatgrass so frequently co-occur in the NGB, these biotic covariates also stand to offer insights relevant to the simultaneous management of the three species groups. Species co-occurrence was indicated by any species observations that were collected in the same

batch and in close proximity. This approach ensured not only spatial, but also temporal, co-occurrence.

Climate and Topographic Data

Climatic and topographic variables (*e.g.*, cumulative annual precipitation and elevation) are a typical component of SDMs, and often used as correlated proxies for more directly relevant factors affecting species distributions (Elith & Leathwick, 2009). Here, I use climatic and topographic variables with functional relevance to the distributions of sagebrush, cheatgrass and juniper across the NGB in the context of restoration and wildfires. The first of these is maximum VPD, taken from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) 30-year normals (1990-2020) at an 800-meter resolution. VPD, a metric of the extent to which atmospheric water content is below the saturation point, contributes to fuel aridity and, by extension, to the size and severity of wildfires across the American West (Abatzoglou & Williams, 2016; Iglesias et al., 2022). VPD also directly contributes to drought-induced plant mortality, with most species exhibiting a VPD survival threshold (Grossiord et al., 2020). Together, VPD, the sensitivity of plants to water limitations (*e.g.*, drought), and climate change all drive wildfire regimes (Rao et al., 2022). VPD is also notably underexplored as a factor in semi-arid plant species distributions, and despite the fact that the more commonly-used covariate of precipitation is a relatively weak predictor of sagebrush in particular (Still & Richardson, 2015).

Both slope (steepness in degrees) and aspect (the direction a slope faces) relate the abiotic conditions driving species-specific site suitability and species ability to recover from disturbances (R. F. Miller & Tausch, 2002). Mountain big sagebrush (*Artemisia*

tridentata Nutt. ssp. *vaseyana* [Rydb.] Beetle) and Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), for example, exhibit stronger natural and post-restoration recovery on north-facing slopes (Davies & Bates, 2017). Meanwhile, more drought-prone (*i.e.*, southerly) aspects may delay recovery among some *A. tridentata* subspecies (Nelson et al., 2014) and provide greater support for cheatgrass populations (Davies & Bates, 2017). Slope can determine aridity conditions, which affect sagebrush, cheatgrass, and juniper distributions (Condon et al., 2011; Requena-Mullor et al., 2019). Together, the steepness of catchment-scale slopes and more northern-facing aspects also increase the probability of fire refugia, which has implications for the occurrence of all three species of interest (Meigs et al., 2020).

The topography-vegetation-fire nexus points to the utility of a topographic metric that combines both slope and aspect. Here, I first derived both slope and aspect in R (R Core Team, 2021) using USGS 1/3 arc-second digital elevation model data, which is approximately equivalent to 10-meter resolution (USGS, 2021). I then used site exposure as a metric to combine slope and aspect, calculated by the equation:

$$\text{slope} \times \cos\left(\pi \times \left(\frac{\text{aspect}-180}{180}\right)\right),$$

where slope and aspect are in degrees, and the output exposure values range from -100 to 100, ranging from less exposed to more exposed, or generally cooler to warmer (Balice et al., 2000). This index has demonstrated efficacy in a modeling context as a topographic metric that combines aspect and slope (Balice et al., 2000).

Wildfire Covariates

To account for the influence of disturbances on species distributions, models included a predictor variable for number of fires based on the 1878-2019 USGS Combined

Wildfire Datasets for the United States and Certain Territories, which includes information from Monitoring Trends in Burn Severity and other federal, state, and local agencies (Welty & Jeffries, 2020). For models looking only at distributions for species that have experienced fire, I also included fire size in acres and time since fire, where the number represented the year post-fire in which a species point was observed in the LFRDB.

Land Treatment Digital Library

Restoration data come from the Land Treatment Digital Library (LTDL; <https://ltdl.wr.usgs.gov/>), a database of over 55,000 records of BLM restoration work and management activities that is maintained and annually updated by the USGS (Pilliod et al., 2021). Treatments include, among others, seeding, planting, fencing, herbicide application, and prescribed burning. I retained all treatments categorized as “Implemented” in the LTDL polygon records, then assigned each species presence or absence point a “Treatment” or “No Treatment” category based on whether or not the area of the species observation had been treated before the LFRDB point collection. Within the NGB, there were 749 Treatment and 6626 No Treatment points for sagebrush, 482 Treatment and 3997 No Treatment points for cheatgrass, and 104 Treatment and 1948 No Treatment points for juniper. Among absences, there were 287 Treatment and 6185 No Treatment points.

Species Distribution Modeling

The inherently spatial nature of SDMs requires addressing spatial autocorrelation among species presence and absence points. Here, I elected to use a conditional autoregressive (CAR) modeling approach, in which the model structure accounts for the proximity of areal units—in this case, BLM grazing allotments—to address spatial dependencies across presence/absence points and within model outputs. CAR models are

most useful in cases where the spatial position of model input data likely influences the data themselves. One consistent use case for multilevel CAR models has been in epidemiological studies, where exploiting adjacencies of non-overlapping areal units can facilitate deeper understanding of disease spread (*e.g.*, Bivand et al., 2013; Djeudeu et al., 2022; Lee et al., 2014). The applicability of multilevel CAR models for ecological problems has been unexplored, but holds promise for understanding ecological processes that occur across human-managed spaces.

Model Implementation

I conducted all spatial and statistical analyses in R 4.1.1 (R Core Team 2021). For each of the three species of interest, I constructed a multilevel logistic CAR model in the R package CARBayes (Lee, 2016). CAR models specifically handle spatial dependencies by modeling spatial autocorrelation via a set of spatial random effects via a variety of implementations, all of which rely on adjacency matrices of the modeled areal units (Besag et al., 1991; Lee, 2016). This allows for easier interpretation of spatial variability in models than a non-CAR implementation while also maintaining high precision and low bias (Beale et al., 2010). Here, I constructed a multilevel CAR model for each species' SDM via the CARBayes function 'S.CARmultilevel' (Lee, 2016), implemented with a binomial likelihood and variation modeled by the following decomposition:

$$\psi_k = \phi_k ,$$

$$\phi_k | \phi_{-k} \sim N \left(\frac{\rho \sum_{j=1}^K w_{kj} \phi_j}{\rho \sum_{j=1}^K w_{kj} + 1 - \rho}, \frac{\tau^2}{\sum_{j=1}^K w_{kj} + 1 - \rho} \right),$$

$$\tau^2, \sigma^2 \sim \text{Inverse Gamma} (a, b).$$

$$\rho \sim \text{Uniform} (0,1).$$

Here, $\phi = (\phi_1, \dots, \phi_k)$ represents the spatial variation of all individuals within a given area, where k is the total number of areas in the model. I used the default CARBayes priors for τ^2 and σ^2 ($a=1$, $b=0.01$), as well as ρ proposed by Leroux et al. (2000), and set a regularizing prior on β to constrain the model space to values closer to zero and avoid model overfitting (McElreath, 2019; Polson & Sokolov, 2019). While there are a number of options for CAR priors in a Bayesian framework, the Leroux prior appears to outperform others, especially for models with a large (>100) number of areas (Aswi et al., 2020).

To account for both spatial autocorrelation among species and absence points, as well as to acknowledge the role of grazing and rangeland management in the NGB's ecological function, I used grazing allotments as the spatial varying intercept for each of the sagebrush, juniper, and cheatgrass SDMs, represented by k in the above decomposition. While the NGB partially or wholly contains 1415 grazing allotments overseen and allocated by the BLM, I retained 515 of these that allotments both contained LFRDB points and had adjacencies with other grazing units, which is necessary for CAR models, which rely on a neighborhood matrix, \mathbf{W} , to indicate areal unit adjacency (De Oliveira, 2012; Lee, 2016; Morris et al., 2019).

Based on Requena-Mullor et al. (2019), who found that model performance in sagebrush systems improved with the inclusion of fire variables (number of fires and fire occurrence) I included number of fires as a covariate in each species' SDM, with additional fire characteristics as predictor variables in the fire-only models (see below). Beyond number of fires, each model included predictor variables for implemented LTDL treatments, a site exposure index value, and maximum VPD from PRISM 30-year normal.

Each model also contained covariates for co-occurrence of the other two species of interest.

See Figure 2 for a conceptual diagram of the CAR model workflow.

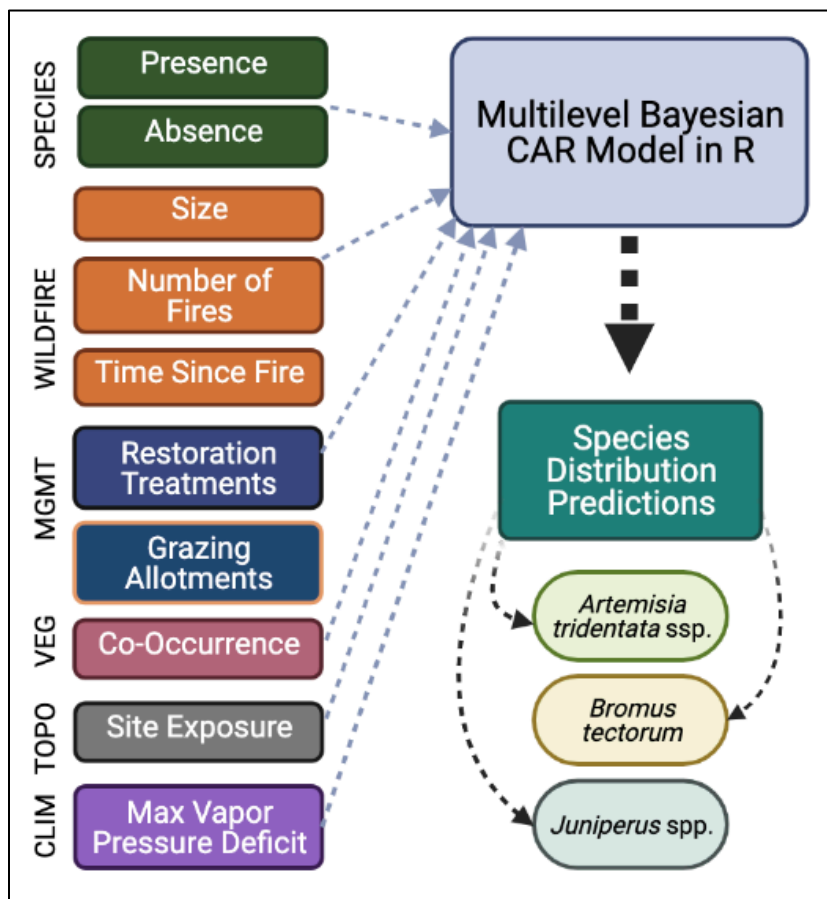


Figure 2. Conceptual diagram of workflow for CAR model implementation. Orange highlight around “Grazing Allotments” indicates its use as the areal unit implemented as a spatial varying intercept. *N.B.* Fire size and time since fire were just included in fire-only versions of all SDMs. Diagram created using BioRender.com.

I standardized all continuous predictor variables (maximum VPD, site exposure, number of fires) to a mean of 0 and standard deviation of 1 (Gelman, 2008), before fitting each model on three chains. Each chain of the sagebrush CAR model ran for 90,000 iterations with a warmup of 40,000 samples and thinned to every fifth draw, resulting in 30,000 total post-warmup samples. Both the cheatgrass and juniper CAR models ran on three chains for 100,000 iterations with 60,000 burn-in samples, then thinned to every fifth

draw, for 24,000 total post-warmup samples. The cheatgrass and juniper CAR implementations required a higher number of iterations and burn-in samples to achieve consistent convergence. I assessed model convergence and proper mixing using traceplots and R-hat values of less than 1.01, as well as Geweke diagnostic values in the range -1.96 to 1.96 (S. P. Brooks & Gelman, 1998; Geweke, 1992).

In addition to the baseline models for all three species, I ran another SDM for each species using only the LFRDB points that had experienced historical fire. These models retained the same covariates as the initial SDMs, and also included fire size and time since fire to offer more robust insights into the effects of fire characteristics on species distributions in historically burned areas. These models replicated the priors from the initial SDM for each species, but included a much smaller dataset, with 1652 species presence/absence points and 141 grazing allotments. Each fire-only model ran on three chains with 90,000 iterations and 40,000 warmup samples thinned to every fifth draw, for a total of 30,000 post-warmup samples.

Model Validation

To validate the models, I used block k-fold cross-validation with 515 folds, each of which corresponded to a single grazing unit, followed by an assessment of log-loss, overall classification accuracy, and balanced classification accuracy as error metrics. While k-fold cross-validation is a typical approach for assessing SDMs' performance, using a blocking strategy may even further prevent overfitting and improve estimates of prediction errors (Merow et al., 2014; Roberts et al., 2017). Since the grazing allotments serve as the spatial random effect, this blocking method helps account for both spatial autocorrelation within the model and for the random effect structure (Roberts et al., 2017). The small size of these

blocks also limits extrapolation, while still allowing for prediction into areas lacking initial species observation points (Roberts et al., 2017).

To assess classification accuracy, I compared the matrix of predicted presence/absence values for each point in a given left-out grazing allotment (*i.e.*, a fold) to the actual presence/absence value for the same point. This allowed me to propagate model uncertainty through the error assessment before calculating the overall and balanced classification using the R package “yardstick” (Kuhn & Vaughan, 2021). Overall accuracy measures the number of correct predictions out of the total predictions, generally resulting in a somewhat more optimistic accuracy figure. Balanced accuracy corrects for imbalanced data, such as the LFRDB species presence/absence points, by taking the mean of sensitivity (number of correctly predicted true positives divided by total number of predicted positives) and specificity (number of correctly predictive true negatives divided by the total number of predicted negatives), which generally results in a somewhat less optimistic classification accuracy (Brodersen et al., 2012).

To calculate log-loss for each model, I estimated the predicted probability of occurrence of points in each left-out allotment in each of the 515 folds. This resulted in 1000 posterior predictive draws for each initial species presence/absence point in all three models (20,225,000 total predictions), which I then compared to the initial observed values in each allotment via the log-loss function. Log-loss represents the negative log likelihood of the test data produced in the k-fold cross-validation process; in other words, it assesses the uncertainties of probabilities estimated by the models by comparing fitted probabilities to the actual data (Phillips & Dudík, 2008; Requena-Mullor et al., 2019). Here, higher log-loss indicates worse model performance, and the log-loss values can also be compared

across SDMs as a measure of relative performance across multiple logistic regression models.

I repeated the same process to validate the fire-only models, using just the 141 grazing allotments that contained fire, species presence/absence points, and were contiguous with at least one other allotment as the “folds.” This resulted, again, in 1000 posterior predictions for each of the initial 1652 species presence/absence points in the fire-only grazing allotments, for a total of 1,652,000 predictive posterior draws from which to calculate log-loss. To calculate overall and balanced accuracy, I compared the predicted presence/absence values from each left-out fold to the observed presence/absence values for the points in the corresponding fire-only grazing allotment.

Model Interpretation

I interpreted all regression coefficients whose Bayesian 95% credible intervals did not contain 0 as providing strong evidence of the given variable having an effect on the probability of species occurrence. This is, in some respects, a Bayesian analog to a frequentist p -value, but can be directly interpreted as the probability of either a positive or negative effect of a particular covariate. Conversely, for the purposes of these models, I considered regression coefficients whose Bayesian 95% CIs crossed zero to not have a strong directional effect on species occurrence, although these coefficients and CIs may still offer some ecological insights into the effects of the specific predictors (Kruschke & Liddell, 2018).

Model Predictions

Using the model fits for both the initial and fire-only models, I created spatially explicit predictions of sagebrush, juniper, and cheatgrass distributions, respectively, in the

NGB. Each of the initial predictor variable datasets served as the new spatial layers on which to predict model outputs, with the exception of species presence/absence, which was LFRDB point data. To establish non-point spatial representations of sagebrush and cheatgrass presence in spatial predictions of the models, I used the National Land Cover Database (NLCD) Rangeland Condition Monitoring Assessment and Projection (RCMAP) sagebrush cover and annual herbaceous cover layers, respectively, from 2009 to represent the new test data for the correct time period.

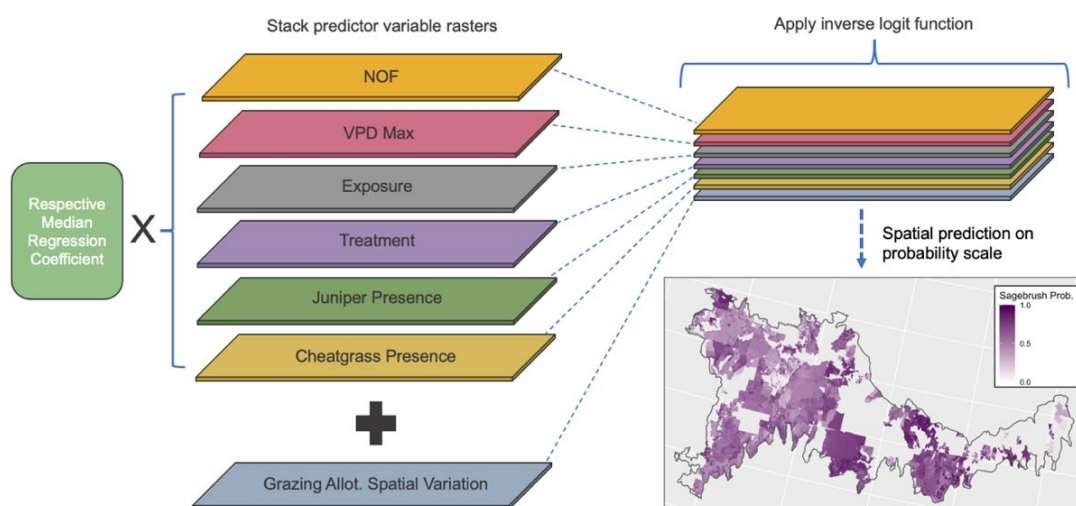


Figure 3. Conceptual diagram of raster-based model prediction process.

To represent juniper presence, I used 2009 remotely-sensed estimates of pinyon-juniper biomass in the Great Basin (Filippelli et al., 2020). I set a threshold such that any pixel in the NLCD data with $\geq 15\%$ cover counted as species presence (*i.e.*, the pixel value became 1) per Bradley *et al.*, who considered 15% a threshold for “high abundance” based on remotely sensed data classification (Bradley et al., 2018). Given that pinyon-juniper biomass is predicated on the presence of pinyon-juniper, the any non-zero pixel from the 2009 biomass layer represented juniper presence. I then stacked, scaled, and centered these

variable rasters to use as prediction layers. See Figure 3 for a visual explanation of this prediction process.

RESULTS

Conditional Autoregressive Models for All NGB Grazing Allotments

Overall, the three SDMs that included both burned and unburned areas indicate that species co-occurrence, number of fires, and maximum VPD have a nonzero effect on the probability of species occurrence in the NGB. Each species also exhibits different spatial responses to the predictor variables used herein (Map 4).

Sagebrush Model

Juniper co-occurrence exhibits the largest—over 5.5 times greater than the next-most influential predictor—and most certain effect on sagebrush presence, increasing the probability of occurrence in the NGB by 71.7% (95% credible interval [CI]: 70.3%, 73.0%). Cheatgrass co-occurrence also has a substantial positive effect on sagebrush presence, increasing the likelihood of sagebrush occurrence by 22.3% (95% CI: 20.1%, 24.5%). Restoration treatment increases the probability of sagebrush presence by 9.35% (95% CI: 5.97%, 12.9%). Maximum VPD increases sagebrush occurrence probability by 43.8% as maximum VPD increases from 8.76 kPa (the minimum observed 30-year normal value in the NGB) to 20.69 kPa (the maximum observed 30-year normal value in the NGB), but with a large amount of uncertainty (95% CI: 36.5%, 51.0%). Number of fires is the only covariate that negatively affects the probability of sagebrush occurrence. As the number of historical fires increases from zero to five, the probability of sagebrush occurrence decreases by 16.7% (95% CI: -21.84%, -8.36%). Site exposure has no discernable effect on sagebrush occurrence (see Figure 4). The sagebrush SDM had an

overall classification accuracy of 66.28% (95% CI: 65.21%, 67.18%), a balanced classification accuracy of 63.58% (95% CI: 62.64%, 64.44%), and a log-loss of 0.548 (95% CI: 0.534, 0.567). See Table 1 for a comparison of errors for all model iterations.

Table 1. Comparison of overall accuracy, balanced accuracy, and log-loss assessments for full CAR and fire-only versions of sagebrush, juniper, and cheatgrass SDMs. Error assessments used a k-fold process that held out a single grazing allotment (fold) of data in each model run.

Model Version	Overall Acc. (95% CI)	Balanced Acc. (95% CI)	Log-loss (95% CI)
<i>Sagebrush</i>	66.28% (65.21, 67.18)	63.58% (62.64, 64.44)	0.548 (0.534, 0.567)
<i>Cheatgrass</i>	92.04% (91.66, 92.37)	89.20% (88.91, 89.48)	0.161 (0.155, 0.170)
<i>Juniper</i>	89.41% (88.78, 90.01)	82.63% (81.90, 83.19)	0.155 (0.150, 0.166)
<i>Sage. (Fire-Only)</i>	57.93% (55.75, 60.23)	55.62% (53.45, 57.96)	0.897 (0.878, 0.922)
<i>Cheat. (Fire-Only)</i>	78.63% (76.82, 80.39)	77.92% (76.34, 79.57)	0.496 (0.485, 0.515)
<i>Jun. (Fire-Only)</i>	84.20% (83.35, 84.93)	74.06% (71.39, 76.97)	3.949 (3.946, 3.953)

Juniper Model

Sagebrush co-occurrence conversely has the greatest effect on the likelihood of juniper, increasing the probability of occurrence by 88.1% (95% CI: 84.7%, 90.7%), with an overall effect more than 10 times stronger than that of any other covariate. Meanwhile, cheatgrass co-occurrence has very little effect on the likelihood of juniper presence in the NGB, increasing the probability of occurrence by just 0.409% (95% CI: 0.0126%, 0.944%). Number of fires decreases the likelihood of juniper occurrence by 1.11% (95% CI: -1.49%, -0.386%) as the number of historical burns goes from zero to five. As maximum VPD moves from 8.76 kPa to 20.69 kPa, the probability of juniper occurrence decreases by 12.8% (95% CI: -10.3%, -7.70%). The application of treatment has a weak effect on juniper occurrence, with the 95% CI crossing zero, although the 50% CI

demonstrates that restoration treatments somewhat reduce juniper presence (see Figure 4). Based on these models, site exposure has a weak effect on juniper occurrence. The juniper SDM had an 89.41% overall classification accuracy (95% CI: 88.78, 90.01), 82.63% balanced classification accuracy (95% CI: 81.90%, 83.19%), and a log-loss of 0.155 (95% CI: 0.150, 0.166; Table 1).

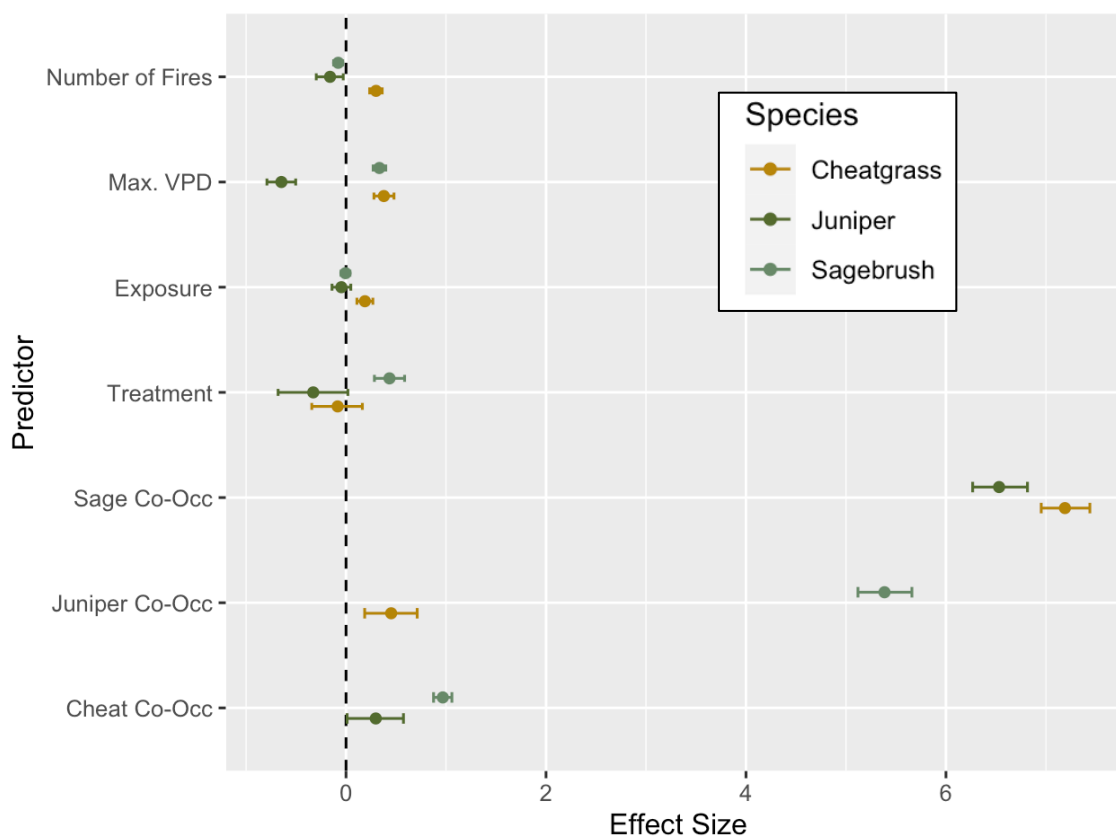
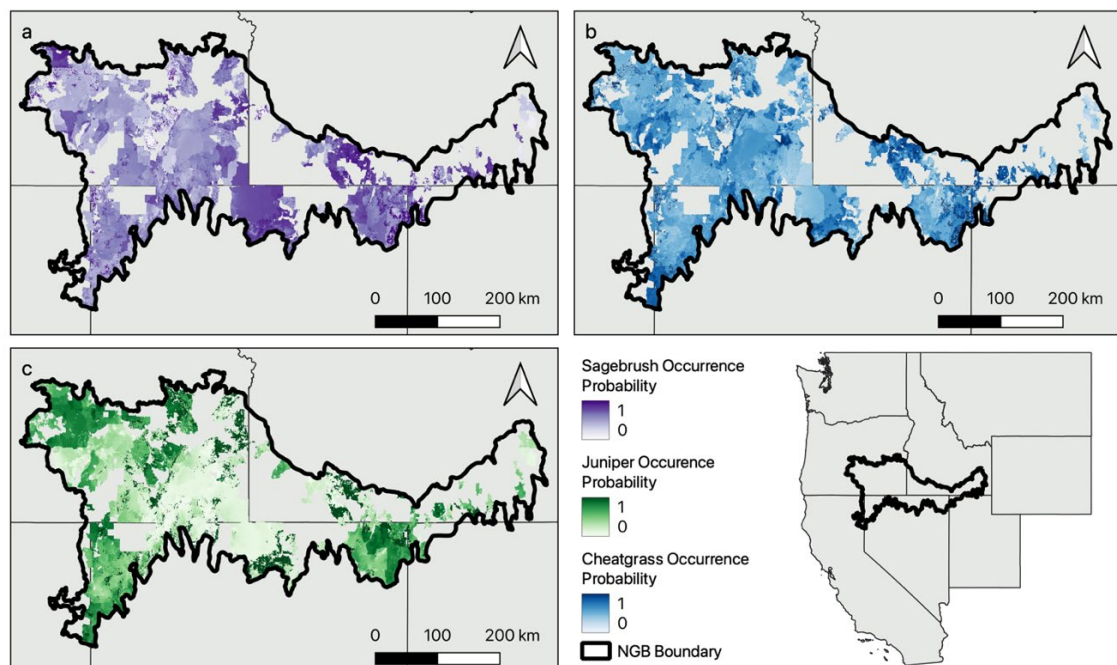


Figure 4. Combined effect size plot for all three SDMs across all NGB grazing allotments. Lines crossing zero indicates that the 95% CI contains 0. Dots indicate median effect size based on regression coefficients. Cheatgrass Model

As with juniper, sagebrush co-occurrence has the largest influence on the probability of cheatgrass. Sagebrush co-occurrence has an effect on cheatgrass nearly 16 times more influential than the next-strongest predictor, increasing the likelihood of presence by 94.3% (95% CI: 93.7%, 94.9%) compared to no co-occurrence. Juniper co-

occurrence also positively affects the probability of cheatgrass presence, but by a much smaller amount, 2.03% (95% CI: 0.757%, 3.63%), while holding other conditions at their mean. By magnitude, number of fires has the second strongest effect on cheatgrass occurrence. As the number of historical fires increases from zero to five, the likelihood of cheatgrass presence increases 69.8% (95% CI: 49.2%, 83.2%). The probability of cheatgrass occurrence increases 11.4% (95% CI: 7.83%, 15.6%) as maximum VPD goes from 8.76 kPa to 20.69 kPa. Cheatgrass likelihood also increases 10.0% (95% CI: 5.12%, 16.56%) as the site exposure index value moves from -15.1 to 21.6, corresponding to a shift from more north-facing to more south-facing. The application of restoration treatments has a weak effect on cheatgrass occurrence (see Figure 4). The cheatgrass SDM performed slightly better than the juniper SDM, with an overall classification accuracy of 92.04% (95% CI: 91.66%, 92.37%), a balanced classification accuracy of 89.20% (95% CI: 88.91%, 89.48%), and a log-loss of 0.161 (95% CI: 0.155, 0.170; Table 1).



Map 4 Spatial predictions for sagebrush (a), cheatgrass (b), and juniper (c) CAR SDMs in historically burned and unburned NGB grazing allotments. Data: US Census Bureau, US EPA, USGS, BLM, NLCD, PRISM, SRTM, LFRDB.

Spatial Autocorrelation

Each CAR model's structure included a grazing allotment adjacency matrix that allowed the model to explicitly handle inherent spatial autocorrelation across points in neighboring allotments. Each model then produced results for spatial autocorrelation, or spatial dependence, across allotments represented by ρ , a value between 0 (total independence) and 1 (total dependence). Posterior estimates for the spatial dependence term, ρ , are 0.712 (95% CI: 0.562, 0.830) for sagebrush, 0.531 (95% CI: 0.244, 0.768) for cheatgrass, and 0.878 (95% CI: 0.757, 0.944) for juniper, with higher values indicating higher spatial autocorrelation between grazing units (Figure 5). Juniper presence exhibits markedly higher spatial dependency across grazing units than sagebrush, and vastly more than cheatgrass.

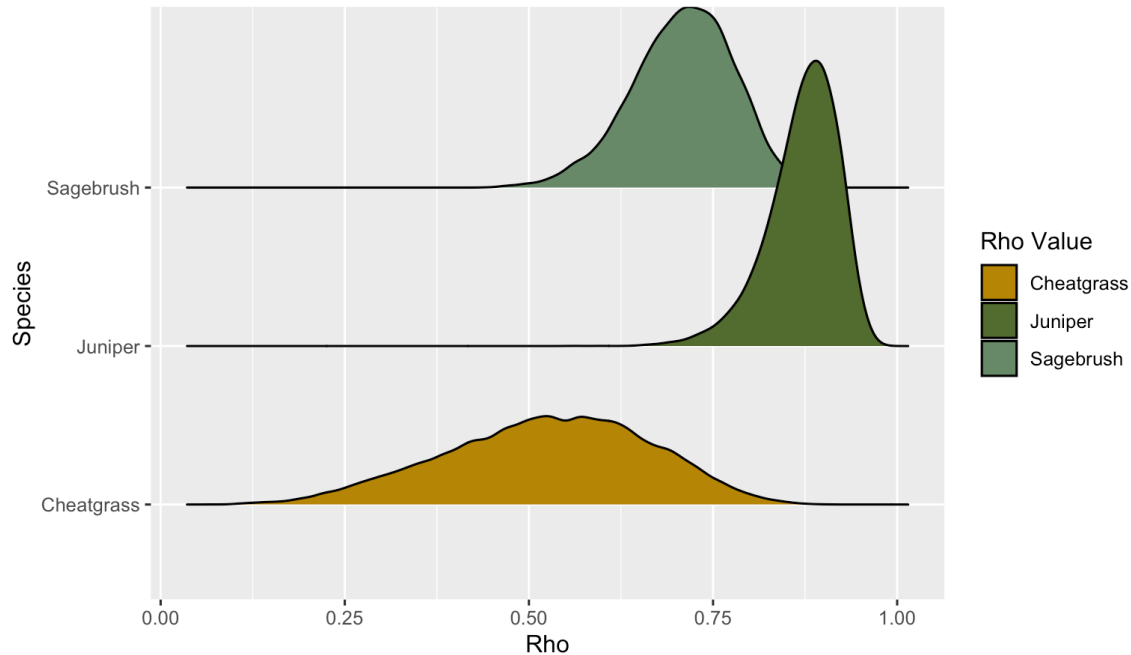


Figure 5. Density plots comparing rho value distributions for sagebrush, juniper, and cheatgrass. Higher rho value indicates greater spatial dependency of species presence across grazing allotments.

Fire-Only Models

In the fire-only models, the direction and relative magnitude of covariates' respective effects remain consistent with the initial model iterations, with species co-occurrence continuing to exhibit the strongest influence on other species' presence. The fire-only models also do not provide evidence of post-fire treatment efficacy for the three species of interest. See Map 5 for explicit spatial predictions of each species distribution in historically burned portions of the NGB.

Fire-Only Sagebrush Model

Juniper co-occurrence continues to have the largest effect on sagebrush presence—4.5 times bigger than the next-strongest covariate, cheatgrass co-occurrence—in previously burned areas, increasing the likelihood of sagebrush occurrence by 42.62% (95% CI: 35.25%, 49.62%). The probability of sagebrush increases by 11.38% (95% CI:

5.887%, 16.83%) when cheatgrass co-occurs and by 50.44% (95% CI: 25.74%, 68.87%) as maximum VPD goes from 10.69 kPa to 20.42 kPa in areas that have experienced at least one fire. Notably, time since fire has a greater effect on sagebrush occurrence than number of fires, also increasing the probability of presence by 48.62% (95% CI: 27.90%, 63.59%) as time since fire goes from two to 87 years. Number of fires continues to negatively impact sagebrush, reducing the likelihood of occurrence by 25.66% (95% CI: -30.53%, -19.55%) as number of fires increases from one to five. Fire size, site exposure, and treatments have no meaningful effect on sagebrush occurrence in previously burned areas (Figure 6). The fire-only sagebrush model performed worse than its initial CAR counterpart, with an overall accuracy of 57.93% (95% CI: 55.75%, 60.23%), a balanced accuracy of 55.62% (95% CI: 53.45%, 57.96%), and a log-loss of 0.897 (95% CI: 0.878, 0.922; Table 1).

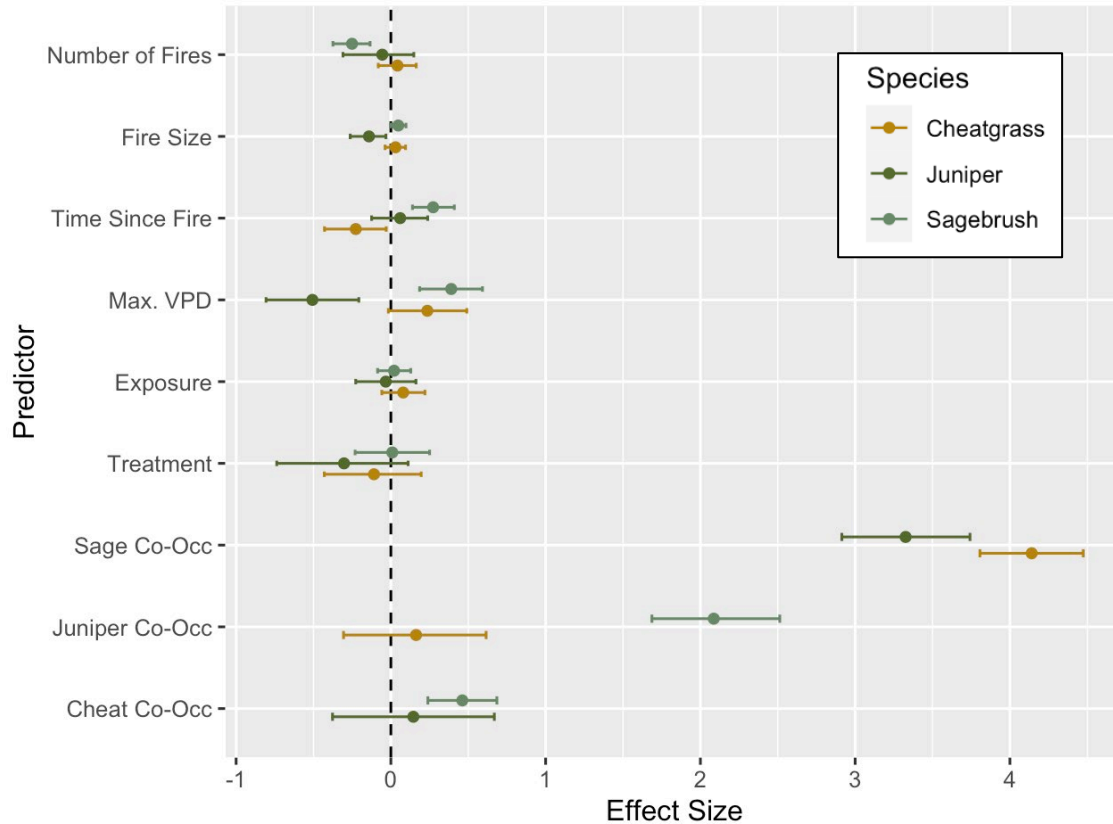


Figure 6. Combined effect size plot for all three SDMs in previously burned grazing allotments in the NGB. Lines crossing zero indicates that the 95% CI contains 0. Dots indicate median effect size based on regression coefficients.

Fire-Only Juniper Model

Sagebrush co-occurrence has over six and a half times more influence than the next-most impactful predictor on juniper presence where fires have occurred, increasing the likelihood of occurrence by 56.93% (95% CI: 41.77%, 68.91%). Maximum VPD exhibits the next-strongest effect on juniper occurrence, followed by fire size, reducing likelihood of presence by 17.66% (95% CI: -38.81%, -5.664%) and 4.226% (95% CI: -9.357%, -1.218%), respectively, as VPD moves from 10.69 kPa to 20.42 kPa and fire size increases from a minimum of 7 acres to a maximum of 95,148 acres. For areas with historical fires, unlike in NGB grazing allotments more broadly, cheatgrass co-occurrence has no discernable effect on juniper presence, nor do number of fires, time since fire, or site

exposure (Figure 6). The fire-only juniper model performed worse than its initial counterpart, and with a much higher log-loss than either the cheatgrass or sagebrush fire-only models. Log-loss for this model was 3.949 (95% CI: 3.946, 3.953), overall accuracy was 84.20% (95% CI: 83.35%, 84.93%), and balanced accuracy was 74.06% (95% CI: 71.39%, 76.97%; Table 1).

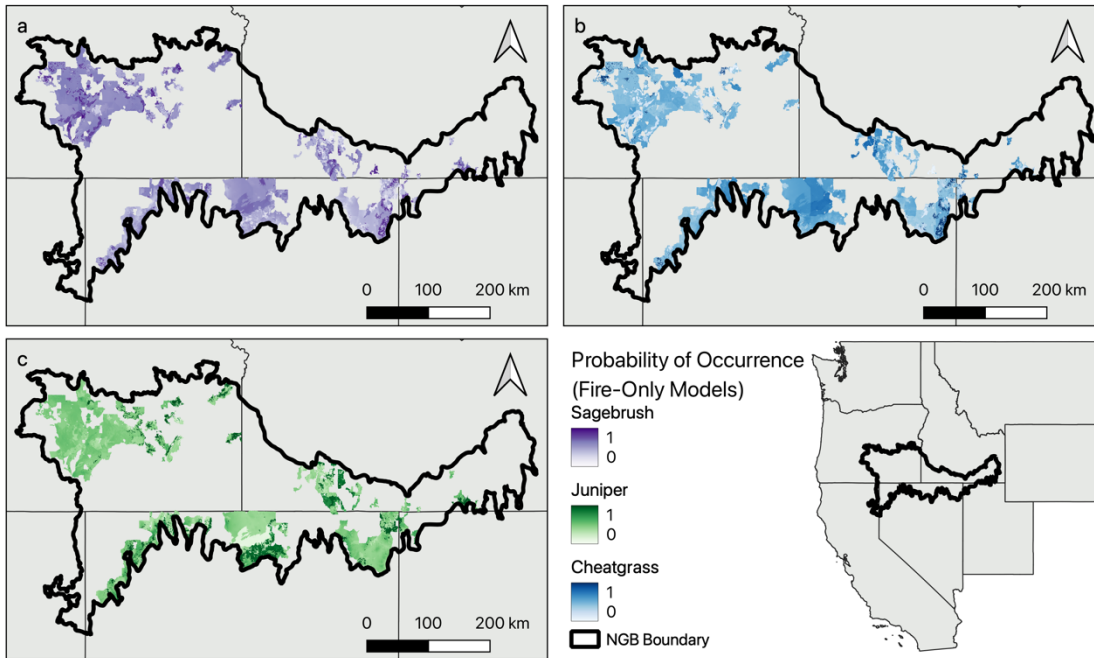
Fire-Only Cheatgrass Model

Based on the fire-only cheatgrass SDM, sagebrush co-occurrence is the strongest predictor—over 17.5 times more influential than the next-strongest meaningful covariate—for cheatgrass presence in previously burned areas, increasing likelihood of occurrence by 76.87% (95% CI: 72.98%, 80.09%). Conversely, time since fire negatively impacts cheatgrass, decreasing probability of occurrence by 13.85% (95% CI: -23.70%, -2.679%) as time since fire extends from two years to 87 years. For historically burned areas, maximum VPD, juniper co-occurrence, treatment application, site exposure, number of fires, and fire size have no meaningful effect on cheatgrass occurrence (Figure 6). The fire-only cheatgrass model also performed worse than the initial cheatgrass CAR SDM, with an overall accuracy of 78.63% (95% CI: 76.82%, 80.39%), a balanced accuracy of 77.92% (95% CI: 76.34%, 79.57%). Log-loss for the cheatgrass fire-only model was 0.496 (95% CI: 0.485, 0.515; Table 1).

Spatial Autocorrelation for Fire-Only Models

Compared with the initial CAR models, the fire-only SDMs indicated both weaker spatial dependencies across grazing allotments and also much greater uncertainty around the level of spatial dependency for each species based on the models' respective ρ values. The sagebrush fire-only model had an overall ρ of 0.598 (95% CI: 0.0752, 0.943), juniper

had a ρ of 0.388 (95% CI: 0.0183, 0.906), and cheatgrass had a ρ value of 0.559 (95% CI: 0.0764, 0.885). See Appendix A for ρ value density plots for fire-only SDMs.



Map 5. Spatial predictions for sagebrush (a), cheatgrass (b), and juniper (c) fire-only SDMs in previously burned NGB grazing allotments. Data: US Census Bureau, US EPA, USGS, BLM, NLCD, PRISM, SRTM, LFRDB.

DISCUSSION

Implications and Applications

In response to the question *How do vegetation co-occurrences, wildfire histories, and human interventions influence the distributions of sagebrush, juniper, and cheatgrass in the NGB?*, these results highlight the importance of abiotic and biotic disturbances as drivers of species' distributions in the semi-arid sagebrush steppe of the NGB, as well as the interconnectedness of ecological impacts and management outcomes. In particular, the relative strength of disturbance factors, such as wildfire and invasive species presence, compared to that of climatic and topographic predictors—maximum VPD and site exposure, respectively—points to the necessity of accounting for invasive species and wildfire in defining the plausible operating space for keystone rangeland vegetation, including sagebrush. These same disturbance regimes are equally critical to understanding the dynamics of competing species such as juniper and invasive annual grasses such as cheatgrass. This is particularly important given that many management and restoration decisions currently rely on slope, aspect, and other topographic features, which may miss key considerations.

The results of using a multilevel CAR modeling approach with a management unit as the spatial varying intercept also underscore the relevance of long-term natural resource decision-making, here represented by a type of cadastral data, in broader ecological function and composition (Barber et al., 2022). Incorporating BLM grazing allotments into the three species' CAR models revealed meaningful spatial dependencies of sagebrush,

juniper, and cheatgrass across grazing units, likely pointing to the effects of similarities in both management practices and biophysical characteristics across allotments (Niemi et al., 2018).

Notably, each of the models performed differently, with sagebrush exhibiting by far the highest error rate of the three species of interest, and a poor overall performance for the fire-only model in particular. Since the LFRDB data were richest and most widespread across the NGB for sagebrush, this may indicate a flaw in parameterization for sagebrush specifically, which could be further explored and rectified in future research. Conversely, the low level of error for cheatgrass and juniper models suggests that the selected predictor variables adequately captured the disturbance-management-biophysical dynamics of these species without overfitting. In all cases, these SDMs' respective performance accuracies represent an improvement over the previous effort by Requena-Mullor *et al.* (2019) to model sagebrush distributions in response to wildfire and restoration. These improved accuracies, particularly for juniper and cheatgrass, may point to opportunities for using similar models for on-the-ground predictive purposes.

The role of species co-occurrence

One of the most notable implications of the full CAR models (*i.e.*, not fire-only) for sagebrush, juniper, and cheatgrass is the substantial role of species co-occurrence as a driver of species presence for all three species. In particular, the strong influence of sagebrush co-occurrence on both cheatgrass and juniper presence supports the known pattern of both species' expansion into native sagebrush ecosystems. Juniper co-occurrence as a strong predictor for sagebrush also reinforces the fact of juniper's adaptations to and expansion within much of the NGB (Coates et al., 2017; Falkowski et al., 2017). Since the

study period (post-2009), the trajectory of pinyon-juniper woodlands has reversed course, with sharp declines in overall biomass (Filippelli et al., 2020).

Overall, the role of co-occurrence in all six of these SDMs points to potential competition and invasion dynamics, and underscores some of the conditions of co-occurrence that outstrip the effects of other landscape-scale climatic, management, and disturbance factors, including drought, restoration efforts, and wildfire. This finding also reinforces the value of jointly modeling species that consistently interact across landscapes and therefore likely influence each other's distributions in complex ways beyond the role of climatic and topographic factors (Meier et al., 2010; Pollock et al., 2014). While incorporating co-occurrence is not, in and of itself, evidence of vegetation interactions (Blanchet et al., 2020) its clear relevance as a predictor opens the door for more particular questions about the mechanisms underpinning vegetation dynamics (*e.g.*, dispersal, regeneration time, etc.) that influence species distributions in sagebrush ecosystems. However, the relatively smaller effect (or lack thereof) of species co-occurrence in the fire-only models suggests that co-occurrences may become less relevant in areas that have burned. Additionally, these relationships are not entirely bi-directional; while cheatgrass does predict for sagebrush when considering the whole NGB, it has a much weaker effect on juniper presence, and no meaningful effect on either sagebrush or juniper for areas that have experienced at least one fire.

One potential implication of sagebrush co-occurrence as a predictor for cheatgrass is that cheatgrass invasions do not necessarily require a prior disturbance, such as wildfire. Instead, this result indicates that cheatgrass can and does invade relatively intact sagebrush systems, or at minimum that its invasion can precede the wholesale disappearance of

sagebrush and associated native species. Although these data cannot account for the exact extent to which any sagebrush system remains intact on the ground, nor the abundance of cheatgrass, this result may counter the narrative that cheatgrass primarily invades already-degraded areas (*e.g.*, Whisenant, 1990). At the same time, widespread, long-term grazing across the NGB also lessens the likelihood that any given area remains truly undisturbed, and indeed itself increases the probability of cheatgrass spread (Williamson et al., 2020). The hypothesis that cheatgrass may invade relatively undisturbed sagebrush systems merits further research.

Specific influences of fire on species distributions

One of the primary takeaways from both SDM iterations for all three species is the relevance of fire as a predictor of and influence on species distributions in the NGB, responding directly to my second research question: *How do wildfire characteristics such as size, frequency, and time since fire influence plant species distributions in the NGB in the context of other abiotic and biotic drivers?* In particular, a higher number of fires reduces the likelihood of both sagebrush and juniper presence, which squares with the slow post-fire recovery of sagebrush and the general lack of fire tolerance of juniper (Chambers, Miller, et al., 2014). The inverse finding that a higher number of fires increases the likelihood of cheatgrass presence also confirms, at a landscape scale, cheatgrass's success at infiltrating and becoming established in burned areas, generally at the expense of native species (Fusco et al., 2019; Whisenant, 1990). However, the influence of number of fires changes markedly when accounting only for areas that have experienced at least one fire, rather than the entire NGB. The fire-only models demonstrate that time since fire and fire size outweigh the relevance of number of fires in these areas. This holds true for all three

species, with time since fire exhibiting a stronger, and inverse, influence on both sagebrush and cheatgrass presence, and fire size having a larger negative effect than number of fires on juniper presence.

These results build on the finding in Requena-Mullor *et al.* (2019) that using fire occurrence and number of fires as covariates improves SDM performance, confirming that characteristics beyond fire occurrence and number of fires, such as time since fire and fire size, matter for species distributions in historically burned areas. The time since fire result, in particular, supports previous findings that sagebrush recovery improves with increased time since fire (Shinneman & McIlroy, 2016). Importantly, these fire characteristics remain relevant even when accounting for the respective influences of species co-occurrence and management activities. Collectively, this implies that a fire regime in the NGB that more closely approximates historical normal for fire return interval and fire size may better serve sagebrush and juniper species while potentially limiting cheatgrass spread. Conversely, this means that the ongoing shift toward shorter return intervals and larger fires will likely reduce the presence of sagebrush and juniper in sagebrush ecosystems and result in conversion of shrublands to herbaceous-dominated landscapes (Ellsworth *et al.*, 2020).

The decision to focus on number of fires, time since fire, and fire size stemmed from their relevance to the specific species of interest in this research, as well as historical data availability. While other fire characteristics such as ignition source, severity, and seasonality certainly have influences on species survival, competition, and distribution (Abatzoglou & Kolden, 2011; Bradley *et al.*, 2018; Chambers *et al.*, 2019; Roundy *et al.*, 2018), number of fires, time since fire, and fire size were considered important landscape-scale, management-relevant factors here (Paul Makela and BLM staff, personal

communication, 16 Mar. 2022). Data on ignitions and burn severity also did not become consistently available until the 1980s, rendering it less applicable as a long-term historical fire predictor variable. Future research exploring additional fire variables would likely add granularity to this work and offer additional insights to conservation and restoration decision-makers.

Effects of maximum vapor pressure deficit

Maximum VPD, a proxy for “droughtiness,” affects the probability of presence or absence for all three species of interest, though not necessarily in the expected directions. VPD exerts a negative effect on juniper, decreasing its likelihood of occurrence, which aligns with juniper species’ known lack of drought tolerance and the broader role of drought conditions in mass tree die-offs (Breshears et al., 2005; Flake & Weisberg, 2021).

Conversely, the cheatgrass model indicates a positive impact of increased maximum VPD on species presence, suggesting that cheatgrass is at least relatively more drought-tolerant than sagebrush or juniper in the NGB. Unlike sagebrush and juniper, cheatgrass adapts to increased VPD by germinating earlier in the year, when moisture tends to be higher (Mahood et al., 2021). Increased cheatgrass at higher maximum VPD may also indicate concurrent, overlapping effects of VPD and multiple fires; in other words, higher VPD supports more wildfires, which in turn create suitable openings for cheatgrass during the long recovery periods of less fire-tolerant species like sagebrush and juniper (Chambers, Bradley, et al., 2014).

Somewhat counterintuitively, the big sagebrush SDMs indicate that increased maximum VPD actually also increases the likelihood of sagebrush occurrence. This may reflect the differences in sagebrush subspecies’ adaptations to drought and generally more

xeric conditions (Kolb & Sperry, 1999), ability to respond to changing climatic conditions (Kleinhesselink & Adler, 2018), and capacity for post-fire re-establishment (Brabec et al., 2017). Sagebrush can also take decades to exhibit adaptations to changing climatic and other ecological conditions (Germino et al., 2019). In other words, the sagebrush CAR model may have had some averaging effect, resulting in an overall positive increase associated with VPD that likely smooths through adaptive lag effects and differential subspecies responses to changing climatic conditions. Still, the sagebrush model here points to the need for additional research on sagebrush responses to projected future increases in VPD (*e.g.*, A. P. Williams et al., 2019) under a warming climate.

Restoration treatment efficacy

Outputs of the initial CAR models (with and without fires) indicate that restoration treatments in the LTDL reduce the probability of juniper occurrence and increase the probability of sagebrush presence. In other words, these treatments may have been effective to some extent at accomplishing broad restoration goals: reducing juniper density and supporting sagebrush habitat. Conversely, cheatgrass model outcomes do not provide evidence of treatment efficacy at reducing cheatgrass occurrence, which also aligns with known difficulties mitigating its spread and impacts (Pilliod et al., 2021).

In the fire-only models, the lack of interpretable effect of restoration treatments on the occurrence of any of the species of interest in previously burned areas also does not provide evidence of restoration treatment efficacy, at least at the scale of the NGB. Previous studies on post-fire sagebrush ecosystem restoration support the difficulty and time-consuming nature of recovery processes (*e.g.* Ellsworth et al., 2016; Nelson et al., 2014), and much of the research on successful treatments has occurred in experimental settings

rather than on a landscape scale (Davies & Bates, 2017). The lack of evidence for post-fire restoration efficacy may also align with Barker *et al.*'s (2019) finding that invasive annual grasses have likely invaded the most fire-prone portions of sagebrush ecosystems pre-fire, and have in turn led to post-fire landscapes dominated by the same invasive grasses, a state that is notoriously hard to reverse (D'Antonio & Vitousek, 1992; Fusco et al., 2021; Pilliod et al., 2021). In other words, the combined difficulty of treating cheatgrass and the invasive annual grass-fire cycle have collided to reduce the landscape-scale efficacy of restoration treatments, particularly in areas where time since fire is shorter.

The specific locations of restoration treatments may be another important factor in post-fire restoration treatment effectiveness. Post-fire restoration often occurs the BLM's Emergency Stabilization and Rehabilitation (ESR) program, which requires rehabilitation plans within 21 days of a fire's containment. Funding for these projects is also often allocated for the hardest-hit areas, and does not necessarily include resources for monitoring and evaluating treatments (personal communication, BLM staff, March and June 2021). To some extent, then, the conditions surrounding rehabilitation efforts may affect overall chances of success. However, it is unclear to what extent any of these circumstances applied to the 513 points in the fire-only model data in areas that had previously been treated (see Appendix B for maps of species points in previously burned and treated areas in the NGB). Additionally, the LTDL data do not necessarily include every treatment, and the approach used here does not disaggregate by treatment type. This means that some treatments included may have an effect on one species but no effect on another, which further research could clarify. Future research could also explore which wildfires and otherwise degraded areas actually receive treatments, which could partially

determine restoration outcomes. Ultimately, the inclusion of restoration treatments as a model covariate may be more important as a way to represent management realities than as a means of exploring the specific landscape-scale outcomes of restoration activities.

Spatial dependencies across grazing allotments

The use of multilevel CAR models with grazing allotments as a spatial random effect demonstrates spatial dependencies across neighboring units. This suggests that the likelihood of species presence or absence—particularly for sagebrush and juniper—will be most similar in adjacent allotments, a finding that connects to a complex and variable history of grazing management. Livestock grazing in the western United States dates back to the introduction of cattle and sheep in the 1800s, prior to the establishment of federal land management agencies. For decades, ranchers grazed cattle across the West with the tacit approval of the federal government, including on off-limits indigenous reservation lands, resulting in wide-scale degradation and desertification. In 1934, Congress passed the Taylor Grazing Act to directly respond to livestock-induced disturbances. The law sought to mitigate the degradation of rangelands by initiating a system of grazing allotments overseen by the Forest Service and Grazing Service (which later merged with the General Land Office to become what is now the BLM). This system remains in use today, and is managed on a state-by-state basis to give ranchers low-cost, fixed-term access to public lands for their operations while also preventing overgrazing. While the Taylor Grazing Act and subsequent federal legislation such as the Federal Land Policy and Management Act and Public Rangeland Improvement Act should serve as unifying guidance for rangeland management in theory, the majority of ground-level grazing policy implementation occurs at the level of local field offices (Wilkinson, 1992). Setting aside

the political, economic, and even ecological implications of this system, the inconsistency of implementation has resulted in a set management regimes whose effects on species distributions are difficult to track (but see the Public Employees for Environmental Responsibility's BLM Rangeland Health Status (2020) [interactive map](#), which provides an assessment of the level of degradation of grazing allotments on public lands). Between this history and the fact that livestock grazing is still the most prevalent type of land use in sagebrush ecosystems of the American West, grazing allotments remain critical to these landscapes' structure, function, and management (Chambers et al., 2017).

In other words, management and disturbance regimes in the NGB have long been, and continue to be, inextricably linked. Unsurprisingly, then, including grazing allotments as a spatial component of plant SDMs helps capture the effects of underlying management, which inherently vary by unit. This research is one of the first efforts to capture these spatial effects in a statistically rigorous way through the use of multilevel CAR models that highlight spatial dependencies across neighboring allotments. This novel implementation also directly responds to a call for the inclusion of cadastral data in anthropogenically-informed SDMs in sagebrush systems (Requena-Mullor et al., 2019).

The overall implication of the spatial dependency term, ρ , for each model is that neighboring allotments have similar juniper management approaches, somewhat less similar sagebrush management approaches, and relatively inconsistent (or perhaps simply ineffective) cheatgrass management practices. To some extent, these dependencies may be explained by the fact that a single manager may have a lease on multiple, potentially neighboring grazing allotments, and may therefore make similar decisions for these neighboring units. Other factors at play could be the influence of neighbor interactions (*i.e.*,

hearing how a neighboring allotment is managed) and fear of social sanctions (*i.e.* being viewed negatively by neighbors for not adhering to local management norms), which have been found to motivate invasive species control in other contexts (Niemi et al., 2018). This may be relevant to juniper management in particular, which is a longstanding vexation among ranchers for its rapid densification and substantial water usage. More generally, previous studies suggest that individual invasive management decisions are influenced by the collective nature and norms around weed control (Lubeck et al., 2019), which would potentially substantiate similarities in neighboring allotments. Spatial dependency may also simply reflect biophysical similarities across allotments, but this modeling effort does not specifically parse the various drivers of autocorrelation. However, correlative models like these may serve as a starting point for a mixed-methods social-ecological approach to understanding grazing management approaches and outcomes in sagebrush systems, potentially as a complement to ground-truthing interviews with land managers.

Limitations

As with any ecological-scale modeling effort, several key limitations and caveats accompanied this research. The first of these was in the LFRDB data that underpinned the model's response variable (species presence/absence). SDMs typically employ point-based response variables, making point data like those in the LFRDB ideal for species presences and absences. However, the LFRDB data carry certain drawbacks that may have limited their utility for this research. One of these drawbacks is the age of the LFRDB point data available in the NGB. While data through 2009 offers a useful retrospective understanding of the interactions among wildfire, restoration, and vegetation dynamics, it does little to clarify the current state of management practices, nor does it offer direction for decision-

making approaches. Additionally, the multi-source nature of the data points, along with agencies' prerogative to rescind contributed points in the 2016 Remap process (personal communication, USGS EROS User Services, October 4, 2021), also adds a general level of uncertainty.

The limitations of the LFRDB could be rectified through the use of different data for the species presence and absence points. In particular, remotely sensed data are becoming increasingly valuable—and functional—for use in SDMs, both as predictor and response variables (Randin et al., 2020; Schwager & Berg, 2021; Waltari et al., 2014; West et al., 2016). Alternatively, the BLM maintains the Assessment, Inventory, and Monitoring (AIM) database, which includes point observations of terrestrial data in the Terrestrial AIM Database (TerrADat). AIM data could supplement or supersede LANDFIRE in the absence of more regularly and thoroughly updated data collection in the LFRDB.

Beyond the response data from the LFRDB, the three SDMs required numerous decisions about predictor variable selection, data selection for those predictor variables, and cleaning of that data. Among these decisions was the choice to treat all subspecies of big sagebrush as a single species group and all species of juniper in the NGB as a single species. In part, the LFRDB's categorization of sagebrush and juniper as, depending on the year, simply "*Artemisia tridentata*" (no subspecies) or "*Juniperus*" (no species), drove this decision, since it prevented further specification for certain years. Additionally, relatively recent and, at times, debated, identification of differentiable juniper species (see Adams, 2019), as well as known issues with in-field identification of both big sagebrush subspecies and juniper species prevented certainty in further sub-categorization (Terry, 2010; Terry et al., 2000). While these groupings largely exhibited similarities in group and sub-group

means and errors (see Appendix A), the trade-off was an inability to capture how big sagebrush sub-species and juniper species distributionally respond to different disturbance, restoration, and long-term management influences.

Another decision was using NLCD sagebrush and herbaceous cover rasters and a juniper biomass (Filippelli et al., 2020) raster for creating spatially explicit model predictions. While these were imperfect replacements, they obviated the need for creating species co-occurrence rasters via kriging, which would have led to a situation in which kriged co-occurrence layers—themselves model outputs—would have been used in the overall spatial predictions of my SDMs. The rasters I selected provided plausible spatial locations for each co-occurring species while avoiding this circularity.

These models also fail to capture the potential influences of other co-occurring native (e.g., Great Basin wild rye [*Leymus cinereus*], Idaho fescue [*Festuca idahoensis*], bluebunch wheatgrass [*Pseudoroegneria spicata*]) and invasive plant species (e.g., medusahead rye [*Taeniatherum caput-medusae* (L.) Nevski], ventenata (*Ventenata dubia*). While the focus here was on the disturbance, distribution, and restoration dynamics of representative examples of ecologically and management-relevant plant species, such an emphasis may come at the expense of illuminating other key dynamics and ecological realities. In particular, it does little to illuminate the roles of other invasive annual grasses that contribute to the grass-fire cycle and species competition. Recently, there have been calls for research that more fully addresses the disturbance dynamics and management outcomes related to other long-standing and emerging invasive annual grasses across the American West (Aslan & Dickson, 2020; Schroeder et al., 2022). Still other research has suggested that certain parts of the Great Basin have become invasive annual grasslands that

must be managed as a new type of persistent ecosystem, rather than through the more traditional lens of these annual grasses as invasions of other ecosystem types (Davies et al., 2021). There have also been calls for treating juniper dynamics as expansion rather than encroachment—which is a more value-laden proposition—particularly considering they are native to the NGB (BLM staff, personal communication, June 2021). This aligns with another recent call to frame distributional movements of plants across a landscape as adaptations, including to climate change, rather than “invasions” (Urban, 2020). Considering juniper and cheatgrass from these perspectives would shift the paradigm underlying the use of SDMs for understanding restoration treatment efficacy in particular.

Given the primacy of wildfire in my research objectives, maximum VPD was a logical climatic predictor since it has implications for vegetation survival, distribution, and recruitment (Grossiord et al., 2020; Littlefield et al., 2020; Mahood & Balch, 2019), the role of vegetation as fuel, and fire behavior more broadly (Abatzoglou & Williams, 2016). This decision also allowed the models to focus on the specific effects of fire histories and restoration treatments, with climate and topography serving more as baseline context. However, VPD captures a narrow swath of the broader climatic realities of species’ environmental niches; precipitation, particularly of the antecedent year, may have added granularity to the results. The effects of minimum temperature on sagebrush distributions also remain largely unexplored, although current research suggests that sufficiently high minimum temperature is a determinant of sagebrush seedling survival, and also varies by subspecies and seasonality (Brabec et al., 2017; Lazarus et al., 2019).

Although a primary objective of this research was to disentangle the roles of different fire characteristics in species distributions, the models ultimately relied on a

relatively small number of fire attributes to represent wildfire histories. Fire severity, for example, which has been altered by vegetation shift and can dictate abundance and proximity of post-fire seed sources, could have supplemented number of fires, fire size, and time since fire as a covariate (Chambers et al., 2017; Littlefield et al., 2020). This may also have accounted for some of the remaining unexplained variance in the fire-only models. In future iterations of this modeling, a more remote sensing-driven approach would open new possibilities for fire data from MODIS or other fire-related remotely sensed data that could expand the characteristics considered.

Finally, BLM grazing allotments were selected as the areal unit representing spatial random effects to reflect the reality of Western land management. However, choosing a different areal unit such as pastures, counties, census tracts, or even states, could have altered model results and interpretation. Additionally, the models do not point to benefits or shortcomings of any given allotment or associated management strategy.

Future Directions

There are several potential extensions of this work that would further improve its relevance to landscape-scale management of sagebrush ecosystems in the NGB. The first would be to update the data such that the models would reflect species distributions up to the present, rather than stopping at 2009. To achieve this, as aforementioned, might require the use of remotely sensed data or other ground-level field observations, such as BLM TerrADat records.

Another obvious pathway for this research would be to explicitly incorporate future climate projections in order to help managers anticipate the future outcomes of management-disturbance-vegetation dynamics. While climate change will directly drive

future species distributions to some extent, the concomitant changes in species' interactions and mechanisms, as well as responses to shifting disturbance regimes, might actually be the most relevant climate-related processes to capture. This would both increase ecological applicability (Guisan et al., 2013; Sinclair et al., 2010) and avoid issues with predicting species' likely "idiosyncratic" responses to non-analog climates (Fitzpatrick & Hargrove, 2009; Lewis, 2006). Additionally, research has suggested that, at least for big sagebrush, wildfire and invasive annual grasses may play a greater role in future species distributions and survival than the direct effects of a changing climate (Schlaepfer et al., 2021). This proposed role of future biotic and abiotic disturbance regimes, combined with the evident strength of species co-occurrence as a predictor in this work, points to a need for more research modeling the future relationships among sagebrush, juniper, and cheatgrass in the context of multiple, overlapping disturbances that capture unexpected, nonlinear effects and interactions.

Future work might also include a more finely-resolved temporal component that could track changes in predicted distributions throughout time, rather than presenting a prediction for a single, historically-informed time step (*e.g.*, Schliep et al., 2018). Theoretically, this might allow for better identification of the trajectories of overlapping disturbance and climate change processes, instead of assuming linear relationships between climate change and species distribution patterns (Austin, 2007; Elith et al., 2010; Hughes et al., 2019; Pearson & Dawson, 2003). Alternatively or additionally, future work could directly consider mechanistic components of species distributions, including, among other mechanisms, dispersal, post-fire regeneration, and other disturbance response processes (*sensu* Case & Lawler, 2017). This would move the work away from its current correlative

structure, and could improve overall model performance under changing environmental conditions (Buckley et al., 2010; Urban et al., 2016; Zurell et al., 2009).

Critically, any expansion on this research should involve iterative communication with BLM staff—as well as other agency staff, private land managers, and Indigenous peoples—involved in management decisions related to sagebrush, juniper, cheatgrass, wildfire, and/or restoration. These interactions could directly improve the performance and relevance of future modeling efforts (Guisan et al., 2013). A collaborative approach could also offer predictive insights that support vegetation and restoration monitoring efforts, particularly in the Botany and Emergency Stabilization and Rehabilitation (ESR) departments of the BLM. In concert with the aforementioned incorporation of future climate projections, these efforts could also support adaptive management decision-making processes on the ground by highlighting plausible ecological transitions.

CONCLUSIONS

The conditional autoregressive species distribution models of sagebrush, juniper, and cheatgrass used here point to three key management-relevant takeaways: 1) Species distributions depend not only on abiotic and biophysical factors, but also on species co-occurrence, which has the strongest effect by far on occurrence; 2) Fire characteristics beyond fire occurrence meaningfully influence sagebrush steppe species distributions; 3) While restoration treatments have generally had some success with sagebrush and juniper, there is little evidence of landscape-scale efficacy of post-fire restoration of juniper, sagebrush, and cheatgrass; and 4) Drought conditions—here represented by maximum VPD—are a major driver of distributions even within the context of other disturbance and management factors at play.

More broadly, these models collectively confirm that both biotic (*e.g.*, invasive and quasi-invasive vegetation interactions) and abiotic disturbances (*e.g.*, climate and wildfire) are linked to the distributions of plant species in the sagebrush steppe of the NGB. At the same time, direct human interventions, both in the form of restoration treatments and longer-term management regimes via grazing allotments, have bearing on ecological outcomes, and should be accounted for in any realistic SDMs. Together, these findings highlight ecological realities in light of inextricably linked, long-term disturbance, vegetation, and management interactions. In particular, explicating the relative roles of wildfire, biological invasions, and restoration on overall species distributions helps to define the space of plausible ecological futures. Doing so through a Bayesian framework

captures the uncertainties inherent in these disturbance-management-ecology relationships and dynamics and thus presents the full possibility space of their outcomes at a landscape scale. Notably, this work also points to the inherent spatial dependencies at play across grazing allotments in the grazing-dominated NGB. The use of multilevel areal unit modeling to address an ecological problem has broader promise in ecology and human-environment systems science, and may help to contextualize the disturbance-management confluence in other social-ecological landscapes.

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APPENDIX A

Supplemental Information

Historical Wildfire Trajectories in the NGB

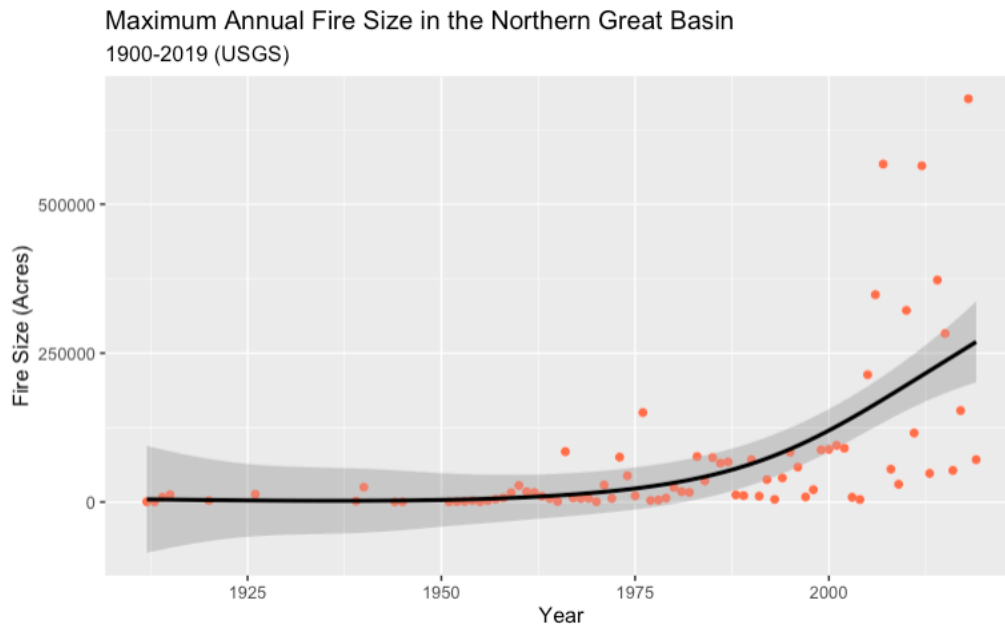


Figure A.1.1. Historical trend of maximum fire size in the NGB. The biggest fires have gotten bigger since the early 20th century, indicating that extreme fires are becoming increasingly extreme.

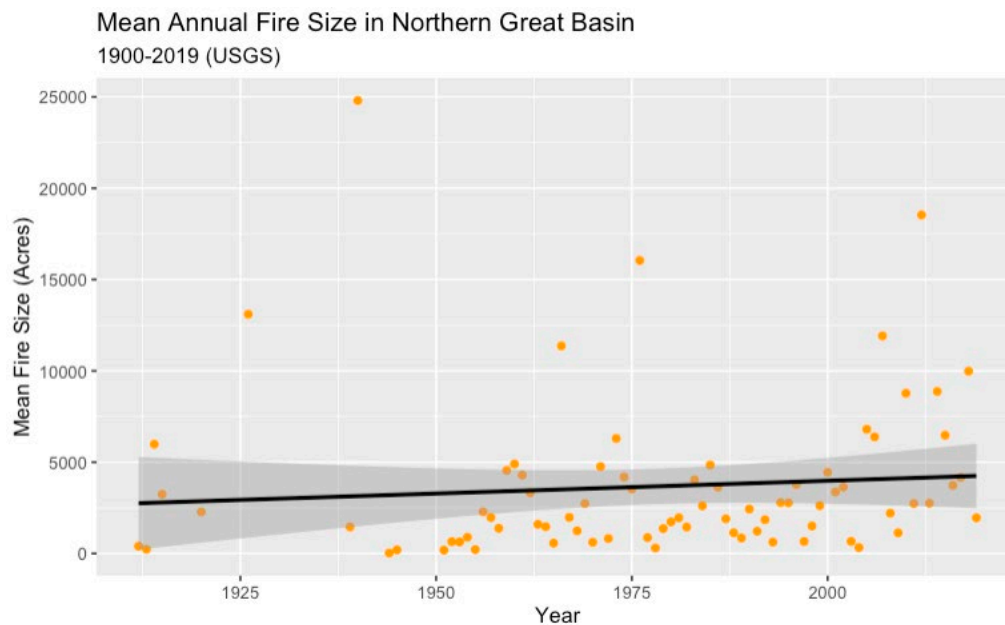


Figure A.1.1. Historical trend of mean fire size in the NGB. Average fire size has increased in the NGB since the start of the 20th century.

Fire Characteristics by Species

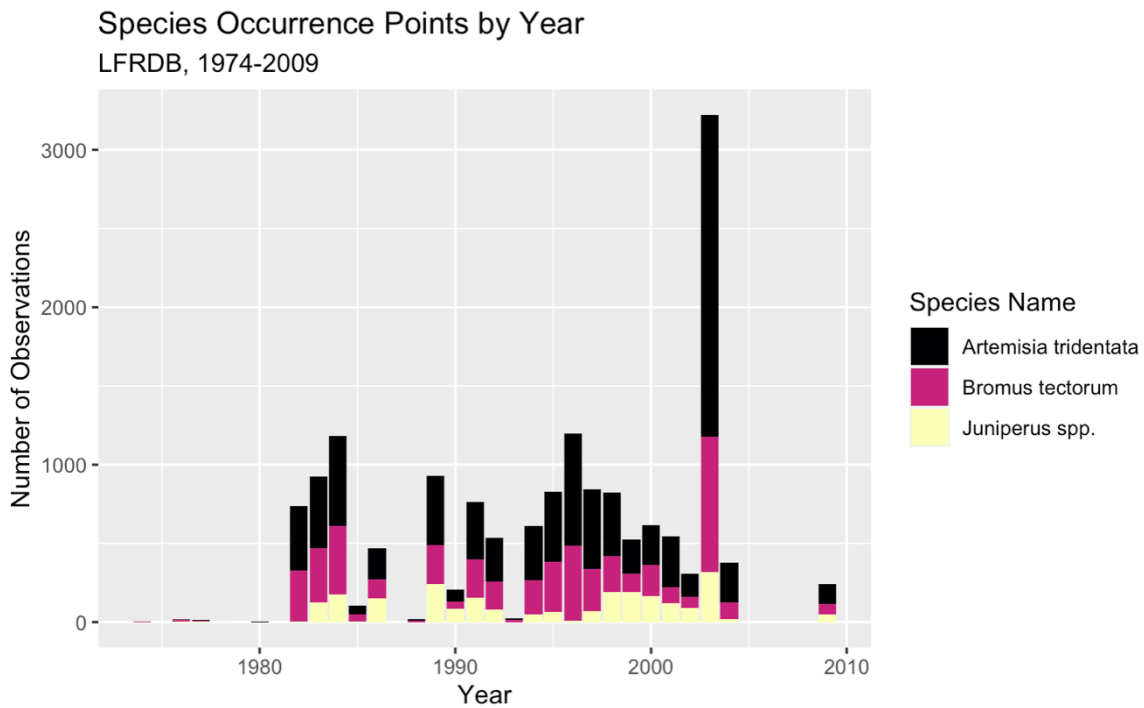


Figure A.2.1. Number of species presence points collected by year in the NGB between 1974 (the first year of LFRDB point collection in the NGB) to 2009 (the most recent collection year in the NGB for species of interest).

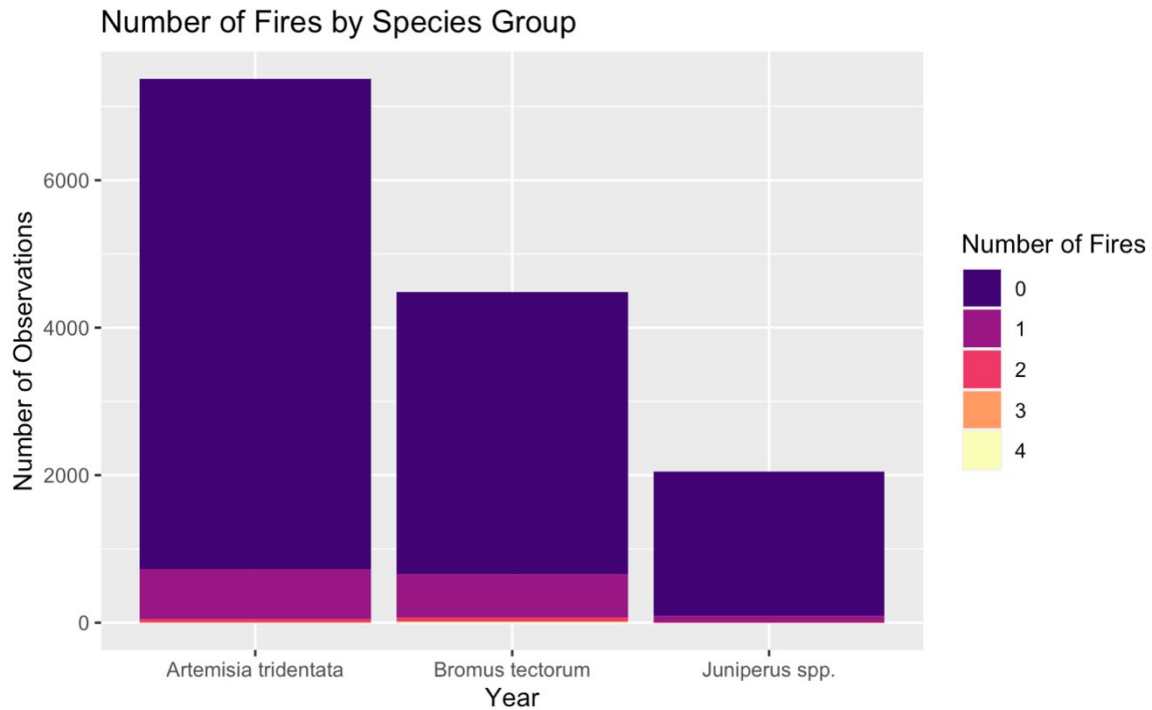


Figure A.2.2. Number of historical fires that occurred at each species presence point between 1912 and 2009 in the NGB.

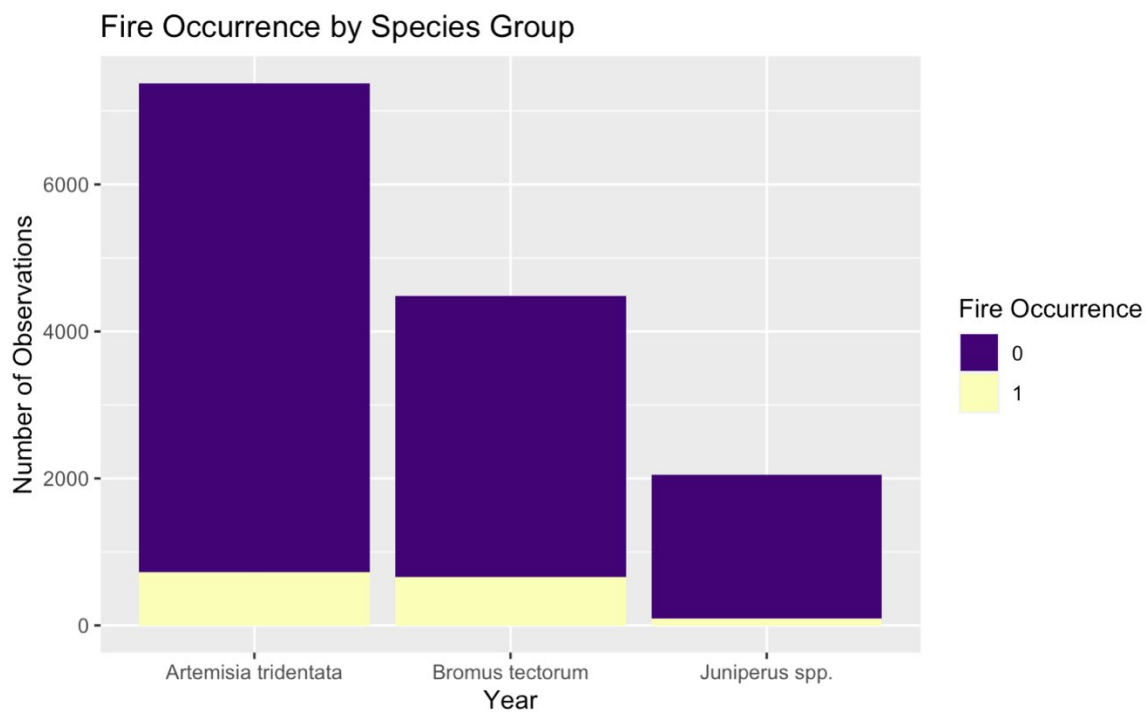


Figure A.2.3. Proportion of each species presence points that experienced at least one fire prior to LFRDB observation.

Group and Individual Species Means and Errors for Elevation and Exposure

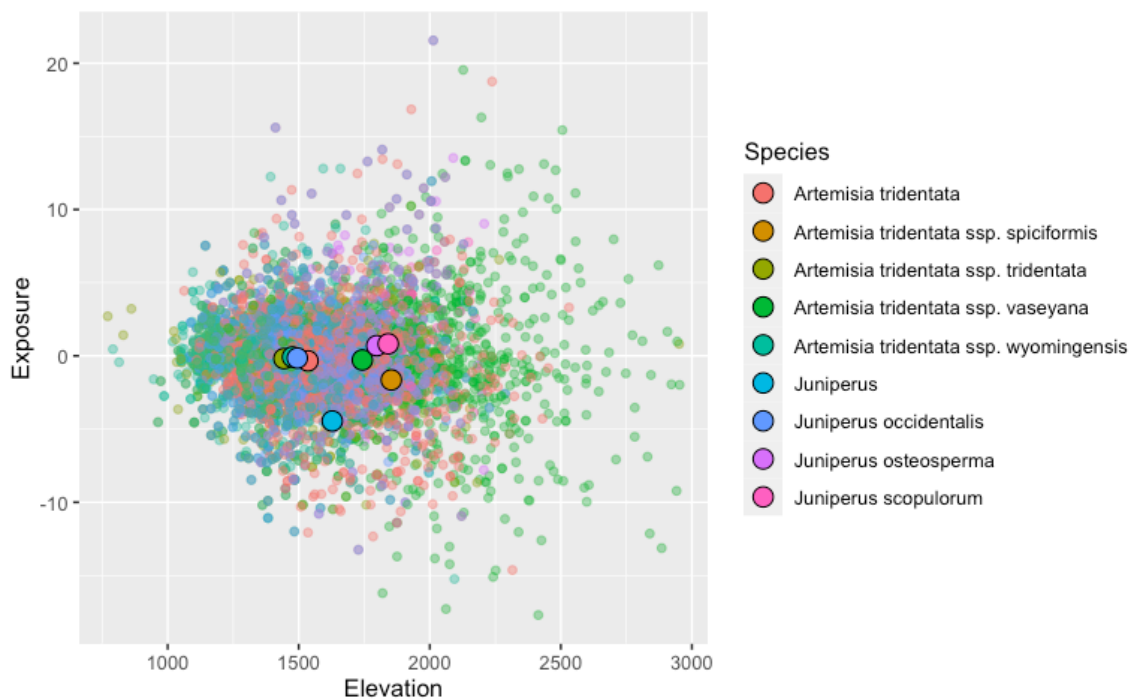


Figure A.3.1. Individual presence point values and group means for elevation (in meters) and site exposure for sagebrush and juniper, respectively broken into subspecies and species.

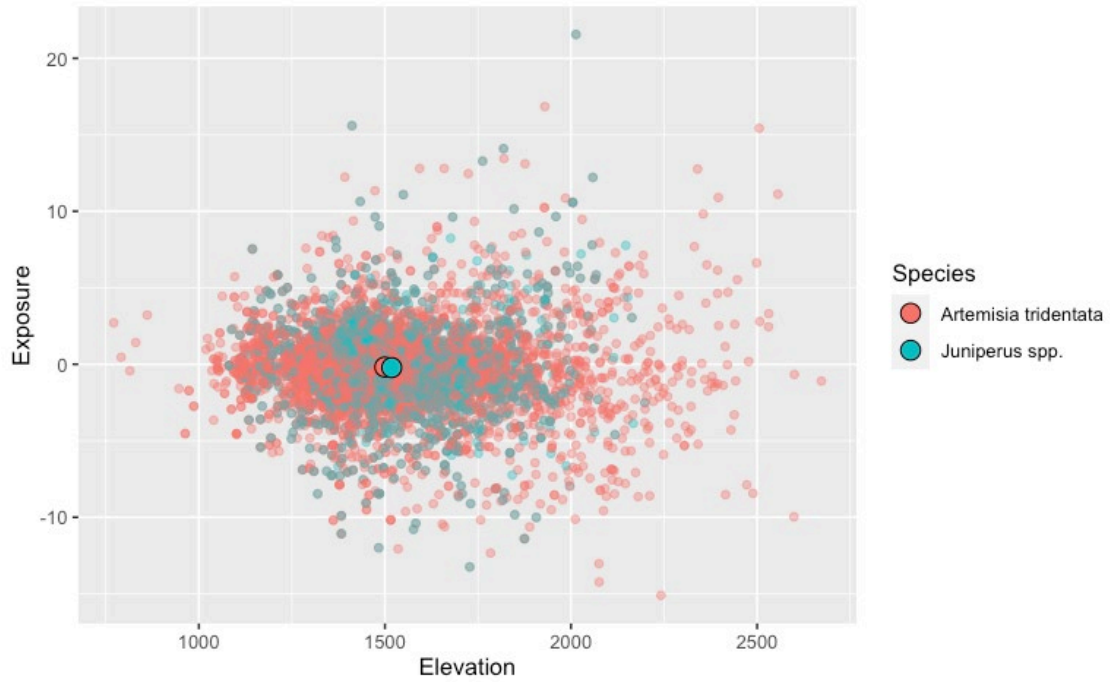


Figure A.3.2. Individual presence point values and group means for elevation (in meters) and site exposure for sagebrush and juniper.

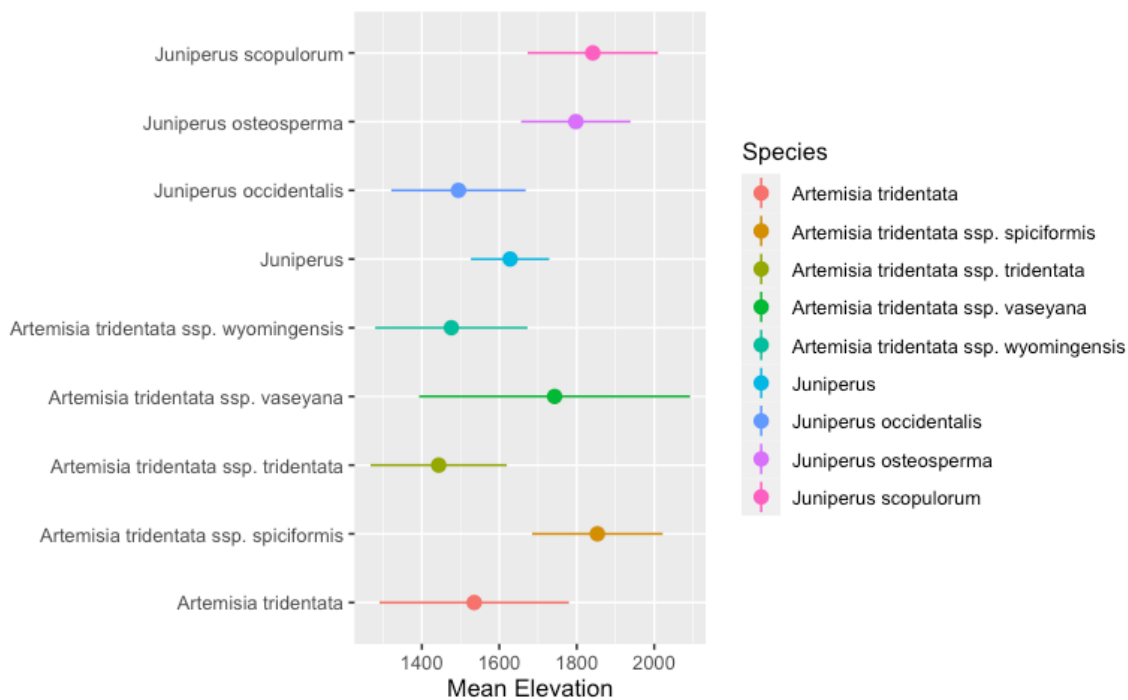


Figure A.3.3. Group elevation means and standard errors for all sagebrush subspecies and juniper species points in the NGB.

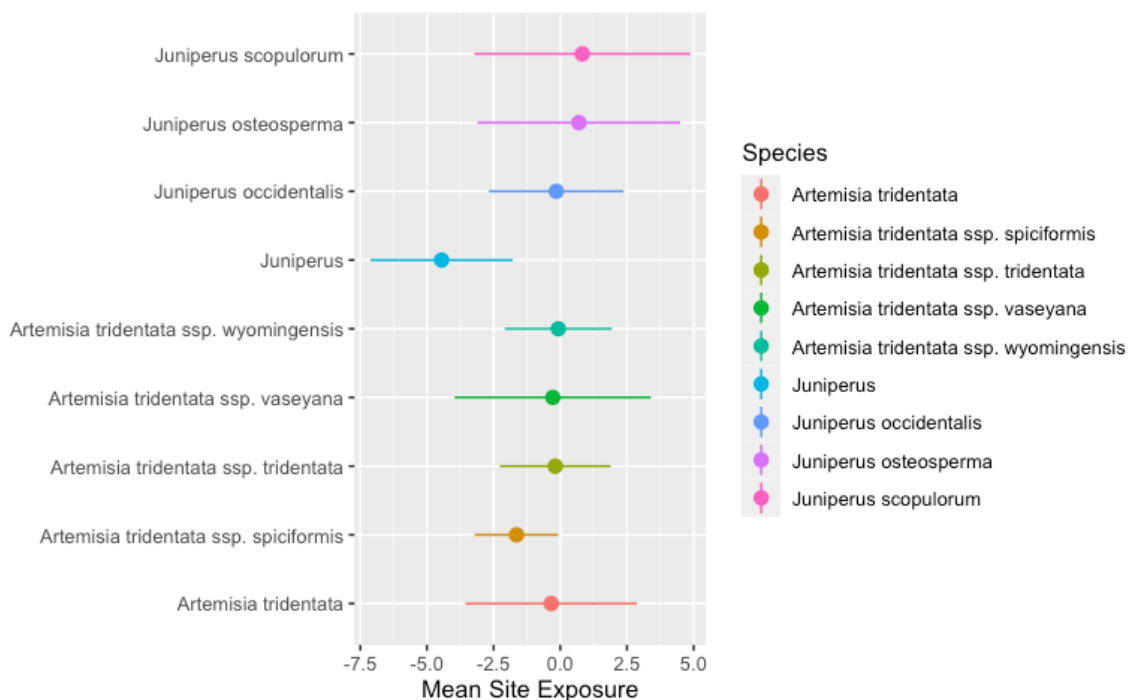
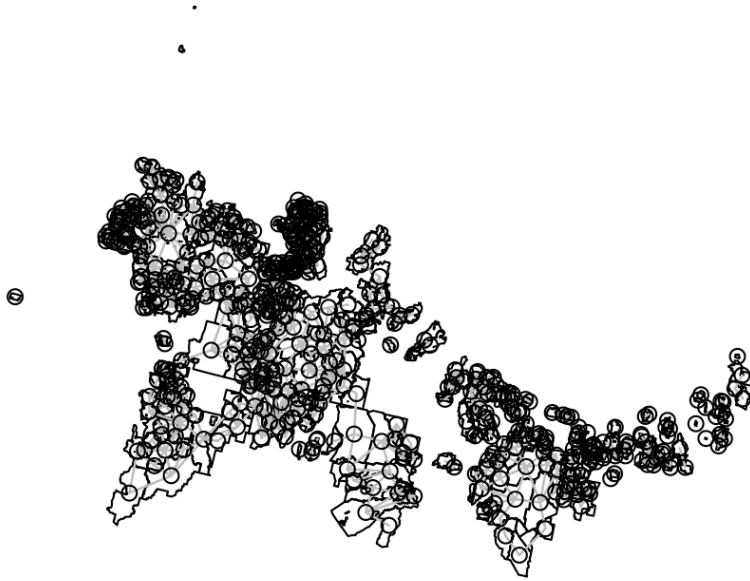


Figure A.3.4. Group site exposure index means and standard errors for all sagebrush subspecies and juniper species points in the NGB.

Adjacency Matrix Network Maps

Map A.1.1. Network of neighboring grazing allotments used to determine values for adjacency matrix in full CAR models (for burned and unburned areas). Spatial network construction relied on the R packages “sdpep” (Bivand & Wong, 2018), “igraph” (Csardi & Nepusz, 2006), and “spatialreg” (Bivand et al., 2013).



Map A.1.2. Network of neighboring grazing allotments used to determine values for adjacency matrix in fire-only CAR models. Spatial network construction relied on the R packages “sdpep” (Bivand & Wong, 2018), “igraph” (Csardi & Nepusz, 2006), and “spatialreg” (Bivand et al., 2013).

Conditional effects plots for full CAR models

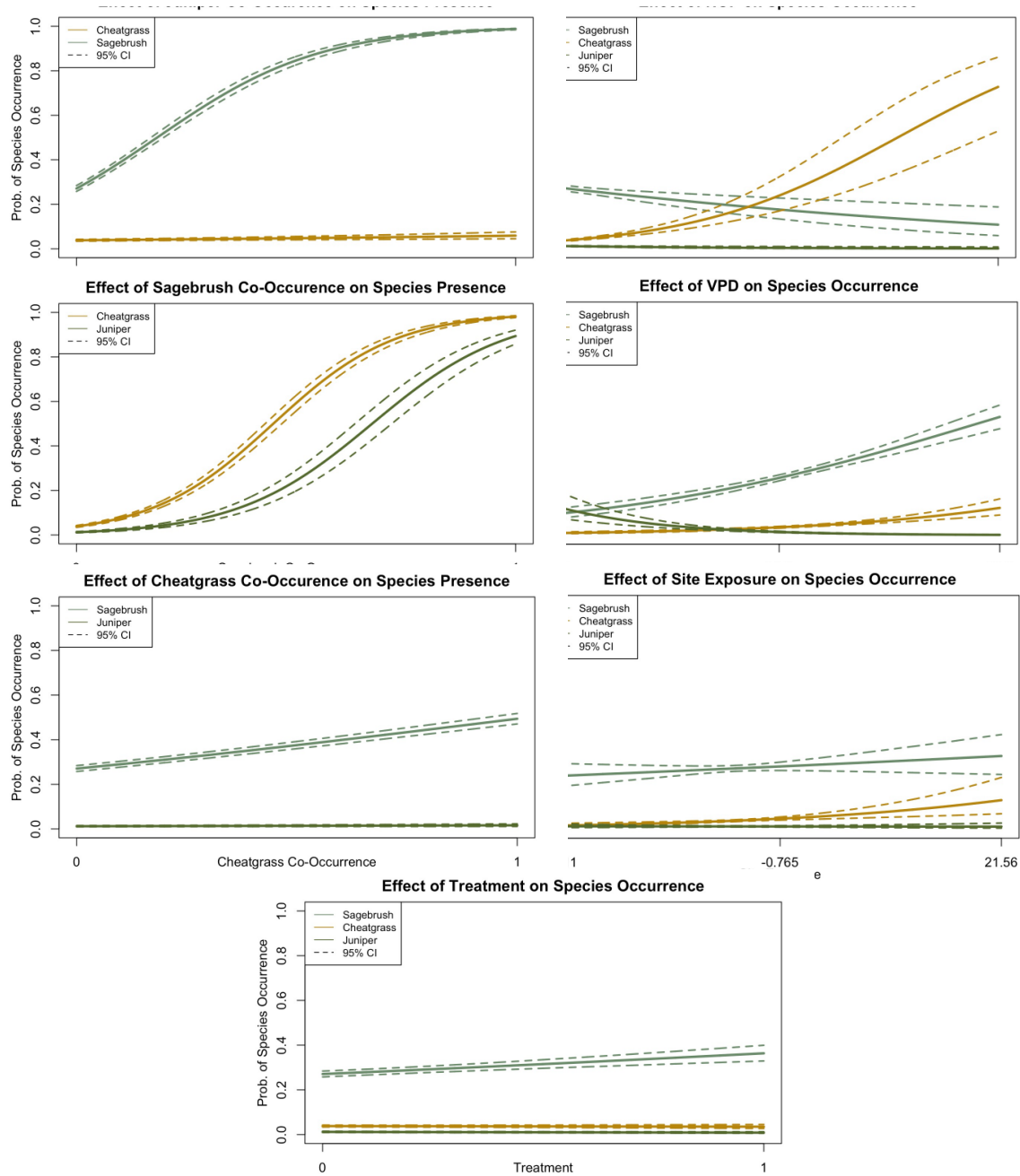


Figure A.4. Counterfactual plots for the effects of each covariate on sagebrush, juniper, and cheatgrass. Clockwise from top left: juniper co-occurrence, number of fires, maximum VPD, site exposure, restoration treatment, cheatgrass co-occurrence, and sagebrush co-occurrence. N.B. Not all predictor variables had interpretable effects in all models (see Results).

Rho Density Plots—Fire-Only Models

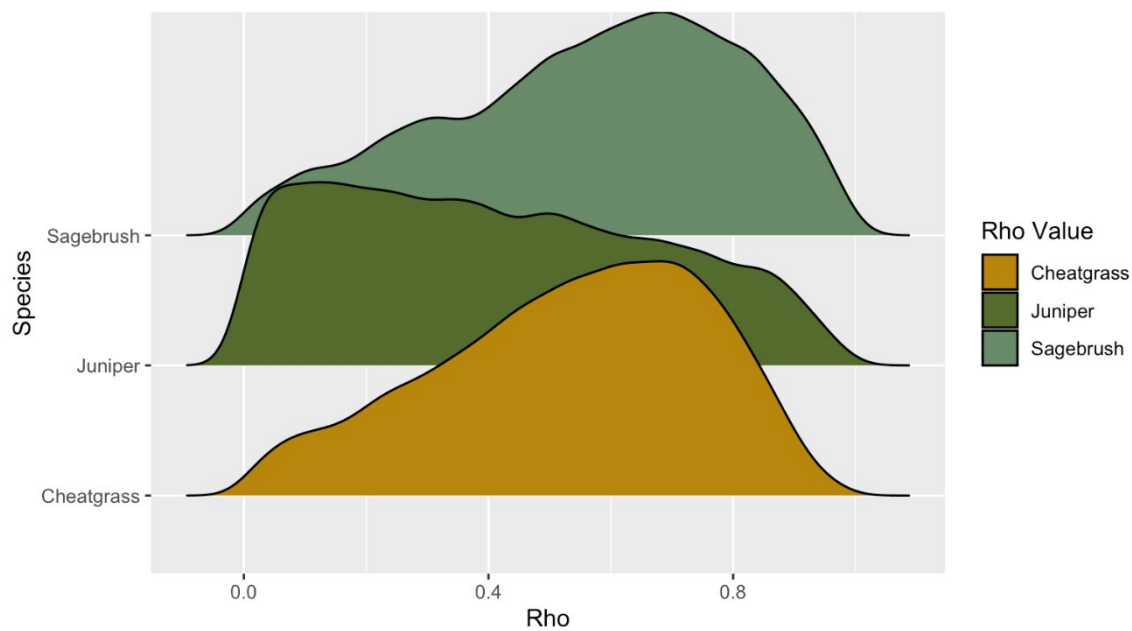
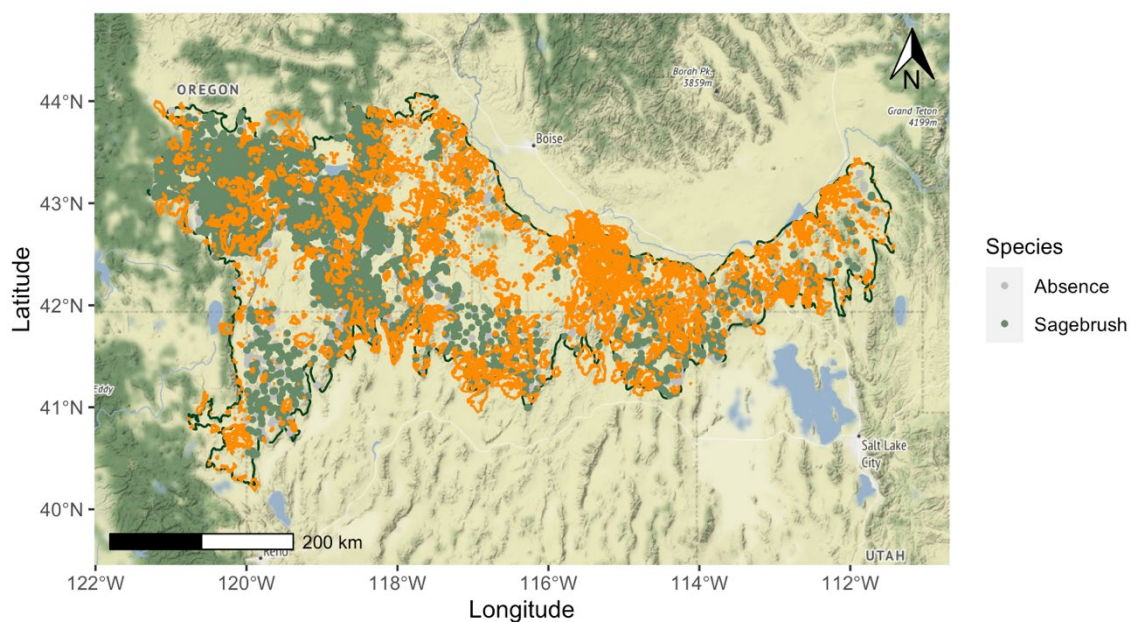


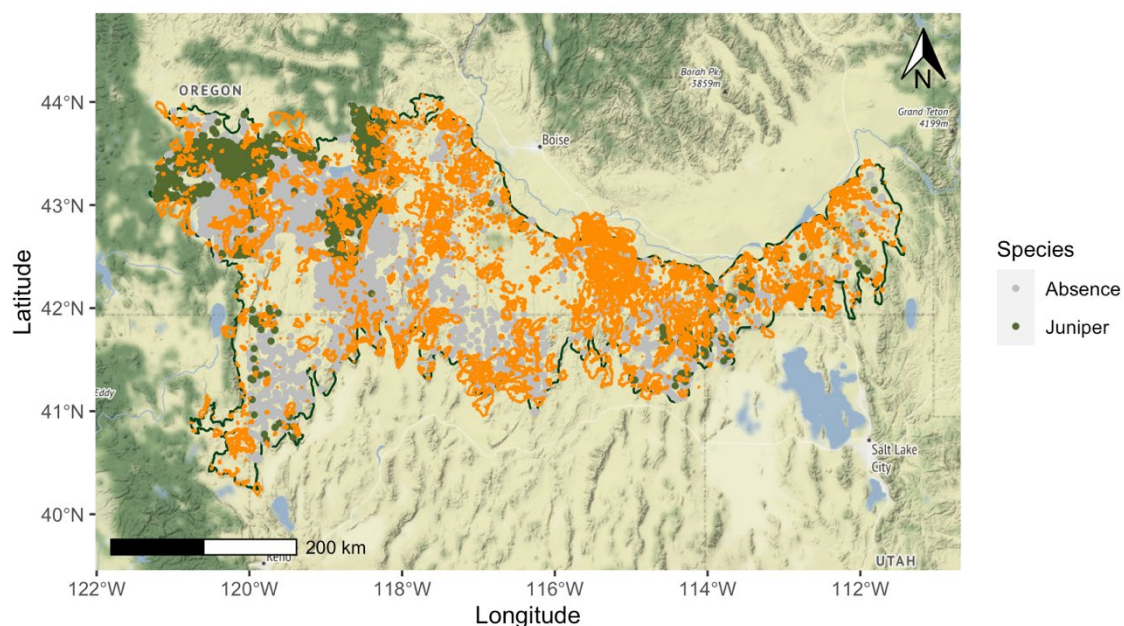
Figure A.5. Density plots of rho values from the posterior of the fire-only CAR SDM for each species of interest. Rho values account for spatial dependency, with higher values indicating more spatial dependency of species across neighboring allotments.

APPENDIX B
Supplemental Maps

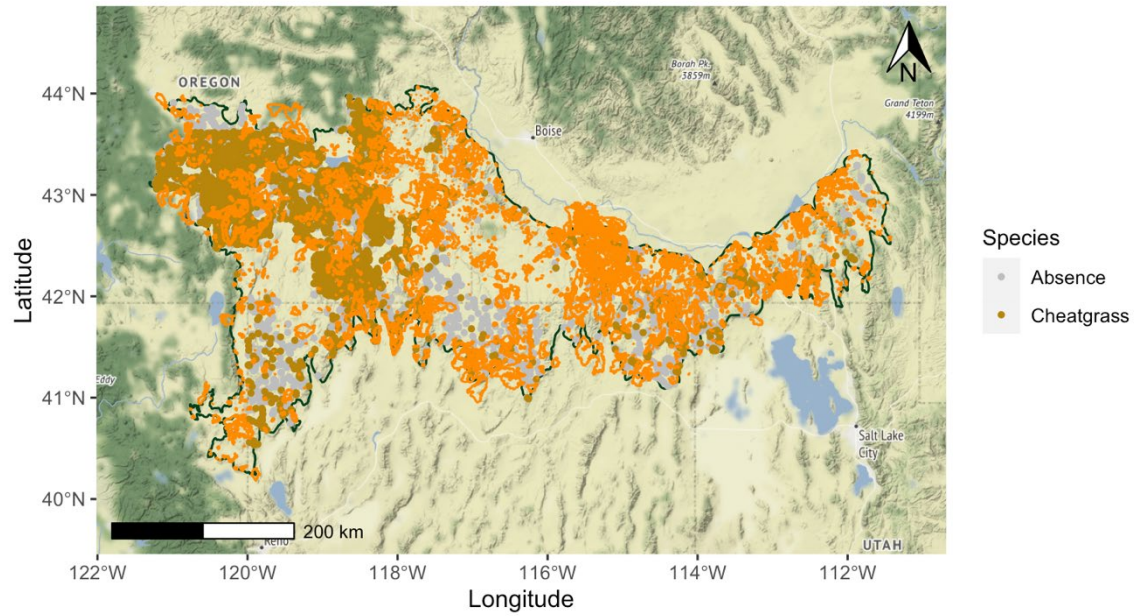
Species presence and absence points in areas in the NGB with historical fire



Map B.1.1. Figure B.1.3. Species presence and absence points for full sagebrush CAR model in the context of all NGB historical wildfires between 1912 and 2009. Orange polygons indicate wildfire boundaries. Data: EPA, USGS, LFRDB, Stamen.

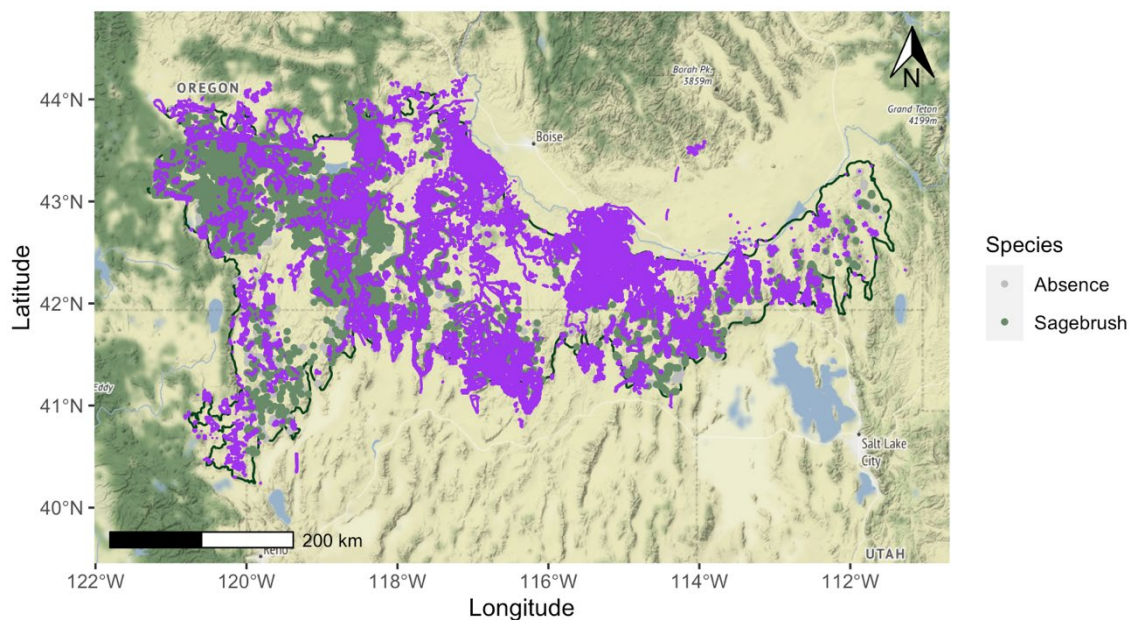


Map B.1.2. Species presence and absence points for full juniper CAR model in the context of all NGB historical wildfires between 1912 and 2009. Orange polygons indicate wildfire boundaries. Data: EPA, USGS, LFRDB, Stamen.

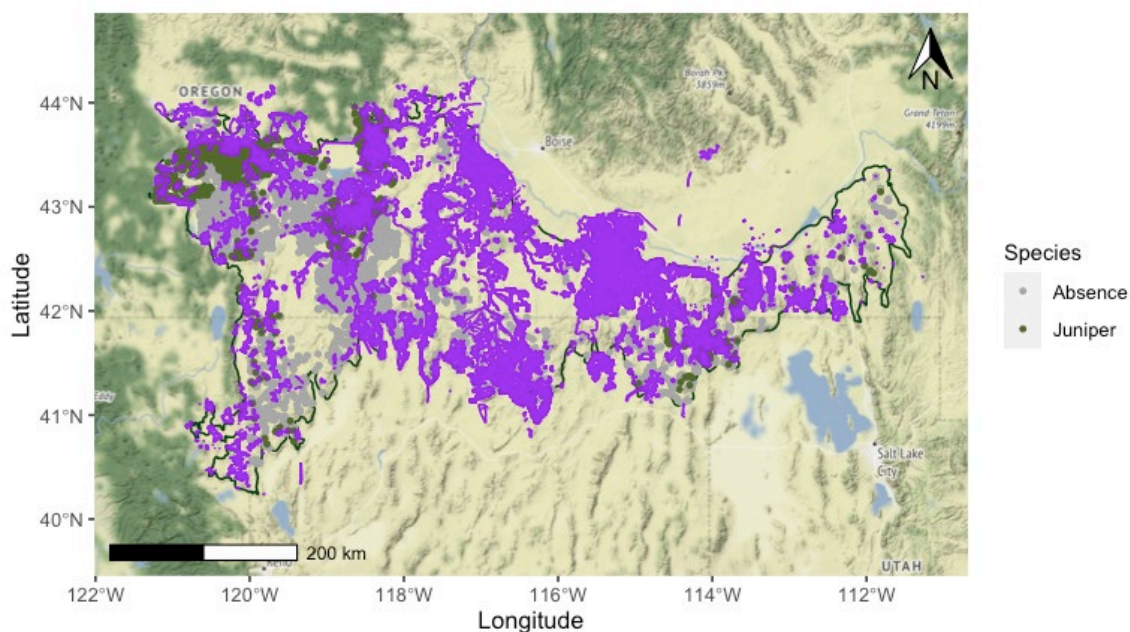


Map B.1.3. Species presence and absence points for full cheatgrass CAR model in the context of all NGB historical wildfires between 1912 and 2009. Orange polygons indicate wildfire boundaries. Data: EPA, USGS, LFRDB, Stamen.

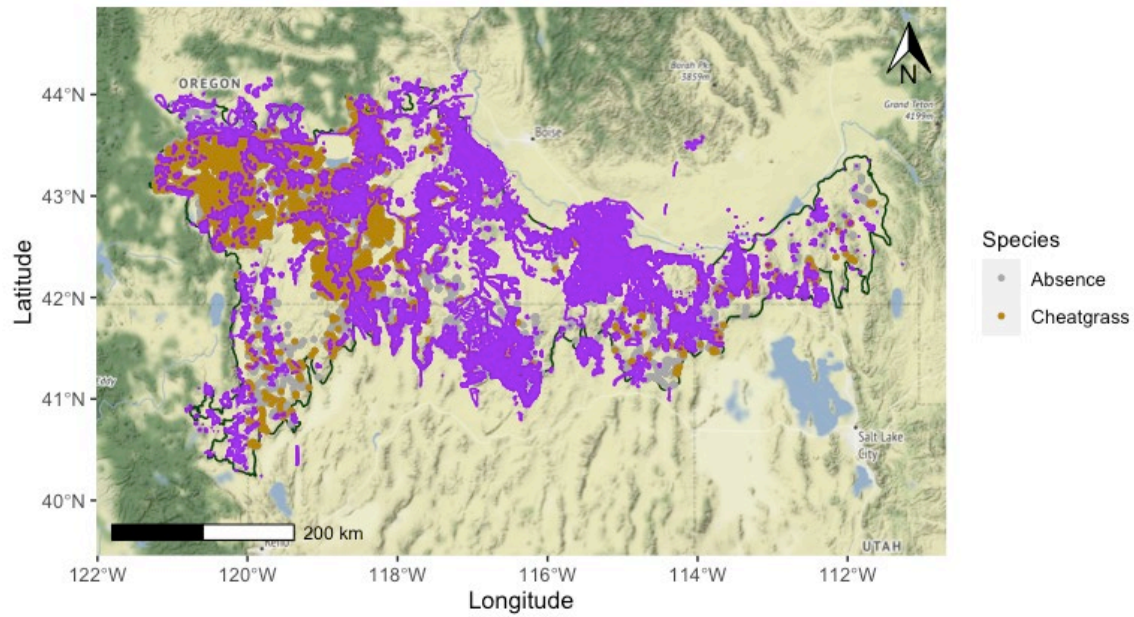
Species presence and absence points in previously treated parts of the NGB



Map B.2.1. Species presence and absence points for full sagebrush CAR model in the context of restoration treatments conducted in the NGB prior to 2009. Purple polygons indicate restoration areas. Data: EPA, LTDL, LFRDB, Stamen.



Map B.2.2. Species presence and absence points for full juniper CAR model in the context of all restoration treatments conducted in the NGB prior to 2009. Purple polygons indicate restoration areas. Data: EPA, LTDL, LFRDB, Stamen.



Map B.2.3. Species presence and absence points for cheatgrass CAR model in the context of all restoration treatments conducted in the NGB prior to 2009. Purple polygons indicate restoration areas. Data: EPA, LTDL, LFRDB, Stamen.