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journal homepage: <http://www.elsevier.com/locate/rama>Differential Species Responses to Aspects of Resistance to Invasion in Two Columbia Plateau — Protected Areas[☆]Daniel M. Esposito^a, Thomas J. Rodhouse^b, Ricardo Mata-González^c, Matthew Hovland^{c,*}^a USDA — Natural Resource Conservation Service, Central Point, OR 97502, USA^b Upper Columbia Basin Network, National Park Service, OSU Cascades, Bend, OR 97702, USA^c Department of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR 97330, USA

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ABSTRACT

Protected-area sagebrush steppe ecosystems are few in number and increasingly important to the North American conservation network as sagebrush steppe faces growing threats from land use, climate change, and invasive species. We analyzed the distribution and abundance of native perennial and invasive annual plants to better understand patterns of plant invasion within two protected areas: John Day Fossil Beds National Monument (JODA), located in central Oregon, and Craters of the Moon National Monument and Preserve (CRMO), located in south-east Idaho. We used multivariate analysis to examine vegetation monitoring datasets and illuminate geographic variation in plant cover along gradients of well-known aspects of resistance to plant invasion (elevation, exposure [slope and aspect], precipitation and proximity to disturbance). Topographically mediated resistance to invasion appeared to manifest in the park with greater topographic variability (JODA), while increased elevation was more strongly associated with resistant sites in the park, which spanned a greater elevational gradient (CRMO). Factors that may mitigate moisture-mediated resistance also differed between sites. Slope and aspect were factors of apparent resistance for bunchgrass communities in JODA, while high crop year precipitation appeared to benefit medusahead (*Taeniatherum caput-medusae* [L.] Nevski) and the weedy native subshrub broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby) over bunchgrasses and Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young). Increased elevation and distance to disturbed areas were the most important factors of resistance in forb-rich communities at CRMO, with the invasive annuals cheatgrass (*Bromus tectorum* L.), tumbled mustard (*Sisymbrium altissimum* L.), and *Descurainia* spp. Webb & Bethel. invading in low elevations and in close proximity to roads or agricultural fields. Such complexity underscores the idiosyncratic nature of the manifestation of resistance and the need for place-based empirical studies to provide information for guiding protected-area management.

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Introduction

Intense and persistent invasion of rangelands by exotic plant species has caused shifts in ecologically stable states (D'Antonio and Vitousek, 1992; DiTomaso 2000) and in turn encouraged management to shift away from concepts of managing for static systems (Walker, 1993; Stringham et al., 2003), toward concepts of managing for resistance to invasion and resilience to disturbance (Gunderson, 2000; Walker et

al., 2004; Briske et al., 2008). Important in the operationalization of these concepts are decision tools that identify resistant and invasion-prone areas, assisting in predicting future conditions and prioritizing sites for protection and restoration (Davies et al., 2010; Rodhouse et al., 2014; Maestas et al., 2016). Process-based resistance distribution mapping may be preferable over more traditional species distribution maps (Tulloch et al., 2016), and is created by identifying links between plant species cover and aspects of resistance to exotic plant invasion, either in situ (e.g., Rodhouse et al., 2014) or a priori (e.g., Maestas et al., 2016). Although both methods may be limited by the spatial extent or resolution of available datasets, maps based on a priori knowledge exchange specificity in management guidance for broad applicability. For instance, abiotic factors providing greater moisture availability in semi-arid systems are currently considered proximal aspects of resistance (Miller et al., 2013; Chambers et al., 2014a; Germino et al., 2018). However, individual species may differ in their responses to greater moisture availability due to physiological adaptations and requirements or

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altered biotic interactions including mycorrhizal colonization, herbivory, and plant competition (Esch et al., 2018; Walter, 2018). Therefore, sites labeled as resistant to exotic plant invasion may be harboring and resisting only select plant species or under certain levels of environmental stress (e.g., drought, grazing, fire).

The efficacy of decision tools such as resistance maps is reliant, in part, on the extent and resolution of both plant community and environmental data (Wilson et al., 2005). Although resistance models created solely from field data may yield the greatest accuracy (Barnard et al., 2019), acquiring environmental field data such as soil texture and microclimate can be tedious and difficult to apply at a landscape management scale in systems with heterogeneous soils (Kabat et al., 1997) and topography (Rodhouse et al., 2017). Because field data—based models using digital data as predictor variables may have similar predictive value as full field data models (Barnard et al., 2019), it may be more efficient to acquire topographic metrics (slope, aspect, elevation) digitally (e.g., GIS layers) due to the increasing reliability, resolution, and availability of digital elevation models (Moudrý et al., 2018). This is particularly meaningful to resistance distribution mapping, as slope and aspect are the main components of common solar-heat indices (along with latitude and elevation) (Pierce et al., 2005; McCune, 2009) and have been implicated as major drivers of plant community structure in grassland systems (Rodhouse et al., 2014; Srinivasan et al., 2015; Bernards and Morris, 2017). Increases in elevation may also correlate with reduced invasive plant cover (Averett et al., 2016; Bangert and Huntly, 2010), in part due to decreased temperatures (i.e., adiabatic cooling rate). However, as elevation increases often coincide with increased distance from disturbance (e.g., agriculture, roads), high-elevation sites may only appear to benefit from climate-mediated resistance and instead may harbor intact native plant communities due to a lack of invasive plant propagule pressure (Pauchard and Alaback, 2004).

The sagebrush steppe biome in western North America has been heavily degraded by a host of anthropogenic impacts including heavy livestock grazing, weed invasion, altered fire and disturbance regimes, energy development, and climate change (Brooks et al., 2004; Davies et al., 2011). The biome is one of the most threatened ecosystem types in the United States (Noss et al., 1995) and is underrepresented within the network of American parks and protected areas (Caicco et al., 1995; Noss et al., 1995; Stoms et al., 1998; Aycrigg et al., 2013). National parks in the Columbia Plateau represent the majority of the biome managed for nonextractive purposes (Stoms et al., 1998). Although these areas are intended and assumed to provide for more intact ecosystems than surrounding mixed-use landscapes (Fancy et al., 2009; Rodhouse et al., 2016), it is not clear whether this is being effectively accomplished. In general, there is an increasing recognition that the performance of existing global protected-area networks to achieve biodiversity goals is uncertain (e.g., Gaston et al., 2008) and that the principles of restoring impaired systems to historical levels of “naturalness” are no longer appropriate for guiding their management (Cole et al., 2008; Hobbs et al., 2010). Rather, because protected areas are also experiencing rapid rates of environmental change from historical legacy and the outside-in forces of climate change and biological invasion, a more dynamic approach using concepts like ecological integrity and resilience has been advocated (Hobbs et al., 2010). However, as salient as these contemporary concepts are for protected-area management, there is a tremendous need for empirical studies to help translate and guide the integration of emerging theory and concepts into tangible management practice at appropriate scales.

As climatic shifts are predicted to further alter abiotic drivers of plant community composition (e.g., water availability) in North American rangelands (Polley et al., 2013), understanding the abiotic factors contributing to invasive species distribution becomes more imperative. Specifically, understanding the variability in the influence of multiple factors contributing to local moisture availability (e.g., slope, aspect, elevation, precipitation) on individual plant species (both native and

invasive) would allow researchers and managers to more accurately predict species distributions and improve applicability of resistance mapping based on a priori knowledge (i.e., concept transferability). A deeper understanding of moisture-mediated resistance to invasion is especially relevant in sagebrush steppe, which is a broad-ranging, moisture-limited biome that spans considerable variation in climate and soils (Holechek et al., 2001). Researchers have attempted to categorize the resistance levels of multiple sagebrush steppe plant communities (Miller et al., 2013; Chambers et al., 2014b), but management guidance is largely aimed at supporting the most susceptible regions, such as those dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) (e.g., Pyke et al., 2014; Reed-Dustin et al., 2016; Swanson et al., 2018) and commonly focuses on resistance to a single invasive plant species—cheatgrass (*Bromus tectorum* L.) (e.g., Chambers et al., 2007, 2014a, 2016; Roundy et al., 2018). Although research focusing on the most common issues and areas affected may yield the greatest management impacts, the efficacy of management outside of research areas may suffer from a lack of transferability.

Our study draws on a large, spatially extensive vegetation monitoring dataset and was designed to provide foundational knowledge of individual plant species responses to site characteristics often associated with resistant plant communities. We surveyed plant cover in two federally protected parks within the Columbia Basin of contrasting size, elevation, and use history to provide a broad backdrop for describing the geographic variation of resistance and ascertain the important environmental factors associated with native and exotic grass, forb, and shrub species cover. The ultimate goal of this study is to contribute to evidence-based species distribution modeling and finely focused, resistance- and resilience-based, protected-area management.

Methods

Study Areas

Our study involved multivariate analyses of large and spatially extensive replicate samples of vegetation in two parks: the 5 800-ha John Day Fossil Beds National Monument (JODA) in central Oregon and the 304 000-ha Craters of the Moon National Monument and Preserve (CRMO) in southern Idaho (Fig. 1). In JODA, the study occurred along rugged, topographically heterogeneous gradients ranging from 421 to 1 255 meters above sea level (m a.s.l.) primarily within the Wyoming big sagebrush vegetation type, a relatively dry sagebrush ecosystem considered of lowest resilience to disturbance and resistance to plant invasion (Chambers et al., 2014b). In CRMO, the study occurred along a much broader gradient of elevation and vegetative productivity, spanning an elevation range of 1 624–2 355 m a.s.l. The southern portion of the park is lower in elevation and dominated by Wyoming big sagebrush, while the northern, higher-elevation sites are more mesic (Fig. 2) and characterized by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle) and low sagebrush (*Artemisia arbuscula* [Nutt.] H.M. Hall & Clem.). Notably, the legacy of historic grazing before park establishment in the 1970s is much more extensive in JODA than in CRMO, which was established in 1924 (expanded in 2000) and where in some places is surrounded by lava flows so expansive that livestock grazing is believed to have been entirely absent over the historic settlement era (Tisdale et al., 1965). Mean annual precipitation in JODA is ~250 mm. Soils in the park are volcanic ash—derived clays and clay-loams with aridic soil moisture and mesic soil temperatures. Mean annual precipitation in CRMO ranges from ~250 mm in the southern portion to ~350 mm in the northern portion of the park (see Fig. 2). Soils on lava flows include Folists, Entisols, Aridisols, and Mollisols with xeric soil moisture throughout the park, but a gradient of mesic to frigid soil temperature regimes that closely follows the north-south elevation gradient.

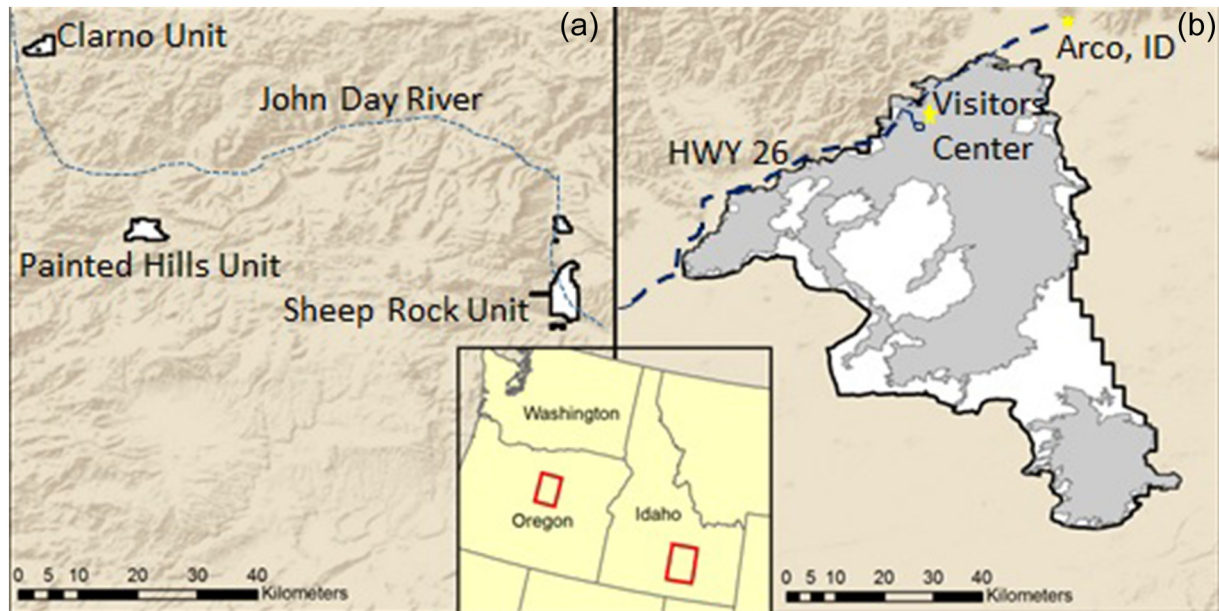


Figure 1. Study areas showing **a**, the distinct units of the John Day Fossil Beds National Monument and **b**, the large expanse of Craters of the Moon National Monument and Preserve.

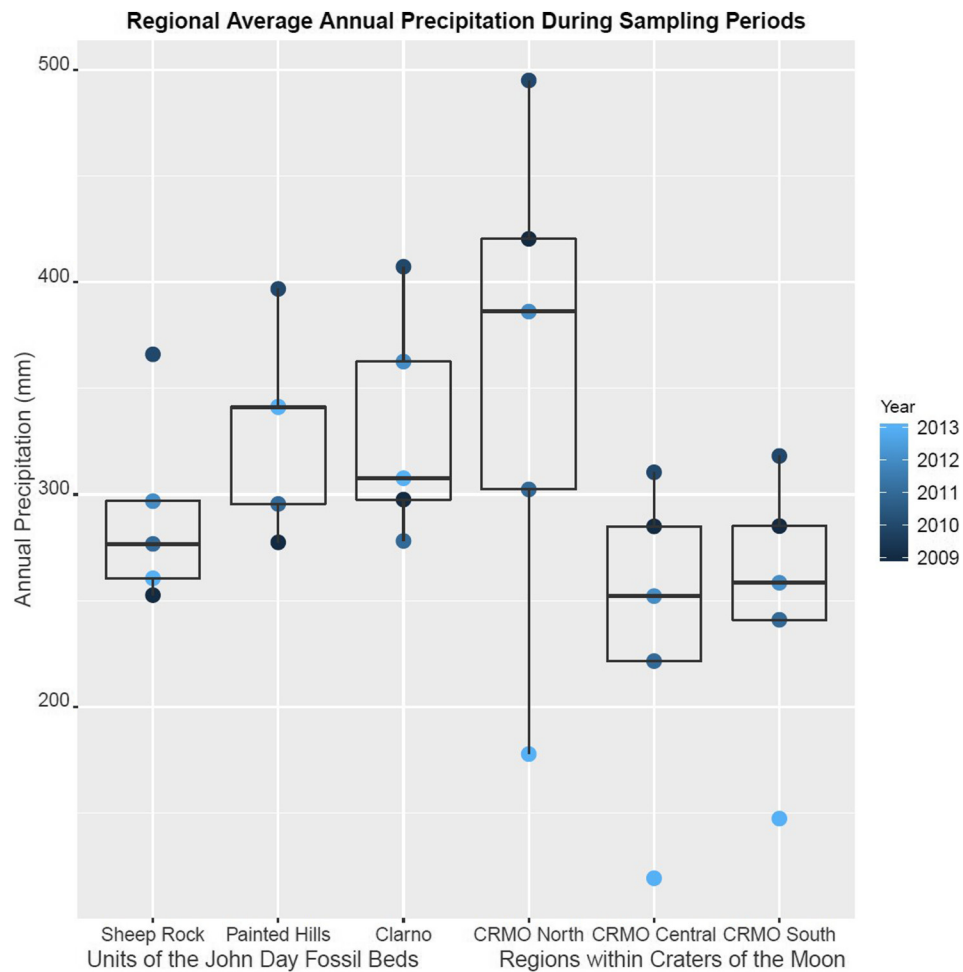


Figure 2. Annual precipitation (mm) for 2009–2013 for three units of the John Day Fossil Beds National Monument and locations at the northern, midlatitude, and southern portions of Craters of the Moon National Monument and Preserve. Craters of the Moon experiences a broader range of annual precipitation throughout the park, as well as greater interannual variation than John Day Fossil Beds. (Source: PRISM Climate Group's 4 000-m resolution annual values)

Field Sampling

Plant cover observations were collected during early summer 2009–2013 (2009 and 2011 for JODA, 2010 and 2013 for CRMO) in 1-m² quadrats. In each quadrat, ocular estimates of plant cover were recorded for principle native and non-native species following Daubenmire (1959) cover classes (0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%). We evaluated 1 169 quadrats in JODA and 2 502 in CRMO. For each year of sampling, quadrats were distributed randomly within sampling frames by way of a spatially balanced algorithm (generalized random-tessellation stratified [GRTS; Stevens and Olsen, 2004; Yeo et al., 2009]). The natural continuity of sagebrush vegetation across JODA allowed for continuous sampling across the sagebrush landscape, and the sampling frame within that park included all uplands except for steep slopes and cliffs > 30 degrees. The expansive and naturally fragmented (from lava flows) landscape of CRMO required a nonrandom placement of twenty-five 12-ha macroplots within sagebrush steppe communities along the elevation gradient, each macroplot functioning as independent sampling frames from which 50 newly randomized quadrat locations were subsequently surveyed for each year of sampling.

Statistical Analysis

Nonmetric multidimensional scaling (NMDS) was used to ordinate the sample units in species space. This type of analysis is ideal for ecological community data due to the inherent complexity of interactions between species and the environment. NMDS was performed using PC-ORD (ver: 6.12, MjM Software, Gleneden Beach, OR), which follows the methods for NMDS outlined in Mather (1976) and Kruskal (1964). Before running the NMDS, cover class records were converted to their respective median values in order to better represent the proportion of cover for each species. For CRMO, average species cover for all quadrat sample units within each frame (50 units within each of 25 frames) for both years were generated for use in analysis. This resulted in a data set representing average abundance patterns at the macroplot (12-ha sample frame) scale. The extensive park-wide sampling frame at JODA permitted direct ordination of quadrats. The suite of species within each park community analysis was reduced by eliminating rare species (those that occurred in < 5% of sample units), and a generalized log transformation was performed on the remaining species. These

modifications served to reduce possible influence of rare and/or highly abundant species, as well as to reduce noise and enhance user ability to interpret relationships within the ordination space (McCune and Grace, 2002). Elevation, slope, aspect, topography (measured as topography = $\sin(\text{slope}) \cdot \cos(\text{aspect})$, producing a variable ranging from -1 for steep south-facing slopes, 1 for steep north-facing slopes, and 0 for flat plains), distance to park boundaries and distance to boundaries of disturbed areas were generated in a GIS using US Geological Survey (USGS) 10-m digital elevation models (DEMs). Precipitation data (total average annual precipitation and crop year precipitation) were derived from the PRISM Climate Group's 800-m resolution raster data products (Daly et al., 2008). Crop year precipitation was calculated as the total amount of precipitation received between September and May.

Sørensen's (Bray-Curtis) proportion coefficient distance measure was used in conjunction with a random starting location using the autopilot mode in PC-ORD, which performed 50 runs with real data and 50 runs with randomized data; 200 iterations were used in the final NMDS for JODA. The same procedure was used for CRMO, performed with 200 runs with real data and 200 runs with randomized data; 80 iterations were used in the final CRMO NMDS. The final dimensionality of each ordination was selected automatically by the software. NMDS test results were examined for stress and instability. Final stress did not exceed 20 and instability < 10^{-4} (McCune and Grace, 2002). Joint plots were overlaid on the ordination to determine which environmental variables exhibited the strongest correlation with each of two ordination axes. Variables chosen for further analysis were those with an $R^2 \geq 0.1$. Species with the highest R^2 values were selected for further analysis, as well as non-native invasive species of interest.

Nonparametric, multiplicative regression was used to evaluate how species cover was related to the strongest NMDS community gradients using HyperNiche (ver: 2, MjM Software) (McCune, 2011). Nonparametric, multiplicative regression is based on a multiplicative kernel smoother and requires no assumptions on the relationships between predictor variables, which represents clear advantages over usual statistical models (e.g., generalized linear) that are too rigid to accommodate complex responses (McCune, 2006, 2011). Nonmetric multidimensional scaling scores for the two ordination axes were used as predictors, as these scores represent the complex interaction of environmental variables to the patterns of species composition within the ordination space (Averett et al., 2016).

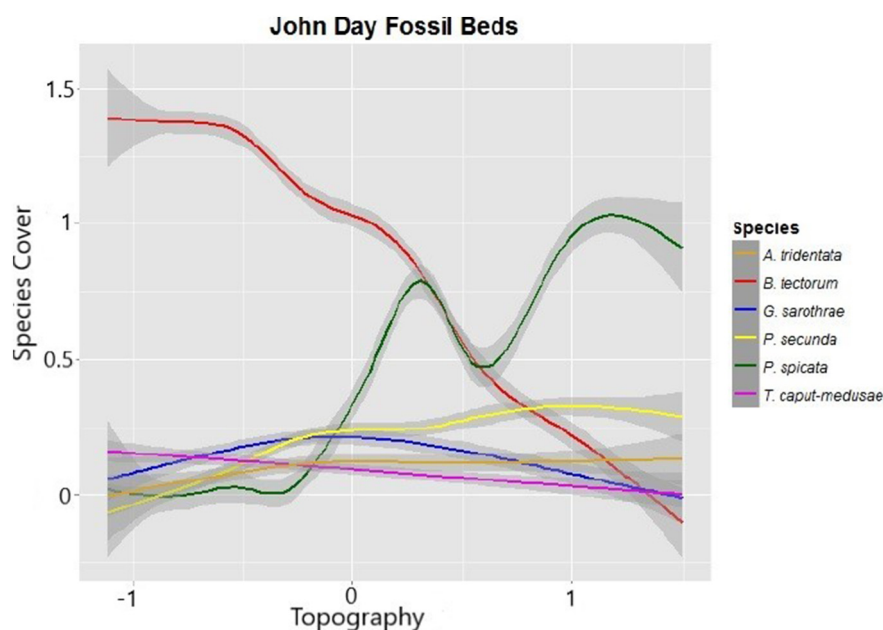


Figure 3. Nonparametric multiplicative regression response curves illustrating the correlation between species cover and topographic variation from steep south-facing to steep north-facing slopes (from left to right) in the John Day Fossil Beds National Monument. The x-axis is a nondimensional and unitless measure of spatial separation.

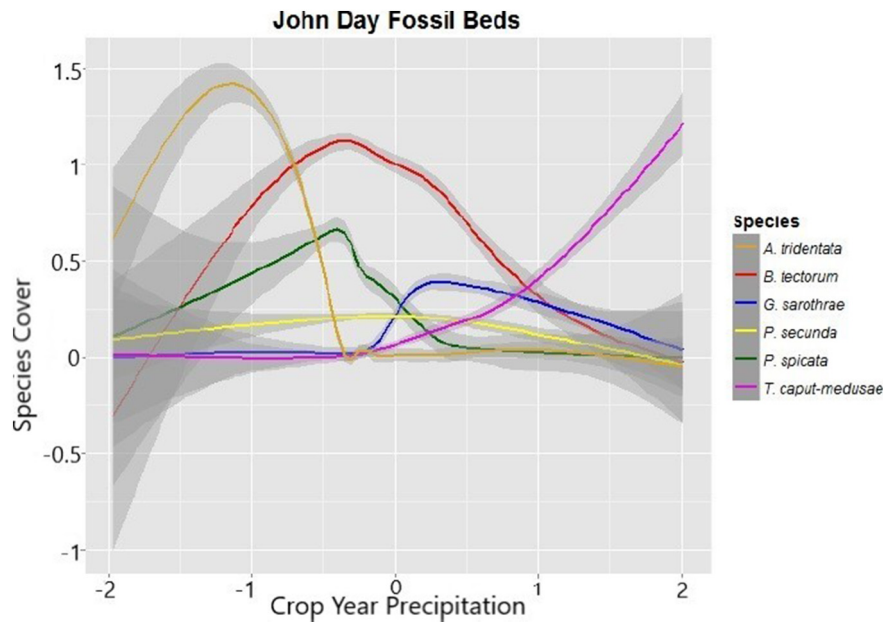


Figure 4. Nonparametric multiplicative regression response curves illustrating the correlation between species cover and crop year (September–May) precipitation in the John Day Fossil Beds National Monument. The x-axis is a nondimensional and unitless measure of spatial separation.

Results

John Day Fossil Beds

The non-native invasive annual-grass species cheatgrass and medusahead (*Taeniatherum caput-medusae* L.) were mainly distributed along south-facing slopes in JODA (Fig. 3). Of the 1 169 quadrats surveyed in 2009 and 2011, 92% contained some cheatgrass and 51% were highly invaded (> 25% cover of the species). Fourteen percent of quadrats contained some medusahead, and 4% were highly invaded (> 25% cover of the species). Numerous other non-native annual grasses including other *Bromus* and *Poa* species and invasive forbs were also widespread among quadrats.

The JODA NMDS resulted in a three-dimensional solution, which explained 83% (cumulative $R^2 = 0.836$, Axis 1 $R^2 = 0.366$, Axis 2 $R^2 = 0.315$, Axis 3 $R^2 = 0.155$) of the variation in species cover estimates (Monte Carlo test result, $P = < 0.02$). The three-dimensional solution resulted in a final stress of 17.73 and final instability of 0.0037. Variation in species cover within the ordination was best described by the topographic gradient and crop year precipitation. Topography was positively correlated with Axis 1 ($R^2 = 0.101$), and crop year precipitation was positively correlated with Axis 2 ($R^2 = 0.109$).

Nonparametric multiplicative regression indicated that the relative cover of the annual grasses cheatgrass and medusahead and the native perennial subshrub broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby) appeared to be most influenced by topography

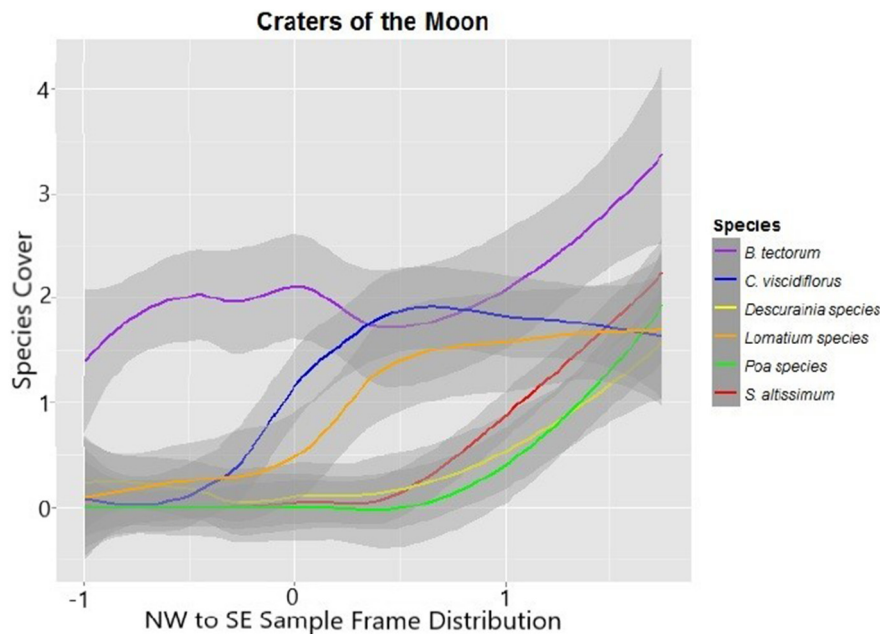


Figure 5. Nonparametric multiplicative regression response curves illustrating the correlation between species cover and Axis 1 representing the spatial separation of sampling frames from northwest to southeast, a gradient of decreasing elevation and increasing aridity. The x-axis is a nondimensional and unitless measure of spatial separation.

(Fig. 3). These three species decreased along Axis 1 as topography increased. Conversely, relative cover of the native perennial bunchgrasses bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Sandberg bluegrass (*Poa secunda* J. Presl.) and, to a lesser extent, Wyoming big sagebrush increased along Axis 1 toward steep north-facing slopes. With respect to crop year precipitation, as it increased along Axis 2, the cover of Wyoming big sagebrush and cheatgrass decreased while the cover of broom snakeweed and medusahead increased (Fig. 4).

Craters of the Moon

Cheatgrass abundance was greatest in the southern, lower portion of the elevation gradient in CRMO (Fig. 5). Of the 2 502 quadrats surveyed in CRMO in 2010 and 2013, 50% contained some cheatgrass and 9% were heavily invaded by it (> 25% cover). Unlike JODA, no plots contained medusahead, although as in JODA, numerous other invasive annual grasses and forbs were widespread across the study area.

The CRMO NMDS resulted in a two-dimensional solution, which explained 90% (cumulative $R^2 = 0.90$, Axis 1 $R^2 = 0.68$, Axis 2 $R^2 = 0.22$) of the variation in species cover estimates (Monte Carlo test result, $P = 0.004$). The two-dimensional solution resulted in a final stress of 12.454 and final instability of < 0.0001 with 80 iterations. Axis 1 represented geographic separation of sample frames within the study area. The variables most correlated with this axis indicate a gradient spanning from southeastern to northwestern frames in the Monument following the elevational gradient. Universal Transverse Mercator (UTM) X coordinates (easting) show positive correlation with Axis 1 ($R^2 = 0.393$), and UTM Y coordinates (northing) show negative correlation with Axis 1 ($R^2 = 0.206$). Axis 2 represented a combination of environmental and geographic variation in the study area. Distance to trails was negatively correlated with Axis 2 ($R^2 = 0.383$), while all other significant ($R^2 \geq 0.1$) environmental variables showed positive correlations with Axis 2; elevation ($R^2 = 0.343$), distance to roads ($R^2 = 0.318$), annual precipitation (mm) ($R^2 = 0.293$), UTM Y coordinates ($R^2 = 0.27$), distance to boundary ($R^2 = 0.184$), and crop year precipitation ($R^2 = 0.182$).

Nonparametric multiplicative regression indicated that numerous principle plant species correlated ($R^2 \geq 0.1$) with one or more axes. As frame locations transitioned from northwest portions of the Monument

to southeast areas, cover of species associated with relatively dry conditions such as green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), cheatgrass, *Poa* spp., the invasive mustards tall tumbledustard (*Sisymbrium altissimum* [L.]) and *Descurainia* Webb & Bethel. spp., and the native forb *Lomatium* Raf. spp. increased along Axis 1 (see Fig. 5). As elevation, precipitation, and distance to roads and boundaries increased along Axis 2 (Fig. 6), the relative cover of the native forbs western stonecrop (*Lithospermum ruderales* Douglas ex Lehm) and *Eriogonum* Michx. spp. and the mesic perennial native grass basin wildrye (*Leymus cinereus* Á. Löve) increased, while non-native invasives cheatgrass, tall tumbledustard, and *Descurainia* spp. and dry site – associated *Poa* spp. decreased.

Discussion

We examined vegetation cover data from a large set of spatially extensive, randomized plot-based surveys to make inferences about plant species responses to aspects of ecological resistance to plant invasion across two Columbia Basin sagebrush steppe – protected areas. Although similar studies have been conducted at both JODA (Rodhouse et al., 2014) and CRMO (Bangert and Huntly, 2010), they were both focused on more generally describing patterns of resistance and invasion rather than describing individual native and non-native plant species abundances along gradients of topographic correlates to water availability and disturbance. Our study adds to the empirical evidence base for management of steppe-protected areas, which are relatively few in number and have generally been overlooked in the biome relative to the focus given to multiuse (i.e., grazed) landscapes (Sayre et al., 2012).

As expected from theory and previous studies (Miller et al., 2013; Chambers et al., 2014a, 2016), patterns of invasion resistance were higher where local-scale topographic features might allow for higher moisture availability and where disturbance and propagule pressure were lowest. However, we found considerable variation in the proximal topographic correlates of moisture availability and the manifestation of resistance to invasion between the two park study areas. In the park with greater topographic variability (JODA), topographic position (slope and aspect) emerged as the primary correlate of weed invasion (see Fig. 3), whereas in the park, which spanned a greater elevational gradient (CRMO), elevation and proximity to disturbance were the

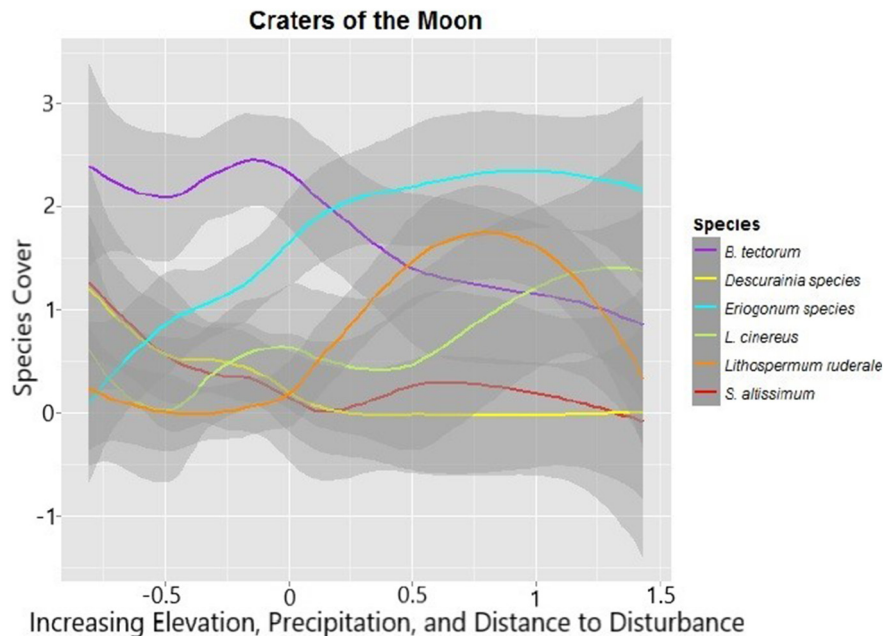


Figure 6. Nonparametric multiplicative regression response curves illustrating the correlation between species cover in Craters of the Moon National Monument and Preserve and environmental gradients derived from NMDS ordination scores for Axis 2. Axis 2 represents increasing elevation, precipitation, distance to roads, and the monument boundary. The x-axis is a nondimensional and unitless measure of spatial separation.

primary correlates of influence (see Fig. 6). Furthermore, the correlations observed between noncheatgrass invaders and environmental variables encourages the identification of proximal aspects of resistance to invasion for individual invasive plant species.

John Day Fossil Beds

Within JODA, higher proportions of the invasive annual grasses cheatgrass and medusahead occurred on steep, south-facing sites, while higher proportions of the native perennials bluebunch wheatgrass and Sandberg bluegrass occurred on steep, north-facing sites (see Fig. 3). These findings are consistent with other studies from the park (Kauffman et al., 1997; Rodhouse et al., 2014) and elsewhere in the Columbia Basin steppe (Bernards and Morris, 2017). Although bluebunch wheatgrass is considered a biological aspect of resilience and resistance to plant invasion in sagebrush steppe systems, due to its ability to survive periodic fire and compete effectively against annual grasses (Sheley and James, 2010; Davies and Johnson, 2017), forb diversity has also been linked to greater resistance to invasion (Allen and Meyer, 2014). The lack of correlation between topography and perennial forb cover doesn't exclude this plant functional guild from the resistant communities; it simply reflects a lack of response to the variables tested (i.e., forbs might persist throughout a broad range of sites), and further analysis is required. Until then, we cannot claim that at JODA managers should expect topography or the presence of bluebunch wheatgrass to promote a more diverse community.

The distribution of plant species in JODA also correlated with crop year precipitation. Although Wyoming big sagebrush and bluebunch wheatgrass are late seral species, well adapted to semiarid conditions, and resistant to yearly variations in precipitation (Mata-González et al., 2008), cover for both species was greater when crop year precipitation was relatively low (see Fig. 4). In general, more precipitation in spring and less in fall and winter can lead to reduced plant productivity in sagebrush steppe (Bates et al., 2006). Shinneman and McIlroy (2016) found that although postfire sagebrush cover appeared to benefit from higher than average precipitation when it occurred the first year after the fire, sites had lower sagebrush cover if precipitation was again higher the following winter, and this was especially true in soils with greater moisture availability. Cheatgrass was similarly negatively correlated with crop year precipitation (see Fig. 4), indicating the competitive advantage of this species in relatively dry sites as noted by Rodhouse et al. (2014) and highlighting the lower resistance of dryer sites in general (Miller et al., 2013; Chambers et al., 2014a).

Broom snakeweed had a positive correlation to crop year precipitation in this study (see Fig. 4) and commonly displays a strong density and cover response to winter and spring precipitation (Ralphs and Sanders, 2002; Ralphs and McDaniel, 2011). In addition, as soil moisture decreases, broom snakeweed can maintain a high degree of stomatal opening (Ralphs and McDaniel, 2011), which may reduce available soil moisture and provide a competitive advantage (Ralphs and Sanders, 2002). Native bunchgrasses and deep-rooted shrub species such as big sagebrush can inhibit the establishment and density of broom snakeweed (Ralphs and McDaniel, 2011). However, Wyoming big sagebrush and bluebunch wheatgrass can be displaced after a fire when more fire-tolerant species are present (Mata-González et al., 2008). The history of fire in JODA has contributed to a low abundance of big sagebrush, which seemingly has been capitalized by the opportunistic broom snakeweed increasingly assuming shrub dominance in JODA (Mata-González et al., 2018). Once established, broom snakeweed has been shown to suppress the establishment and growth of native grass and forb species (Thacker et al., 2008; Ralphs and McDaniel, 2011), which may have otherwise conferred resistance to annual grass invasion (Sheley and James, 2010; Davies and Johnson, 2017). Furthermore, significant reduction of big sagebrush cover can increase available resources, increasing the chance of invasive species establishment (Germino et al., 2004; Prevey et al., 2010).

Medusahead also appeared to benefit from higher crop year precipitation (see Fig. 4). The positive correlation of medusahead to crop year precipitation in JODA may be due to a high need for available spring moisture (Dahl and Tisdale, 1975; Bansal et al., 2014). Dahl and Tisdale (1975) reported that in areas with higher moisture availability, such as depressions, which accumulate runoff, medusahead established readily, provided that the native perennial vegetation had been previously reduced, as is the case across much of JODA. According to the NPS vegetation data analysis website [Vegviz.org](http://vegvis.org), it appears that between 2011 and 2017 both medusahead and broom snakeweed expanded into higher slopes, and medusahead especially increased in percent cover. In 2009–2011, the highest broom snakeweed cover class (50–75% cover) was restricted to lower slopes (5–10%), but in 2011–2017 it expanded to slopes of up to 20% ([Vegviz.org](http://vegvis.org)).

Our findings indicate that areas similar to JODA, which have been converted to broom snakeweed dominance, have potentially lowered resistance and should be considered areas of concern and at risk of additional invasive species establishment. The dominance of broom snakeweed is also of concern because of the expected patterns of climate change involving augmented late fall to early spring precipitation for the region (Palmquist et al., 2016). Such patterns would favor the dominance of the opportunistic broom snakeweed and medusahead over foundational species such as Wyoming big sagebrush (Bates et al., 2006). In light of our findings of invasive species establishment and expansion along gradients of moisture availability, resource managers dealing with similar issues should prioritize protection and prevention (of invasion) in areas where resistance appears to be highest (i.e., north-facing slopes). Nonetheless, the effects of wildfire on native plant density and diversity may play a greater role in the dominance of invasive species than the variation of physical factors such as topography or available water (Mata-González et al., 2012). Continued monitoring of invasive species encroachment and a better understanding of forb diversity and responses to precipitation (in an extended data series) in situations such as this may clarify the need for intervention in order to assist the manageable (i.e., biological) aspects of resistance.

Craters of the Moon

Species distribution across Craters of the Moon can largely be explained by the effects of elevation and precipitation on plant habitat suitability. An inflated correlation between plant community and precipitation is possible due to the effect of the 2013 drought yr data (see Fig. 2). However, this should have inflated positive correlations between annual species and precipitation, and this was not observed, at least for cheatgrass and the weedy mustard species (see Fig. 6). The drought year effect was likely dampened by the precipitation gradient found throughout the park (see Fig. 2) and resolution of climate data, but including additional sampling years would further decrease the effect. Elevation and precipitation decrease from north to south across CRMO as cover of invasive species such as cheatgrass and tall tumbled mustard increase (see Fig. 6). Bangert and Huntly (2010) also reported native species occurrence and richness at CRMO to be most influenced by environmental conditions associated with elevation and a greater occurrence and richness of exotic species in the warmer, drier, lower-elevation sites typical of southern portions of the park. Unlike at JODA, resistant sites at CRMO are harboring increased cover of perennial forbs. Increased *Eriogonum* spp. cover at resistant sites may be more associated with the lack of competition with cheatgrass than by other habitat requirements. Sulphur-flower buckwheat (*Eriogonum umbellatum* Torr.) responded positively in stem height to snow removal and lacked a response to experimental warming in a study at Grand Teton National Park in Wyoming (Sherwood et al. 2017). Furthermore, although sulphur-flower buckwheat root growth rate appears to be unaffected by neighboring native bunchgrasses, it was reduced by 42% when in competition with cheatgrass (Parkinson et al., 2013). Basin wildrye, the mesic perennial bunchgrass positively associated with

CRMO's aspects of resistance (see Fig. 6), is likely to contribute to site resistance. In a co-planting study with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), a highly competitive exotic perennial bunchgrass, basin wildrye was able to maintain its original planting density, while 3 out of 6 bunchgrasses in the study, including bluebunch wheatgrass, decreased from their original densities (Nafus et al., 2015). This may be partially due to basin wildrye's extensive lateral root system (Abbott et al., 1991) and competitiveness for soil moisture (Anderson and Toft, 1993).

Environmental constraints are likely negatively affecting the establishment of cheatgrass in northern, more mesic, portions of CRMO; however, variable climatic patterns may reduce the buffering effect of elevation (on resistance) now present in CRMO. Wade and Loik (2017) observed that cheatgrass at a high elevation site (~2100 m a.s.l.) on the eastern slope of the Sierra Nevada Mountains increased photosynthetic rates in response to precipitation pulses in dry springs to a greater degree than two native bunchgrasses and a native forb. The Sierra Nevada site is of similar elevation to northern CRMO and exhibited high annual precipitation variability (130–557 mm). The precipitation variability at CRMO is exemplified by the annual precipitation in the two sampling years in this study. In 2010, the north end of CRMO recorded ~495 mm of precipitation, while in 2013 the same area only received ~177 mm (see Fig. 2). This leads us to believe that elevation alone may not confer enough site resistance to exclude cheatgrass from high-elevation sites like those at northern CRMO if a drought year was coupled with sufficient propagule pressure.

Similar to other studies from the region (Knapp, 1996; Bangert and Huntly, 2010), this study found exotic species occurrence more heavily concentrated with increased proximity to a railroad, where at CRMO it follows the southern border of the park (due to lava flows acting as fire breaks) have allowed for invasive species to expand from southern agricultural and other disturbed areas (i.e., roads), the highway that borders the northern extent of the park, as well as the visitor's access loop road and wilderness trails, are also likely avenues for plant invasion (Davies et al., 2013). Resource managers should consider the potential fragility of resistance in high-elevation, drought-prone sites, such as northern CRMO, and closely monitor to identify changes in plant communities possibly driven by climate, anthropogenic disturbance, or exotic introductions and take preventative measures to mitigate the risk of future invasive plant expansion.

Implications

The occurrence and distribution of non-native species within our study areas highlight an apparent lack of insularity conferred by the protected status of these landscapes and raise important conservation concerns for what has been deemed the most imperiled ecosystem type in the United States (Noss et al., 1995; Chambers and Wisdom, 2009). Sagebrush steppe ecosystems provide critical habitat for native species of concern (e.g., greater sage-grouse, Columbia Basin pygmy rabbit), as well as ecosystem services and economic possibilities (i.e., grazing). Parks and protected areas are unique to these landscapes in that they prioritize biodiversity and intrinsic values (e.g., visitor experience), but their rarity across the biome and their degradation from outside-in forces and historical legacy, in part revealed by our study, suggest that the current protected-area network will not provide for meaningful amounts of representative components of the biome in the future. Resistance patterns in the topographically variable JODA are based on the relatively intact native plant communities that are favored by higher-elevation and northern exposures, while fire and altered precipitation regimes may allow expansion of invasive plants into sites currently considered to be benefitting from aspects of resistance. Resistance patterns in the relatively flat but expansive CRMO are based mostly on elevation, but location with respect to anthropogenic disturbances, as well as precipitation variability at the park, may

jeopardize resistant sites. The concepts of resilience and resistance to invasion provide for a dynamic framework to understand and cope with the ecological changes under way in sagebrush steppe ecosystems. The transferability of these concepts from current research areas to protected areas and beyond will likely rely on identifying the idiosyncratic variation in manifestations of resistance. Further studies identifying the most influential aspects of resistance and invasibility for specific areas could not only increase the accuracy of local decision tools but also identify patterns of resistance applicable to areas with similar climates, plant communities (e.g., big sagebrush subspecies), or landscape attributes. Nonmetric multidimensional scaling of digitally acquired topographic and environmental datasets, combined with nonparametric multiplicative regression using field data, appears to be an effective method of observing relationships between resistant and invaded communities and their environments. Future research should attempt to incorporate digital soils maps (Maestas et al., 2016), topographic variables, disturbance history, and more complex water balance metrics into models of resistance and resilience, especially for areas that are affected by invasive plant species from multiple functional guilds.

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