RESEARCH ARTICLE

Spatiotemporal patterns of cheatgrass invasion in Colorado Plateau National Parks

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Abstract

Context Exotic annual grasses are transforming native arid and semi-arid ecosystems globally by accelerating fire cycles that drive vegetation state changes. Cheatgrass (*Bromus tectorum*), a particularly widespread and aggressive exotic annual grass, is a key management target in national parks of the western United States due to its impacts on wildfire and biodiversity loss. Cheatgrass is known for its high interannual variability and can grow in a wide range of conditions.

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Objectives The objectives were to (1) map the presence and persistence of cheatgrass in national park units across a 11-year period using remote sensing, and (2) identify the biophysical parameters that correlate with cheatgrass persistence.

Methods We used remote sensing and GIS tools to develop a systematic model to characterize the status and environmental correlates of cheatgrass invasions in seven national park units in the western United States.

Results On average cheatgrass covered 3.8% of park areas, each park ranging from 0.8 to 24.8% coverage. Where cheatgrass was detected, persistent populations across time (hotspots) made up on average 13% of cheatgrass areas. Hotspots were found in areas with deeper plant-available water, lower elevations, colder mean winter temperatures, flatter slopes, higher soil clay content, and lower mean fall precipitation.

Conclusion Study results identified spatiotemporal patterns of plant invasions and key environmental drivers that influence invasion patterns. GIS tool development and analysis from this study were used to generate invasion maps for each park, which can be used to mitigate wildfire and biodiveristy loss.

Keywords *Bromus tectorum* · Cheatgrass · Plant invasion · Wildfire · Remote sensing · GIS · Spatial modeling

Introduction

Invasive grasses are transforming ecosystems, incurring great socioeconomic and environmental costs (Vitousek et al. 1996; Pimentel et al. 2005). These costs accumulate due to reductions in biodiversity, productivity, nutrient cycling, and altered fire regimes (D'Antonio and Vitousek 1992; Brooks et al. 2004). The rapid spread and success of invasive annual grasses can be explained by their short life cycles, large investment in reproduction, and opportunistic response to favorable climate conditions (Chambers et al. 2007). Future replacement of native plant communities by exotic annual grass species is likely to be fueled by increases in land use intensification and climate change (Dukes and Mooney 1999). While exotic grass invasions are occurring globally, dryland ecosystems of western North America are being converted to non-native grass communities at a particularly rapid pace (Bradley et al. 2018).

Understanding the spread of invasive grasses is challenging because of their high spatial and temporal variability. The interaction of landscape position and microenvironment create large spatial heterogeneity, in both the presence and productivity of invasive grasses, and their persistence through time (Bradley and Mustard 2006; Horn and St Clair 2017). Explaining temporal and spatial patterns of invasion is a critical dimension of developing a comprehensive invasive species management strategy (Ashton et al. 2016). There is substantial interannual variability in the abundance and density of invasive annuals that is driven by weather (Horn et al. 2015; Ashton et al. 2016), population structure (Mack and Pyke 1983), and community processes (Germino et al. 2015; St. Clair et al. 2016). This temporal variability can amplify responses to environmental change relative to native plant communities (Elmore et al. 2003), making it difficult to detect and explain patterns of invasion and the underlying mechanisms at landscape scales. To capture both temporal and spatial dynamics associated with plant invasions has required either modeling or using spectral signals unique to invasive species in certain climate conditions and analyzing long-term remote sensing imagery (Balch et al. 2013; Biganzoli et al. 2013).

Cheatgrass (*Bromus tectorum*), an invasive annual grass from Eurasia, is one of the most insidious exotic plants in western North America (Balch et al. 2013;

Reisner et al. 2013) where it has spread across 22.7 million ha. (Duncan 2004) and is expected to establish into new areas given future climate predictions (Bradley 2009b). Cheatgrass is phenotypically plastic and genetically diverse, allowing it to occupy a diversity of habitats (Concilio et al. 2013; Reisner et al. 2013; Meyer et al. 2016). It is highly competitive with a great deal of native vegetation, often altering plant community structure by promoting recurrent wildfire and altering nutrient dynamics (Booth et al. 2003; Urza et al. 2017). Because of its widespread impacts, cheatgrass is a critical species to understand, and its unique phenology makes it an ideal species to study using remote sensing techniques (Bradley et al. 2018). In the Colorado Plateau, cheatgrass mainly germinates in the fall, develops an extensive root system during the winter and reaches maximum biomass in mid-spring, compared to early summer for native plants (Mack and Pyke 1983; Munson et al. 2011). This temporal difference in greenness allows for the identification of landscape locations dominated by cheatgrass. The distribution of cheatgrass on the Colorado Plateau, a physiographic region bounded by the Rocky Mountains and deserts areas in western North America, is particularly alarming because it spans even into well-protected national parks who's primary focus is conservation (Munson et al. 2015).

Remote sensing can be an ideal tool to detect and monitor invasive grasses, because it can reveal abundance and spread at high resolution, across large spatiotemporal scales, at relatively low cost (Bradley and Marvin 2011; Bradley et al. 2018). Combining remote sensing, geographic modelling, and statistical modelling allows for the quantification of the spatial extent of grass invasion and how it changes with variation in biophysical conditions. We took the approach of combining a novel remote sensing technique, known as Detection of Early Season Invasives software (henceforth DESI) (Kokaly 2011), with Hotspot analysis, a spatial analysis tool (ESRI 2011), to characterize patterns of cheatgrass invasion. Hotspot analysis has been previously used for analysis of road incidents, urban crime analysis, and epidemiologic studies (Craglia et al. 2000; Maciel et al. 2010; Songchitruksa and Zeng 2010), but to our knowledge has not been applied to track the establishment and spread of invasive species and identify the biophysical correlates underlying plant invasions.

The objectives of this study were to develop an innovative method to systematically model and identify the spatial extent and temporal patterns of cheatgrass, and characterize the environmental associates of cheatgrass invasions in seven national parks in the Colorado Plateau region of western North America. We specifically examined cheatgrass invasion in national parks because of its direct and negative impacts on key management objectives of the National Park Service related to invasive grass-fire cycles and biodiversity conservation. Our study objectives were to:

(1) Map the presence and persistence of cheatgrass in seven national park units across a 11-year period on the Colorado Plateau.

(2) Identify the important biophysical factors that associate with the presence and persistence of cheatgrass across space and time.

Methods

Site description

Seven national park units were selected across the Colorado Plateau region: Arches, Bryce Canyon, Canyonlands, and Capitol Reef National Parks (NP), Dinosaur and Natural Bridges National Monuments (NM), and Glen Canyon National Recreation Area (NRA). These national park units are extremely popular tourist destinations visited by millions of people each year (Utah Office of Tourism 2017). The study areas span from the low elevation (930 m) southern unit of Glen Canyon NRA, with a mean annual precipitation of 181 mm year^{-1} and mean annual temperature of 15.6 °C, to the higher elevation (2700 m) unit of Bryce Canyon NP with a mean annual precipitation of 370 mm year^{-1} and mean annual temperature of 5.7 °C (Table 1). These park units have large elevational ranges within and among them (930–2700 m) (Table 1). The low elevation areas are arid to semi-arid and composed of shrublands and grasslands. Woodlands dominated by pinyon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), and various shrubs occupy middle elevation areas. At high elevation, mixed conifer forests are the primary plant community. Cheatgrass was introduced to Washington, Utah and British Columbia, during the mid

nineteenth-century, originating from populations in Europe (Mack and Pyke 1983). By 1930 its range expanded throughout perennial grassland and shrublands in western North America (Morrow and Stahlman 1984). The greatest cheatgrass abundance occurs within the Great Basin and Columbia Basin regions where it is adapted to a variety of soil types and moisture conditions. It is an increasing concern in the Colorado Plateau where disturbances are negatively impacting native plant and biological soil crust communities increasing invasion potential (Schwinning et al. 2008). Cheatgrass has been mapped extensively across the Great Basin (Balch et al. 2013; Bradley et al. 2018) but not much is known about its distribution on the Colorado Plateau at large scales.

Experimental design and analysis

Landsat imagery, DESI software (Kokaly 2011), and Hotspot spatial analysis (ESRI 2011) were used to identify cheatgrass abundance and persistence and correlate it to environmental variables. Landsat satellite imagery was obtained from 1999 to 2009 and converted to DESI maps for individual years using the methods of Kokaly (2011) outlined here. The DESI software is comprised of programs written in Interactive Data Language that run with ENvironment for Visualizing Images (Harris Geospatial Solutions, Boulder, CO) and uses Landsat 5 TM and Landsat 7 ETM images to calculate a seasonal normalized difference vegetation index (NDVI) values using surface reflectance. In contrast to native vegetation, cheatgrass has a distinct peak greenness in the early spring, and no greenness in mid-summer, associated with senescence. Therefore, we calculated a difference NDVI (dNDVI) at a pixel-level to create a map of cheatgrass presence/absence using the following equation:

$$dNDVI = NDVI_{early-season} - NDVI_{mid-summer}$$

The optimal window for the early-season satellite image in our study area was previously found to be between March 30 and April 23 and the mid-summer image between June 18 and July 12 (Kokaly 2011). Cloud cover can distort the radiance and reflectance of vegetation so images with high cloud cover were not used for analysis. Cloud-free images in the optimal time window were used to produce dNDVI values at a pixel-level within park boundaries. We used

Table 1 Climate, elevation, cheatgrass cover, and cheatgrass persistence (hotspot—spatially significant persistent populations of cheatgrass, ephemeral—spatially insignificant temporally variable populations of cheatgrass) in each park unit and park group

National Park Unit	Park characteristics					Cheatgrass % of total park area (%)	Hotspot analysis of total cheatgrass	
	Average annual precipitation (mm)	Average T_{max} (°C)	Average T_{min} (°C)	Elevation range (m)	Area (km^2)		Hotspot (%)	Ephemeral (%)
Arches National Park	209.6	22.2	6.3	1245–1723	310	2.6	10.3	89.7
Bryce Canyon National Park	369.5	13.3	− 1.9	2400–2700	145	1.5	2.6	97.4
Canyonlands National Park	212.5	19.0	5.5	1128–2170	1365	5.9	12.1	87.9
Captiol Reef National Park	189.0	18.6	5.5	1800–2700	979	0.8	2.7	97.3
Dinosaur National Monument	227.8	16.3	2.7	1432–2700	853	24.8	16.8	82.9
Glen Canyon National Recreation Area	181.7	21.8	9.5	930–2319	5075	5.7	11.3	86.6
Natural Bridges National Monument	299.6	17.2	3.7	1600–2000	31	14.8	13.0	86.9
All parks	241.4	18.3	4.5	930–2700	8758	3.8	12.9	85.9
AN park group	218.5	19.8	6.1	930–2700	7760	5.0	11.3	87.2
BD park group	298.6	14.8	0.4	1432–2700	998	2.5	16.6	83.1

AN park group Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges; *BD park group* Bryce Canyon and Dinosaur

previously established dNDVI thresholds for our study region to designate a high or low probability of a pixel containing cheatgrass (Kokaly 2011). The threshold for a high probability of a pixel containing cheatgrass was dNDVI > 0.1, and the threshold for low probability of a pixel containing cheatgrass was 0.075 < dNDVI < 0.1. Pixels with dNDVI < 0.075 were designated as a pixel absent of cheatgrass and assigned a value of 0 for subsequent analysis. Maps were produced for all seven parks showing presence (low and high probability combined) and absence of cheatgrass.

We extracted cheatgrass cover estimates from 4121 unique site × year combinations from 1999 to 2009 at permanent monitoring plot (30 × 30 m) and transect (100 m) locations within the study area (Munson et al. 2011; Miller 2018) to perform an accuracy assessment and ground truth the maps. Cheatgrass was considered present if it occurred at > 10% canopy cover inside monitoring plots (Munson et al. 2011; Miller 2018). We randomly selected 1200 monitoring locations and compared cheatgrass presence to the DESI maps. Overall accuracy was found to be 85–92% across all years of the study period. Map accuracy was confirmed by park staff with expertise on cheatgrass locations.

Kokaly (2011) identified confidence levels for whether individual pixels were dominated by cheatgrass. The highest confidence pixels, given a value of 2, had a high probability of cheatgrass (dNDVI > 0.1) and more than 1 of the 8 neighboring pixels with a dNDVI > 0.075 (low probability threshold). Moderate confidence pixels, given a value of 1, had a lower probability of cheatgrass (0.1 > dNDVI > 0.075) and 1 or more of the 8 neighboring pixels with a dNDVI > 0.075. All DESI cheatgrass maps for each study site were combined using the GIS software, ArcMap 10 × (ESRI 2011). Each pixel in this integrated map is a summed cheatgrass value of all years ranging between 0 and 22. A value of zero corresponded to no annual pixels over the period of record having any probability of cheatgrass. If each year had a high confidence value across all years, a pixel value of 22 was assigned. The end result was one raster layer where each pixel represented all DESI images from each year added together (the final DESI layer) (Online Appendix 1—Fig. S1). Higher pixel values suggest greater cheatgrass persistence across years in that specific pixel location.

Hotspot analysis (ESRI 2011) provided a means to statistically evaluate cheatgrass persistence across space and time in the DESI maps. The final DESI

layer was converted from raster to vector data, in which the centroid of each pixel became a point with the associated cumulative value of cheatgrass detection probability from all years. Hotspot Analysis calculates the Getis-Ord Gi*statistic (Ord and Getis 1995), which evaluates the sum of an individual point and all surrounding points proportionally to the sum of all points in an individual DESI layer. Z-scores and associated p-values from the Gi* statistic were then calculated for each point. If a point and its neighboring points had a large positive z-score and p > 0.05, there is significant spatial clustering called a *hotspot*. In this study, *hotspots* represent greater persistence of cheatgrass due to spatial clustering of populations with detection that occurred most years throughout the study. If the z-scores were close to zero and resulted in an insignificant *p* value, the point had no spatial clustering and thus cheatgrass presence was considered *ephemeral*. *Coldspots* were populations with low or infrequent presence (detection did not occur most years) that had a significant spatial clustering.

Elevation, slope, and aspect, were calculated from a digital elevation model (DEM) (State of Utah Division of Technology and Information Services 2003). Slope and aspect were calculated using the ArcMap v.10x Slope and Aspect Tool with each of the DEM layers. Soil texture (percent sand and clay at 0–20 cm depth) were obtained from the NRCS Web Soil Survey (Soil Survey Staff 2015). Depth of plant available water, at a 25 cm profile depth, downloaded from the NRCS Web Soil Survey (Soil Survey Staff 2015) is a measurement that aggregates available water supply at field capacity with corrections for salinity, and rooting depth. Climate data for this study included the mean Standardized Precipitation and Evapotranspiration Index (mean SPEI) (https://wrcc.dri.edu/wwdt/time) from the previous September through May of a DESI image, and antecedent mean summer, fall, winter, and spring precipitation and summer, fall, winter and spring temperature for each year of a DESI image (e.g., 1999 fall precipitation was used for the 2000 DESI image). Precipitation and temperature data were collected from PRISM climate datasets (Daly et al. 2002). All PRISM data were resampled using a cubic convolution to match the 30 m × 30 m pixel size of the DESI output image.

Because national parks in our study area experience a large number of visitors that can affect cheatgrass distributions, we compiled spatial layers of park boundaries, visitor centers, campgrounds, roads, and trails from the National Park Service GIS data portal (https://irma.nps.gov/DataStore/). We digitized the most current park and trail maps to include published trails and other points of interest from the National Park Service. We created a 200 m buffer around these high human use areas using ArcMap (ESRI 2011) to include invasive annual plant growth that may occur near human impacted locations. For instance, cheatgrass does not grow on paved roads, but likely occurs on the road shoulder or land adjacent to a road (Gelbard and Belnap 2003).

Statistics

We used a principal components analysis (PCA) to identify whether parks could be grouped together to increase the spatial scale of analysis. We expected cheatgrass dynamics to vary depending on general physical attributes such as common climate and topographic variables (e.g. elevation distributions); therefore, analyzing grouped parks with shared attributes increases spatial scale compared to analyzing each park individually. We used a correlation matrix to determine whether the biophysical factors including precipitation, temperature, elevation, slope, and soil characteristics could be pooled for use in a Principal Components Analysis (PCA). Mean summer, fall, and spring temperature and winter precipitation were left out of the PCA (Pearson's correlation > 0.85) due to uneven loading potential (Smith 2002). Using a benchmark cumulative Eigenvalue of 70%, the parks were categorized into like groups (see results below). PCA was performed using JMP 13pro (JMP Pro 1989–2012).

To test which biophysical factors were significant in explaining cheatgrass occurrence and persistence using the Hotspot analysis, a stepwise discriminant analysis was performed using SAS© software (SAS Institute 1990). However, due to the very low proportion of *coldspots* (<1.2% for total park area) that caused a violation of the general 9:1 *hotspot:coldspot* ratios assumption (Zuur et al. 2007), the *coldspots* were dropped from the analysis. Because of high correlations between temperature and precipitation data, all temperature data except for mean winter temperature was left out of the discriminant analysis. Our decision to keep precipitation data over temperature is due to the evidence that fall temperatures are

likely to be favorable for cheatgrass growth as long as there is sufficient water (Germino et al. 2015). Mean SPEI was also a way to incorporate temperature as a biophysical component. To avoid violating the assumption of spatial independence, we performed a repeated simulation of randomly selecting 1000 points from each Hotspot analysis category and ran the stepwise discriminant analysis 1000 times with no repeated samples. The order in which variables were used for the discriminant functions were recorded in summary tables to identify which biophysical attributes best discriminated against hotspot categories in a weighted frequency table (Table 2). Weighted frequency was calculated by taking into account the order in the discriminant function (1st, 2nd, 3rd, etc.) and how frequent the variable was used at that order. This was done for all parks combined and then for each group of parks categorized by the PCA. Once those biophysical variables were identified in the weighted frequency table, a discriminant function was made for each grouping.

To test whether the mean values of the biophysical characteristics were statistically significant across *hotspots, ephemeral,* and *no cheatgrass* points, we performed a pairwise comparison using Wilcoxon rank sum test with a Bonferroni correction method using the stats package in R (Hollander et al. 2013; R Development Core Team 2016). A random sample

with minimum distance set by the inverse distance weighting measurement used in the hotspot analysis was used to ensure spatial independence of the samples because points outside of that distance range were not used to assess hotspot categorization during the hotspot analysis phase.

Kernel density estimation plots were used to visually characterize the most important biophysical variables in explaining cheatgrass presence of each park group. Kernel density estimation, approximates the probability of the distribution for the population of a particular measured biophysical variable based on the sample population for that biophysical variable. These estimates are then used to visualize differences in distributions of the characterizing biophysical attributes between each hotspot analysis category for each park group when displayed on the same plot. Kernel density estimation plots were created using ggplot2 package in R (R Development Core Team 2016; Wickham 2016).

Results

PCA

Two principal components were found to be important in categorizing park groups (Fig. 1). Component One

Table 2 Biophysical attributes weighted frequency in discriminating among hotspots, ephemeral, and no cheatgrass

	All parks (%)	AN group (%)	BD group (%)
Aspect	0.6	1.9	0.2
Depth of plant-available water (cm)	38.1[a]	6.3[a]	12.0[a]
Distance to human infrastructure (km)	0.3	6.0[a]	2.9[a]
Distance to park boundary (km)	0.5	1.2	0.3
Elevation (m)	20.6[a]	22.5[a]	5.5[a]
Mean fall precipitation (mm)	3.4	4.9	7.4[a]
Mean spring precipitation (mm)	2.9	4.0	0.1
Mean Standardized Precipitation and Evapotranspiration Index (SPEI)	0.3	0.9	3.9[a]
Mean summer precipitation (mm)	2.7	3.5	2.7
Mean winter precipitation (mm)	7.4[a]	12.6[a]	2.8
Mean winter temperature (°C)	13.0[a]	0.4	23.8[a]
Percent clay in top 20 cm of soil	3.9[a]	33.5[a]	1.5
Percent sand in top 20 cm of soil	0.8	1.5	2.6
Slope	5.5[a]	0.8	38.3

[a]Denotes attributes included in the best discriminant function for each park group

Fig. 1 PCA biplot showing the loading for each variable. Park groupings were determined mainly by the clustering along Component 1 axis. Bryce Canyon NP (BRCA) and Dinosaur NM (DINO) became BD park group. Glen Canyon NRA (GLCA), Capitol Reef NP (CARE), Natural Bridges NM (NABR), Canyonlands NP (CANY), and Arches NP (ARCH) were grouped into the AN park group. Eigenvalues for each component given in each axis title
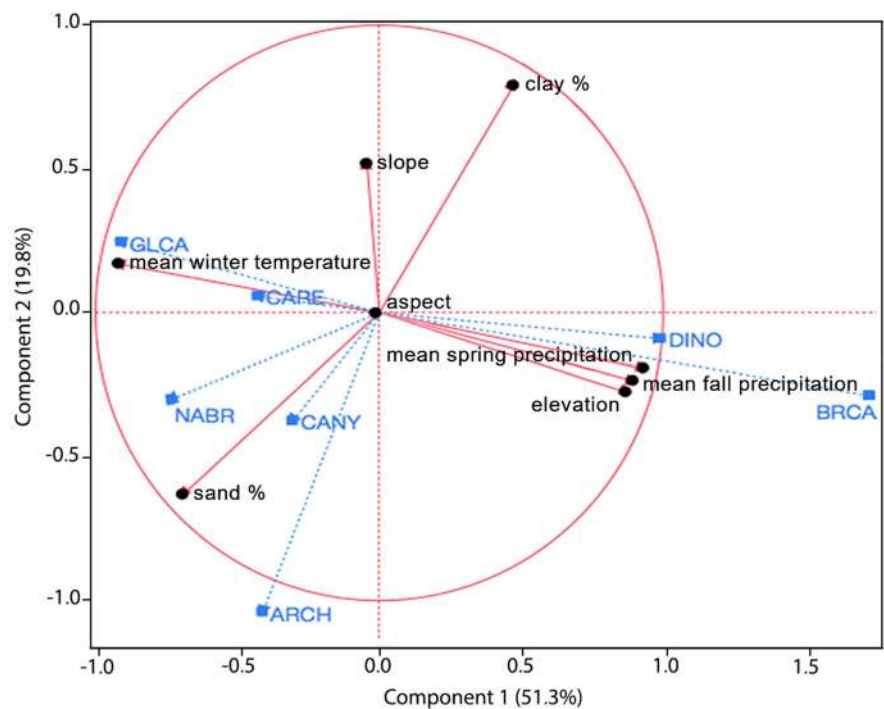
(Eigenvalue = 51.3%) was largely driven by mean fall and spring precipitation, mean winter temperature and elevation, with relatively equal contributions from each variable. The second component (Eigenvalue = 19.8%) largely consisted of clay and sand content with equal contributions from each of these two variables. Component One clustered the parks into two main groups: hot, dry parks (AN group: Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges) and the cold, wet parks (BD group: Bryce Canyon and Dinosaur).
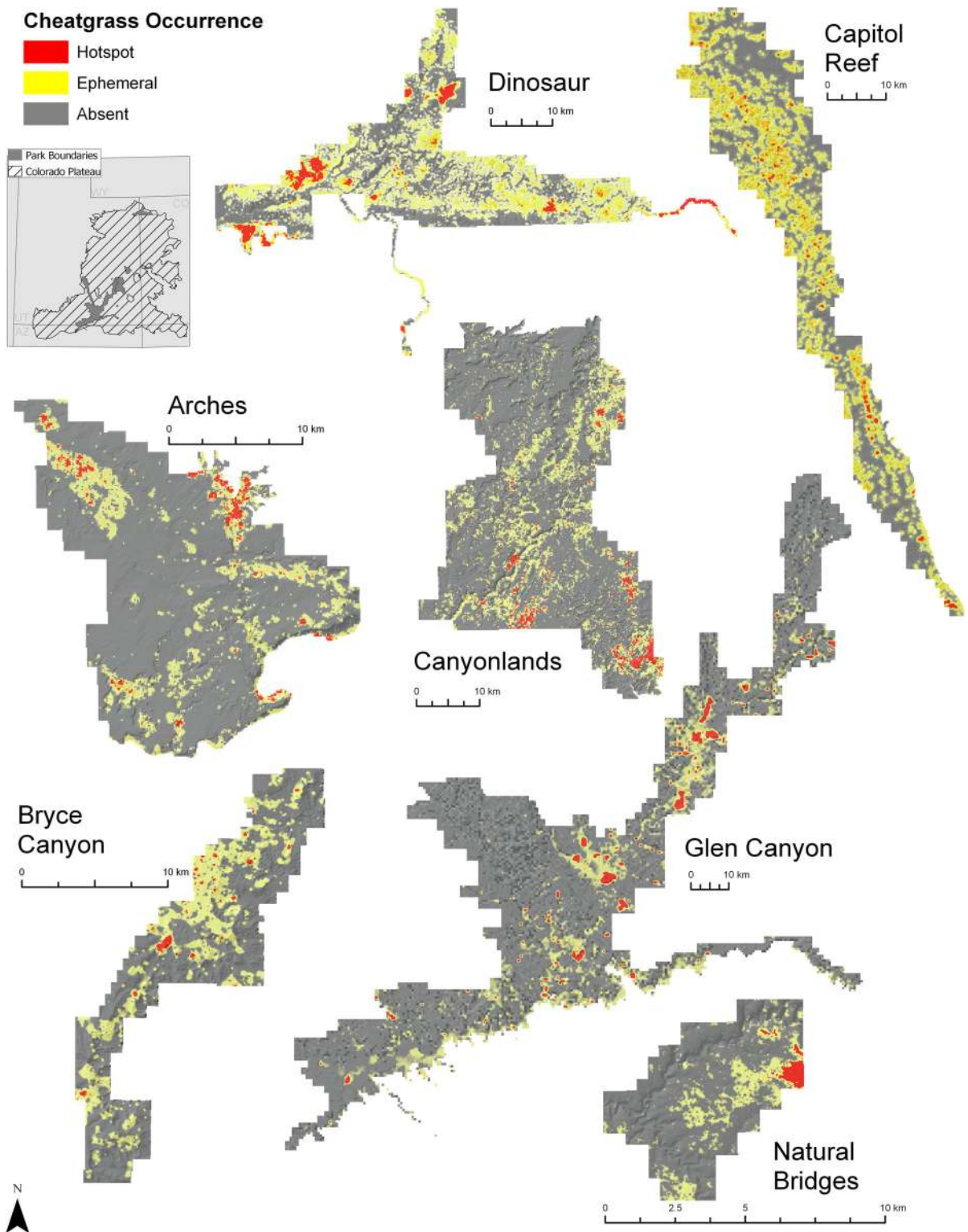
Hotspots

Cheatgrass had a value of at least 1 in the final composite layer (all years combined) in 3.8% of the area across all parks (Table 1, Fig. 2). Within the 3.8% area where cheatgrass was detected, *hotspots*, *ephemeral*, and *coldspots* populations covered 12.9, 85.9, and 1.2% respectively (Table 1). The AN park group had twice as much cheatgrass cover as the BD park group but the BD park group had slightly more hotspots (Table 1). The two smallest parks, Dinosaur NM and Natural Bridges NM, had the highest cheatgrass detection where 24.8% and 14.8% of the

parks were covered in cheatgrass in addition to the highest proportion of hotspots (Table 1).

Biophysical attributes by park group

All parks

For all parks combined, the best discriminant function combined the following six variables in decreasing order of importance: depth of plant-available water, elevation (m), mean winter temperature (°C), mean winter precipitation (mm), slope (°), and percent clay ($\Lambda = 0.8836213$, F = 7349, $P \leq 0.0001$) (Table 2). Percent weight for each variable decreased nearly 2-fold in descending order (Table 2). Because the top four variables for each park group comprised > 80% of the discrimination, we report only them (though results for all variables can be viewed in Online Appendix 2—Table S1). *Hotspots* had a higher probability of occurring in areas with deeper plant-available water ($P \leq 0.05$) and a lower elevation by 90–100 m ($P \leq 0.05$) compared to *ephemeral* populations and *no cheatgrass* areas. *Hotspots* also had 1 °C colder mean winter temperatures ($P \leq 0.05$) than *ephemeral* but no difference in mean winter temperatures compared to *no cheatgrass* ($P > 0.05$).

Fig. 2 Hotspot maps visualizing each park and the locations of hotspots, ephemeral populations, and areas of no detectable cheatgrass growth. Each park base layer is an elevation relief

Table 3 Top four biophysical attributes in order for best discriminant function

	Top four weighted biophysical attributes			
	Depth of plant available water (cm)	Elevation (m)	Mean winter temperature (°C)	Mean winter precipitation (mm)
All parks				
No cheatgrass	1.96 ± 001	1645 ± 1	0.02 ± 004	43.4 ± 0.02
Ephemeral	2.14 ± 0.001	1585 ± 1	0.30 ± 0.005	44.04 ± 0.02
Hotspots	2.5 ± 0.003	1497 ± 1.5	− 0.35 ± 0.01	43.48 ± 0.05
Pairwise comparisons				
NC × Hotspots	144,447***	302,590***	2,556,078	1,486,500
NC × Ephemeral	1,302,367***	1,706,133***	1,377,300**	93,324
Ephemeral × Hotspots	120,327***	81,642*	80,655*	237,137
	Percent clay in top 20 cm of soil	Elevation (m)	Mean winter precipitation (mm)	Depth of plant available water (cm)
AN group—hot, dry				
No cheatgrass	11.17 ± 0.02	1460 ± 0.5	40.4 ± 0.02	1.79 ± 0.001
Ephemeral	14.6 ± 0.02	1398 ± 0.6	41.05 ± 0.02	1.99 ± 0.001
Hotspots	15.15 ± 0.05	1302 ± 1.6	41.44 ± 0.08	2.07 ± 0.003
Pairwise comparisons				
NC × Hotspots	112,343 ***	361,217***	249,627*	148,160*
NC × Ephemeral	1,108,367***	1,864,667***	1,472,367	1,202,567***
Ephemeral × Hotspots	106,437*	63,422***	85,469	109,227***
	Slope	Mean winter temperature (°C)	Depth of plant available water (cm)	Mean fall precipitation (mm)
BD group—cold, wet				
No cheatgrass	14.98 ± 0.03	− 3.51 ± 0.00	2.25 ± 0.01	91.98 ± 0.03
Ephemeral	8.8 ± 0.02	− 3.31 ± 0.00	2.42 ± 0.002	92.03 ± 0.03
Hotspots	3.7 ± 0.02	− 3.75 ± 0.003	3.04 ± 0.004	83.33 ± 0.06
Pairwise comparisons				
NC × Hotspots	403,463***	36,797***	101,121***	353,160***
NC × Ephemeral	2,021,367***	1,487,967	1,280,467***	461,900
Ephemeral × Hotspots	46,890***	41,653***	136,557***	43,954***

Mean ± SE presented for each cheatgrass population type: no cheatgrass (NC), ephemeral, hotspots, in the top three rows of each park group. Pairwise comparisons were done using Wilcoxon rank sum test. W-values and significance indicated by asterisks: *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$ in the bottom three rows of each park group

Hotspots had fairly similar mean winter precipitation values of 43.5 mm/winter ($P > 0.05$) (Table 3, Fig. 3). *Ephemeral* populations had a higher probability of being found in areas with: deeper plant-available water ($P \leq 0.05$), a 60 m lower average elevation ($P \leq 0.05$) and warmer mean winter temperatures ($P \leq 0.05$), but similar mean winter precipitation ($P > 0.05$) when compared to *no cheatgrass* areas (Table 3, Fig. 3).

Arches, Canyonlands, Capitol Reef, Glen Canyon, Natural Bridges Park Group

The best discriminant function for the hot, dry parks (AN group) used five variables in decreasing order of importance: percent clay, elevation, mean winter precipitation, depth of plant-available water, and distance to human infrastructure (km) ($\Lambda = 0.88265$, $F = 4808.2$, $P \leq 0.0001$) (Table 2). Clay content was
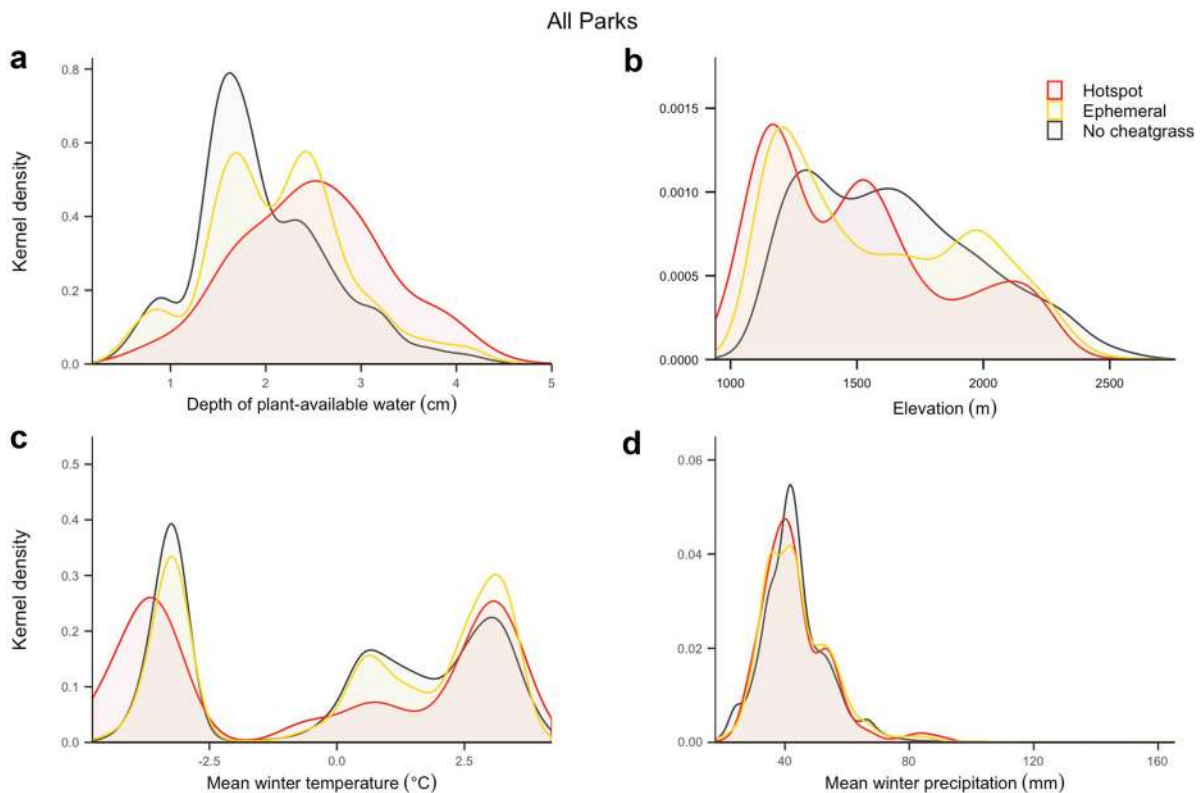
All Parks

Fig. 3 Kernel density plots of the top four weighted variables when all parks are combined: **a** plant available water depth (38.1%), **b** elevation (20.6%), **c** mean winter temperature (13.0%), and **d** mean winter precipitation (7.4%)

$4 \pm 0.02\%$ higher in *hotspots* compared to *ephemeral* or *no cheatgrass* locations (Table 3, Fig. 3) ($P \leq 0.05$). *Hotspots* were 100-160 m lower elevation ($P \leq 0.05$) and were on average a 0.5 km closer to human infrastructure ($P \leq 0.05$) compared with *ephemeral* populations and *no cheatgrass* areas (Table 3, Fig. 3). *Hotspots* had 1 mm more mean winter precipitation and deeper plant-available water ($P \leq 0.05$) than *no cheatgrass* areas ($P \leq 0.05$). There was no difference in mean winter temperature and plant available water between *hotspots* and *ephemeral* populations ($P > 0.05$). *Ephemeral* populations had higher probability of being found in 3% higher percent clay ($P \leq 0.05$) than *no cheatgrass* areas. *Ephemeral* populations had lower elevations by 62 m on average ($P \leq 0.05$), and deeper plant-available water depths ($P \leq 0.05$) compared to *no cheatgrass* areas. There were no differences in *ephemeral* and *no cheatgrass* areas mean winter precipitation ($P > 0.05$) (Table 3, Fig. 4).

Bryce Canyon and Dinosaur Park group

The best discriminant function for the BD group used seven variables in decreasing order of importance: slope, mean winter temperature, depth of plant available water, mean fall precipitation, elevation, and mean SPEI, and distance to human infrastructure ($\Lambda = 0.7164597$, F = 6996.7, $P \leq 0.0001$) (Table 2). *Hotspots* had a 2.4- and 4-fold decrease in slope ($P \leq 0.05$) compared to *ephemeral* and *no cheatgrass* areas (Table 3, Fig. 5). *Hotspots* had a 0.35 °C drop in mean winter temperature ($P \leq 0.05$), deeper plant-available water ($P \leq 0.05$), and nearly 9 mm less mean fall precipitation ($P \leq 0.05$) than *ephemeral* populations and *no cheatgrass* areas (Table 3, Fig. 5). *Ephemeral* populations had a 1.7-fold decrease in slope ($P \leq 0.05$), a similar mean winter temperature ($P > 0.05$), deeper plant-available water ($P \leq 0.05$), and similar mean fall precipitation when compared with *no cheatgrass* areas ($P > 0.05$) (Table 3, Fig. 5).
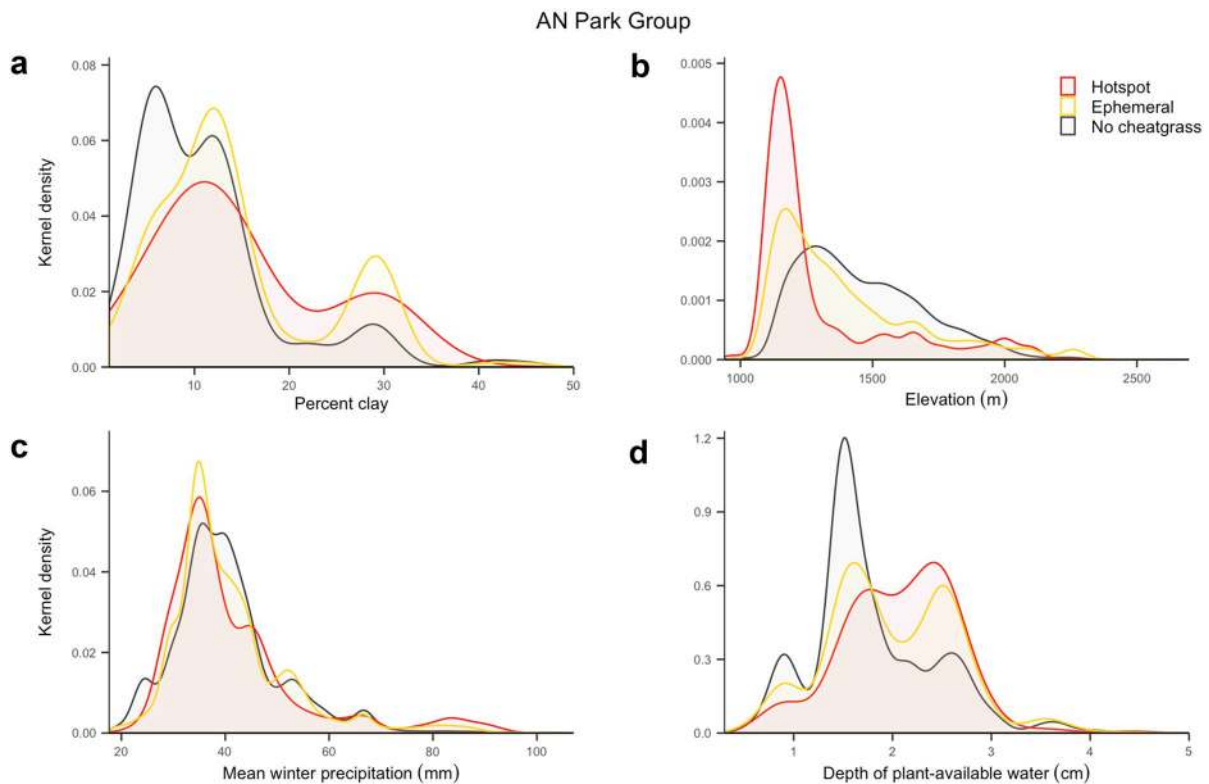
Fig. 4 Kernel density plots of the top four weighted variables for the AN Park Group (Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges): **a** percent clay (33.5%), **b** elevation (22.5%), **c** mean winter precipitation (12.6%) and **d** plant available water depth (6.3%)

Discussion

The systematic model that we developed as part of our first objective demonstrated that there are strong spatial and temporal factors associated with the distribution of cheatgrass in the Colorado Plateau national parks. By combining the insights and results derived from remote sensing, detection algorithms, and hotspot analysis, the data indicate that cheatgrass can be mapped on large landscape scales with high accuracy and efficiency (Fig. 2) allowing an examination of the biophysical correlates driving its distribution (Tables 2, 3, Figs. 3, 4 and 5). Our findings indicate that *hotspots,* areas with persistent cheatgrass, are found across the Colorado Plateau and appear to be most strongly correlated with deeper plant available water, lower elevations, colder mean winter temperatures, flatter slopes, and lower mean fall precipitation compared to *ephemeral* populations and *no cheatgrass* areas (Table 3). However, there are notable landscape

differences between the two park groups, and their separation creates a more tailored suite of biophysical characteristics with which to examine cheatgrass distribution. This is important information in understanding where future invasions and possible expansions are likely with projected climate change (Bradley et al. 2018).

Presence and persistence of cheatgrass

Cheatgrass dominates nearly 4% of the total area of Colorado Plateau's national parks (Table 1, Fig. 2). This is likely an underestimate of cover, given the required detection thresholds (Kokaly 2011; Bradley et al. 2018) and the more robust alpha level cutoffs we used (see "Methods" section). Of particular concern is Dinosaur NM, where hotspots covered nearly 25% of the park area (Table 1). In this park, grazing and fires have created widespread disturbance in the past 150 years (Sherrill and Romme 2012) that promote
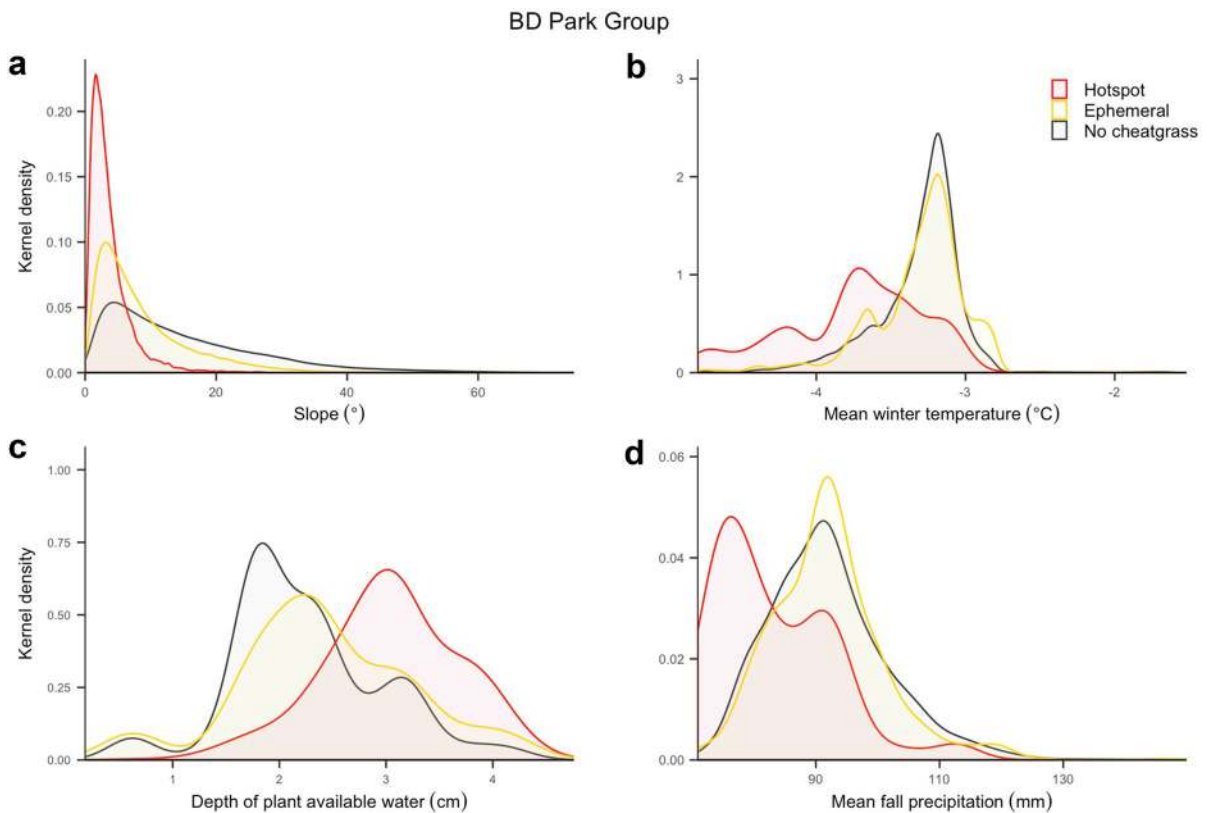
BD Park Group

Fig. 5 Kernel density plots of the top four weighted variables in the discriminant function for the BD Park Group (Bryce Canyon and Dinosaur): **a** slope (38.3%), **b** mean winter temperature (23.8%), **c** plant available water depth (12.0%), and **d** mean fall precipitation (7.4%)

cheatgrass establishment and spread (St. Clair et al. 2016). Cheatgrass is considered one of the most aggressive invasive plant species and its successful establishment increases the likelihood of more frequent and larger fires (Bradley et al. 2018). This suggests that parks which have a high percentage of cheatgrass hotspots, like Dinosaur NM, are at increased risk of shorter fire intervals (Sherrill and Romme 2012). Increases in fire occurrence will substantially degrade visitor experiences (Bowman et al. 2011), reduce ecosystem services and biodiversity (St. Clair et al. 2016), and diminish the ability of the National Park Service to meet its mandate to conserve native species (National Park System Advisory Board 2001; Thompson et al. 2011).

Spatial patterns of cheatgrass invasion may have a foundation in the historical and current land use of the parks. Patterns seen in Glen Canyon NRA show ephemeral populations are spatially spread along the

Lake Powell reservoir and Colorado river's edge (Fig. 2). Receding water levels in response to drought and increased water demand in Glen Canyon NRA exposes more land every year, causing concern that cheatgrass may colonize in those locations (Bureau of Reclamation 2016). High numbers of recreationists in those areas in Glen Canyon compound the problem, as cheatgrass is an opportunistic invader that responds well to disturbance (Gelbard and Belnap 2003; Bradford and Lauenroth 2009). Other land uses, such as historical agricultural use, have led to a degraded - state of native plant communities previous to park establishment (Knapp 1996; Munson et al. 2016). In Canyonlands, where hotspots are found mostly in the south and southeastern parts of the park (Fig. 2), continuous and heavy grazing from the mid-1800s until park establishment in 1964 has facilitated dense invasions and as a result native plants have struggled to re-establish and rebound even after > 40

years of no grazing (Fick et al. 2016). Grazing in semi-arid and arid ecosystems can lead to an increase in invasibility by removing biotic resistance from the perennial herbaceous vegetation (Walker et al. 1981; Knapp 1996).

Biophysical correlates

Hotspots and *ephemeral* populations had a higher probability of being located in areas with deeper plant available water (Table 3; Figs. 3, 4 and 5). Soil moisture is a strong regulator of seed germination and a strong determinant of plant establishment success (Roundy et al. 2007; Prevéy and Seastedt 2014; Horn et al. 2015). Cheatgrass is a good competitor for soil water because of fast growing roots and a long growing season particularly when it germinates in the fall (Mack and Pyke 1983; Melgoza et al. 1990). Soil moisture is typically recharged with late summer monsoons on the Colorado Plateau, which can favor winter annual plants like cheatgrass that germinate in the fall when there is adequate soil moisture (Munson et al. 2011). Soil moisture at the surface can be vulnerable to evaporation in warmer temperatures, therefore having deeper soil moisture available after summer precipitation will favor establishment after fall germination before transitioning to winter (Cline et al. 1977; Miller et al. 2006).

Precipitation timing influences plant productivity and germination but may not be as good of an indicator for discriminating between cheatgrass population groups (Table 3) (Prevéy and Seastedt 2015; Horn et al. 2017). Our results show that *hotspot* distributions were not strongly correlated with differences in the amount of precipitation in spring, summer, or winter periods and only slightly with fall precipitation compared to *ephemeral* or *no cheatgrass* (Table 3, Figs. 3, 4, and 5). *Hotspots* were found in areas with lower mean fall precipitation compared to *ephemeral* and *no cheatgrass* areas (Table 3, Fig. 5d). We expected increased mean fall precipitation to play an important role in determining persistent populations of cheatgrass because of the positive effect of early precipitation on fall germination (Prevéy and Seastedt 2014; Horn et al. 2017; Gill et al. 2018). However, as the data show this is not the case (Table 3; Fig. 5d). One potential reason why there is an increased probability of hotspots with lower fall precipitation is that when soils have water at depths greater than 0.5 m, the

soil water partitioning between native species and cheatgrass increases (Schwinning and Ehleringer 2001; Bradford and Lauenroth 2009). Lower fall precipitation may not wet the soil deep enough, to benefit native species with relatively deeper root systems, such that they are not able to persist and/or compete with cheatgrass for limited water resources higher in the soil profile; thereby increasing potential persistence of cheatgrass (Cline et al. 1977; Chambers et al. 2007). Our findings also show that ephemeral populations and no cheatgrass areas have near identical mean fall precipitation (Table 3, Fig. 5d). This may imply that ephemeral populations are growing in well-established native woody communities in which the natives are not as susceptible to cheatgrass' competitive effects (Booth et al. 2003). Climate scenarios predict changes to fall precipitation that could favor the increase of ephemeral populations (Christensen 2007; Horn and St Clair 2017). More ephemeral populations could eventually mean more hotspots by increasing propagule availability (Mazzola et al. 2011; Horn et al. 2017).

Persistent populations of cheatgrass were found in areas with lower mean winter temperature (Table 3; Fig. 3 and 4). Temperature influences soil–water relations and long-term survival of cheatgrass seedlings (Davis et al. 2000; Chambers et al. 2007). Cheatgrass can germinate at cold temperatures and harden off before winter temperatures drop too low or grow throughout the winter (Meyer et al. 1997; Chambers et al. 2007). Cooler temperatures result in less evapotranspiration which would increase favorable soil–water conditions (Meyer et al. 1997; Davis et al. 2000; Chambers et al. 2007). Even at higher elevations, slower accumulation of degree-days favors cheatgrass density and population growth due to a lower risk of detrimental winter germination (Griffith and Loik 2010). Ephemeral populations are more likely found in warmer mean winter temperatures than areas of no cheatgrass and persistent populations (Table 3, Figs. 3 and 4). Without sufficient precipitation, a warmer winter could prevent persistence in cheatgrass growth through the lack of suitable soil moisture (McMichael and Quisenberry 1993).

Cheatgrass establishment can vary strongly across elevation gradients (Abella et al. 2012; Prevéy and Seastedt 2014). *Hotspots* and *ephemeral* populations had a higher probability of being found below elevations of 1300 m (Table 3; Fig. 3b), similar to

the results of Chambers et al. (2007), and may be limited by long term soil freezing and increased snow cover at higher elevations (Griffith and Loik 2010). Higher elevations typically have later snow pack melt which delays cheatgrass growth and emergence (Concilio et al. 2013). Lower elevations that still have some snow cover have warmer soils and earlier spring melt which is conducive to cheatgrass germination and growth (Chambers et al. 2007; Roundy et al. 2007). Climate variability also increases with lower elevations which increases susceptibility to invasion in an arid or semi-arid environment (Dukes and Mooney 1999; Chambers et al. 2007).

Hotspots were more likely in areas with higher percent clay (Table 2, Fig. 4). Soil characteristics greatly affect the germination and establishment of plants through their influence on water relations and nutrient holding capacity (Marschner 1983). Higher clay content has higher water and nutrient holding capacity (Hillel 1998). Cheatgrass showed higher germination and establishment in areas with greater clay content in wet years (Miller et al. 2006) likely due to better water availability in the upper profile of the soil where cheatgrass typically can outcompete native plants (Bradford and Lauenroth 2009).

We found more hotspots in flatter landscape settings (Table 3, Fig. 5a), possibly because of greater soil stability and increased land use compared with places with steep slopes. Flatter slopes typically experience less water induced soil erosion and increased soil depths which favor water retention (Morgan 2009). Studies have shown downslope patterns in clay and silt content which would create more suitable conditions for cheatgrass persistence (Neff et al. 2005; Reynolds et al. 2006). Flatter landscapes also experience and are more easily accessible for animal and human use (Morgan 2009). Cheatgrass has a well-documented positive interaction to disturbance and increased land use (Gelbard and Belnap 2003; West et al. 2017; Bradley et al. 2018) which could be intensified in areas that have easier access. Soil erosion, removal of native vegetation, and decreased biological soil crusts have adverse impacts that increase susceptibility and success of invasion by cheatgrass (Cline et al. 1977; Belnap et al. 2001; Levine et al. 2003).

Our results did not show that human infrastructure such as trails, roads, and visitor centers played a key role in discriminating between *hotspots*,

ephemeral, and *no cheatgrass* areas (Table 2). However, *hotspots* were on average closer to human infrastructure compared to *ephemeral* and *no cheatgrass* (Online Appendix 2—Table S1). Legacy effects of historic land uses could lead to the persistence of cheatgrass in certain areas of these parks and historical disturbance is likely to play a key role in how the biophysical correlates interact (Mack et al. 2000; D'Antonio and Thomsen 2004; Neff et al. 2005). For example, as parks like Canyonlands experienced heavy and continuous grazing before park establishment, biological soil crusts that are known to be able to resist and prevent cheatgrass establishment by creating physical barriers for germination and growth are disrupted creating an opportunity for invasion (Deines et al. 2007; Serpe et al. 2008). Areas of the park that meet the landscape criteria for *hotspots* in the AN park group (low elevation, higher clay, flatter slopes, and deeper soils) (Table 3, Figs. 3, 4) are also areas that have had these historical land disturbances that have shown long term legacy effects in other studies (Fig. 2) (Fick et al. 2016; Munson et al. 2016).

GIS remote sensing

The results of this study have broadened our understanding of landscape level biophysical factors that are associated with cheatgrass establishment and persistence. The combination of remote sensing and GIS technology we used was both cost- and time-effective, unlike many previous efforts (Mack 2010). Previous GIS remote sensing studies of cheatgrass distribution had to be highly selective in what years were used (Bradley and Mustard 2006; Bradley 2009a; Balch et al. 2013), were restricted by the coarse resolution of MODIS (250 m and 1 km) (Stohlgren et al. 2010; Balch et al. 2013; Bradley et al. 2018), and required > 40% plant cover for accurate detection (West et al. 2017). Although our DESI analysis used commercial software [*ENVI version 4.8* (*Exelis Visual Information Solutions,* Boulder, Colorado)], comparing NDVI images from different seasons can be more widely adopted on publicly available cloud-computing platforms to detect cheatgrass and other invasive species with distinct phenologies. This approach can lead to highly accurate detection, across different landscapes, with relatively low invasive cover, an increased number of years, and at greater spatial resolution.

Conclusion

The expansion of cheatgrass is a major concern for the national park service and land managers because of its ability to accelerate fire cycles and create vegetation state changes (D'Antonio and Vitousek 1992). The hotspots we identified provide an ideal target for high priority management, as these areas are likely seed sources for the future expansion of cheatgrass populations (Mazzola et al. 2011). By reducing hotspots, expansion may be halted or slowed. *Ephemeral* populations are problematic in certain years, especially those with above-average precipitation, and can perpetuate habitat degradation potentially creating more *hotspots* (Pilliod et al. 2017; Bradley et al. 2018). As the understanding of what causes big fire years and the biophysical traits associated with invasive species-fire cycles improves (Balch et al. 2018), knowing the geographic locations of potential *hotspots* and *ephemeral* populations based on predictive modelling would enable more preventative management measures. In addition, these areas need to be analyzed and assessed under future climate conditions or expected changes in land use, as invasion potential may change (Bradley 2009b; Prevéy and Seastedt 2015). Using our data combined with future climate models might provide preliminary predictions about future establishment and spread of cheatgrass across the Colorado Plateau. Preventing unnatural wildfire damage would decrease economic, ecologic, and human health hardships associated with wildfire (Bowman et al. 2011; Thompson et al. 2011). Areas with no cheatgrass are important to identify so that limited management resources can be applied elsewhere. This hierarchical management approach allows more effective utilization of resources and likely better outcomes in these changing landscapes.

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