



Biophysical factors control invasive annual grass hot spots in the Mojave Desert

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Abstract Invasive annual grasses can promote ecosystem state changes and habitat loss in the American Southwest. Non-native annual grasses such as *Bromus* spp. and *Schismus* spp. have invaded the Mojave Desert and degraded habitat through increased fire occurrence, severity, and shifting plant community composition. Thus, it is important to identify and characterize the areas where persistent invasion has occurred, identifying where subsequent habitat degradation has increased. Previous plot and landscape-scale analyses have revealed anthropogenic and

biophysical correlates with the establishment and dominance of invasive annual grasses in the Mojave Desert. However, these studies have been limited in spatial and temporal scales. Here we use Landsat imagery validated using an extensive network of plot data to map persistent and productive populations of invasive annual grass, called *hot spots*, across the entire Mojave Desert ecoregion over 12 years (2009–2020). We also identify important variables for predicting *hot spot* distribution using the Random Forest algorithm and identifying the most invaded subregions. We identified *hot spots* in over 5% of the Mojave Desert mostly on the western and eastern edges of the ecoregion, and invasive grasses were

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detected in over 90% of the Mojave Desert at least once in that time. Across the entire Mojave Desert, our results indicate that soil texture, aspect, winter precipitation, and elevation are the highest-ranking predictive variables of invasive grass *hot spots*, while anthropogenic variables contributed the least to the accuracy of the predictive model. The total area covered by *hot spots* varied significantly among subregions of the Mojave Desert. We found that anthropogenic variables became more important in explaining invasive annual establishment and persistence as spatial scale was reduced to the subregional level. Our findings have important implications for informing where land management actions can prioritize reducing invasive annual persistence and promoting restoration efforts.

Keywords *Bromus* · Invasion · *Schismus* · Remote sensing · Invasive non-native annual grasses

Introduction

Invasive annual grasses can degrade ecosystems by altering community structure and enhancing or changing disturbance regimes (D'Antonio and Vitousek 1992; Pimentel et al. 2005; Vitousek et al. 1997). Annual grass invasions can accelerate fire return intervals, compete with native species, and change biogeochemical cycles (Brooks et al. 2004; D'Antonio and Vitousek 1992; Wilcox et al. 2012). The rapid spread of invasive annual grass, often accelerated by climate change, calls for an urgent need to understand the current distribution of successful invaders, spatial patterns of productive populations, and the biophysical and anthropogenic factors associated with those invasions (Abatzoglou and Kolden 2011; Bradley 2009; Sandel and Dangremond 2012). The distribution and abundance of invasive annual grasses vary interannually making characterizations of invasions at relevant scales has been a costly and difficult task in past years. Recently, the advancement of remote sensing monitoring technologies has helped improve the detection and spread of invasive plants across spatial and temporal scales (Bradley 2014; Dahal et al. 2022; Klinger et al. 2019; Pastick et al. 2021).

Invasive annual grasses have been documented in regions throughout the world, and have been particularly influential in the American Southwest and

West, where wildfire occurrence has dramatically increased in some areas, such as in the Mojave Desert and Great Basin (Brooks and Matchett 2006; Fusco et al. 2019; Vitousek et al. 1997; Vitousek et al. 1996; Whisenant 1990). The drylands of this region feature large gaps between native perennials, providing available habitat for opportunistic invasion of non-native grasses (Beatley 1966; Chambers et al. 2007; Gill et al. 2018). Specifically, species invading the Mojave Desert include winter annuals from the genus *Bromus*, primarily *Bromus rubens* L. and *Bromus tectorum* L., and the genus *Schismus*, primarily *Schismus barbatus* var. *arabicus* (Nees) and *Schismus barbatus* (L.) Thell. These Eurasian grasses are thought to have been introduced to western North America sometime in the latter half of the nineteenth century or early twentieth century (Brooks 2000a; Salo 2005), and have a wide physiological tolerance for both cold and warm extremes (Bykova and Sage 2012; Loria and Noy-Meir 1979). As winter annuals, they are primarily fall and winter germinating species (Brooks 2000a, 2000b), with the most significant growth occurring in the early spring, but they can also germinate following sufficient rainfall in the spring and summer (Beatley 1974). High spatial and temporal variation in precipitation in arid systems contributes to variability in the distribution of productive populations of annual plants between years, with extremes represented in super bloom years within the Mojave Desert (Beatley 1974; Wallace and Thomas 2008). Invasive annual grasses in the west and southwestern United States can green-up earlier in the spring and often senesce earlier in the summer compared to native perennial plants (Beatley 1974; Brooks 1999a; DeFalco et al. 2007). These phenological differences make invasive annuals good targets for remote detection of invasion and have been key in many important studies examining the distribution of invasive plants using satellite imagery (Bishop et al. 2019; Bradley 2014; Bradley et al. 2018; Dahal et al. 2022; Villarreal et al. 2019). However, inferences made from remote sensing about invasive annual plants are informed by plot-scale studies which have effectively investigated correlates to invasion and consequences of invasion by annual grasses in the Mojave Desert.

Prior plot-scale studies have yielded important conclusions about annual grass invasion patterns and consequences over relatively short time periods and small spatial extents (Abella et al. 2012; Brooks and

Berry 2006). Annual grass invasion has been consistently found to increase fine fuel loads, fuel continuity, and fire occurrence in the region (Brooks and Matchett 2006; Davies and Nafus 2012; Germino et al. 2015). These changes pose risks to fire-intolerant native species due to the absence of evolutionary pressures resulting from historically infrequent fires in the region (Brooks 1999a; Brooks et al. 2004). Additionally, non-native annual grasses alter hydrology and negatively impact important vertebrate habitats throughout the Mojave Desert (Brooks and Esque 2002; Rowland and Turner 1964; Wilcox et al. 2012). Studies examining correlates of invasion have differed in focus and conclusions. For example, invasive annuals were found dominating areas near dirt roads and in years with lower-than-average rainfall in the western Mojave (Brooks and Berry 2006). In contrast, work in the central Mojave near Lake Mead found that *B. rubens* populations were found at middle to high elevations and were correlated with higher-than-average rainfall (Abella et al. 2012; Duniway and Palmquist 2020). In addition, soil characteristics and nutrient additions such as nitrogen input have been found to locally control abundance as investigated in Joshua Tree National Park (Allen et al. 2009). Differences in focus and correlated variables of previous plot-scale studies of invasive annual grasses in the Mojave Desert could be a result of interannual variability, biogeographical differences within the region, or differing study designs. The causes of these differences create challenges in mapping the distribution of invasive annual grasses, a priority for invasive species management and research (Foxcroft et al. 2017; Shelley & Smith 2012; USDA 2017).

To accomplish the important task of mapping invasive plant distribution, remote sensing can expand the spatial and temporal scale of monitoring invasive annual grasses and identify the most productive and dense areas of invasion that are of greatest management concern (O'Neill et al. 2021). Mapping invasive annuals over multiple years with remote sensing can help identify hot spots, or areas of persistent invasive populations, an important task for annual grasses in dryland ecosystems with high interannual variability (Bishop et al. 2019). Hot spots are statistically significant clusters of frequently detected invasives and can be distinct from areas of initial invasive establishment as well as from the interannual variability due to differing climatic conditions (O'Neill et al. 2021; Ord

and Getis 1995). Large landscape-level maps help prioritize conservation goals but can be difficult to create depending on both spatial and temporal scales and sensor availability. Tools like small uncrewed aerial vehicles (sUAVs) are useful to map invasive species on a small preserve scale (Bishop and Errigo 2023), but lack the depth in time and space to apply to large landscape level management objectives common with agencies such as the US Bureau of Land Management. Therefore, the use of satellite imagery is important for identifying persistent and productive hot spots across larger spatial and temporal scales. These maps can then be useful for revealing where ecosystems have potentially been most negatively affected by invasion, allowing for understanding of the environmental factors that correlate with invasion success. (Lyons et al. 2020; O'Donnell et al. 2012; Wan et al. 2016). Historically, identification of invasion hot spots aids management, public outreach in biodiversity conservation, anthropogenic change mitigation, and can be used to prioritize where management treatments occur (Cowling et al. 2003; Ganzhorn et al. 2001).

To understand patterns of invasive grass distribution across the Mojave Desert ecoregion, we developed three aims. First, we aimed to identify the most persistent and productive populations within the Mojave Desert over 12 years using Landsat satellite imagery and spatial analysis to identify invasion hot spots. Our second aim was to learn which biophysical and anthropogenic variables are most important for predicting the spatial distribution of invasive annual grass hot spots in the Mojave Desert. Finally, we set out to identify the most invaded subregions of the Mojave Desert ecoregion, which we defined as subregions with the greatest proportion of the total area occupied by persistently detected populations. We hypothesized that hot spots will be primarily distributed in the basin and ranges in the Western Mojave Desert where a combination of early fall rains and lowering temperatures in the fall and winter cause potential germination events and on the extreme western edges where the climate is transitional to a wetter Mediterranean climate (Hereford et al. 2006). We also hypothesized that due to the seasonality of annual grass germination and growth, fall and winter precipitation will be important predictive variables, and due to their ability to withstand to disturbance,

proximity to human infrastructure would also be an important predictive variable.

Methods

Study area

The Mojave Desert is a geologically and biologically unique ecoregion in the southwest United States due to a mixture of climatic and topographic extremes. It spans over 12 million hectares and four different states, California, Nevada, Arizona, and Utah. The Mojave Desert contains 16 subregions that are each characterized by unique geological and climate conditions (Omernik & Griffith 2014; Tagestad et al. 2016). The region is one of the hottest and driest ecoregions in the US and is characterized by north–south-oriented basins and ranges, creating significant elevational gradients. The highest peak in the Mojave is Mt. Charleston in Nevada at 3632 m, while Death Valley reaches 86 m below sea level, the lowest point in North America. Death Valley has recorded the hottest surface temperature on earth at 56.7 °C and only averages 50 mm of precipitation annually (El Fadli et al. 2013), while Mt. Charleston has an average January temperature of −7.1 °C with nearly 600 mm of precipitation annually. The Mojave Desert hosts a diverse suite of ecotypes and plant communities. The middle elevations of the Mojave Desert ranges and footslopes are primarily inhabited by creosote bush (*Larrea tridentata* (DC.) Coville) and white bursage (*Ambrosia dumosa* (A. Gray) Payne) scrub and blackbrush (*Coleogyne ramosissima* Torr.) shrubland with iconic Joshua tree (*Yucca brevifolia* Engelm.) communities scattered throughout much of the desert (St. Clair and Hoines 2018). Higher elevations throughout the Mojave ranges include piñon-juniper communities and big sagebrush (*Artemisia tridentata* Nutt.), especially in the northern areas. The lowest elevations of the Mojave basins are dominated by saltbush scrubland (*Atriplex* spp.). Perennial grasslands cover small areas throughout the eastern Mojave Desert basins (McAuliffe 2016).

In addition to varied environmental conditions, the Mojave Desert is home to a variety of land uses and population densities, and is managed by many different land management agencies. The largest city in the

Mojave Desert is the Las Vegas metropolitan area, NV, with over 2 million people. Other notable cities in the Mojave Desert are St. George, UT, in the northeast, and Victorville, Lancaster, and Palmdale, CA, in the southwest. Additionally, the Mojave Desert is a short drive from Los Angeles and Phoenix, bringing large numbers of human visitors that also contribute to land use disturbance through recreational use. Over 1.3 million ha of the Mojave Desert is occupied by U.S. Department of Defense installations used for military training and testing, with 85% of the desert managed by federal agencies in some capacity. Renewable energy is a growing sector in the Mojave Desert, with solar and wind facilities being added every year (Hernandez et al. 2015). The region is also home to Joshua Tree and Death Valley National Parks as well as the Mojave National Preserve, comprising more than 3.4 million ha combined. While much of the Mojave Desert is absent of large permanent human settlements, roads traverse the entire region. There are more than 125,000 km of roads and a history of unregulated and extensive recreation off-highway vehicle use (OHVs), particularly in the 1970s and 1980s (U.S. Census Bureau 2015; Woodhouse 2019).

Detection of early season annuals

To identify persistently productive populations of invasive annual grasses we first classified Landsat imagery using Detection of Early Season Invasives (DESI) methods (Kokaly 2010a), then performed Getis-Ord G_i^* Hot Spot Analysis (Ord and Getis 1995) following the methods of Bishop et al. (2019). Cloud-masked Landsat 5, Landsat 7, and Landsat 8 surface reflectance data were processed from 2009 to 2020 in Google Earth Engine (Gorelick et al. 2017) to generate a 12-year time series of invasive grass occurrence (Landsat 5: 2011–2012, Landsat 7: 2012–2013, and Landsat 8: 2013–2020). We removed 2012 due to issues with the scan line corrector on Landsat 7. The DESI workflow is based on the observation that invasive annuals can quickly exploit available soil moisture and therefore green up earlier than most native perennial plants, and that locations with early-season pulses of greenness can be identified by comparing spring imagery to late-summer imagery when winter annuals have senesced (Beatley 1974; DeFalco et al. 2007; Kokaly 2010b). Using an early season period of

January–May and a mid-summer period of June–July, we calculated differential NDVI values (dNDVI) with the following equation:

$$\text{dNDVI} = \text{Maximum NDVI}_{\text{early - season}} \\ - \text{Median NDVI}_{\text{mid - summer}}$$

To avoid dependence on a single scene for each season, we calculated the NDVI for every cloudless scene available during the early season window was calculated and selected the maximum NDVI value for each pixel across the study region. Next, we calculated the median NDVI value of mid-summer scenes to create a median pixel NDVI composite for dNDVI calculations. This allowed us to classify an entire ecoregion while accounting for regional differences in the timing of peak greenness across environmental gradients. We used the dNDVI values to classify pixels by likelihood of invasive annual occurrence using threshold values as determined by testing dNDVI thresholds against field data measuring percent invasives cover values to attain the highest overall classification accuracy and kappa statistic.

For threshold testing and accuracy assessment ($n=274$), we used field data collected from 2012 to 2020 from the Bureau of Land Management Assessment, Inventory, and Monitoring terrestrial monitoring plots (Toevs et al. 2011); National Park Service's Inventory and Monitoring program for the Mojave Desert Network (Hupp et al. 2020); and two projects implemented by the United States Geological Survey (Duniway et al. 2012; Duniway and Palmquist 2020). These studies all used the line-point intercept method (LPI) to collect plant foliar cover and we calculated percent cover from LPI data using the terradactyl R package (McCord et al. 2022). We used field data collected between January 1 and April 15 to capture the peak greenness period for the target invasive species (*Bromus rubens*, *B. tectorum*, *B. madritensis*, *Brassica tournefortii*, *Erodium cicutarium*, *Schismus arabicus*, and *Schismus barbatus*). Target species were identified by including invasive species frequently found in our plots and determining they could be accurately identified as a group using our methods to ensure maximization of our kappa statistic. According to the field data, *B. rubens*, *B. tectorum*, and both *Schismus* species were the most common, and invasives represented 52% of the total annual herbaceous cover, so our discussion is focused primarily on those

four target invasive species. We tested invasive annual cover thresholds between 1 and 15% and dNDVI thresholds between 0.005 and 0.150 and selected the combination of percent cover and dNDVI thresholds that maximized the Kappa statistic. Ultimately, the thresholds for high probability pixels were $\geq 14\%$ rooted cover, with $\text{dNDVI} \geq 0.115$ (Kappa=0.418; overall accuracy=90.9%). In high probability pixels, invasives made up 55.6% of the total annual herbaceous cover. For low probability pixels, the thresholds were invasives $\geq 1\%$ cover, with $\text{dNDVI} \geq 0.030$ (Kappa=0.336; overall accuracy=70.4%). In low probability threshold pixels, invasives represented 52.4% of the total annual herbaceous cover (see supplementary material Figure S1). Following the categorical classification scheme outlined in Table 1, pixel values were rescaled for each classified year in the time series (Bishop et al. 2019; Kokaly 2010b). We then aggregated the classified rasters, and summed individual pixel values across 11 years, so that the values ranged from 0 (no detection in any years) to 22 (high probability pixel all 11 years).

Using the GAP/LANDFIRE 2011 National Terrestrial Ecosystem data (U.S. Geological Survey 2016), we masked pixels classified as water, human development, or agriculture from subsequent analysis to avoid errors in hot spot identification. Additionally, we masked stitching lines from the initial mosaicked Landsat scenes through the middle of the raster. We then converted the remaining pixels to point features and the categorical rescaled values (Table 1) were used in a Getis-Ord G_i^* Hot Spot Analysis in ESRI's ArcGIS Pro (version 2.9.0, Esri Inc., Redlands, CA, USA; ESRI Developer Network 2011; Ord and Getis 1995). Hot Spot analysis is a spatial statistical tool which uses the Getis-Ord G_i^* statistic to identify areas of significant clustering of high and low values. We used an inverse distance weighting rule of 120-m or 4 pixels. Additionally, we applied false discovery rate (FDR) correction to increase confidence in the identified hot spots (Caldas de Castro and Singer 2006; Ord and Getis 1995; Watson 1985). FDR is a method which accounts for the spatial autocorrelation common within large geographic datasets, by raising the threshold for significant values and ensuring independence. We classified values with high z -score and $p < 0.05$ as *hot spots*, and areas with low z -scores and significant p values, $p < 0.05$, as *cold spots*, however, there were no *cold spots* in this analysis. Pixels with

Table 1 Classification of DESI Imagery with rescaled values for hot spot analysis

DESI pixel value (Kokaly 2010a)	Description	Rescaled value (Bishop et al. 2019)
0	Masked from analysis	0
1	Low dNDVI threshold was not exceeded, and none of the eight surrounding pixels exceeded a threshold	0
2	Above the low probability threshold, but only one of eight surrounding pixels exceeded the low threshold	0
3	Exceeded high probability threshold, but only one of eight surrounding pixels exceeded the low threshold	1
4	Exceeded the low threshold, and more than one of eight surrounding pixels exceeded the low threshold	1
5	Exceeded the high dNDVI threshold, and more than one of eight surrounding pixels exceeded the low threshold	2

z-scores near zero and p values > 0.05 were classified as *ephemeral* populations. Our *ephemeral* class is defined by pixels where we detected at least one year of invasion with no spatial clustering of similar values during our study period meaning some pixels are a low temporal threshold (1 year), and a low DESI threshold (lower uncertainty/abundance threshold). Conversely, the *ephemeral* class also contains pixels that frequently exceeded the high threshold during our study period but did not have any statistically significant clustering. The raw aggregated DESI values (1–22, mentioned above) represent the range within the ephemeral class, with pixels with a value of 1 indicating low abundance probability and lower frequency, meanwhile, *ephemeral* pixels with a value of 22 represent high probability of high abundance and high frequency but no significant spatial clustering. We include the *ephemeral* class to highlight pixels that are neither *hot spots* or *none* that have measured detection at some point in our study period where low abundance of invasive annuals may occur with high temporal variation. Our categorical classification scheme is similar to (Sheley and Smith 2012), which recommends three classes to categorize invasion status are ideal for rangeland invasion mapping to prioritize areas for ecologically based management strategies (Christensen et al. 2011). The names of the classes are italicized, *hot spots*, *ephemeral*, and *none*, to clearly identify our specific statistical class. We then converted the results into a 30-m by 30-m resolution raster of *hot spot* occurrence. We tabulated and summarized the results of the hot spot analysis

by the EPA level IV Mojave subregions (Keys 1981; Omernik and Griffith 2014). The DESI annual prediction and the hot spot rasters are available from the USGS ScienceBase-Catalog (Villarreal et al. 2023).

Correlational analysis

We resampled elevation data from the USGS 1 arc-second digital elevation model and generated slope and aspect (Keys 1981; U.S. Geological Survey 2017). We used the aspect data to calculate northness $\left(\cos\left(\text{aspect} \times \frac{\pi}{180}\right)\right)$ and eastness $\left(\sin\left(\text{aspect} \times \frac{\pi}{180}\right)\right)$ and flat areas were included as zero values for both indices. We downloaded the soil nitrogen, percent clay, percent sand, soil organic carbon, electrical conductivity (EC), and bulk density data layers from Ramcharan et al. (2017) at point depths of 0, 5, 15, and 30 cm; values for these variables were calculated to 30 cm depth using a trapezoidal approximation for a definite integral. Data on coarse fragments down to 5 cm depth was downloaded from soil grids at 250-m resolution (Hengl et al. 2017). In the absence of measured or modeled soil hydraulic property data, we used a pedotransfer function (Saxton & Rawls 2006), to calculate percent soil moisture at permanent wilting point (PWP) incorporating percent sand, percent clay, and soil organic matter content (SOC * 1.72). We used PWP because of its relevance in water-limited systems and its incorporation of variables that were available at

the scale of our analysis. High PWP values correspond to soils dominated by fine pores (clays and clay loams), and low values correspond to soils with mostly large pores (sands). We downloaded PRISM seasonal precipitation totals and average seasonal temperature data and averaged the layers over the study years to create a raster of average seasonal climate conditions from 2009 to 2020 (Daly et al. 2002). Anthropogenic (human-related, i.e. roads) variables including surface management agency and grazing allotments were extracted as polygon layers from BLM's surface management agency dataset, and U.S. Geological Survey's Protected Area Database (PAD-US) conservation status layer was used for conservation status (U.S. Geological Survey 2020). As a proxy for human infrastructure, we used U.S. Census Bureau level 3 TIGER datasets to compile all roads within the Mojave Desert (U.S. Census Bureau 2015). We extracted the Euclidean distance to the nearest road for each pixel, using a point to line rule with the centroid of each pixel. The variables here are meant to represent the conditions related to invasive annual persistence, rather than effects of persistence, necessitating the notable exclusion of fire from the analysis. All of the covariates included were resampled using cubic convolution to match the 30-m \times 30-m pixels of the hot spot map. To avoid bias in the ranking of variable importance due to potential collinearity, we removed correlated variables (Pearson correlation coefficient, $r > |0.7|$). We removed seasonal temperature variables because of high collinearity with elevation; spring and summer precipitation were also highly correlated with fall precipitation, so we kept fall because the relationship annual plants traditionally have with fall precipitation. PWP is highly correlated with clay and sand content, so we chose to include it as a proxy for both. All of the geographic data processing was completed using ESRI's ArcGIS Pro 2.9 (version 2.9.0, Esri Inc., Redlands, CA, USA; ESRI Developer Network 2011).

To characterize which variables are the most important in distinguishing between invasion classes, the Random Forest classification algorithm was used to classify sample points based on predictive variables, and predictive variables were ranked according to their permutation importance (Breiman 2001). To ensure spatial independence, we used a GIS to sample 320,000 points in the study area using equalized stratified random sampling by invasion class (*hot spot*,

ephemeral, *none*), where an equal number of random samples from each class were recorded. Each data point contained all previously mentioned predictive variables. For simplicity and to keep the focus on the characterization of hot spots, we sampled ephemeral populations as a single class rather than as a gradient. We repeated this process ten times to ensure the sample points were representative of the entire system. Of the sampled points, 80% were used for training data, and 20% were set aside as test samples. The R package 'randomForest' was used to implement the model (Breiman 2001; Liaw and Wiener 2002) Random Forest is an ensemble machine learning method that creates a 'forest' of decision trees for classification. We used permutation importance or mean decrease accuracy as the variable importance mode, and 500 trees were made for each forest. Permutation importance randomly permutes the algorithm to exclude a particular variable and the output importance is an index of how much the predictive accuracy of the model decreases when the variable is excluded. We used the caret package (Kuhn 2015), and the previously allotted test dataset to create a confusion matrix and calculate a value for McNemar's test for identifying the reliability of our confusion matrix. We averaged the confusion matrices, McNemar's tests, and variable importance over ten iterations using the ten sample sets. We calculated standard error for each of the variable importance estimates to ensure an accurate understanding of relative importance. Finally, to understand the differences between hot spot group means, a Wilcoxon-rank sum test was performed on 999,999 sample data points (Hollander et al. 2013). We created kernel density plots using ggplot2 to identify the distribution of values for important predictive variables by hot spot response group (Wickham 2016). To better understand how these results may vary among highly invaded subregions of the Mojave Desert, we repeated the process within the six Level IV subregions where the highest percentage of *hot spots* were identified. For each of these six subregions, the same random forest protocol was repeated but only with one sample set of 125,000 points.

Results

The DESI classification revealed that 93.8% of analyzed pixels had values of at least 1, indicating at least

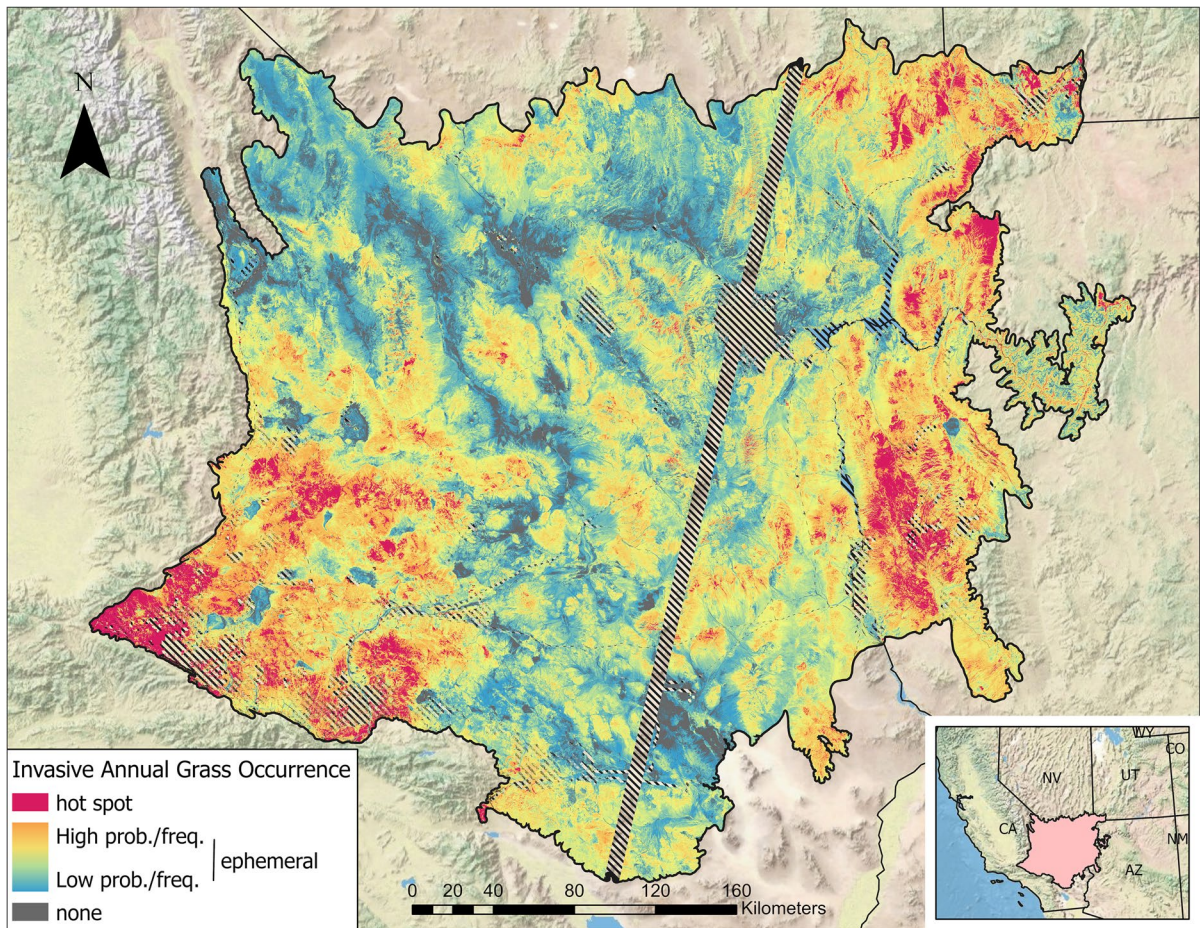


Fig. 1 Map of invasive annual grass occurrence in the Mojave Desert, outlined and defined by EPA level III ecoregion from 2009 to 2020 (Omernik and Griffith 2014). Ephemeral pixels are represented on a continuous scale derived from the raw DESI aggregation values (1–22), to show the variation

of detection frequency and invasive abundance probability within the class. Masked pixels include satellite stitching errors and areas classified as roads, water, agriculture, or developed land. *Hot spots* represent the most persistently productive and detectable populations over the study period

one year of detection of annuals at a low confidence threshold. Only 6.2% percent of analyzed pixels had no detectable populations of invasive annuals over the study period. The hot spot analysis revealed that *hot spot*, *ephemeral*, no invasive (*none*) pixels represented 5.4, 88.4, and 6.2% of the Mojave Desert area, respectively (Fig. 1). Although nearly the entire ecoregion detected *ephemeral* populations of invasive annuals, *hot spots* were primarily found in the eastern and western boundaries of the Mojave. The *hot spots* and pixels with no invasive annuals (*none*) were highly clustered into subregions rather than dispersed throughout the entire ecoregion.

Characterizing by subregion revealed that subregions with the highest percent of *hot spot* coverage were found in Western Mojave Basins, Eastern Mojave Mountain Woodland and Shrubland, Western Mojave Low Ranges and Arid Footslopes, Eastern Mojave Basins, and Eastern Mojave Low Ranges and Footslopes (Fig. 2; see supplementary material Table S1 for full summary). Meanwhile, the areas with the fewest *hot spots* and greatest percentage of no invasives (*none*) were Mojave Sand Dunes, Mesquite Flat/Badwater Basin, Death Valley/Mojave central trough, Amargosa Desert, and the Mojave Playas (Fig. 2).

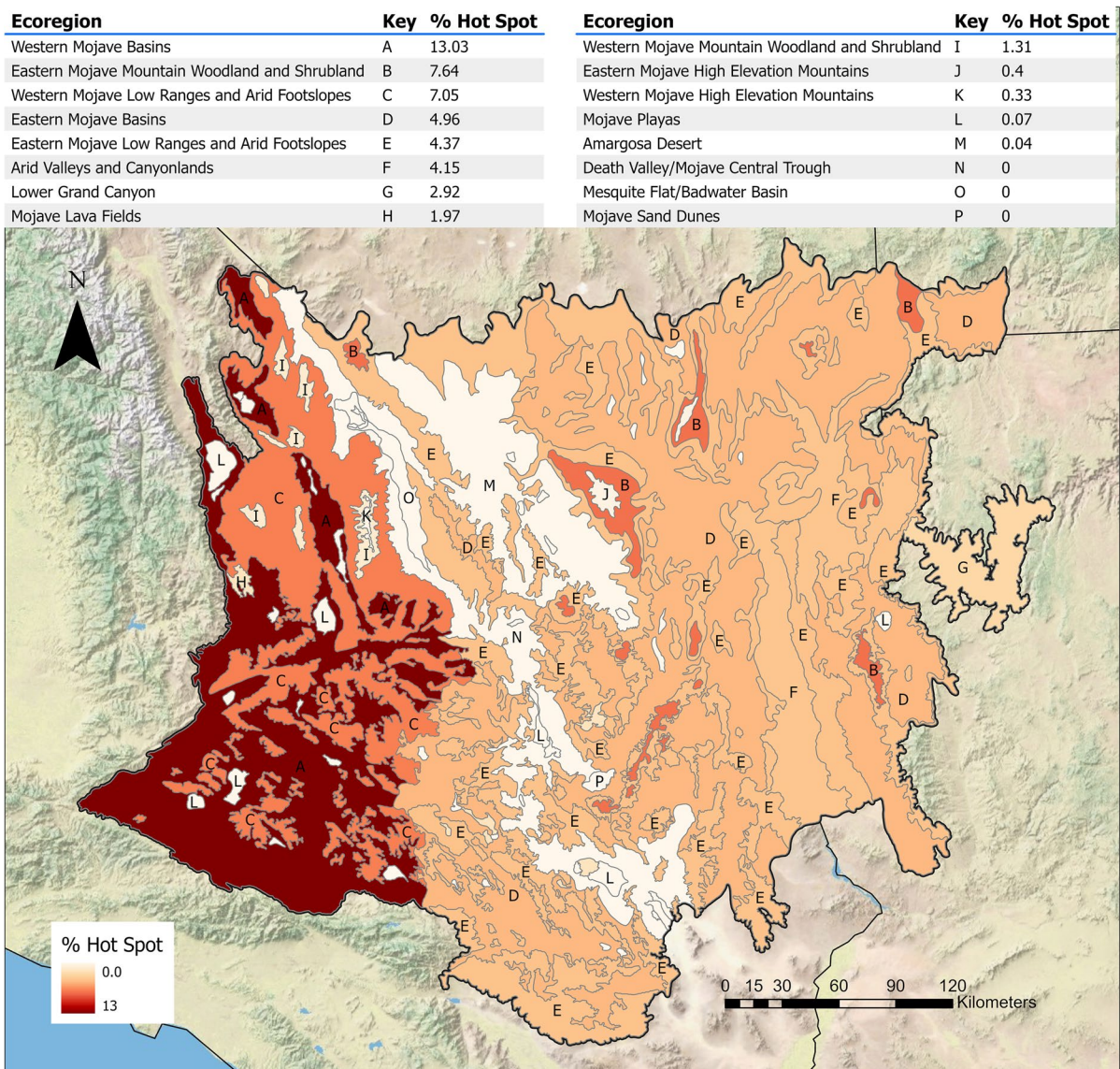


Fig. 2 Hot spots summarized by EPA level IV ecoregions (Omernik and Griffith 2014), ranked by percent area covered by hot spots

Variable importance

The mean kappa statistic across ten random forests was 0.80, and McNemar’s test was significant at $p < 0.0001$. The average overall accuracy of the models was 0.86, and hot spots were accurately identified 95.9% of the time, represented in the confusion matrix (Table 2).

Topographic, soil, and climate variables were all among the top-ranked variables (Fig. 3). Specifically, the top six ranked variables from the Random

Forest analysis were soil moisture at permanent wilting point (PWP), bulk density, northness, eastness, winter precipitation, and elevation. The bottom four ranked variables were all anthropogenic: distance to road, management agency, conservation status, and grazing allotment.

Due to the large sample size, the Wilcoxon-rank sum test indicated that the mean of all numerical variables was statistically significant between response groups. Therefore, rather than statistical significance, the practical significance of means was considered.

Table 2 Accuracy of the Random Forest model trained from 80% of 320,000 sampled pixels with selected correlated variables used for prediction represented as a confusion matrix

		Reference			Accuracy
		Ephemeral	Hot spot	None	
Prediction	Ephemeral	159,078	10,656	22,957	0.83
	Hot spot	25,015	202,745	640	0.89
	None	23,893	124	165,317	0.87
	Accuracy	0.77	0.95	0.88	0.86

Accuracy measured through model prediction of test data derived from the remaining 20% of the overall 320,000 point sample size

We found the means of the PWP parameter to differ between *hot spots* (7.5%), *ephemeral* pixels (7.7%), and pixels with no invasive annuals detected (*none*) (9.3%). *Hot spots* and *ephemeral* populations were more common in soils with a larger pore size (sandier) than pixels classified as *none*. While overall, the dominant soil texture in the Mojave Desert is sandy loam, *hot spots* had a narrow PWP distribution compared to pixels classified as *none*, which

aggregated over ten iterations with separate sample datasets. Bold values indicate the number of pixels accurately identified for each class

were wider and skewed right (Fig. 4a). Average bulk density in *hot spots* was 1398.6 kg m^{-3} , while it was 1395.3 kg m^{-3} in *ephemeral* pixels, and 1369 kg m^{-3} in *none* pixels, suggesting that low-bulk density soils support fewer invasive annuals. *Hot spots* were associated with northern facing slopes (0.06), while areas with no invasives were likely to be found on southern facing slopes (-0.13 ; Fig. 4b). *Hot spots* had the most winter precipitation, with an average of 89.7 mm,

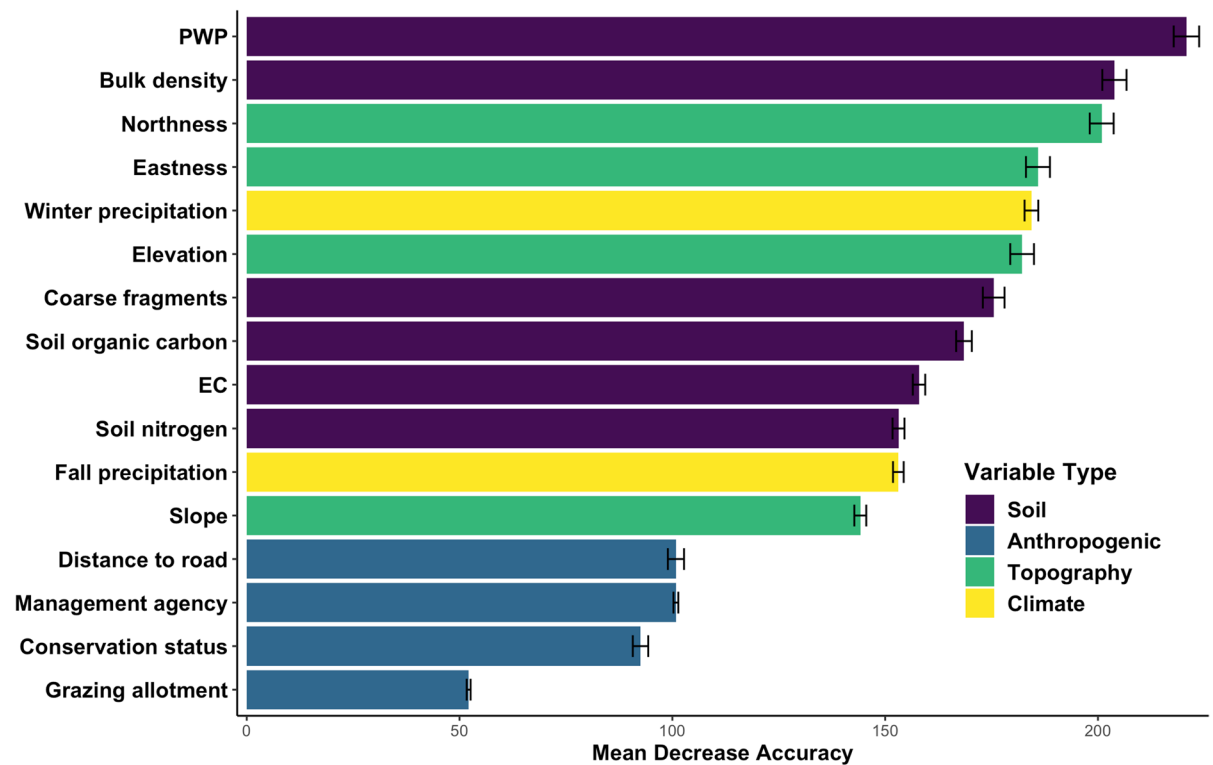


Fig. 3 Random Forest variable importance, ranked by contribution of accuracy to the model and grouped by variable type. Standard error bars were calculated from ten random forest tri-

als. PWP and EC refer to percent weight at wilting point and electrical conductivity, respectively

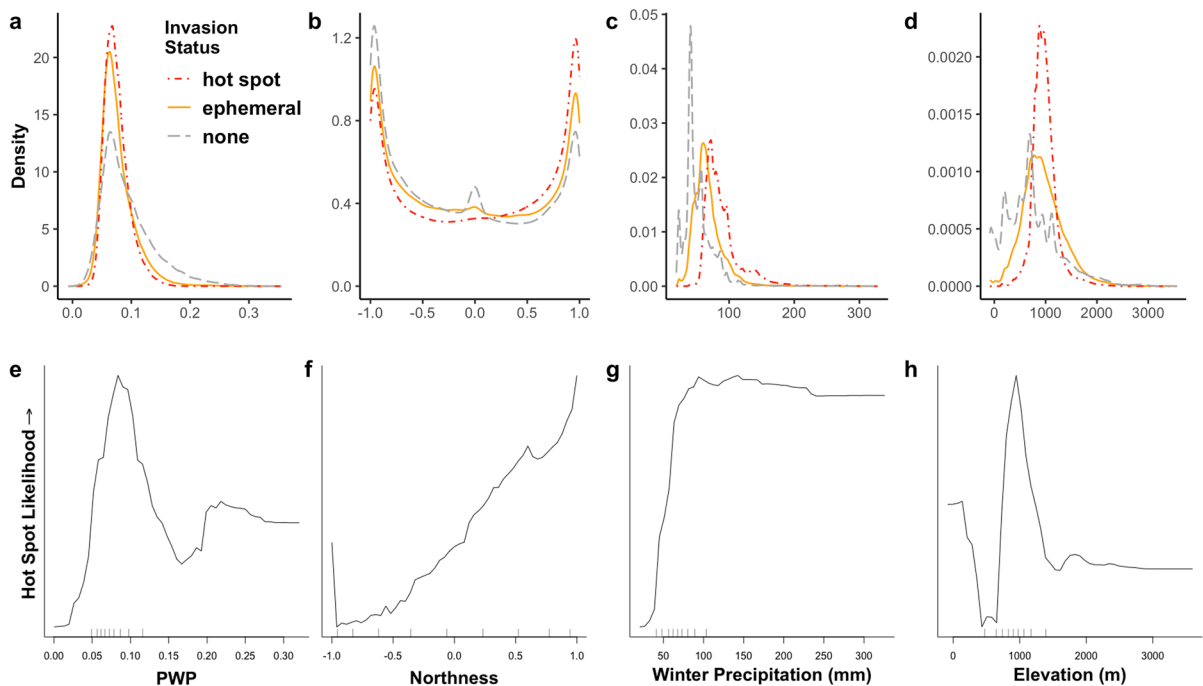


Fig. 4 Kernel density plots of four top-ranked variables. Grouped kernel density plots separated by hot spot response group (a–d), and partial dependence plots illustrating the likelihood of hot spot classification along variable gradients (e–h)

while *ephemeral* was next highest with 67.6 mm, and areas with no detected invasion (*none*) had an average of only 53.0 mm of winter precipitation. The overall distribution of winter precipitation in the Mojave Desert was multimodal, and *hot spots* had the highest winter precipitation of the three classes (Fig. 4c). The average elevation of *hot spots* was only slightly higher than *ephemeral* areas, with averages of 974.3 and 947.7 m, respectively, while areas with no invasives detected over the 12-year span were lower in elevation, averaging 733.9 m (Fig. 4d). It is important to note that both the *ephemeral* and *none* classes had flatter distributions than *hot spots*, and *hot spots* consistently had very narrow distributions in these top-ranked variables (Fig. 4).

The subregional random forest predictions for the six subregions had a mean kappa statistic of 0.81 and McNemar's test was significant at $p < 0.0001$. The mean overall accuracy of these models was 0.88 and *hot spots* were accurately identified 94.59% of the time. However, there were some differences in variable importance between subregions and the entire Mojave Desert, including that distance to roads was a top variable in multiple regions, and coarse fragments

and slope data were frequently more useful in the subregional models than in the full Mojave Desert (see supplementary material Figs. S2 and S3). In the regions where coarse fragments were ranked as top variables, *hot spots* preferred substrate with fewer coarse fragments relative to other classes and overall distributions of the subregions, except in arid valleys and canyonlands, where *hot spots* were found in areas with more coarse fragments. In subregions where slope was a top variable, *hot spots* trended toward areas of a moderate slope relative to the overall distribution of each respective subregion. Finally, in the western Mojave low ranges and arid footslopes, electrical conductivity (EC) was a top variable and *hot spots* were most commonly found in areas of lower EC (supplementary material Figs. S4–S9).

Discussion

Our work leveraged the distinct phenological attributes of invasive annual grasses to identify spatially clustered groups of pixels with persistent and long-term detection of early season invasive annuals

(2009–2020; *hot spots*) and the variables associated with their distribution (Bishop et al. 2019). In this study, *hot spots* of early season invasive annual grasses in the Mojave Desert over 12 years were successfully identified and found to be primarily on the eastern and western margins of the Mojave Desert ecoregion. Coverage of *hot spots* was found to vary across subregions, with Western Mojave Basins containing far more *hot spots* proportionally than any other subregion. The wide distribution of the *ephemeral* class indicates nearly all subregions of the Mojave Desert support some level of occasional annual grass invasion with no significant spatial clustering. At the Mojave Desert ecoregional scale, we found that biophysical variables, rather than anthropogenic variables, were better predictors of *hot spot* distribution, but all variables included contributed positively to the accuracy of the model. The spatial distribution of our *hot spots* largely overlapped with the distribution of previous invasive annual detection and suitability modeling in the Mojave Desert (Dahal et al. 2022; Klinger et al. 2019; Underwood et al. 2019). Our full ecoregional insights largely agree with the biophysical controls of invasion investigated by prior plot or landscape scale studies, while subregional analysis yielded results supported by the literature, such as increased importance of anthropogenic variables at subregional or smaller spatial extents (Abella et al. 2012; Brooks & Berry 2006). Our work adds important management-relevant knowledge of long-term patterns of persistence on a Mojave Desert ecoregional scale, capturing large biophysical and anthropogenic gradients. Information on persistent populations of invasive annuals is useful for prioritizing management on areas that are most likely to cause ecological issues in the future. The wide-ranging prevalence of *ephemeral* grass distributions compared with *hot spots* demonstrates the usefulness of aggregating over time to identify hot spots, which are likely high-priority areas for invasive species management.

The temporal and spatial resolution of our remote sensing approach was ideal for identifying invasive populations at a scale fine enough to detect variation due to biophysical variables yet large enough spatial resolution not to overwhelm computational power during analysis (Kennedy et al. 2014). Our temporal aggregation and hot spot analysis help to reduce uncertainty, because invasive annuals commonly form

dense patches that germinate every year, meanwhile the growth and germination requirements for native plants are often much more stringent resulting in less consistent productivity (Beatley 1974; Brooks 1999b, 2003). The byproduct of temporal aggregation is the broad *ephemeral* class, which in addition to including “superbloom” years in the Mojave Desert, also includes pixels of a lower dNDVI detection threshold and therefore higher variation in invasive cover abundance and uncertainty. While we are confident in our detection of invasives, it is possible that native annuals coincident with the phenology of invasives are included in our detection in the *ephemeral* class in particular and therefore it is important to not overestimate the dominance of invasives in the *ephemeral* category. However, the broad *ephemeral* class provides important context for the identified persistent *hot spots*, and understanding propagule dynamics, and is evidence of the need to conduct multi-year assessments to identify focus areas to account for interannual variability and to avoid detection error. As with any remote detection method, it is important to practice caution with application, and any *hot spots* should be field validated before management decisions are made.

Even with the varied physiological tolerances within the Mojave Desert of the four target invasive species we studied, the treatment of these species as a coherent functional group is supported by the narrow set of conditions under which they form *hot spots* as well as the similar effects they have on ecosystems (Bykova & Sage 2012; Hufft and Zelikova, 2016; Wu & Jain 1978). The similar effects of invasive annuals on ecosystems are likely due to shared characteristics such as possessing a shallow fibrous root system, germination cohorts following precipitation pulse events throughout the fall and winter, the ability to photosynthesize at low temperatures, rapid growth, early seed set, and high seed production. While these common physiological traits confer advantages that allow opportunistic invasion in favorable conditions, they also impose limits on their environmental tolerances (Armstrong & Huenneke 1992; Griffith et al. 2014). Therefore, despite detecting multiple species within the invasive annual grass functional group, the group’s shared physiological characteristics lead us to infer *hot spots* mapped here are within a narrow biophysical envelope where invasive annual grasses can maintain persistence on the landscape.

Predictors of invasive hot spots

The narrow frequency distributions for *hot spots* in the top-ranked variables (Fig. 4), indicate that *hot spots* exist in a specific set of soil, topographic, and climatic conditions, which is supportive of research finding soil texture, and topographic variables to be important determinants of annual plant cover in the Mojave on a plot scale (Duniway and Palmquist 2020; Munson et al. 2015). *Hot spots* favored coarse-textured sandy loam soils with relatively low PWP, and higher average bulk density than the other classes. However, the texture related conditions commonly found with *hot spots* in our study contradict a prior assessment from the Lower Grand Canyon subregion in the eastern Mojave Desert (Grand Canyon-Parashant National Monument) that indicated *Bromus rubens* was found mostly in finer soil textures (Duniway and Palmquist 2020). These discrepancies are likely the result of differences in spatial and temporal scale as well as the specific geographic location of the referenced study. Closer examination of the Lower Grand Canyon subregion indicates *hot spots* in this area prefer finer soils (PWP=9.7%) relative to other classes in the area as well as *hot spots* in the rest of the Mojave Desert. In the eastern part of the Mojave, where fall and summer monsoonal precipitation contribute significantly to the total annual precipitation, retention of summer and fall precipitation in finer-textured soils would be more important for overwintering annuals (Tagestad et al. 2016). Invasive annuals show relatively wet wilting points (-1 MPa), significantly wetter than Mojave native plants and even wetter than average agricultural plants (Germino et al. 2015; Link et al. 1990). As such, *hot spots* appear to occur in areas with relatively high precipitation during fall and winter, and soils have relatively few fine pores in the top 30 cm that retain water below wilting point of these species (< -1.5 MPa, PWP used here). These low PWP soils are typically sandy allowing the fibrous root systems to quickly and easily extract water during germination and early growth following rain events (DeFalco et al. 2003). Another possible mechanistic explanation for our result on the ecoregion scale is that *hot spots* are found in areas where invasive grasses are less likely to experience evaporative water loss such as in sandier soils and north-facing aspects. Greater downward infiltration of sandy soils limits evaporative loss more than finer soils

in arid systems, and support higher productivity in water-limited, high evaporative demand systems like the Mojave Desert (Noy-Meir 1973; Sala et al. 1988). Additionally, northern-facing slopes have lower solar radiation and therefore, lower evaporative loss than southern counterparts, which are likely important for invasive annuals with no waxy cuticle like many other desert plants (Yeats & Rose 2013). Similarly, *hot spots* were also more likely to be found on western facing slopes, perhaps a function of rain shadow with moist weather systems approaching from the coast as well as eastern slopes being exposed to hot and dry continental Santa Ana winds.

Seasonal precipitation and elevation were both among the most useful variables, reflecting the physiological limits of invasive annual grasses. Research suggests that pulses in precipitation are important for germination and growth in invasive annual grasses in the Mojave Desert (Horn et al. 2017). Our early season NDVI measurements are likely related to winter survivability and growth, providing a mechanism as to why areas with mean winter precipitation of 90 mm or greater are likely to be hot spots. Timing of precipitation is especially important considering that invasive annual grasses lack the ability for deep soil-water extraction (Ryel et al. 2008). Some of the areas with the highest precipitation of the Mojave Desert are also at high elevation, but *hot spots* were common at middle elevations (~ 1000 m). In this case, elevation is partly a proxy for temperature, as in our initial variable selection process, we found elevation and temperature to be highly correlated in the Mojave Desert. Thus, the cool winter and spring temperatures at high elevations likely decrease photosynthetic rates while the high temperatures and soil conditions found in low elevations likely make seed survival and water extraction difficult for annual grasses (Bykova and Sage 2012). Furthermore, the upper elevation cold limitations of *hot spots* is evidence of the potential for *hot spots* to spread to higher elevations as the climate warms (Bradley et al. 2016). Furthermore, previous observations suggest that run-off onto alluvial fans and toeslopes common at middle elevations in the eastern Mojave could be contributing to the surprising amount of *hot spots* in the area. Further plot-scale research would allow for more specific mechanistic understanding of patterns observed here.

Our results notably found anthropogenic variables to be comparatively less predictive across the entire

Mojave Desert, but frequently predictive of *hot spots* on a smaller subregional scale. Humans can act as a vector for spread and distribution of invasive species which has been connected with energy development, unpaved road density, OHVs, and proximity to cattle water sources (Brooks and Berry 2006; Duniway and Palmquist 2020; Salo 2005; Villarreal et al. 2019). For the entire Mojave Desert ecoregion on average, *hot spots* were found closer to roads than the *ephemeral* and *none* classes, and areas with high levels of conservation protection were somewhat less likely to contain *hot spots*. However, the lack of high predictive ranking of anthropogenic variables across the entire Mojave Desert likely is indicative of broad scale naturalization of invasive annuals in the entire ecoregion and their potential to invade even undisturbed areas (Beatley 1966; Belnap et al. 2006; Bowers et al. 2006). Our analysis focused on the continued persistence of invasive annual grass populations, rather than initial spread and establishment, which can be distinct from persistent hot spots (O'Neill et al. 2021). Therefore, humans undoubtedly play a role in the establishment of these non-native species, but perhaps one that is not detectable when examining persistence over a 12-year period within an entire ecoregion after the initial introduction and establishment in the late nineteenth and early twentieth centuries. It is likely that we missed a temporal window when human expansion and development drove the initial spread of propagules throughout the twentieth century and they are now self-sustaining populations (Beatley 1966; Bowers et al. 2006; Salo 2005). Finally, variation in the importance of anthropogenic variables between spatial and temporal scales accentuate the need to have multiple studies across gradients of temporal and spatial scales in addition to robust data on human use and presence on the landscape.

Historic land-use and fire history, along with other legacy variables, likely have had a lasting impact on the distribution of invasive plant *hot spots* in the Mojave Desert. However, the anthropogenic spatial data used here primarily represents current land use and management and do not capture such historical activities. Throughout the last two centuries, human activities such as ranching, cultivated crops, widespread clearing, and groundwater pumping have taken place throughout the Mojave Desert, with some areas of high intensity in the Western Mojave Basins,

where much of the hot spots have been recorded (Carrico and Norris 1978; Norris 1982). Plot scale experiments have indicated that invasive annual grasses thrive in areas of increased disturbances and have the potential to quickly invade areas cleared for agriculture that have been subsequently abandoned (Brooks et al. 2006; Marushia and Allen 2011; Williamson et al. 2020). Previous studies on these invasion processes have been primarily focused on local scales, but understanding the initial sites of introduction and disturbance on a regional scale can also yield important information to how these grasses might spread and how their range might have expanded over time. Therefore, while our analysis characterizes the role that soil, climatic, topographic variables, and current land-use and management play in the continued productivity of invasive annual grasses, we cannot assume that these are independent of fire history and historical land uses. Investigating the roles of fire, abandoned farmland, and historical livestock grazing in the establishment of invasive annuals throughout the Mojave remains an important topic and direction for future studies.

Subregional assessments

The Mojave Desert is a biogeographically diverse ecoregion, and we found that some subregions had nearly 10% or more of their total area in *hot spots* while other subregions were completely lacking *hot spots*. This subregional variability highlights the importance of biophysical factors at this scale and provides some insight into which plant and animal communities are most affected by annual grass invasions. Western Mojave Basins (13.0% *hot spot* cover), Eastern Mojave Mountain Woodland and Shrubland (7.6% *hot spot* cover), and Western Mojave Low Ranges and Arid Footslopes (7.0% *hot spot* cover) are the most persistently invaded subregions within the Mojave Desert. All three of these subregions are characterized by mixed shrub and woodlands, including Joshua trees and mixed pinyon-juniper woodlands (Omernik and Griffith 2014). These heavily invaded subregions are all characterized by relatively high rainfall, and stable substrate (Mack et al. 2000). These are also regions where historical agricultural land-use has been intensive, which may also contribute to the prevalence of *hot spots* in the region. The subregions with the lowest fraction of *hot spots* detected

were Mojave Sand Dunes (0% *hot spot* cover), Mesquite Flat/Badwater Basin (0% *hot spot* cover), and Death Valley (0% *hot spot* cover). In contrast to the most persistently invaded subregions, all three of these subregions are in the central Mojave and are low-elevation areas, with biota adapted to hotter and drier conditions than the rest of the Mojave Desert. The Mojave Sand Dunes do not provide a stable substrate for annual grasses to persistently establish, and most dune species are native low-growing herbaceous perennials (Pavlik 1985). Mesquite Flat, Badwater Basin, and Death Valley are host to some of the most extreme climatic and soil conditions in North America, therefore *hot spots* are unlikely to form in these more extreme habitats, despite available space.

While largely similar to the full ecoregional results, the random forest models from the most invaded subregions yielded insights into the unique characteristics of invasion in Mojave subregions and additionally illustrated the importance of spatial scale within invasion ecology. In eastern subregions (Eastern Mojave Mountain Woodland and Shrubland, Eastern Mojave Basins, Eastern Mojave Low Ranges and Arid Footslopes, Arid Valleys and Canyonlands), fall precipitation was frequently ranked as a top variable, with *hot spots* preferring areas with high fall precipitation averages as well as areas where average PWP is similar but is slightly higher than average (8.3%) compared to the entire Mojave Desert. This reinforces our assumption that retention of early rainfall is particularly important in subregions where summer and fall monsoonal rains contribute to a large portion of the total annual precipitation. The importance of topographic variables in mountains and footslopes is supported by work suggesting that herbaceous plants are especially sensitive to topography due to the importance of water retention in mountainous areas subject to run-off, even under favorable climatic conditions (Munson et al. 2015). Coarse fragments were consistently highly ranked in most subregional models with *hot spots* in subregions preferring soils with fewer coarse fragments. This is likely due to the reduced water-holding capacity of surface soils with large amounts of coarse fragments limiting the productivity of invasive annuals and *hot spots* being less commonly detected. However, coarse fragment importance and trends with *hot spots* was inconsistent among ecoregions (not in the top variables for Eastern Mojave Woodland and Mountain Shrubland and the opposite

trend in Arid Valleys and Canyonlands). This contrasting importance or association of coarse fragments between subregions has been observed in field-based studies (Duniway and Palmquist 2020) and is potentially due to interactions of soil ecohydrologic properties, aridity, and plant community interactions (Munson et al. 2015).

The difference in scale of the subregional models resulted in proximity to human infrastructure being ranked consistently higher than in the models of the entire Mojave Desert (Brooks and Berry 2006; Villarreal et al. 2019). It was ranked particularly high in the Eastern Mojave Mountain Woodlands and Shrublands and Arid Valleys and Canyonlands. Both subregions are situated near two of the largest cities in the Mojave Desert (Las Vegas, Nevada and St. George, Utah), and a primary use of these areas is for recreation. Furthermore, previous agricultural land-use in these subregions may have been less intensive than in the Western Mojave, suggesting modern population growth is influencing the spread of invasive populations. It would be interesting to have a more in-depth analysis on the effects of varying land-use legacies on invasion (Carrico and Norris 1978; Lovich and Bainbridge 1999), however, currently a lack of comprehensive and spatially explicit data for the Mojave Desert prevents meaningful conclusions on their relationships with *hot spots*, even at the subregional level.

Conclusions

Non-native annual grass invasions contribute to the environmental change in the American Southwest as climate change and the human footprint may expand favorable conditions for invasion. Here we have identified the most productive and persistent populations of invasive annual grasses in the Mojave Desert, revealing that invasive grass persistence and productivity at the entire Mojave Desert ecoregion scale is primarily predicted by soil, topographic, and climatic factors. This understanding is useful for modeling future distributional changes caused by the changing climate as invasion fronts for these species may move into different ecoregions such as the Great Basin (Bradley et al. 2016). Efforts for understanding future distribution of invasive annuals could utilize this dataset for time–space clustering and trend detection to identify areas where invasives may be growing in frequency and area. The ecoregional analysis

allows us to discern ecological patterns such as the importance of rainfall in driving patterns of invasion, or the areas that are unsuitable for most herbaceous invaders such as Death Valley. Furthermore, the inclusion of our *ephemeral* class identifies potential areas where invasives can occur that can be examined as to whether they could become persistently productive enough to be classified as *hot spots*. Identified *hot spot* populations are important to help narrow down management targets, and invasion dynamics and prevent possible catastrophes related to increased risk of fire and chance of altering plant community structure in the ecoregion. While hot spots of annual grass invasions represent an increased risk, they also present a significant opportunity for targeted management and active restoration.

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Declarations

Conflict of interest Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Department of Agriculture.

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