

## Original Research

Plot-Measured Variables Indicate Landscape-Scale Patterns of Annual Grass Invasion in Northwestern US Rangelands<sup>☆</sup>

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## ABSTRACT

Introduced annual grasses (IAGs) have invaded tens of millions of hectares of western US rangelands, displacing native vegetation and altering ecosystem functions and services. Our main goal was to assess the influence of introduced annual grasses by 1) exploring the relationships among IAG cover, species richness, diversity, and cover of other plant functional groups; and 2) identifying biotic and abiotic indicators of IAG cover. Using data from 64 sites and 420 plots from rangelands of the northwestern United States, we explored linear correlations between IAG cover and species richness, Shannon index, and plant functional group cover. We also used Least Absolute Shrinkage and Selection Operator (LASSO) regression and nonmetric multidimensional scaling to select environmental variables and plant functional groups that were associated with IAG cover. Our findings revealed a negative correlation among IAG cover and species richness, Shannon index, native perennial grass cover, and other perennial species cover and a positive correlation with other annual species cover. Our results identified several indicators: cover of native perennial grass; other perennial species (forbs and shrubs); litter; bare ground/rock; soil attributes (pH, bulk density, clay, and nitrogen); and mean annual temperatures. Our results showed that perennial vegetation, especially native perennial grasses, have a negative correlation with IAG. Warmer mean annual temperatures, but not higher daily extreme temperatures, and higher bulk density were important indicators for IAG preferred sites, while lower soil nitrogen may denote soil changes due to invasion. Given the fundamental role of disturbance in determining the magnitude and scale of IAG invasion, our results provide important insights for scientists and managers.

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## Introduction

Introduced annual grasses (IAGs) represent an unprecedented threat to native perennial-dominated ecosystems of western North

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America (Mack 1981; D'Antonio and Vitousek 1992; Brooks et al. 2004; Davies et al. 2021). They have invaded tens of millions of hectares (Mein et al. 2009; Bradley et al. 2018), with a projected expansion rate of about 200 000 ha per yr (Smith et al. 2022). Among IAG, *Bromus arvensis* (*Bromus japonicus*), *Bromus tectorum*, *Taeniatherum caput-medusae*, and *Ventenata dubia* pose major concerns because of their ability to displace perennial-dominated communities, converting the native ecosystem into introduced annual-dominated communities (Knick and Rotenberry 1997; Davies 2011) and consequently altering ecological functions (DiTomaso 2000; Masters and Sheley 2001; Bradley and Mustard 2005; Simberloff 2005; Clinton et al. 2010; DiTomaso et al. 2010; Davies 2011). Annual bromes typically germinate in au-

tum through winter; are abundant in several rangeland ecosystems, such as sagebrush-dominated ecosystems (Smith et al. 2021); and have been a part of the landscape for more than a century (Symstad et al. 2021). *Ventenata dubia* typically germinates in autumn and has rapidly established in northwestern North America, invading pasturelands, croplands, grasslands, sagebrush steppe, ponderosa pine forests, and woodlands (Wallace et al. 2015; Averett et al. 2016; Bernards and Morris 2017; Jones et al. 2018; Downing et al. 2020; Ridder et al. 2021; Hart and Meador 2021). *T. caput-medusae* has expanded to at least 17 states, invading more than 973 000 ha (Miller et al. 1999; Duncan et al. 2004; Bateman et al. 2020).

As introduced species cover increases, native plant diversity often decreases, likely due to asymmetric competition of IAG (Nasri and Doescher 1995; Rafferty and Young 2002; Davies 2011). Introduced annual grasses may have a higher relative growth rate than natives at earlier stages, depleting limited water and soil resources, competing for light excluding natives (Melgoza et al. 1990; D'Antonio and Vitousek 1992; Humphrey and Schupp 2004; Eiswerth et al. 2009), and negatively impacting wildlife and livestock species that depend on native perennials for food (Stewart and Hull 1949; Davies 2011; Balch et al. 2013). Furthermore, IAG can alter wildfire regimes by increasing the quantity and continuity of dry fine fuels (Knapp 1995; Davies and Nafus 2013; Pilliod et al. 2017; Fusco et al. 2019), which contribute to more frequent, larger, and higher-intensity fires that are detrimental to fire-intolerant native vegetation such as big sagebrush (*Artemisia tridentata*) (Young and Evans 1978; D'Antonio and Vitousek 1992; Brooks et al. 2004). Introduced annual grasses can modify soil nutrient cycling and soil biological activity (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; Dickens et al. 2013) impacting carbon (C) and nitrogen (N) cycles, pH, and bacterial abundance (Caspi et al. 2019). Furthermore, IAG can have a significant impact on grazing and livestock production in areas where these activities are major economical drivers. Specifically, IAG can reduce the quality and quantity of native forage species, increasing overgrazing and pasture degradation (D'Antonio and Meyerson 2002). Livestock tend to avoid areas dominated by IAG because of their low palatability, altering grazing patterns and resulting in significant economic losses on land, livestock, and infrastructure. The effects of IAG will likely become more severe in the future due to anthropogenic-induced events such as climate change (Ziska et al. 2005; Abatzoglou and Kolden 2011; Creutzburg et al. 2015). Because of these detrimental effects on ecosystem function, important efforts have been undertaken to remove IAG and restore native vegetation. To facilitate the management and restoration decision-making process, as well as to inform allocation of resources, analyzing ecological relationships among IAG, native plant communities, and environmental factors is critical (Bansal and Sheley 2016). Abiotic and biotic factors, such as interactions with other plant functional groups, climate and topographic characteristics, and soil properties, are associated with the distribution and abundance of IAG (Melgoza et al. 1990; Anderson and Inouye 2001; Gelbard and Belnap 2003; Blank et al. 2007; Chambers et al. 2007; Maestre et al. 2010; Bansal et al. 2014a, 2014a; Bansal and Sheley 2016). Investigating these relationships can allow managers to identify invasion risk and the invasion stage and then implement the most effective management response (D'Antonio and Meyerson 2002; Davies et al. 2009). Despite the availability of numerous local individual studies documenting negative impacts of IAG on native perennial ecosystems, a comprehensive review and analysis of these trends for the western United States has not been produced. The abundance and distribution of species is influenced by a set of abiotic (such as climate and soil) and biotic factors, with the former affecting their distribution at landscape scale (> 10 000 m<sup>2</sup>) and the latter at finer scale (< 100 m<sup>2</sup>) (Bansal and Sheley

2016). Therefore, we collected species cover, topographic, climatic, and soil data from existing studies distributed in the northwestern United States. We used this dataset to investigate relationships between IAG cover and associated plant communities across rangelands in the northwestern United States. Specifically, we address the following questions: 1) What are the relationships among IAG, species richness, diversity (Shannon index), and plant functional group cover? 2) Which biotic (plant functional groups) and abiotic (climate and soil) factors are indicators of the cover of all IAG species as a functional group? Answering these questions will help clarify patterns and consequences of invasion and direct efforts to assess other areas at risk.

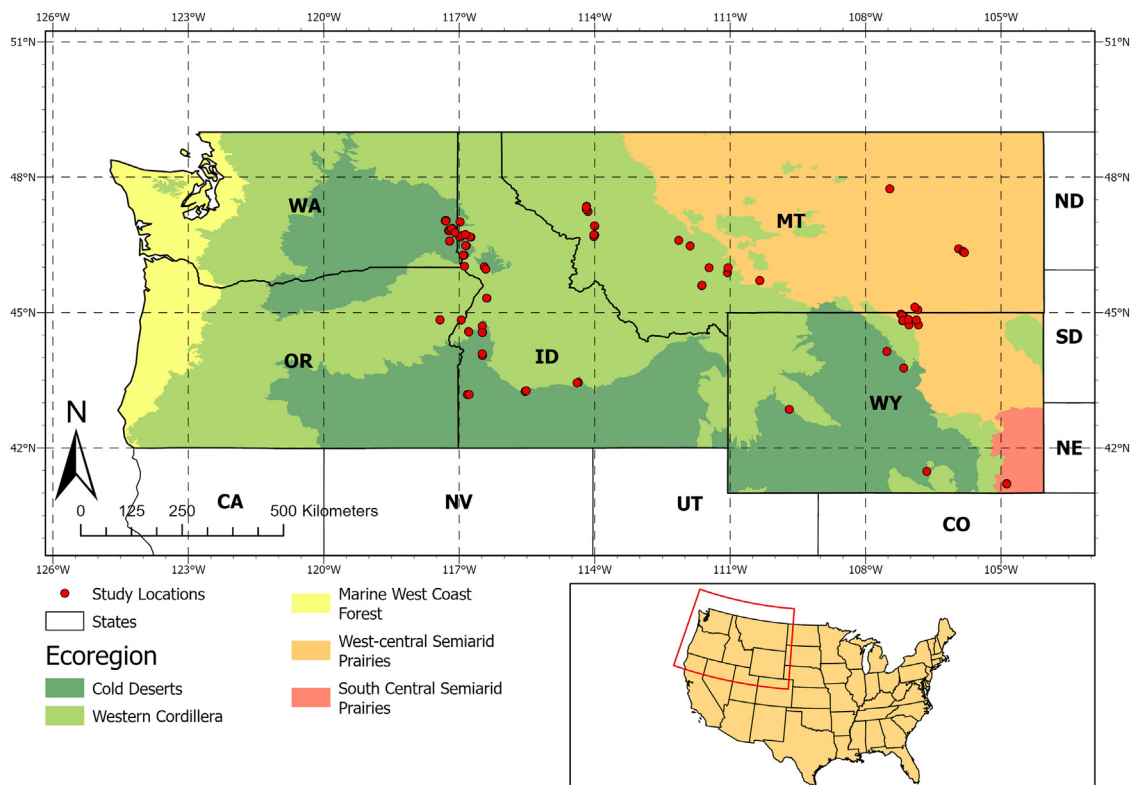
## Methods

### Study locations

We collected datasets from existing studies at 70 sites located in five states across the northwestern United States (Idaho, Montana, Oregon, Washington, and Wyoming, roughly from 104.8934972 W to 117.4713003 W and from 47.8561868 N to 41.298413 N) and distributed within four level II EPA ecoregions (Cold Deserts, South Central Semiarid Prairies, West Central Semiarid Prairies, Western Cordillera) (Omernik and Griffith 2014) (Figure 1). Because only two sites were located within the South-Central Semiarid Prairies ecoregion, we merged them with sites in the West Central Semiarid Prairies into one ecoregion (West and South-Central Semiarid Prairies). We used level II ecoregions because they provide a detailed description of large ecological areas and they are useful for national and subcontinental overviews of ecological patterns, whereas level I ecoregions are too coarse and level III ecoregions are too narrow for our scope. Specifically, we included 16 sites and 156 plots in Idaho, 16 sites and 100 plots in Montana, 3 sites and 9 plots in Oregon, 7 sites and 26 plots in Washington, and 22 sites and 129 plots in Wyoming. Of these, 162 plots were in Cold Deserts, 93 in West and South-Central Semiarid Prairies, and 165 plots in Western Cordillera. We used cover data before any restoration treatment to understand baseline conditions. To be included in our analyses, sites had to be on rangelands > 2 ha that were historically dominated by shrub or herbaceous vegetation appropriate for browsing or grazing by domestic or wild herbivores (Nusser and Goebel 2004; Reeves and Mitchell 2011). Agricultural land and sites dominated by trees were excluded from our analyses. Our dataset originates from the efforts of a multistate consortium, which includes sites mostly characterized by high IAG cover. The sites were often used in previous research projects related to IAG control methods (Greet et al. 2016; Jones et al. 2018, 2020; Metier et al. 2018; Seipel et al. 2018; Lehnhoff et al. 2019; De Stefano et al. 2021; Hart and Meador 2021; Wood and Meador 2022) and were not treated (chemical, mechanical, grazing, and prescribed fire) in the past few years. More information about the published data can be found in Supplementary Material, available online at table.

### Plant data

Plants were identified and categorized on the basis of their native status, life cycle, and growth habit according to the US Department of Agriculture (USDA) Plants Database (<https://plants.usda.gov/>). In some cases, species were only identified by the genus (e.g., *Lupinus* sp. in the case of an unidentified lupine) and species not fully identified were recorded as unknown 1, unknown 2, etc. (61 unknown species in total). When a certain species presented more than one life cycle duration habit (e.g., either annual or perennial) in the USDA Plants Database, we determined the duration using several regional field guides. Species defined as bien-



**Figure 1.** Locations of study sites and their respective EPA level II ecoregions in Idaho, Montana, Oregon, Washington, and Wyoming.

nial were included in the annual class. Unknown species were excluded from the analyses. Plant cover assessment was conducted either using line-point intercept or quadrat-based methods. For quadrats, frames were quadrat-based belt transects, and species canopy cover was visually estimated. For line-point intercept, a certain number of sampling points were established at regular intervals on the transect (e.g., every 0.3 m). At each sampling point, a pin was dropped vertically to the ground and the canopy estimation was conducted by recording when a species was “hit” by the pin. Next, the percentage cover was calculated by dividing the total number of “hits” for a species by the total number of points sampled in the plot. De Stefano et al. (2021) found that the quadrats and LPI have a reasonable level of agreement when it comes to measure plant cover; therefore, we decided to run all the analysis pooling together the data coming from the two methods.

We identified the following functional groups: native annual forbs, native perennial forbs, native annual grasses, native perennial grasses, native shrubs (including tree species that were rare), introduced annual forbs, introduced perennial forbs, introduced annual grasses, introduced perennial grasses, and introduced shrubs. For analysis purposes and because of their functional similarities, we merged native perennial forbs, native shrubs, introduced perennial forbs, and introduced perennial grasses into one category (OP, meaning other perennials). For similar reasons, we also combined native annual forbs, native annual grasses, and introduced annual forbs into Other Annuals (OA). Therefore, the functional groups included in the analyses were IAGs, native perennial grasses (NPGs), OPs, and OAs. A comprehensive list of the species can be found in Supplementary Table.

#### Environmental data

Litter, bare ground, and rock cover on the soil surface were measured in the field as part of the sampling methodology described earlier. We merged bare ground and rock cover into one

single category (bare ground/rock cover from now on) for consistency because some originating datasets reported them as separate categories and others as a single category. Other categories, such as livestock dung or animal feces, were included in the bare ground/rock cover, when present. Slope, aspect, eastness, and northness were calculated for each site using 30-m resolution digital elevation model (US Geological Survey 2006) in ArcGIS Pro (Esri, Redlands, CA). Because aspect was expressed as a circular land-surface parameter, north-south and east-west gradients were calculated as sine and cosine of aspect, respectively. Because south-facing slopes receive more potential sunlight than those facing north in the northern hemisphere, the interaction between the north-south gradient and slope was calculated as well. Mean annual temperature, total annual precipitation, and average of daily minimum and maximum temperatures were calculated for each site using 30-yr (1991–2020) normal data obtained from PRISM (PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, data created February 4, 2014, accessed 2022). Despite precipitation seasonality having a critical role in invasion processes, we decided to include total annual precipitation values rather than seasonal values. In our study, it was difficult to determine which months were critical to IAG, considering the heterogeneity of the ecoregions and the variety of the included ecosystems. Soil features at 100-m spatial resolution and 30-cm depth were obtained from Ramcharan et al. (2018) and are listed in Table 1. We considered soil features up to 30-cm depth because of the shallow root system of IAG (see Supplementary Material Table).

#### Data analyses

Our dataset consisted of 420 plots, of which 162 were located in Cold Deserts, 165 in Western Cordillera, and 93 in West and South-Central Semiarid Prairies (Fig. 1). When subplots or multiple transects were present within a plot, we averaged data at the plot

**Table 1**  
Topographic, climatic, soil, and vegetation cover variables.

Variable	Abbreviation	Unit	Resolution	Source
Elevation	Elevation	m above sea level	30 m	USGS digital elevation model (DEM)
Slope	Slope	%	30 m	Calculated from USGS DEM
Aspect	Aspect	Degrees	30 m	Calculated from USGS DEM
North-south gradient	Northness	—	30 m	Calculated as sine of Aspect
East-west gradient	Eastness	—	30 m	Calculated as cosine of Aspect
Mean total annual precipitation	MAP	mm	Station	PRISM Group
Mean annual temperature	MAT	°C	Station	PRISM Group
Daily maximum temperature	T_max	°C	Station	PRISM Group
Daily minimum temperature	T_min	°C	Station	PRISM Group
Soil bulk density	BD	g cm <sup>-3</sup>	100 m	Ramcharan et al. (2018)
Soil nitrogen	N	Weight %	100 m	Ramcharan et al. (2018)
Soil organic carbon	SOC	Weight %	100 m	Ramcharan et al. (2018)
Soil pH	pH	1:1 soil/H <sub>2</sub> O solution	100 m	Ramcharan et al. (2018)
Soil clay	Clay	%	100 m	Ramcharan et al. (2018)
Soil sand	Sand	%	100 m	Ramcharan et al. (2018)
Bare ground/rock cover	Bare/rock	%	Plot	Field measures
Litter cover	Litter	%	Plot	Field measures
Introduced annual grass cover	IAG	%	Plot	Field measures
Native perennial grass cover	NPG	%	Plot	Field measures
Other perennial cover	OP	%	Plot	Field measures
Other annual cover	OA	%	Plot	Field measures

level. All analyses were conducted using R software version 4.2.0 (R Core Team 2021). We calculated species richness (total number of species including IAG) and species diversity as Shannon index ( $H'$ ) using the “vegan” package (Oksanen et al. 2018). Shannon diversity index was calculated using the formula (Eq. 1) presented by Magurran (2004):

$$H' = - \sum_{i=1}^N p_i \ln p_i \quad (1)$$

where  $p_i$  represents the relative proportion (expressed as percent cover) of the  $i^{\text{th}}$  species.

#### Correlation analyses

We used correlation analysis to evaluate relationships among IAG cover and richness, Shannon index, native perennial grass cover, other perennials cover, and other annuals cover (Question 1). Because the normal distribution assumption was violated for some variables, we used Spearman's rank correlation coefficient ( $\rho$ ). Spearman's rank correlation coefficient is a nonparametric measure of correlation that assesses the monotonic relationship between two variables rather than the strength and direction of the linear relationship. Correlation analyses were conducted for all ecoregions pooled and for individual ecoregions.

#### LASSO regression and nonmetric multidimensional scaling (NMDS)

We used LASSO regression as a variable selection method to identify the biotic and abiotic covariates associated with IAG cover (Question 2). LASSO regression is a generalized linear regression approach with an additional regularization parameter,  $\lambda$ , that shrinks or eliminates covariates that contribute least to the model fit, helping to prevent overfitting (Tibshirani 1996). LASSO often results in models with fewer variables and higher predictive accuracy than ordinary least squares regression. Covariates with a zero coefficient were excluded from the model. LASSO presents several advantages over other variable selection methods, such as stepwise regression. In stepwise regression,  $R^2$  values can be biased high, standard errors of the parameter estimates can be too small, the confidence intervals around the parameters can be too narrow, collinearity can be exacerbated, and  $P$  values can be too small because of the multiple comparisons (Harrell 2015). LASSO regularization prevents these issues, but the shrinkage of the coefficients

toward zero leads to an estimation bias but also a smaller prediction error due to decreased variance (Hastie et al. 2009a, 2009b, 2009c).

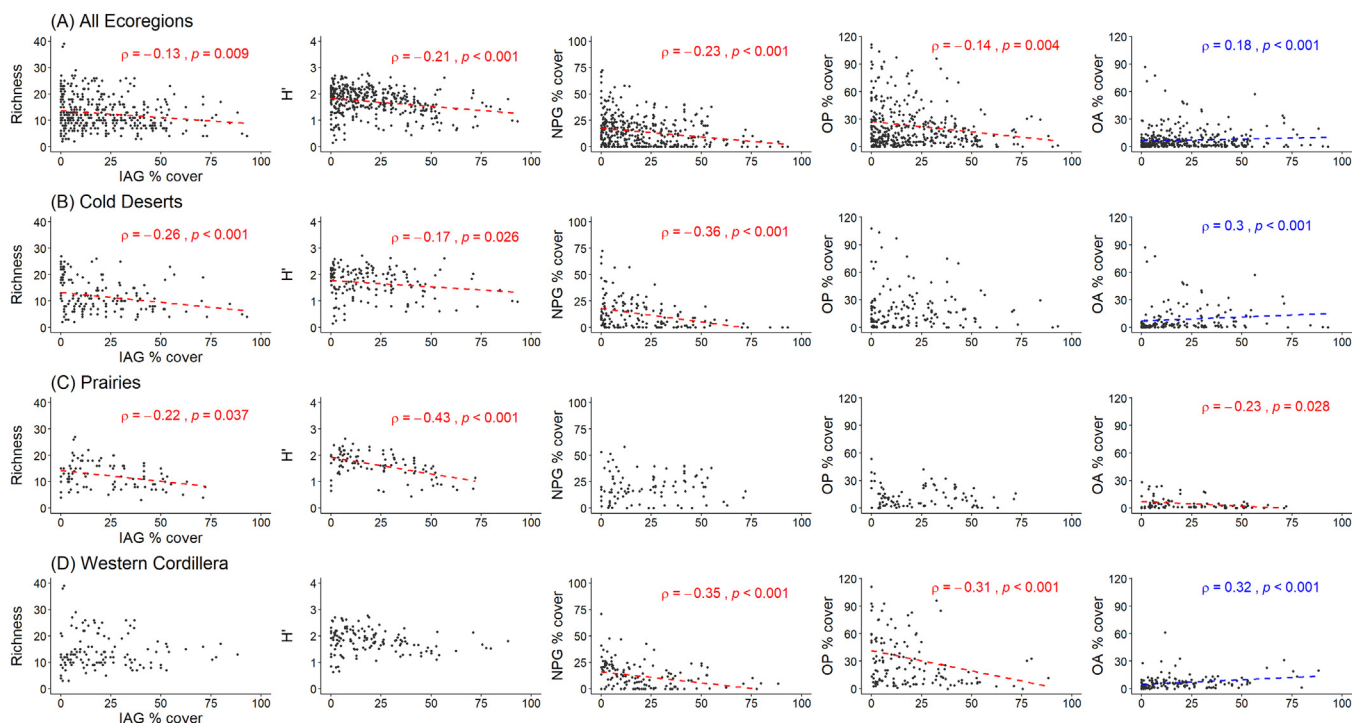
We used k-fold cross-validation to assess the validity of the LASSO regression model. Cross-validation involves splitting the available data into training and test sets, the model is fit to the training data and then assessed, based on its predictions, to the test data (Hastie et al. 2009c). By repeating this process for many different splits (folds) of the data, the average performance of the model is estimated. Cross-validated predictive performance is commonly used to estimate or tune auxiliary parameters (hyperparameters) of a model ( $\lambda$  in this case). The dataset split was 70% for model training and 30% for testing. We used k-fold cross-validation with the training set to tune the hyperparameter  $\lambda$ . Lowest RMSE (root mean squared error) was used to select the model with the best  $\lambda$ . Using this value, we used the trained model to predict the test set and measured the agreement between measured and predicted IAG cover values ( $R^2$ ). Variable importance scores were computed for each variable retained in the model using absolute importance. These scores assess the relative influence of each variable by measuring the change in model's performance (RMSE) if the selected variable is removed from the model (Fisher et al. 2019). We used the “tidymodels” R package (Kuhn and Wickham 2020) to perform the LASSO regression. Introduced annual grass cover was square root transformed to achieve a normal distribution, highly correlated covariates (Pearson's correlation  $r > 0.9$ ) were dropped from the model to avoid multicollinearity, and all covariates were standardized. Outliers were detected by evaluating their Cook's distance and excluded from the analysis when the Cook's distance was  $> 4/n$  (Stevens 1984). For further insights about the relationships between functional group covers and abiotic factors, a non-metric multidimensional scaling (NMDS) ordination using a Bray-Curtis distance was performed using the *vegan* package (Oksanen et al. 2018).

## Results

#### Correlation analyses

Our first specific objective was to quantify correlations among IAG cover, species richness (total number of species), diversity (Shannon index), and plant functional group cover (native perennial grass, other perennials, and other annuals cover). Correlation





**Figure 2.** Scatterplots show the relationship among introduced annual grass (IAG) cover and species number (richness), Shannon index ( $H'$ ), native perennial grass cover (NPG % cover), other perennial cover (OP % cover), and other annual cover (OA % cover) in all Environmental Protection Area level II ecoregions (A), Cold Deserts (B), West and South-Central Semiarid Prairies (C), and Western Cordillera (D). Correlation coefficients are expressed as Spearman's rank correlation coefficient ( $\rho$ ). Red dotted lines represent linear regression lines.

analyses results for all EPA level II ecoregions and each ecoregion individually are reported in Figure 2. For level II ecoregions, there was a negative relationship among IAG cover and species richness, Shannon index, native perennial grass, and other perennials cover, and a positive relationship between IAG and other annuals cover. At the individual ecoregion scale, IAG correlation patterns were similar, but with some notable differences. In the Cold Desert ecoregion, IAG cover was negatively correlated with species richness, Shannon index, and native perennial grass cover, whereas IAG and other annuals covers were positively correlated. In West and South-Central Semiarid Prairies, IAG cover was negatively correlated with species richness, Shannon index, and other annuals cover. Finally, in the Western Cordillera, IAG cover was negatively correlated with NPG and other perennials covers and positively correlated with other annuals cover.

#### LASSO regression model and NMDS

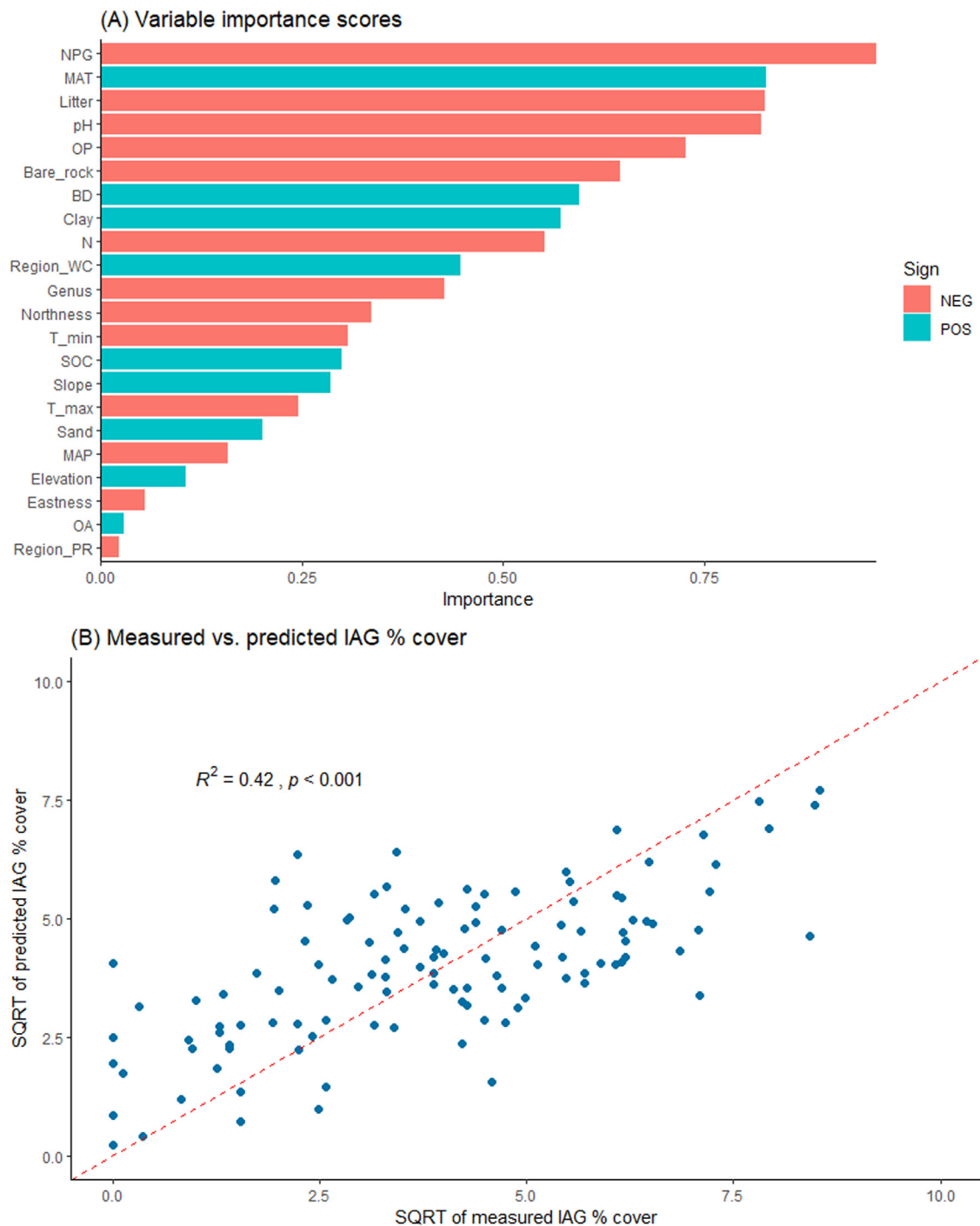
The second specific objective was to identify the abiotic and biotic factors associated with IAG cover, for which we used a LASSO regression model. The biotic factors considered were cover of native perennials, other perennials, other annuals, and cover by genus. The abiotic factors were mean elevation, slope, north-south and east-west gradient, mean annual temperature, total annual precipitation, average daily minimum and maximum temperatures, litter cover, bare ground/rock cover, soil percent sand and clay, pH, soil bulk density, and soil N. Level II ecoregions were also used in the model as a 3-level factor (CD: Cold Deserts, PR: West and South-Central Semiarid Prairies, and WC: Western Cordillera). Hyperparameter tuning revealed a  $\lambda = 0.006$  (RMSE = 1.64,  $R^2 = 0.43$ ) for the final LASSO model, which retained 22 of the 23 initial variables. Variable importance scores and results from the test dataset are shown in Figure 3, while variable coefficients are presented in Table 2.

**Table 2**

Least Absolute Shrinkage and Selection Operator regression standardized coefficients. These coefficients measure the effect of independent variables on the dependent variable, indicating the change in the dependent variable as the standard deviation increases in the independent variable.

Term	Standardized coefficient
(Intercept)	0.006
Elevation	0.106
Slope	0.286
MAP	-0.157
T_min	-0.308
MAT	0.827
T_max	-0.246
Litter	-0.825
Bare/rock	-0.646
Northness	-0.336
Eastness	-0.054
NPG	-0.963
Genus	-0.428
OP	-0.728
OA	0.029
BD	0.595
SOC	0.299
pH	-0.821
N	-0.552
Clay	0.571
Sand	0.201
Region_WC	0.446
Region_PR	-0.023

NMDS analysis results revealed a clear separation in the ordination space between the functional groups, with a more remarkable distinction among IAG, native perennial grasses, and other perennial species (Fig. 4A). The same consideration held for the majority of invasive annual grass species, although some species were found placed closely with other annuals (VUBR–*Vulpia bromoides*) and other perennials (APIN–*Apera interrupta*). IAG were also placed



**Figure 3.** Variable importance scores related to the Least Absolute Shrinkage and Selection Operator regression (LASSO) (A) (see Table 1 for variable abbreviations), and LASSO regression performance evaluated through correlation between model-predicted introduced annual grass (IAG) cover values (calculated using the k-fold cross-validation) and field-measured IAG cover values (B). Red dashed line represents 1:1 line.

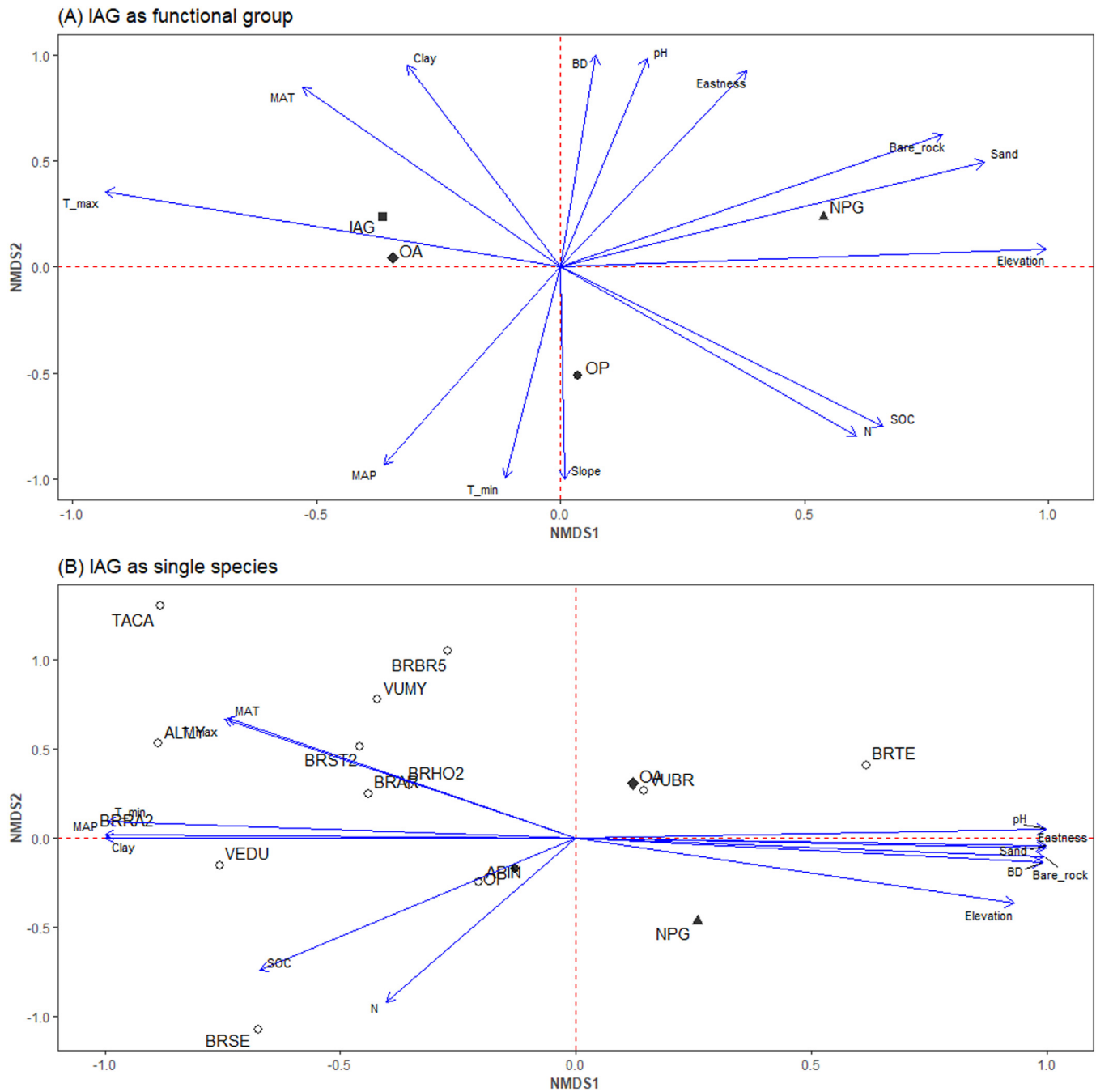
along gradients of increasing mean and daily maximum temperatures (Fig. 4B).

## Discussion

### Correlation analyses

Our results suggest an adverse relationship between IAG as a functional group with native plant communities at a landscape scale because IAG were negatively associated with total species

richness, species diversity (Shannon index), native perennial grass cover, and other perennial plant cover (both native and nonnative). These correlations generally held within each ecoregion, although some deviation from these patterns was detected. Our outcomes are consistent with numerous studies conducted at the local scale in previous literature. For example, in southern Idaho and eastern Oregon, sites located in Western Cordillera and Cold Desert ecoregions, *V. dubia* cover showed a negative response to species diversity and native species richness (Jones et al. 2018, 2020). Similar results were found by Averett et al. (2020) in Pa-



**Figure 4.** Nonmetric multidimensional scaling (NMDS) of all plant functional groups (A) and single invasive annual grass species (B) and other functional groups. For functional groups and environmental variables abbreviations, see Table 1. ALMY indicates *Alopecurus myosuroides*; APIN, *Apera interrupta*, BRAR (*Bromus arvensis*), BRBR5, *Bromus briziformis*; BRHO2, *Bromus hordeaceus*; BRSE, *Bromus secalinus*; BRST2, *Bromus sterilis*; BRTE, *Bromus tectorum*; TACA, *Taeniatherum caput-medusae*; VEDU, *Ventenata dubia*; VUBR, *Vulpia bromoides*; and VUMY, *Vulpia myuros*.

cific Northwest prairies, where increasing *V. dubia* cover corresponded with decreasing native perennial grass and native perennial forb cover. Similarly, Davies (2011) observed a negative relationship among *T. caput-medusae* density and perennial species density, total species richness, species diversity (Shannon index), perennial bunchgrass density, *Poa secunda* (native perennial grass) density, and *Artemisia* species (native shrub) density in *Artemisia*-dominated steppes in southeastern Oregon (Cold Deserts and Western Cordillera). Anderson and Inouye (2001) showed a negative relationship between *B. tectorum* and native species cover, as well as between introduced species and native species cover in

Idaho's *Artemisia* steppe located in the Western Cordillera ecoregion. Also in the Western Cordillera, Larson et al. (2017) showed a negative response between *B. tectorum* and total and native species richness and alpha diversity, in Montana, as did Wood and Meador (2022) between *B. tectorum* and species richness in Wyoming.

Finally, in a field experiment conducted by Humphrey and Schupp (2004) in Cold Deserts, *B. tectorum* decreased *Elymus elymoides* (native perennial grass) density and relative growth rate during the first yr.

With regard to other functional groups, numerous studies have shown a negative correlation between IAG and perennial grasses

(Nasri and Doescher 1995; Lulow 2006; Davies and Svejcar 2008; Leger 2008; Davies and Bates 2010; Larson et al. 2017; Endress et al. 2020; Applestein and Germino 2022; Wood and Meador 2022), shrubs (Leger 2008; Prev y et al. 2010), and perennial forbs (Davies and Svejcar 2008; Leger 2008; Davies and Bates 2010). Our results showed a positive correlation between IAG and other annual plants, a relationship that is inconsistent with the results of other authors (Davies and Svejcar 2008; Davies and Bates 2010; Averett et al. 2020; Watson et al. 2021). Functional groups with similar life cycles and ecological functions to IAG, such as annual forbs, should have a strong negative relationship with introduced grasses because of competition (Lep s 2004) if they emerge and grow at similar times. On the other hand, in a study conducted by Davies (2011), all native plant groups but annual forbs displayed a negative relationship with *T. caput-medusae*. We hypothesize that other annual plants, with sufficient ecological characteristics to IAG, may have been favored by microsites with similar environmental conditions that also favor IAG. However, competition can be a decisive factor in certain environmental conditions, as we observed in South-Central and West Semiarid Prairies, where the relationship between IAG and annual plants was negative.

Overall, our findings support results of other studies at a large geographical scale; that is, increased cover of IAG is negatively associated with floristic diversity and cover of desirable perennial species. The negative correlation of IAG with plant diversity can diminish ecosystem functions and services vital to western rangelands.

#### LASSO regression and NMDS

The variable selection procedure performed by LASSO regression highlighted the importance of perennial vegetation, particularly native perennial grasses. In invaded sites, native perennials may limit the expansion of IAG, probably through direct competition for resources and invasion resistance, regardless of the primary cause of invasion (i.e., disturbance) (Lulow 2006; McGlone et al. 2012; Sebade et al. 2012; Hergert et al. 2015; Herget et al. 2015; Davies et al. 2021). These results were corroborated by our LASSO regression results, which denoted negative coefficients for perennial vegetation (NPG and OP). Furthermore, IAG and NPG were distinctly separated in the NMDS analysis. A similar pattern was observed for bare ground/rock cover, confirmed by results obtained in *Artemisia* steppe in Oregon (Bansal and Sheley 2016), where *B. tectorum*-dominated plots showed a negative correlation with bare ground/rock, shrub, and perennial grass cover. The model also showed a negative coefficient of litter, which contrasts with other reports in the literature that indicate a positive response between litter and introduced species cover (D'Antonio and Vitousek 1992; Gasch et al. 2013; Jones et al. 2018; Jones et al. 2020) but is supported by other studies (Amatangelo et al. 2008; Bansal, Sheley et al. 2014). We postulate that increased litter cover corresponded to less suitable conditions for IAG due to microclimate and microsite changes. Several research papers have positively linked warmer temperatures with IAG cover (Bradford and Lauenroth 2006; Chambers et al. 2007; Bansal and Sheley 2016), and this was supported in our LASSO regression model and NMDS by the positive coefficient of mean annual temperature and negative coefficient of daily minimum temperature. On the other hand, Larson et al. (2017) observed that climate treatments (experimental warming and drying) without sufficient moisture and significant disruption of perennial vegetation did not facilitate *B. tectorum* invasion.

Decreasing daily minimum temperature (daily minimum temperature becomes colder) decreased IAG cover in our model, denoting the preference for warmer climates. On the other hand, our model indicated a negative coefficient for maximum daily tempera-

ture. Within the ecoregions evaluated, IAGs prefer average warmer temperatures but are sensitive to upper and lower extremes that represent their temperature niche. Our model indicated a negative coefficient for total annual precipitation, which substantiates the idea that IAGs are often most successful in drier sites and after disturbance events (Haubensak et al. 2009). Our model also revealed negative coefficients for north-south and east-west gradients and a positive coefficient for slope. Introduced annual grasses are able to successfully establish and colonize south-facing slopes, especially after disturbance and soil erosion (Bradley and Mustard 2006; Bradley et al. 2009; Lovtang and Riegel 2012; Kulpa et al. 2012). In the western portion of the United States, south- and west-facing slopes are generally warmer than north- and east-facing slopes, validating the preference of IAG for warmer sites.

Among soil variables, bulk density, organic carbon, and clay had positive coefficients, while pH and N had negative coefficients. Generally, increased soil bulk density negatively affects soil infiltration, water availability, soil porosity, aeration, plant nutrient availability, and soil microorganism activity, which can reduce introduced species cover (Stohlgren et al. 2005). The positive coefficient of bulk density conflicts with those findings, and its meaning remains unclear. Higher bulk density may reduce fibrous root penetration and therefore limit perennial grass access to soil moisture deeper in the soil. Moreover, the IAG root system (finer compared to perennial grasses) can access more easily to reduced pore space in higher soil bulk density conditions (Ning et al. 2022). Areas invaded by *B. tectorum* undergo changes in soil morphology and physical properties due to the transition from perennial shrub- and grass-dominated systems (lower bulk density) to annual grass-dominated systems (higher bulk density) (Berendse et al. 1992; Norton et al. 2004; Williamson et al. 2004; Boxell and Drohan 2009). Nagy et al. (2021) found the top 10-cm soil organic carbon was significantly higher in *B. tectorum*-dominated sites than in sagebrush-dominated sites, which is consistent with our findings. Soil nutrient availability is sensitive to variations in pH and clay content and can influence IAG performance (Bansal et al. 2014). Therefore, lower pH values and consequently lower nutrient availability can limit IAG cover. Higher clay content might be associated with higher cation exchange capacity, water-holding capacity, and fertility, which can favor IAG expansion, as observed in southern California (Warm Deserts and Mediterranean California ecoregions) where introduced *Bromus* species prefer rich and fertile soils (Caspi et al. 2019). Our model also denoted a negative coefficient of soil nitrogen and supports the nitrogen and nutrient depletion observed by several studies (Corbin and D'Antonio 2004; Vasquez et al. 2008; MacKown et al. 2009). Sites invaded by IAG have their soil resources, including nitrogen, depleted; our coefficient might indicate that invaded sites have lower soil N because of IAG uptake and depletion, while sites with low or no invasion might have higher levels of N. Sites with coarser soil texture and consequently less productivity are more susceptible to invasion (Stewart and Hull 1949; Reisner et al. 2013), as supported by the positive coefficient of sand in our model.

Finally, our model training evaluation (predicted vs. measured IAG covers) indicated  $R^2 = 0.42$ , suggesting that 42% of the variance in measured cover values was explained by the predicted values. The level of dispersion around the ideal 1:1 line might relate to the nature of the dataset, such as discrepancies in cover measure methodology (i.e., line-point intercept vs. belt transects), noise in the data (i.e., species identified only at genus level, without information on the duration life cycle, native status, and form), and sampling locations. Our data originate from previous datasets where the sites were selected because of IAG presence, which constitutes a bias. As such, the sites are not systematically or randomly distributed. We think that adding more data points (better systematic sampling distribution), standardizing the sampling methodol-



ogy in the field, and improving the quality of existing data (e.g., fully identify the genus-only entries) would improve the model validation in terms of goodness of fit ( $R^2$ ).

## Implications

Our study offers a comprehensive examination of the relationship between IAG and biotic and abiotic factors, highlighting that native perennial grass cover had the strongest negative relationship to IAG cover. Hence, monitoring native perennial grass cover can be crucial for scientists and land managers in mitigating the impacts of invasive annual grasses. Identifying specific values of native perennial grass cover correspondent to high level of annual grass invasions (i.e., 50% IAG cover) will help to identify better strategies, including prevention, early detection and rapid response, restoration, and integrated management approaches.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [10.1016/j.rama.2023.10.003](https://doi.org/10.1016/j.rama.2023.10.003).

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