Biol Invasions (2024) 26:1157–1179
https://doi.org/10.1007/s10530-023-03235-9

ORIGINAL PAPER

Non-native plant invasion after fire in western USA varies by functional type and with climate

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Received: 15 May 2023 / Accepted: 18 December 2023 / Published online: 2 February 2024

Abstract Invasions by non-native plant species after fire can negatively affect important ecosystem services and lead to invasion-fire cycles that further degrade ecosystems. The relationship between fire and plant invasion is complex, and the risk of invasion varies greatly between functional types and across geographic scales. Here, we examined patterns and predictors of non-native plant invasion following fire across the western United States. We specifically analyzed how the abundance of non-native plants after fire was related to fire characteristics and environmental conditions, such as climate, soil, and topography, in 26,729 vegetation plots from government networks and individual studies. Non-native plant cover was higher in plots measured after wildfires compared to prescribed burns or unburned plots. The post-fire cover of non-native species varied by plant functional type, and only the cover of short-lived (i.e., annual and biennial) forbs and short-lived C3 grasses was significantly higher in burned plots compared to unburned plots. Cool-season short-lived

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-023-03235-9.

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grasses composed most of the non-native post-fire vegetation, with cheatgrass (*Bromus tectorum*) being the most recorded species in the dataset. Climate variables were the most influential predictors of the cover of non-native short-lived grasses and forbs after fires, with invasion being more common in areas with drier summers and a higher proportion of yearly precipitation falling in October through March. Models using future projected climate for mid (2041–2070) and end (2071–2100) of century showed a potential for increasing post-fire invasion risk at higher elevations and latitudes. These findings highlight priorities for mitigation, monitoring, and restoration efforts to reduce post-fire plant invasion risk across the western United States.

Keywords *Bromus tectorum* · Climate change · Disturbance · Exotic annual grasses · Invasive plants · Management · Wildfire

Introduction

Invasions by non-native plant species following fire can have significant and lasting impacts on ecosystem services such as biodiversity, soil stability, and forage production (Hobbs and Huenneke 1992; Coates et al. 2016; Nagy et al. 2021). Non-native species may also alter trajectories in early successional communities, lead to the exclusion of native early seral species (Kulmatiski 2006), and have negative impacts on other biotic interactions (Mack et al. 2000; Coates et al. 2016). Non-native plants often invade native ecosystems after disturbances such as fire remove established vegetation, which can increase the availability of limiting resources and benefit invasive species establishment (Davis et al. 2000; Davis and Pelsor 2001; Shea and Chesson 2002; Daehler 2003). In some ecosystems, non-native plant invasions can also increase fire risk (Fusco et al. 2019), and create a positive invasion-fire feedback that can result in alternative, less diverse ecosystem states (D'Antonio and Vitousek 1992; Brooks et al. 2004; Davies et al. 2012).

Fire and invasion are both complex processes that are influenced by environmental conditions (climate, soil, topography), human disturbance (grazing pressure, proximity to roads and trails, and the overall intensity of disturbance), fire regime characteristics (past fire regime, departure from fire regime), and biological factors (pre-fire plant community characteristics, non-native propagule pressure, and potential invader characteristics). All these factors interact to influence how "invasible" a given ecosystem is after a fire (Keeley et al. 2003, 2011; Merriam et al. 2006; Perkins et al. 2011; Ellsworth et al. 2016; Williamson et al. 2020). For example, some shrubland ecosystems in western USA historically had long fire return intervals prior to European settlement, but now experience more frequent fires (Bukowski and Baker 2013), and this departure from past conditions can allow new species to invade (Keeley et al. 2011). Fire severity may also influence invasion, as higher severity may lead to greater disturbance, which can increase available resources for invasive plants (Fornwalt et al. 2010; Miller et al. 2010; Sherrill and Romme 2012). Invasion can increase landscape-scale fire spread and severity, which has been linked to tree mortality,

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a shift to non-forest vegetation types, and in some cases increase the potential for invasion (Coop et al. 2020; Kerns et al. 2020; Woolman et al. 2022; Tortorelli et al. 2023). However, to our knowledge there has been no research examining how fire severity may relate to plant invasions across large climate gradients and multiple ecosystem types.

To date, most of the negative impacts associated with the invasion of non-native plants after fire in North America have been in hotter, drier regions of the western part of the USA (D'Antonio and Vitousek 1992; Brooks 1999; Fusco et al. 2019; Wilder et al. 2021). Invasion by non-native plants can increase fine fuel loads and fuel continuity in historically sparsely vegetated and fuel-limited systems. Coupled with hotter and drier weather, invasion can increase the extent and frequency of both subsequent large destructive wildfires and subsequent invasions via a positive feedback (Brooks et al. 2004; Fusco et al. 2019; Wilder et al. 2021). Prescribed fire, which is often used to achieve restoration goals (Ditomaso et al. 2006; Calo et al. 2012), can similarly exacerbate plant invasions in some cases (Keeley et al. 2007; Sherrill and Romme 2012; Roundy et al. 2018). However, not all fires, or fire types, result in invasion by non-native species (Alba et al. 2015), some invasive species can reduce fire spread (Stevens and Beckage 2009), and not all non-native species become abundant after fires (Byers et al. 2002; Smith et al. 2008).

The non-native species that are successful after fires in semi-arid ecosystems are often fast-growing annuals that establish quickly and grow early after disturbances (Wolkovich and Cleland 2011), preempting newly available soil resources and outcompeting slower-establishing native species with more conservative growth strategies (Davis et al. 2000; Montesinos 2022). A changing climate in conjunction with an increase in the size and severity of fires at higher elevations and in more northern regions may lead to an increased risk of post-fire plant invasion in formerly resistant or resilient ecosystems (Concilio et al. 2013; Taylor et al. 2014; Lembrechts et al. 2016; Kerns et al. 2020). Increasingly, the risk of invasion by non-native grasses after disturbances at higher altitudes and in forested ecosystems has been recognized (Kerns et al. 2020; Smith et al. 2022). Forested, formerly invasion-resistant regions may not return to their historical forested state after high severity wildfires with climate change (Coop et al. 2020; Woolman et al. 2022), and this can lead to increased potential for an even broader footprint of plant invasions (Franklin et al. 2006). Land managers are concerned with the higher potential for invasion risks associated with climate change and mega-fires (Williams 2013; USDA 2022), and thus need information to focus limited resources on managing potential invasions after large fires across broad spatial scales.

To deal with threats posed by increasing wildfire activity and intensity under warmer and drier conditions, managers and government officials are directing large amounts of money for prescribed fires and fuels treatments (see, e.g., USDA 2022). Consequentially, understanding the impacts of wildfires and prescribed fires on non-native plants at the landscape-scale is a high priority. Given the large number of interacting factors that can potentially determine post-fire invasion risk, it is difficult to accurately predict areas that are at the greatest risk of invasion after fires, both now and in the future (Beaury et al. 2020). To address the uncertainty associated with the interconnected risks of plant invasion and fire, we performed a quantitative data synthesis to explore how the abundance of non-native plants after fire varies in relation to fire characteristics and environmental conditions such as soils, topography, and climate, using vegetation data collected on the ground from across the western USA. We synthesized this large dataset to examine which types of invasive plants are the most successful invaders after fires and identify where post-fire plant invasions are most common.

We hypothesized the following: (1) Non-native plant species will differ in their successful establishment after fires based on their functional type and life history. Specifically, we hypothesized that non-native short-lived (annual and biennial) herbaceous species would be more abundant in burned plots compared to non-native long-lived herbaceous and woody species, because short-lived herbaceous species may respond to an increase in limited resources following disturbances more rapidly than slower growing plant species (Melgoza et al. 1990; Davis et al. 2000). (2) Non-native plant functional types that increase in cover following fires will be more abundant following wildfires compared with prescribed fires and will be most abundant in severely burned areas and areas that historically had long fire return intervals prior to European colonization of North America. We hypothesized this because

greater levels of disturbance and greater departures from historical conditions may increase invasion risk (Davis et al. 2000; Keeley et al. 2011). (3) Abundance of functional types that increase after fires will vary across climatic gradients. Specifically, we hypothesized that non-native plant functional types that benefit from fire will also be more abundant in regions with greater summer drought, and a greater proportion of yearly precipitation falling outside the traditional growing season, because quick growing and winter-annual non-native plants may more effectively capture limited pulses of resources after disturbances like fire and outcompete natives in these conditions (Melgoza et al. 1990; Davis et al. 2000; Prevéy and Seastedt 2014; Bradley et al. 2018). Strong correlations between climate and post-fire invasion may also indicate that invasion risk could change in the future as the climate changes.

Materials and methods

We compiled a large dataset of non-native plant abundance, fire characteristics, and environmental predictors across the western United States. We focused our analyses on vegetation plots in the Western USA, west of − 100 longitude, as there were too few vegetation plots measured after fires in the eastern part of the country to examine broad-scale patterns there. For these analyses, we combined data from two national-scale datasets of plant species cover data compiled from federal, state, county, and other sources: the Standardized Plant Community with Introduced Status Database (SPCIS; Petri et al. 2022) and the Public LANDFIRE Reference Database from the Landscape Fire and Resource Management Planning Tools program (LANDFIRE 2016a, b). Three of the main contributors of plot-level vegetation data to these databases were the Bureau of Land Management (BLM) Inventory and monitoring program, the National Park Service (NPS) Inventory and Monitoring plots, and U.S. Department of Agriculture (USDA) Forest Service (USFS) Forest Inventory and Analysis Program. The LANDFIRE reference database comes from county, state, and federal government sources that contributed plant cover data to the LANDFIRE project (LANDFIRE 2016a, b). To supplement this dataset, we added plot-level data from numerous targeted post-fire vegetation studies in the western USA (Firmage and Ronsani 2021a, b, Table S1). These studies measured the absolute percent foliar cover of plant species within plots, or frequency of all plant species located at intervals along transects (hereafter, "plots"). We then used fire perimeter data from the combined wildland fire datasets for the United States and certain territories from 1800s to 2020 (Welty and Jeffries 2021), and fire perimeter and severity data from the Monitoring Trends in Burn Severity (MTBS) database, from 1980 through 2020 (www.mtbs.gov/) to identify all plots that were measured up to 50 years following a fire and quantify the number of times plots had burned prior to measurement. We identified the historical mean fire return interval for all fires and historical fire regimes prior to European colonization of North America for each plot using derived layers from LANDFIRE (LANDFIRE 2016b). The resulting combined dataset includes cover data from 237,799 vegetation plots located west of − 100 longitude, measured between 1970 and 2020 (Fig. 1). Of these plots, 26,729 were burned from 1 to 50 years prior to vegetation measurements (Fig. 1). This dataset consists of plots measured at a single point in time; and thus results shown here infer impacts via a space-for-time substitution (Sofaer et al. 2018).

We summed the percent cover of non-native plants by plant functional type and photosynthetic pathway in each plot across the combined dataset, using the following categories: woody (trees and shrubs), short-lived forbs, long-lived forbs, C3 short-lived grasses, C3 long-lived grasses, and C4 grasses. There were very few non-native C4 grasses present in the dataset, so the short-lived and long-lived C4 categories were combined to allow for statistical comparisons of cover between burned and unburned plots. Vines were included in the forb categories. 'Short-lived' indicates annuals and biennials, and 'long-lived' refers to perennial plants. Non-native status and lifeform categories are based on the native status, duration, and growth habit information from the USDA Plants database (USDA and NRCS 2022) and photosynthetic pathway information was derived from Waller and Lewis (1979), Belmonte and de Agrasar (2002) and Bruhl and Wilson (2007). Plots with summed cover values for any functional type that totaled over 100% were converted to 100%.

To address our first hypothesis that some plant functional types would be more abundant after fire than others, we fit separate models with each

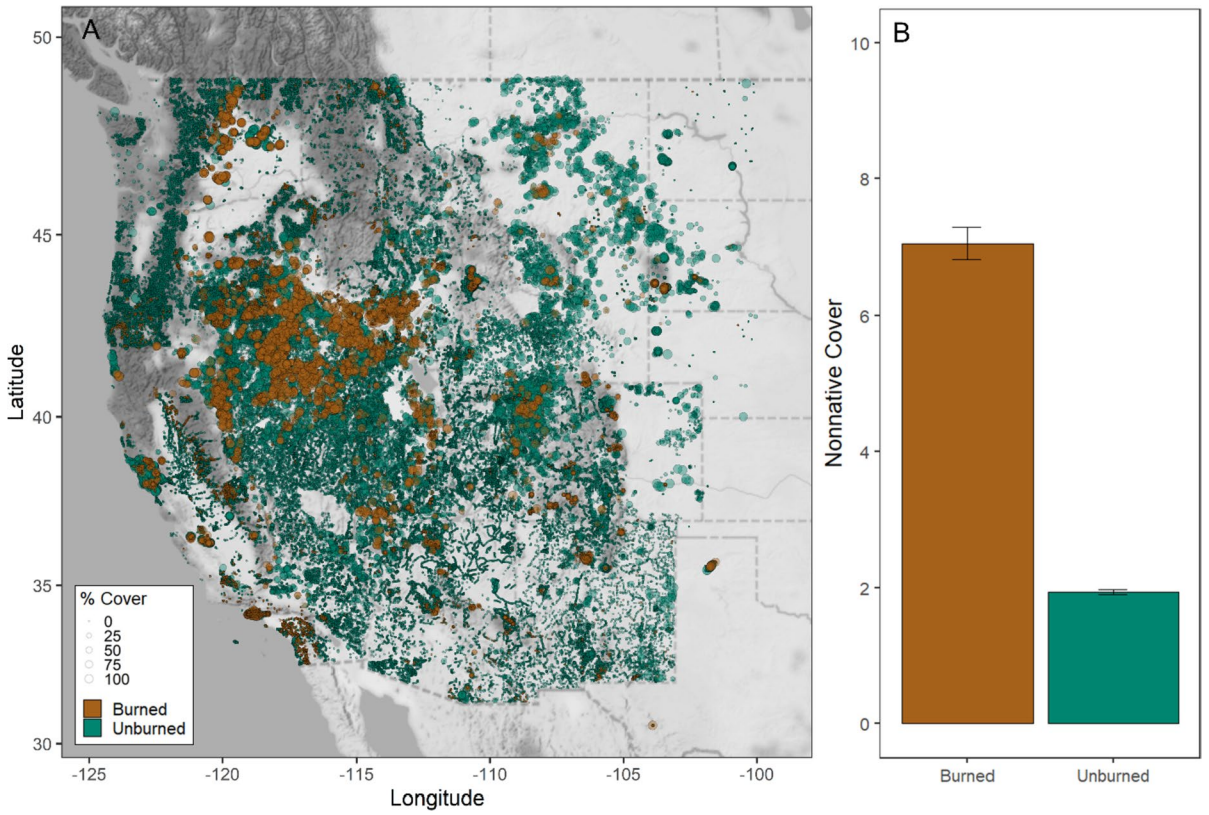


Fig. 1 **A** Locations of all plots in the dataset. Brown points indicate plots that burned up to 50 years prior to vegetation measurements (n = 26,729), and green points indicate plots that were not identified as having burned within 50 years of measurements (n = 211,070). The size of points relates to the percent foliar cover of non-native plant species recorded at that plot. **B** Average cover of all non-native plant species in plots burned up to 50 years prior to measurement, and unburned plots, ± standard error. Map tiles for base map by Stamen Design, under CC BY 4.0. Data by OpenStreetMap, under ODbL

non-native functional type's plot-level cumulative percent cover (hereafter 'cover') as response variables and burn status (burned or unburned) as the predictor variable. To examine our second hypothesis that abundance of non-native plant functional types following fires will depend on fire type and severity, we separately analyzed how fire type of the most recent fire (wildfire or prescribed fire), number of times burned over the past 50 years, time since the most recent fire, severity of the most recent fire based on burn severity mosaics from the MTBS database, historic fire return interval, and fire regime influenced the percent cover of non-native plants. Plots with fire types listed in MTBS as 'unknown' or 'wildland fire use' were grouped with the wildfire category. MTBS thematic burn severity classes were binned into three categories prior to analysis: 'Low', 'Medium', and 'High', based on changes in the Normalized Burn Ratio from LANDSAT images taken from before and after fires (Eidenshink et al. 2007). We performed separate analyses of thematic burn severity for plots located in forested versus grassland or shrubland land cover types according to the North American Environmental Atlas (NALCMS 2015). Fire regime analysis was restricted to categories with over 1000 observations. We tested for significant effects of all above variables using generalized linear mixed-effects models (glmms) in the statistical program R (R Core Team 2022). To accommodate the unbalanced nature of the data and the many plots where no non-native plants were found, we fit models with tweedie distributions using the glmmTMB package (Brooks et al. 2017). Tweedie distributions are generalized power law distributions that have been used

to model continuous data with many zeros (Dunn et al. 2018), and here provided a better fit and convergence than other distributions for our statistical models. For each analysis we also fit mixed-effects models only using data for each functional type in plots where those functional types were recorded (i.e., we removed plots with zero values for that specific functional type). We did this to account for potential biases in the way plot-level vegetation data were gathered. For example, if data on certain types of species were not measured in a plot, this would result in erroneous zero values. Additionally, a lack of cover of a non-native plant species may result from a lack of seed sources in an area, and not necessarily be indicative of responses to fire. Ecoregion, dataset, and survey year were considered random variables in models. Ecoregion categories were based on Level I Ecoregions of North America (Omernik and Griffith 2014), with the 'North American Deserts' category spilt into 'Warm deserts' and 'Cold deserts' to distribute the number of burned plots more evenly between regions (Fig. S1). We calculated pseudo R^2 values for mixed effects models with continuous predictor variables using the DHARMa package (Hartig 2022), and we performed Tukey's post hoc tests for multiple comparisons for models with categorical predictor variables (historic fire return interval and fire regime) using the multcomp package in R (Hothorn et al. 2008). Model assumptions, including lack of dispersion and normality of residuals, were checked visually in quantile–quantile plots, histograms of residuals, and plots of residuals versus fitted values.

To address our third hypothesis and examine how climate and other environmental factors influenced the post-fire invasion risk of functional types that benefited from fire, we modeled the abundance of different functional types using random forest models across the western USA. Random foress models were chosen for this portion of the analysis because they are robust to unbalanced, continuous data with non-normal distributions (Cutler et al. 2007; Mi et al. 2017), and have been found to perform well for spatial predictions of ecological phenomena (Evans et al. 2011). We used plot-level cover of non-native functional types in burned plots as response variables and included ecologically relevant bioclimatic variables derived from ClimateNA normals from 1981 to 2010 (Wang et al. 2016) as potential predictor variables. We also derived several precipitation variables that we hypothesized would be important predictors of non-native plant success. Specifically, we calculated the total precipitation received over the growing season (April–September). We also determined the ratio of yearly precipitation received in winter (October–March), March, and spring (March–May). Our reasoning behind this is that some non-native species may be more successful in regions that receive more precipitation in winter or early spring and less over the traditional growing season (Prevéy and Seastedt 2014). We included a predictor variable calculating distance from roads and trails, as they can be vectors for the introduction and spread of invasive plant species (Gelbard and Belnap 2003). We also considered soil variables (% sand, % clay, bulk density, pH), and geography (slope, aspect, and continuous heat-insolation load index), as gradients in soils and topography are often associated with where plants grow on the landscape (Table 1). Preliminary correlation analyses were conducted to identify predictor variables that were strongly correlated with each other. We removed predictor variables that were correlated at > than 0.7 (Dormann et al. 2013), retaining the set of uncorrelated variables that had the most ecological relevance (Table 1). We also tested the effect of each predictor variable on non-native cover separately using glmms as described above to ensure the final selected variables were also those that explained a significant amount of variance in post-fire non-native plant cover individually. We performed ecoregion specific analyses for our six generalized ecoregions to test whether important predictors of post-fire invasion varied by ecoregion. We compared results to those from random forests trained on spatially thinned datasets that retained data from only 10,000 plots selected to be maximally distant from each other, and we compared results to random forest models only including data from plots where plant functional groups were present. We also compared results for random forests trained with data only from the most common non-native C3 short-lived grass in the dataset, cheatgrass (*Bromus tectorum*), and random forests trained with all non-native C3 short-lived grasses except cheatgrass to examine how these results reflect its influence and whether other annual grasses show similar responses. We fit random forest models using the randomForest package (Liaw and Wiener 2002) in R, and assessed accuracy using Pearson correlations between training and out of bag samples. We assessed spatial

Table 1 All potential predictor variables considered for random forest models of post-fire non-native plant abundance across the western United States

Variable abbreviation	Variable name	Calculations/units	Source
AHM	**Annual heat-moisture index**	**(MAT + 10)/(MAP/1000))**	**Wang et al. (2016)**
April precip	April precipitation	mm	Wang et al. (2016)
August precip	August precipitation	mm	Wang et al. (2016)
BD	Bulk density of soil	kg/cubic-meter	Ramcharan et al. (2018)
bFFP	The day of the year on which the frost-free period (FFP) begins	DOY	Wang et al. (2016)
CHILI	**Continuous Heat-Load Index, based on latitude, aspect, and slope**	**Index between 0 and 1**	USGS (2019)
Clay %	**Percent clay content in top 5 cm of soil**	%	Ramcharan et al. (2018)
CMD	Hargreaves climatic moisture deficit	mm	Wang et al. (2016)
DD_0	degree-days below 0 °C	Number of days	Wang et al. (2016)
eFFP	The day of the year on which FFP ends	DOY	Wang et al. (2016)
EMT	Extreme minimum temperature over 30 years	°C	Wang et al. (2016)
Eref	Hargreaves reference evaporation	mm	Wang et al. (2016)
EXT	Extreme maximum temperature over 30 years	°C	Wang et al. (2016)
FFP	Frost-free period	Number of days	Wang et al. (2016)
FRI	**Historic fire regime interval**	**Mean number of years between fires**	LANDFIRE (2016a, b)
GSP	**April to September precipitation (mm)**	**(mm), Calculated from Climate NA monthly data**	**Wang et al. (2016)**
July precip	July precipitation	mm	Wang et al. (2016)
June precip	June precipitation	mm	Wang et al. (2016)
MAP	mean annual precipitation	mm	Wang et al. (2016)
MAR	**Mean annual solar radiation**	**(MJ m-2 d-1)**	**Wang et al. (2016)**
Mar p	March precipitation	mm	Wang et al. (2016)
MAT	Mean annual temperature	°C	Wang et al. (2016)
May precip	May precipitation	mm	Wang et al. (2016)
MCMT	Mean coldest month temperature	°C	Wang et al. (2016)
MSP	May to September precipitation	mm	Wang et al. (2016)
MWMT	Mean warmest month temperature	°C	Wang et al. (2016)
MWP	October to March precipitation	mm	Wang et al. (2016)
Nitrogen	Nitrogen content	% weight	Ramcharan et al. (2018)
Northness	**Northness**	**Cosine (Aspect in radians)**	USGS (2019)
PAS	**Precipitation as snow between August in the previous year and July in the current year**	**mm**	**Wang et al. (2016)**
pH	Ph of soil	pH	Ramcharan et al. (2018)
Remote	**Remoteness from roads and trails**	**Cost surface based on travel times to nearest road or trail**	US Census (2018)
Sand %	**Percent sand in top 5 cm of soil**	%	Ramcharan et al. (2018)
Sept. precip	September precipitation		Wang et al. (2016)
SHM	summer heat-moisture index	((MWMT)/(MSP/1000))	Wang et al. (2016)
Slope angle	**Slope degrees**	°	USGS (2019)
SOC	Soil organic content	g/kg	Ramcharan et al. (2018)
TD	Temperature difference between MWMT and MCMT, or continentality	Temperature difference in °C	Wang et al. (2016)

Table 1 (continued)

Variable abbreviation	Variable name	Calculations/units	Source
WPR	**% of annual precipitation received in Winter (Oct.-March)**	**%, Calculated from Climate NA monthly data**	Wang et al. (2016)

Variables in bold are the uncorrelated (< 0.07) predictors selected for final random forest models based on correlation analyses. Full citations for sources can be found in the Citations

autocorrelation of model results by visual inspection of residuals across plot locations in the western USA to ensure there were no spatial patterns in areas of over or under prediction.

To project potential climate-driven changes in post-fire invasion risk of functional types that benefited from fire, we used future projections of climate variables across the western USA to map predicted changes in post-fire risk for mid (2041–2070) and end (2071–2100) of century under a medium (SSP245) and a high (SSP585) greenhouse gas emission scenarios (Eyring et al. 2016; Wang et al. 2016). The SSP245 scenario is a medium radiative forcing scenario that predicts an additional radiative forcing of 4.5 W m^2 by 2100, and the SSP585 scenario represents the upper boundary of the range of climate change scenarios and predicts an additional radiative forcing of 8.5 W/m^2 by the end of the twenty-first century (Eyring et al. 2016). We used downscaled future climate projections from a CMIP6 13-model ensemble (Adaptwest Project 2022; Wang et al. 2016, Mahony et al. 2022) to identify regions where climatic conditions matching those predicting current post-fire invasion risk may exist in the future.

Results

Non-native plants were present in only 12% (28,391) of the 237,799 plots in the dataset. There were 667 non-native species identified across all plots in this dataset (Table S2). By non-native functional type, C3 short-lived grasses were present in 19,067 plots, C3 long-lived grasses were present in 6479 plots, short-lived forbs were present in 15,541 plots, long-lived forbs were present in 4873 plots, C4 grasses were present in 429 plots, and shrubs and trees were present in 1256 plots (Fig. S2).

Overall, burned plots had higher cover ($z = 47.13$, $p < 0.0001$) and species richness ($z = 46.10$, $p < 0.0001$) of non-native plants compared with unburned plots (Table 2, Fig. 1). C3 short-lived grasses comprised most of the non-native post-fire vegetation (Fig. 2), and the C3 short-lived grass *Bromus tectorum* was the most common and abundant species in the dataset (Table 3, Table S2). Post-fire cover of non-native species varied by plant functional type, and only cover of non-native C3 short-lived grasses and short-lived forbs were significantly higher in burned plots compared to unburned plots when including all plots, as well as only the subset of plots where the non-native functional types were present (all $p < 0.0001$, Table 2, Fig. 2).

Eleven percent (26,729) of the 237,799 plots in the dataset had burned within 50 years prior to measurement. Wildfire burned 25,661 plots; prescribed fires burned 1067 plots. Cover of non-native C3 short-lived grasses and short-lived forbs was higher following wildfires compared with prescribed burns, both in analyses including zero cover values, and when zero values were excluded (all $p > 0.05$, Table 4, Fig. 3).

We were able to identify the total number of times a plot was burned prior to measurement for 18,306 of the 26,729 burned plots. Of these, 8932 of the plots burned once prior to measurement, 4828 burned twice, 2463 burned three times, 1161 burned four times, and 922 plots had burned 5 or more times prior to measurement. The number of times a plot had burned prior to measurement was weakly correlated with the abundance of C3 short-lived grasses and short-lived forbs (all $p < 0.06$; pseudo $R^2 = 0.01$, Table 4).

We identified the MTBS burn severity data class of the most recent fire for a subset of 6244 plots in the western USA that had burned after 1984 in fires larger than 1000 acres; 3831 of these plots were binned in the 'low' fire severity category, 1577 in the 'medium' category, and 836 plots in the 'high' category. There was no trend for higher cover of C3 short-lived non-native grasses or forbs with higher fire severity across all ecosystem types, or within either the shrubland/grassland or forested ecosystems (all $p > 0.07$, pseudo

Table 2 Estimates of fixed effects of fire status on non-native cover and species richness of the non-native plant functional types, for analyses with and without plots recording 0% cover of the functional type

Non-native functional type	Fixed effect	Model type	Estimate	se	*z*	*p*	# Obs
Total non-native cover	Burned	All plots	1.57	0.03	48.21	< 0.00001	237,799
Total non-native cover	Burned	Non-zero plots	0.60	0.02	27.49	< 0.00001	28,391
Non-native sp. richness	Burned	All plots	0.85	0.02	46.35	< 0.00001	237,799
Non-native sp. richness	Burned	Non-zero plots	0.21	0.01	19.76	< 0.00001	28,391
c3 sl grass	Burned	All plots	1.64	0.04	46.15	< 0.00001	237,799
c3 sl grass	Burned	Non-zero plots	0.57	0.02	24.67	< 0.00001	19,067
c3 ll grass	Burned	All plots	1.86	0.07	25.00	< 0.00001	237,799
c3 ll grass	Burned	Non-zero plots	− 0.02	0.05	− 0.52	0.60	6479
c4 grass	Burned	All plots	0.53	0.56	0.95	0.34	237,799
c4 grass	Burned	Non-zero plots	− 0.18	0.28	− 0.64	0.52	429
sl forb	Burned	All plots	1.54	0.04	38.19	< 0.00001	237,799
sl forb	Burned	Non-zero plots	0.21	0.03	8.13	< 0.00001	15,541
ll forb	Burned	All plots	1.09	0.08	12.95	< 0.00001	237,799
ll forb	Burned	Non-zero plots	− 0.01	0.06	− 0.22	0.83	4873
Woody	Burned	All plots	0.74	0.34	2.20	0.06	237,799
Woody	Burned	Non-zero plots	− 0.22	0.16	− 1.36	0.17	1256

$R^2 < 0.15$, Table 4). There was also no trend for a decrease in non-native C3 short-lived grass or short-lived forb cover based on the amount of time between when a fire occurred and when a plot was measured (all $p > 0.07$, pseudo $R^2 < 0.009$, Table 4). Both short-lived non-native functional types were more abundant in plots that historically experienced longer fire return intervals (all $p < 0.03$, Fig. 4), and were most abundant in fire regime category IV-A, which historically had fire return intervals from 36 to 100 years and experienced replacement fires greater than 66.7% of the time (all $p < 0.05$, Fig. 4, Table 4).

Random forest models that included data from all burned plots throughout the western USA showed that severity of drought, growing season precipitation, and the ratio of yearly precipitation received in winter were the most important variables predicting cover of the two functional types that benefited from fire in this dataset: non-native C3 short-lived grasses and non-native short-lived forbs (Tables 5 and 6, Fig. 5). These variables were also highly significant predictors of post-fire cover in single-variable glmms (Tables S3 and S4). The order of importance of the top two predictor variables did not differ between non-native C3 short-lived grasses and non-native short-lived forbs. The order of importance differed somewhat for random forests including only plots where lifeforms were present, and models only including data from specific ecoregions (Tables S5 and S6). However, a climate variable was always ranked as the most important for each model type, with summer precipitation being the most important variable in most models (Tables S5 and S6). For non-native C3 short-lived grasses, non-native short-lived forbs, only *Bromus tectorum*, and all C3 short-lived grasses excluding *Bromus tectorum*, higher projected post-fire cover was predicted in semi-arid basins and steppes across the western USA for the current time period (Fig. 5). Areas projected to currently have higher post-fire cover of *B. tectorum* differed slightly from those projected to have higher cover of short-lived forbs or other C3 short-lived grasses, with higher predicted cover for *B. tectorum* overall, but relatively higher projected post-fire cover of short-lived forbs and other C3 grasses in the central and Mojave basins of California, and in the northern plains (Fig. 5).

Future predictions of invasion risk based on current relationships between post-fire cover of non-native C3 short-lived grasses and short-lived forbs and important environmental variables indicate that the risk of invasion may increase at higher elevations and latitudes, and in northern portions of the short-grass prairie (Figs. 6 and 7). Future projections show increased probabilities for more severe summer

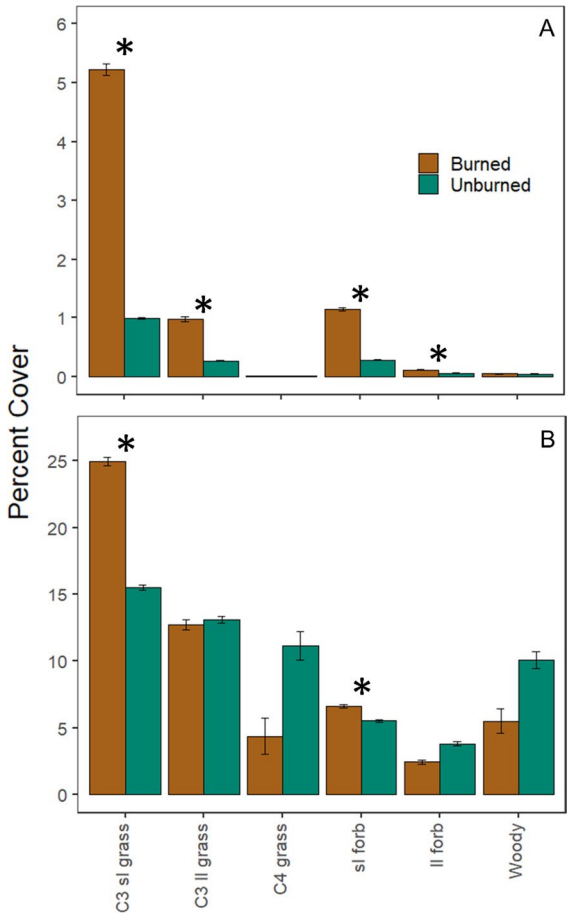


Fig. 2 Mean percent cover of non-native plant functional types in unburned plots and plots in the western United States that had burned in all fire types up to 50 years prior to measurement, ±standard error. Asterisks indicate significant differences in mean cover by burn status. **A** Means of all cover response variables from all plots measured, including plots with 0% cover for the variable. **B** Means of all cover response variables only including plots where the target lifeform was present. Note the change in values on the y-axis. Maps of cover for each lifeform, along with sample sizes, are shown in Fig. S2

drought, as well as an increase in the percentage of total precipitation occurring in winter and early spring and falling as rain rather than snow. The higher SSP585 scenario projects a greater risk of invasion by mid-century with further increases in post-fire invasion risk at higher elevations and latitudes by the end of century, and the lower SSP245 scenario shows a more moderate increase in post-fire invasion risk that stabilizes by end of the century (Figs. 6 and 7).

Discussion

Short-lived non-native plants were more abundant after wildfires than in unburned plots throughout the western USA, as predicted, which is in line with results from studies at smaller spatial scales (Alba et al. 2015; Williamson et al. 2020; Sofaer et al. 2022). Time since fire and fire severity did not significantly correlate with cover of non-native species, although satellite-derived measurements of fire severity may not be highly accurate across forest and shrubland ecosystems (Zhu et al. 2006; Storey et al. 2021). Short-lived non-native species were more abundant in burned areas with historically longer fire return intervals. Departure from historic fire regimes may create a pathway for invasion, as the plant species present in these ecosystems were adapted to disturbance regimes prior to European settlement, and the recent departure from these regimes may allow colonization by new species better evolved to deal with a higher disturbance frequency (Keeley et al. 2011; Brooks and Chambers 2011). This interpretation is reinforced by the relatively higher abundance of these non-natives following wildfire than prescribed fire (which is generally low severity in western forests), though we did not observe an effect of wildfire severity across the entire dataset.

In our dataset, short-lived C3 grasses were the most common non-native plants to establish after fires, with *Bromus tectorum* being the most abundant of these. Post-fire invasion of these non-native short-lived grasses was more likely in areas with low summer precipitation, higher annual heat-to-moisture ratios, and a higher proportion of yearly precipitation falling in winter and early spring. Currently, short-lived non-native C3 grasses are most invasive in semi-arid regions of western North America after fires. In these ecosystems, disturbance and departure from historical fire regimes (e.g. atypically severe or frequent fire) are important factors allowing for plant invasion (Lembrechts et al. 2016). Non-native species that can escape harsh conditions temporally (short-lived) and grow quickly (non-woody) can potentially thrive after disturbances, whereas the native species in these ecosystems often have a more conservative strategy to resist and survive harsh conditions (e.g. long-lived, slow growing, small leaves, thick cuticles, woody). In contrast, in moderate, wetter climates, many native species have evolved to grow quickly

Table 3 The six most frequently encountered non-native species by functional group, the number of plots the species were identified in across the dataset, and the average percent cover of each species in plots where they were present

Lifeform	Species	# of Plots	% Cover
Short-lived C3 grasses	*Bromus tectorum*	14,213	18.6
	Bromus arvensis	2144	11.77
	Bromus rubens	1707	4.73
	Bromus hordeaceus	1371	6.28
	Bromus diandrus	1206	4.9
	Bromus madritensis	804	2.63
Long-lived C3 grasses	*Poa pratensis*	2213	8.71
	Agropyron cristatum	2113	14.37
	Thinopyrum intermedium	1447	7.59
	Poa bulbosa	897	9.38
	Bromus inermis	717	9.27
	Phleum pratense	512	4.37
C4 grasses	*Cynodon dactylon*	87	13.97
	Eragrostis lehmanniana	87	8.09
	Pennisetum setaceum	86	2.97
	Eragrostis cilianensis	68	1.97
	Echinochloa crus-galli	44	1.76
	Setaria viridis	33	4.13
Short-lived forbs	*Sisymbrium altissimum*	2062	4.73
	Alyssum desertorum	1951	6.53
	Tragopogon dubius	1820	0.83
	Erodium cicutarium	1753	4.48
	Lactuca serriola	1427	1.37
	Melilotus officinalis	1262	6.27
Long-lived forbs	*Taraxacum officinale*	2353	1.85
	Cirsium arvense	573	3.24
	Rumex crispus	359	0.9
	Hypochaeris radicata	301	1.86
	Rumex acetosella	248	2.13
	Marrubium vulgare	218	1.08
Shrubs and trees	*Tamarix spp.*	292	10.38
	Nicotiana glauca	189	0.46
	Rubus armeniacus	92	13.62
	Elaeagnus angustifolia	92	16.74
	Genista monspessulana	91	6.36
	Rubus bifrons	66	5.34

A full list of all non-native species found in the dataset is in Table S2

with abundant resources, and thus post-fire native competition and invasion resistance is higher (Chambers et al. 2019; Bekris et al. 2021). Higher cover of native species, and specifically native perennial species, has been shown to provide resistance to winter-annual and short-lived non-native plant invasions (Chambers et al. 2007; McGlone et al. 2011; Reisner et al. 2013; Williamson et al. 2020; Anthony and Germino 2023). As this synthesis shows, and is backed by other research, the importance of climate and competition is especially apparent after disturbances (Taylor et al. 2014; Brummer et al. 2016).

The non-native functional types that increased after fire, short-lived forbs and C3 grasses, were both strongly correlated with climate, and the regions where invasions following fire were predicted to be most likely were similar for both functional types. Furthermore, even though our results for short-lived

Table 4 Estimates of fixed effects of fire type (unburned, wildfire, prescribed fire), the number of times a plot was burned in the last 50 years, the number of years since a fire occurred, the monitoring trends in burn severity (MTBS) fire severity classification, fire regime on percent cover of non-native functional types that increased following fires: short-lived grasses and short-lived forbs

Non-native functional type	Response values included	Fixed effect	Estimate	se	*z*	*p*	# obs
Short-lived grasses	All	Fire type (wildfire)	1.67	0.03	46.26	< 0.00001	25,661
Short-lived grasses	All	Fire type (Rx fire)	0.97	0.16	6.22	< 0.00001	1067
Short-lived grasses	Non-zero	Fire type (wildfire)	0.59	0.02	25.2	< 0.00001	5373
Short-lived grasses	Non-zero	Fire type (Rx fire)	− 0.001	0.11	− 0.02	0.99	193
Short-lived grasses	All	# times burned	0.16	0.05	3.01	0.002	18,306
Short-lived grasses	Non-zero	# times burned	0.17	0.04	4.18	0.05	4610
Short-lived grasses	All	Time since fire	0.004	0.001	2.97	0.003	18,306
Short-lived grasses	Non-zero	Time since fire	0.002	0.001	1.67	0.09	5596
Short-lived grasses	All	Fire severity	− 0.05	0.03	− 1.74	0.08	6244
Short-lived grasses	Non-zero	Fire severity	0.04	0.02	1.36	0.17	3667
Short-lived grasses	All—forest	Fire severity	− 0.50	0.42	− 1.19	0.23	799
Short-lived grasses	All—grass/shrubland	Fire severity	− 0.06	0.03	− 1.79	0.07	5345
Short-lived grasses	All	FRI (36–100)	0.03	0.05	2.1	0.04	9881
Short-lived grasses	All	FRI (200+)	0.16	0.04	3.3	0.0009	8710
Short-lived grasses	All	Fire regime (I-C)	− 1.83	0.09	*4.36	< 0.00001	3206
Short-lived grasses	All	Fire regime (III-A)	− 1.39	0.29	− 3.55	0.0004	2303
Short-lived grasses	All	Fire regime (IV-A)	2.79	0.32	8.47	< 0.00001	7578
Short-lived grasses	All	Fire regime (IV-B)	0.57	0.08	1.7	0.08	6509
Short-lived forbs	All	Fire type (wildfire)	1.56	0.04	38.53	< 0.00001	25,661
Short-lived forbs	All	Fire type (Rx fire)	0.62	0.18	3.40	0.0007	1067
Short-lived forbs	Non-zero	Fire type (wildfire)	0.22	0.03	8.3	< 0.00001	4463
Short-lived forbs	Non-zero	Fire type (Rx fire)	0.005	0.12	0.41	0.96	143
Short-lived forbs	All	# times burned	0.08	0.04	1.99	0.05	18,306
Short-lived forbs	Non-zero	# times burned	0.04	0.03	1.37	0.001	2681
Short-lived forbs	All	Time since fire	− 0.005	0.002	− 2.378	0.017, 0.35	18,306
Short-lived forbs	Non-zero	Time since fire	− 0.0002	0.002	− 0.113	0.91	4639
Short-lived forbs	All	Fire severity	0.06	0.05	1.20	0.23	6244
Short-lived forbs	Non-zero	Fire severity	0.12	0.04	3.22	0.06	2788
Short-lived forbs	All—forest	Fire severity	− 0.23	0.36	− 0.65	0.52	799
Short-lived forbs	All—grass/shrubland	Fire severity	0.01	0.05	0.27	0.78	5345
Short-lived forbs	All	FRI (36–100)	0.12	0.06	1.97	0.05	9881
Short-lived forbs	All	FRI (200+)	0.31	0.06	5.2	< 0.00001	8710
Short-lived forbs	All	Fire regime (I-C)	− 0.18	0.03	− 1.51	0.13	3206
Short-lived forbs	All	Fire regime (III-A)	− 0.14	0.01	− 1.06	0.29	2303
Short-lived forbs	All	Fire regime (IV-A)	0.53	0.01	4.88	< 0.00001	7578
Short-lived forbs	All	Fire regime (IV-B)	0.54	0.01	0.492	0.62	6509

C3 grasses were likely driven by relationships important for the dominant invasive *B. tectorum*, the spatial predictions from models trained on other C3 grasses excluding *B. tectorum* were similar to those from models trained on only *B. tectorum* cover data. These results highlight that semi-arid regions receiving the majority of precipitation in the winter and early spring are susceptible to invasion after disturbances by short-lived non-native species that can germinate and grow quickly outside the historical growing season. Species traits are often the focus of studies of invasions (e.g. Drenovsky et al. 2012; Funk

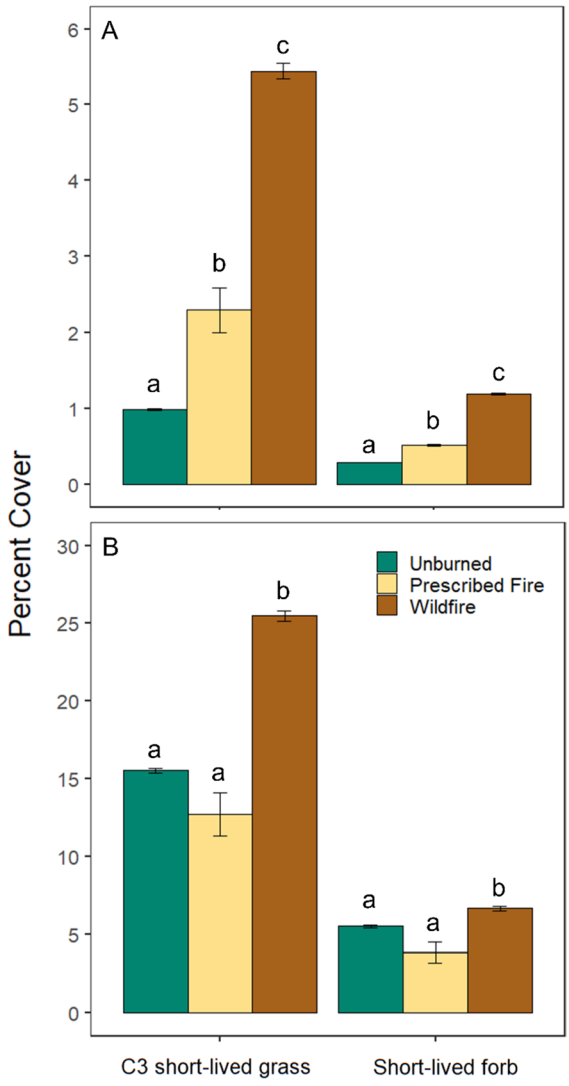
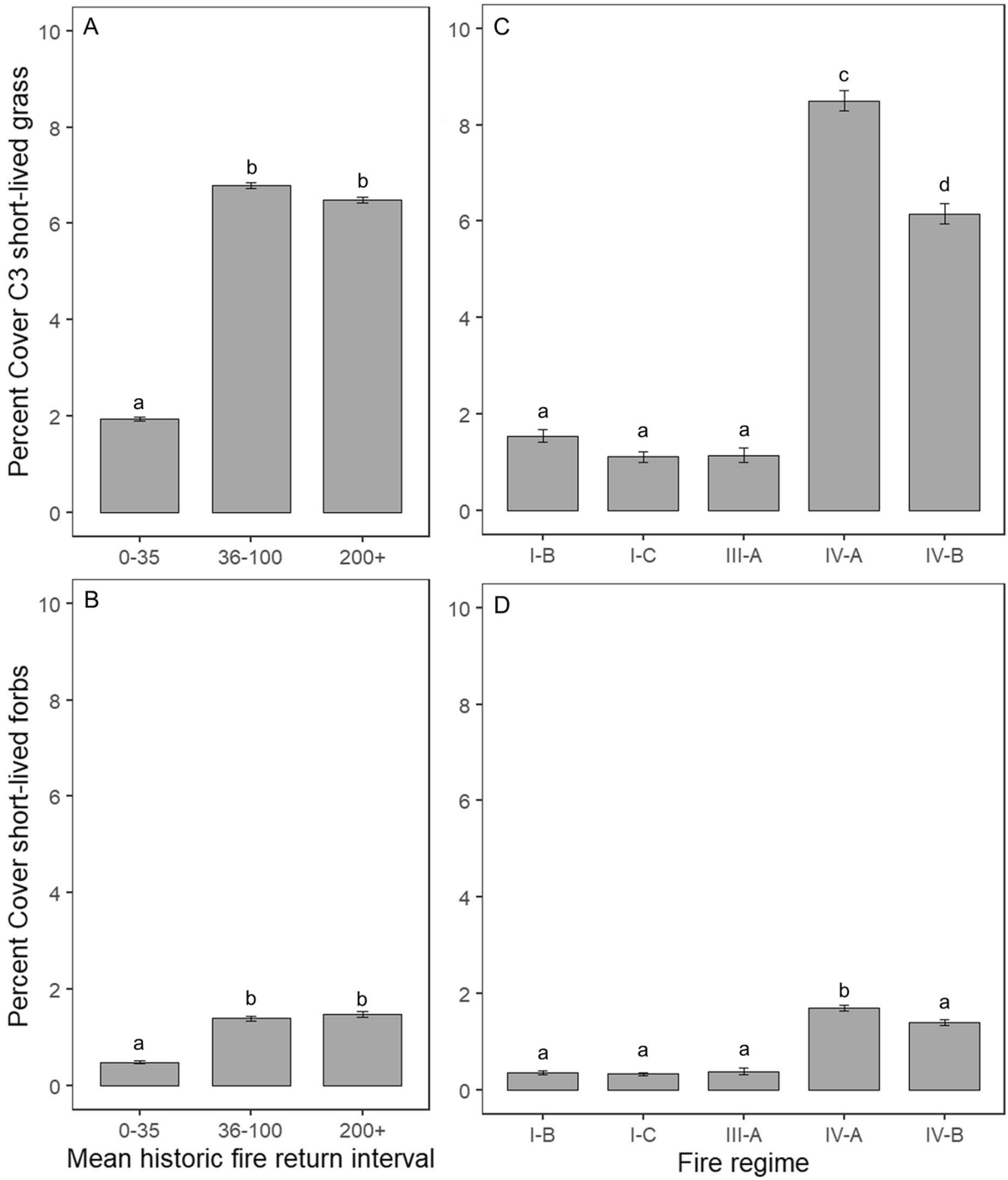


Fig. 3 **A** Mean percent cover of fire-increasing non-native lifeforms in unburned plots (n = 211,071), plots that burned in a prescribed fire (n = 1067), and plots that burned in a wildfire (n = 25,152) up to 50 years prior to measurement, ± standard error, including plots with 0% cover for the variable. **B** Means of all cover response variables only including plots where the target lifeform was present. Note the change in values on the y-axis. Different letters indicate significant differences in mean cover by fire type at $p < 0.05$

et al. 2017), but abiotic factors also play an important role in determining where species become invasive (Davis et al. 2000). In regions with temporally limited resources, there may be a greater fluctuation in these resources after disturbances compared to regions with more moderate climates, and thus there is a greater opportunity for invasion, perhaps regardless of the specific invader characteristics themselves (Davis et al. 2000). Highlighting the environmental conditions that influence ecosystem invasibility after disturbances can help focus management efforts to regions at the greatest risk following disturbance and with climate change.

Climate-driven changes in the timing of precipitation and drought may alter the locations where post-fire plant invasions for the species included in this dataset are most likely and most damaging (Bradley 2009; Taylor et al. 2014; Bradley et al. 2018). There is some evidence that these changes may already be occurring, as long-term monitoring plots from rangelands in western USA show an increase in the cover of annual plants across all regions over time, including in forested mountains and in the Northern Great Plains (Kleinhesselink et al. 2023). Future changes in invasion risk may impact decisions about prescribed fires, thinning operations, herbicide use, restoration planting, and where to increase post-disturbance monitoring for non-natives in higher elevation ecosystems (Brooks et al. 2004; Merriam et al. 2006; Keeley et al. 2011). Our results also highlight regions that may see a decrease in invasion risk by short-lived non-native C3 grasses and forbs in the future based on climate projections. Areas that are projected to see decreased risk of invasion are those that are projected to become very arid in the future, and these regions may become more resistant to invasion as there will be fewer resource pulses to enable non-native colonization following disturbances, potentially favoring the more conservative strategies of some native species (Zefferman et al. 2015). These results need to be interpreted with caution, but they are supported by other similar findings for individual non-native species (Bradley and Wilcove 2009; Allen and Bradley 2016). Targeting areas with a reduced projected invasion risk for restoration treatments could result in greater restoration success as non-natives become less climatically suited and thus less competitive with restored native plantings (Pilliod et al. 2021).

There are many critical caveats that should be considered when interpreting the results of our data synthesis. Perhaps most importantly, this dataset consists of temporally and spatially uneven samples consisting of a single post-fire measurement per plot; and thus results shown here infer impacts via a space-for-time substitution (Sofaer et al. 2018). For example, we


A
Percent Cover C3 short-lived grass
10
8
6
4
2
0
a
b
b
0-35
36-100
200+
C
a
a
a
c
d
I-B
I-C
III-A
IV-A
IV-B
B
Percent Cover short-lived forbs
a
b
b
0-35
36-100
200+
Mean historic fire return interval
D
a
a
a
b
a
I-B
I-C
III-A
IV-A
IV-B
Fire regime

◂**Fig. 4** Average percent cover of functional types that increased following fire in burned plots. **A** non-native C3 short-lived grasses and **B** non-native short-lived forbs in binned categories based on LANDFIRE historic fire return intervals, 0–35 years (n = 7702), 36–100 years (n = 9881), and 200 years or greater (n = 8710). Average percent cover of **C** non-native C3 short-lived grasses and **D** non-native short-lived forbs by LANDFIRE fire regime classification: I-B is categorized as having percent replacement fire less than 66.7%, and a fire return interval of 6–15 years (n = 3114), I-C has 66.7% replacement fire, fire return interval of 16–35 years (n = 3206), III-A has less than 80% replacement fire, fire return interval of 36–100 years (n = 2303), IV-A has greater than 80% replacement fire, fire return interval of 36–100 years (n = 7578), IV-B has greater than 66.7% replacement fire, fire return interval of 101–200 years (n = 6509). Different letters denote significant differences at $p < 0.05$

found that time since fire did not impact non-native plant cover. However, these data are from only a single point in time at each site, so we cannot accurately examine site-level cover changes over time. We also found no relationships between non-native cover and fire severity. Fire severity measurements for grass and shrubland ecosystems have been shown to be highly inaccurate (Zhu et al. 2006; Storey et al. 2021), and site-level analyses have shown that higher fire severity increases prevalence of some invaders in forests (Tortorelli et al. 2020). Additionally, the importance of climate variables as drivers of invasion risk likely results from the large scale of this analysis as well. Topography, soils, past management, and grazing history would likely become more important predictors of where non-native plants are abundant at finer scales (Pearson and Dawson 2003; Ellsworth et al. 2016). Additional data from long-term monitoring plots that are repeatedly measured over time, evenly dispersed across the landscape, and paired with accurate on-the-ground measures of fire severity across a range of habitat types will help refine predictions of post-fire invasion risk.

We did not examine native vegetation here, so we cannot directly infer impacts of competition, biotic resistance, or other plant interactions. This would have only been correlative with this data collection, as these data were taken at a single point in time, and time-series before and after fires would be needed for such analyses. We attempted to limit the influence of pre-existing vegetation in our analyses by only including "recently" burned (i.e., disturbed) plots. However, this type of analysis means we are unable to accurately identify how pre-fire plant community composition or vegetation type influences post-fire invasion patterns. There were also large data gaps that likely hinder the accurate assessment of post-fire invasion risk across the western USA. For example, we have very few data points from burned plots in southwestern hot desert ecosystems, where non-native long-lived grass species may be becoming more prevalent after fires (Brooks and Chambers 2011; Wilder et al. 2021). Additional monitoring data from burned areas in the southwestern region, as well as other under-sampled regions, will help provide more balanced and accurate predictions of post-fire invasion risk across the west. This synthesis is helpful in that it highlights regions where more data are needed.

Another important caveat with these analyses is that we sum the cover of all non-native species within a functional type together prior to evaluating how cover is influenced by environmental variables. This is partially due to the scarcity of data for any single species besides *Bromus tectorum* across the entirety of the western USA, but also stems from the goal to look at broad-scale patterns in invasion rather than replicate species-level distribution models and maps (e.g. Bradley 2009; Bradley et al. 2018; Sofaer et al. 2022). Individual species will respond in different ways to combinations of disturbance and climate (Tortorelli et al. 2020; Applestein and Germino

Table 5 Random forest model results showing R^2 and root-mean-squared-error (RSME) values for predictions from out-of-bag data not in the bootstrapped sample (oob), as well for the bootstrapped data (sample)

Model	R^2 oob	R^2 sample	RSME oob	RSME sample
Short-lived C3 grasses	0.44	0.89	11.63	5.80
Short-lived forbs	0.19	0.83	4.43	2.39

Table 6 Importance values for the final set of predictor variables from random forest models of post-fire abundance of non-native C3 short-lived grasses and short-lived forbs

Lifeform	Variable	Permutation importance
C3 short-lived grasses		
	April-Sept. precipitation	17.80
	Winter precipitation ratio	15.50
	Precipitation as snow	15.16
	Annual heat-moisture index	13.78
	Mean annual radiation	8.65
	Historic fire return interval	8.24
	Remoteness	8.24
	% Sand	6.79
	% Clay	6.70
	CHILI	6.02
	Northness	5.84
Short-lived forbs		
	April-Sept. precipitation	8.04
	Winter precipitation ratio	6.89
	Annual heat-moisture index	6.12
	Precipitation as snow	5.97
	MAR	3.36
	Historic fire return interval	3.17
	% Clay	3.09
	% Sand	2.82
	Remoteness	2.57
	CHILI	1.73
	Northness	1.66

Importance values show how much including the variable in the model increases model accuracy. Variables with higher importance values have greater predictive power. Descriptions of variable abbreviations can be found in Table 1

2022), and thus grouping multiple species together for analyses could obfuscate species-level patterns. In sagebrush steppe, *Ventenata dubia* has been shown to occupy a distinct niche from *Bromus tectorum* and *Taeniatherum caput-medusae* (Applestein and Germino 2022). Additionally, fire may not play as large of a role in enhancing invasion risk of specific species of short-lived non-natives compared to others (Ridder et al. 2021). For example, *Ventenata dubia* is currently a more successful invader at higher elevations than *Bromus tectorum*, and our combined climate predictions for all short-lived grasses may mask more rapid advances to higher elevations of *Ventenata dubia* with a changing climate (Tortorelli et al. 2020).

This synthesis is the first to pull extensively from multiple datasets to examine patterns in post-fire plant invasion risk at a subcontinental scale. We show that non-native invasion after fire in the western USA is overwhelmingly caused by short-lived plant species, and they are most abundant after fires in regions with dry summers and historically long fire return intervals. Our analyses clearly indicate a 'climate space' where non-native plant invasion is more likely after fire, specifically in regions with higher summer drought. This 'climate space' may change as the climate changes and summer droughts become more severe, so risk of post-fire plant invasions may change as well. The spatial projections of the results presented here can help identify hotspots where invasions are the most common following fire now and in the future. These spatial predictions provide an important step to help reduce the risk of

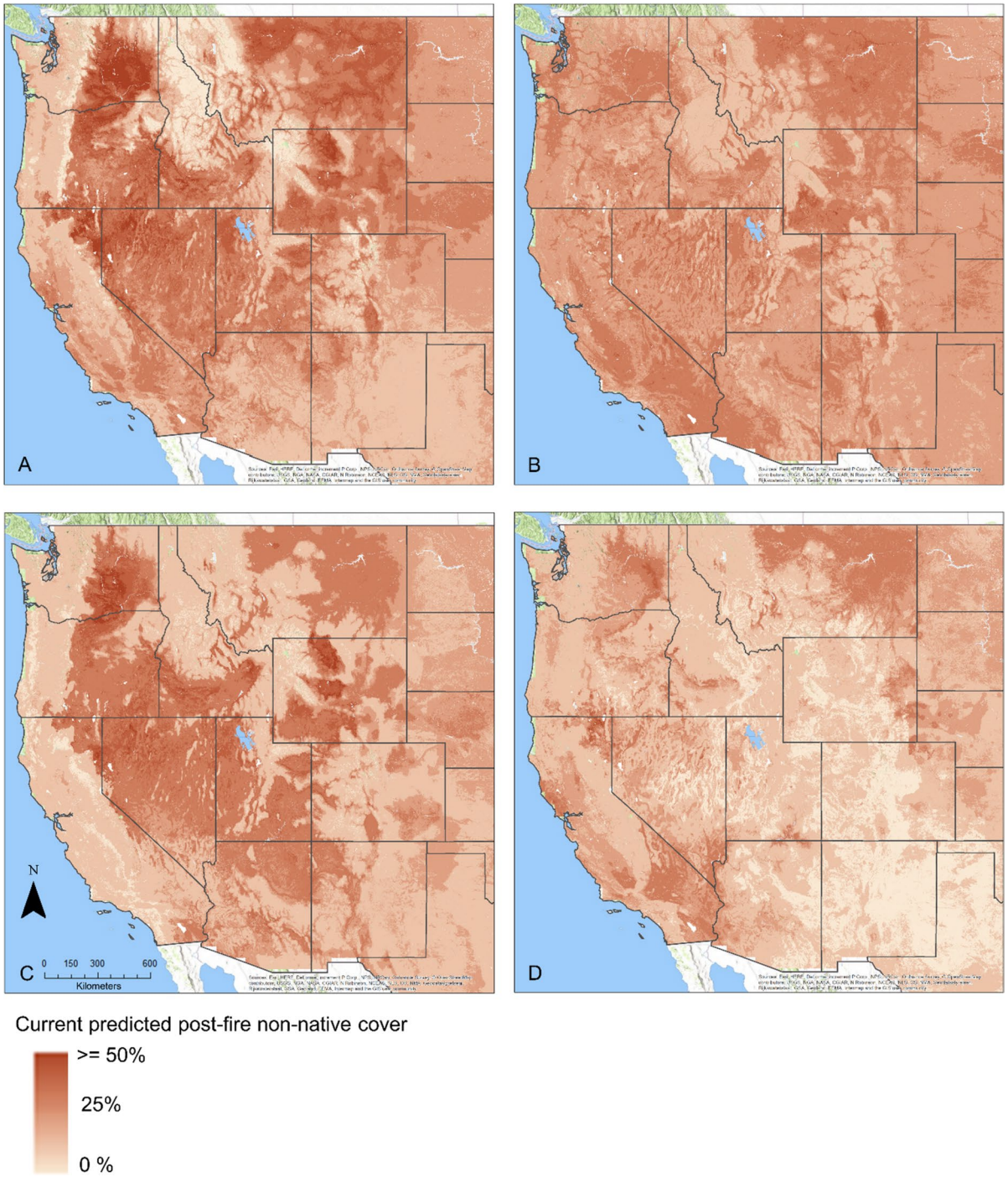


Fig. 5 Projections of post-fire cover of non-native **A** C3 short-lived grasses, **B** short-lived forbs, **C** only *Bromus tectorum,* and **D** all other C3 short-lived grasses except *Bromus tectorum* based on random forests using bioclimatic data for the current (1981–2010) time period. Base map from Esri and its licensors, copyright 2022

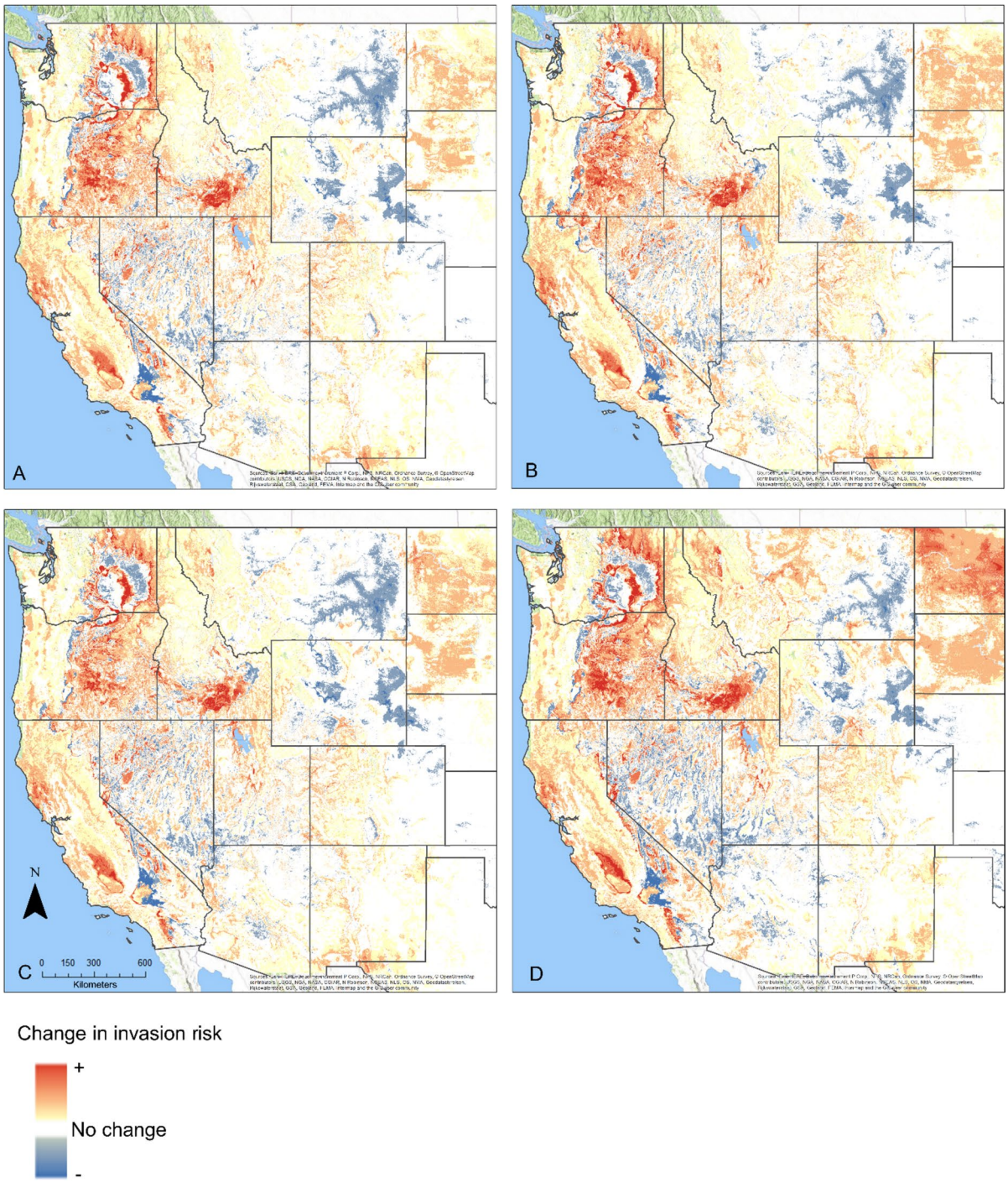


Fig. 6 Projected changes in post-fire abundance of non-native C3 short-lived grasses for **A** 2041–2070 under a medium emissions climate scenario SSP245, **B** 2041–2070 under the highest emissions climate scenario SSP285, **C** 2071–2100 under SSP545, and **D** 2071–2100 under SSP585. Base map from Esri and its licensors, copyright 2022

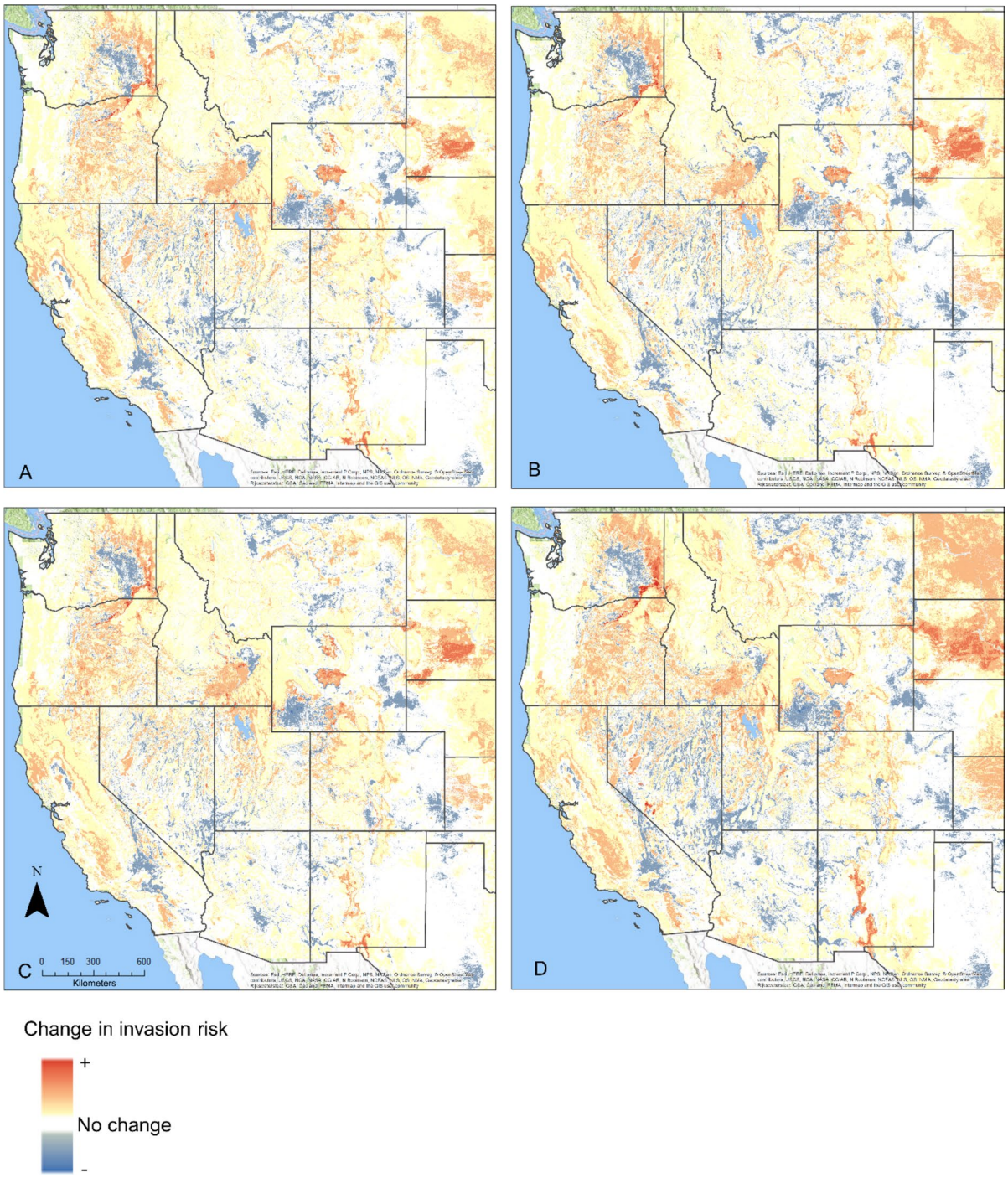


Fig. 7 Projected changes in post-fire abundance of non-native short-lived forbs for **A** 2041–2070 under a medium emissions climate scenario SSP245, **B** 2041–2070 under the highest emissions climate scenario SSP285, **C** 2071–2100 under SSP545, and **D** 2071–2100 under SSP585. Base map from Esri and its licensors, copyright 2022

invasion after wildfires by allowing for more targeted mitigation, monitoring, and restoration.

Acknowledgements The authors thank the many people who helped to collect, record, and make publicly available the data used in this paper. We thank Aleta Nafus for assistance interpreting AIM BLM data, and and Neil Frakes for conversations about the management implications of this research. Funding for this project was provided by the US Geological Survey Land Management Research Program in the Ecosystems Mission Area and the US Geological Survey Risk Research and Applications Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions JSP, ISP, CSJ, conceived of the concept for this synthesis with input from SMM and JTS. KB, JDC, MAD, DF, PF, KH, JJ, BKK, MAK, BM, TN, JR, JDS, CSSR, MTS, and CT collected and contributed data to this synthesis. JSP led the writing of the manuscript and analysis of the data. All authors contributed to writing and edits of drafts of the manuscript and gave final approval for publication.

Funding Funding for this project was provided by the US Geological Survey Land Management Research Program in the Ecosystems Mission Area and the US Geological Survey Risk Research and Applications Program.

Data availability Any unpublished plot-level plant cover data used in this manuscript will be made available upon request from the authors.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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