



Invasive grasses increase fire occurrence and frequency across US ecoregions

Emily J. Fusco^{a,1}, John T. Finn^b, Jennifer K. Balch^{c,d}, R. Chelsea Nagy^c, and Bethany A. Bradley^{a,b}

^aGraduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003; ^bDepartment of Environmental Conservation, University of Massachusetts, Amherst, MA 01003; ^cEarth Lab, University of Colorado, Boulder, CO 80309; and ^dDepartment of Geography, University of Colorado, Boulder, CO 80309

Edited by David Bowman, University of Tasmania, Hobart, Tasmania, and accepted by Editorial Board Member Ruth S. DeFries October 1, 2019 (received for review May 17, 2019)

Fire-prone invasive grasses create novel ecosystem threats by increasing fine-fuel loads and continuity, which can alter fire regimes. While the existence of an invasive grass-fire cycle is well known, evidence of altered fire regimes is typically based on local-scale studies or expert knowledge. Here, we quantify the effects of 12 nonnative, invasive grasses on fire occurrence, size, and frequency across 29 US ecoregions encompassing more than one third of the conterminous United States. These 12 grass species promote fire locally and have extensive spatial records of abundant infestations. We combined agency and satellite fire data with records of abundant grass invasion to test for differences in fire regimes between invaded and nearby “uninvaded” habitat. Additionally, we assessed whether invasive grass presence is a significant predictor of altered fire by modeling fire occurrence, size, and frequency as a function of grass invasion, in addition to anthropogenic and ecological covariates relevant to fire. Eight species showed significantly higher fire-occurrence rates, which more than tripled for *Schismus barbatus* and *Pennisetum ciliare*. Six species demonstrated significantly higher mean fire frequency, which more than doubled for *Neyraudia reynaudiana* and *Pennisetum ciliare*. Grass invasion was significant in fire occurrence and frequency models, but not in fire-size models. The significant differences in fire regimes, coupled with the importance of grass invasion in modeling these differences, suggest that invasive grasses alter US fire regimes at regional scales. As concern about US wildfires grows, accounting for fire-promoting invasive grasses will be imperative for effectively managing ecosystems.

invasive grass | nonnative plant | fire regime | grass-fire cycle

Nonnative invasive grasses can promote fire, creating new fire regimes that are unsuitable for native species and lead to lower diversity and localized extinctions (1, 2). The altered fire regimes also create favorable conditions for the invasive grasses, which recover and spread quickly postfire, resulting in a “grass-fire cycle” (1). Despite the ubiquity of invasive grasses identified as fire-prone (e.g., ref. 3), alteration of fire regimes at a regional scale has been quantified for only a single species, cheatgrass (*Bromus tectorum*; refs. 4–6). Given increasing western US fire frequency (7–9) and the continued spread of nonnative grasses, it is critical to identify the broad-scale effects of the grass-fire cycle.

Grass invasion adds abundant and novel fuels to ecosystems, altering fuel properties in ways that promote fire (1, 2). For example, invasive grasses can increase rates of fire occurrence by providing continuous fine fuels which cure quickly relative to other vegetation types (1, 2, 10), increasing the range of conditions favorable for fire ignition (1). The presence of invasive grasses can increase fire size by creating horizontal and vertical fuel continuity, resulting in faster fire spread and the potential for crown fires (1, 2). Larger fuel loads from grass invasion can also lead to higher fire intensity (2), and hotter fires have been documented in areas occupied by grass species currently invading the United States (e.g., refs. 11–13). Finally, invasive grasses can increase fire frequency because they recover quickly

postfire, providing renewed fuel sources and potentially resulting in shortened fire-return intervals (e.g., refs. 2, 11, 14, and 15). The mechanisms by which invasive grasses promote fire are likely applicable across large spatial scales and in a range of ecosystems; however, regional alteration of fire regimes has not been assessed for the majority of species.

In the United States, nonnative invasive grasses suspected of promoting fire are established in ecosystems across the country, including pine savannah in the southeast (11, 12), temperate deciduous forest in the mid-Atlantic and southeast (16), wetlands in the Great Lakes region (17), deserts in the southwest (18), and semiarid shrublands in the Great Basin (refs. 4–6 and Fig. 1). Invasive grass alteration of fire regimes is likely to negatively affect native species regardless of region, from ecosystems where fire is infrequent (e.g., sagebrush systems in the intermountain west; ref. 14) to those that were historically fire-dependent (e.g., pine savannah in Florida; ref. 11) by increasing fire frequency to historically unprecedented rates at which native vegetation is unable to recover (19). One exception may be the US central Great Plains regions where fire-adapted native grasses are dominant (20). In addition, increased fire intensity associated with grass invasion has been demonstrated to adversely affect native plants which evolved with lower-intensity fires (13).

Nonnative, invasive grasses are introduced and dispersed by people (21, 22). However, despite the prevalence of invasive grasses and the pronounced economic and ecological consequences of

Significance

One of the most notorious impacts of nonnative, invasive grasses is the alteration of fire regimes. Yet, most evidence of these impacts comes from local-scale studies, making it unclear whether they have broader implications for national and regional fire management. Our analysis of 12 invasive grasses documents regional-scale alteration of fire regimes for 8 species, which are already increasing fire occurrence by up to 230% and fire frequency by up to 150%. These impacts were demonstrated across US ecoregions and vegetation types, suggesting that many ecosystems are vulnerable to a novel grass-fire cycle. Managing existing grass invasions and preventing future introductions presents a key opportunity to remediate the ecological and economic consequences of invasive species and fire.

Author contributions: E.J.F. and B.A.B. designed research; E.J.F. and B.A.B. performed research; E.J.F. and J.T.F. analyzed data; and E.J.F., J.T.F., J.K.B., R.C.N., and B.A.B. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. D.B. is a guest editor invited by the Editorial Board. Published under the [PNAS license](#).

Data deposition: Data are available at UMass Scholarworks (DOI: [10.7275/ndsz-eh64](https://doi.org/10.7275/ndsz-eh64)).

¹To whom correspondence may be addressed. Email: efusco@cns.umass.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1908253116/-DCSupplemental.

First published November 4, 2019.

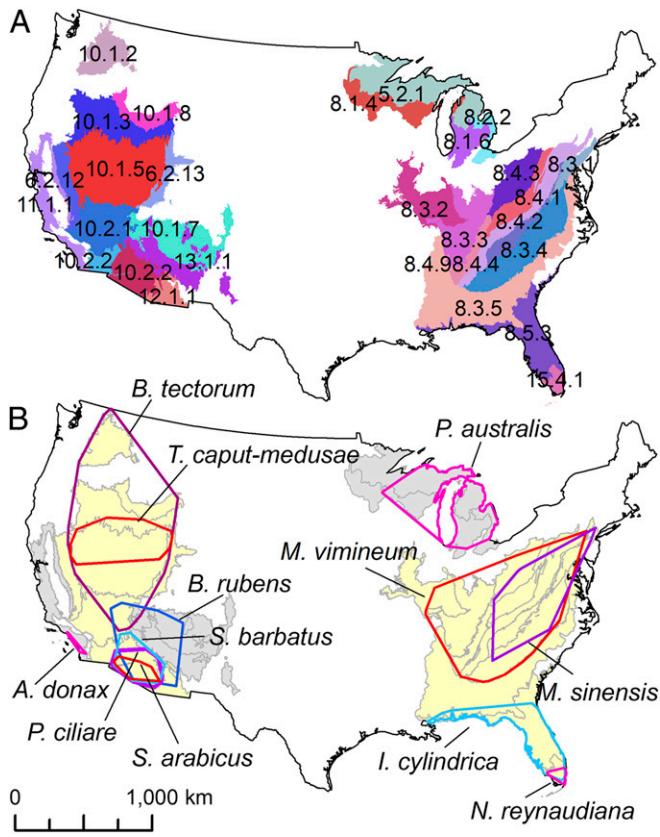


Fig. 1. The grass species analyzed span US ecoregions. (A) Twenty-nine EPA level III ecoregions were included in the analysis. Ecoregion names are listed in *SI Appendix, Table S2*. (B) Study areas for the target invasive grass species were based on convex hull polygons of invaded pixels located in fire-prone ecoregion(s), and regions with demonstrated fire impacts are highlighted in yellow. Both maps are displayed in US Albers equal-area conic projection.

increased wildfires (23, 24), the regional impacts of these grasses on fire regimes remain unknown. Here, we calculate differences in fire occurrence, fire size, and fire frequency on invaded vs. uninhabited landscapes for 12 invasive grass species to quantify the magnitude and geography of altered fire regimes. We further model these fire-regime parameters (i.e., occurrence, size, frequency) as a function of anthropogenic and ecological variables to explore the association between nonnative grass invasion and observed fire regimes. This national-scale analysis spans multiple ecoregions and provides a comprehensive analysis of the effect of invasive grasses on US fire regimes.

Results

Based on our literature review, we identified 18 fire-promoting invasive grass species in the conterminous United States (*SI Appendix, Table S1*). Of these, 12 species were determined to have sufficient spatial abundance data for analysis (Table 1 and *SI Appendix, Table S1*). These 12 grass species were located in 29 EPA level III ecoregions (Fig. 1), and numbers of invaded pixels (pixel = 500 m square used for analysis) ranged from 35 for *Arundo donax* to 9,388 for *B. tectorum* (median = 344; *SI Appendix, Table S2*). All 12 species are in the family Poaceae and are graminoids (grass-like) with the exception of *A. donax* and *Phragmites australis*, which are shrub/subshrub in addition to graminoid (25). Half of the species are annuals, and half are perennials. They range in size from less than 1 m in height for *Schismus* spp. and *Bromus* spp. to 8 m for *A. donax* (Table 1 and refs. 3 and 26).

Eight of the 12 grass species had a significantly higher proportion of fire occurrence on invaded pixels compared to uninhabited pixels, with significant increases ranging from 27 to 230% (Fig. 2A). Of these 8 species, *Schismus barbatus* showed the highest rate of increase, with 5% of uninhabited pixels burning during the 2000–2015 time period vs. 16.5% of invaded pixels. There was no significant difference for 3 species, and for *P. australis*, fire occurrence was significantly lower in invaded pixels (Fig. 2A). For fire size, *I. cylindrica* and *Miscanthus sinensis* were associated with significantly larger fires, while *B. tectorum*, *Pennisetum ciliare*, and *Taeniatherum caput-medusae* were associated with significantly smaller fires (Fig. 2B). Fire frequency was significantly higher in invaded pixels for all 6 species with sufficient data to be tested (Fig. 2C). For *Neyraudia reynaudiana*, average fire frequency more than doubled in invaded pixels (0.38 vs. 0.87 fires/16 y/pixel; $P < 0.001$).

For grasses with significant differences in fire-regime parameters, we created generalized linear models (GLMs) to predict fire occurrence, size, and frequency as a function of environmental variables, anthropogenic variables, and grass invasion. The model results generally supported that grass invasion increased aspects of fire regimes (Table 2). Of the 9 fire-occurrence GLMs, presence of invasive grass was a significant predictor in all models except *P. australis*. The deviance explained for these models ranged from 2.3% for *Microstegium vimineum* to 13.8% for *N. reynaudiana*. Similarly, grass presence remained a significant predictor in all 6 of the fire-frequency models tested (Table 2). The total deviance explained in these models ranged from 3.9% in *M. vimineum* to 14.8% for *T. caput-medusae*. The deviance explained by the invasive grass ranged from 0.08% (Δ AIC [Akaike information criterion] 1.3) for *I. cylindrica* fire frequency to 5.9% (Δ AIC 44.9) for *N. reynaudiana* fire occurrence (Table 2). Where it was included in the best model, invasive grass ranked as the first or second most important variable in 9 of 14 models based on percent deviance explained (*SI Appendix, Table S3*). Invasive grass was not a significant predictor in any fire-size models.

Discussion

People undoubtedly influence fire regimes (24, 41): increasing fire occurrence by providing ignition sources (e.g., refs. 9 and 42–44), changing climate (e.g., refs. 7 and 45), and altering fuels through the introduction of nonnative, invasive species (1, 2, 5). While there has been a focus on national- and regional-scale impacts of climate and human ignition on fire, little exists to quantify regional impacts of invasive grasses on fire regimes across the United States. Our results are consistent with previous work showing regional increases in fire occurrence associated with *B. tectorum* (5, 6). We provide evidence for significant alteration to regional fire regimes for 7 additional nonnative, invasive grass species across ecoregions: *T. caput-medusae* in the Great Basin, *P. ciliare* and *S. barbatus* in the desert southwest, *M. vimineum* and *M. sinensis* in eastern temperate deciduous forests, and *I. cylindrica* and *N. reynaudiana* in southern pine savannah and pine rockland communities (Fig. 1).

Although climate change has received considerable attention as a factor in altered fire regimes, invasive grasses are similarly important. Individually, climate change is expected to increase the potential for fire occurrence by 150% by the end of the century based on projected changes in temperature and precipitation (46). Here we show that 8 invasive grass species are already associated with increased rates of fire occurrence by 27 to 230% (Fig. 2A), and 6 invasive grass species are associated with increased mean fire frequency by 24 to 150% (Fig. 2C and *SI Appendix, Fig. S1*), compounding current and future fire risk across the United States. Further, understanding climate change and invasive grass interactions is necessary for predicting future fires. For example, increased variability in precipitation allows grasses to accumulate biomass during wet years, which cures during subsequent dry periods, increasing fire risk (5, 47). Climate change

Table 1. Twelve invasive grass species chosen for analysis and their reported impacts on fire regimes

Scientific Name	Common Name	Duration	Height (meters)	Fire-Regime Impact	Selected Literature
<i>Arundo donax</i>	giant reed	perennial	2–8	high flammability, high intensity, increased fuel load, and continuity	(15, 27, 28)
<i>Bromus rubens</i>	red brome	annual	0.1–0.7	increased fire frequency, fuel load, occurrence, and spread, persistent flammability, low intensity	(18, 28–30)
<i>Bromus tectorum</i>	cheat grass/downy brome	annual	0.1–0.8	increased fire frequency, horizontal continuity, spread, contributor to large fires in the Great Basin	(5, 6, 14, 31)
<i>Imperata cylindrica</i>	cogon grass	perennial	1	increased fuel loads, horizontal continuity, vertical continuity, fine fuels, and intensity	(11, 12, 32)
<i>Microstegium vimineum</i>	Japanese stiltgrass	annual	1–1.5	potential to increase fine-fuel load, increased flame height, easily ignitable, particularly a hazard after senescence and in dry climates	(16, 33)
<i>Miscanthus sinensis</i>	Chinese silvergrass	perennial	1–3	increased fuel load, high flammability, particularly a hazard after senescence and in dry climates	(34, 35)
<i>Neyraudia reynaudiana</i>	silk reed, burma reed	perennial	1–5	increased fuel load, fine fuel, vertical continuity, spread, severity, and frequency	(12, 36)
<i>Pennisetum ciliare</i>	buffelgrass	perennial	0.1–1.5	increased fine-fuel load, flame length, spread, intensity, and frequency, creates consistent fire hazard	(13, 37)
<i>Phragmites australis</i>	common reed	perennial	up to 6	highly flammable, increased fire spread and fuel loads	(17, 38)
<i>Schismus arabicus</i>	Arabian schismus	annual	0.4	increased fine fuel and continuity	(18, 26, 28)
<i>Schismus barbatus</i>	common Mediterranean grass	annual	0.4	increased fine fuel and continuity	(18, 26, 28)
<i>Taeniamia caput-medusae</i>	medusahead	Annual	0.2–0.5	increased fire frequency, and horizontal continuity, highly flammable, high volumes of long-lasting dry litter	(39, 40)

is also likely to promote the growth and spread of invasive grasses (48, 49), further enhancing the grass-fire cycle.

Grass invasion was an important predictor of increased fire occurrence and frequency for 8 and 6 invasive grass species, respectively, suggesting the grasses increase fuel ignitability (ref. 2, Table 2, and *SI Appendix*, Table S3). Higher ignitability could be due to increased fuel loads and horizontal fuel continuity, which change fuel properties and increase the likelihood of ignition (ref. 2 and Table 1). Another mechanism could be the tendency of fine fuels from grasses to cure quickly, making them ignitable under a wide range of climatic conditions (1, 2). Only *P. australis*, a wetland species, had significantly lower rates of fire occurrence (Fig. 2A). However, *P. australis* invasion was no longer significant when additional covariates were included in the model, suggesting that other ecological and anthropogenic variables better explain this pattern (Table 2).

Invasive grass presence, anthropogenic predictors, and ecological variables were significant in the majority of fire-occurrence and frequency models (Table 2). The significance of grass invasion with anthropogenic covariates highlights the importance of human activity alongside the ecology of natural systems in understanding modern fire regimes. In the United States, human ignitions account for 84% of wildfires (9). Invasive grasses are also strongly associated with human activity (21) and are introduced by people. Our analysis underscores the importance of both human activity and invasive grasses on the grass-fire cycle and suggests that these fire-regime drivers are likely inextricable. Further, these interactions are present across nearly 25% of US ecoregions (Fig. 1). The human grass-fire link is concerning because it indicates that increased fire probability and frequency are occurring where people live, posing threats to human lives and livelihoods.

Invasive grass association with human activity may also explain why we found little evidence for regional impacts on fire size

(Fig. 2B). For the few species that demonstrated a significant difference in fire size, our models suggest these differences are a result of ecological and anthropogenic variables rather than grass invasion. For example, the significance of development in predicting fire size for *I. cylindrica* and *B. tectorum* (Table 2) could be due to heightened fire suppression in invaded areas near development. Suppression could decrease observed fire spread and size in invaded areas, adding small-fire records and potentially obscuring changes in fire size. While grass invasion may promote fire spread and size at the event level (e.g., ref. 15), it remains challenging to identify a regional link between fire size and grass invasion.

Another challenge associated with interpreting this type of pyrogeographic analysis is the relatively low deviance explained by the “invaded” covariate (0.08 to 5.9%) and by each of the top-ranked models (4 to 15%, Table 2). These numbers are not surprising given that the data were synthesized from multiple sources, collection methods, and times. Consistent and repeated collection of invasive species abundance information is rare but critical for understanding impacts (50) and could improve our models. Therefore, given the nature of these data, our results likely provide a conservative estimate of invasive grass impacts on fire.

Wildfires are costly both ecologically and economically (23, 24), and climate change and human ignition sources have contributed to a regional-scale increase in the United States for both wildfire occurrence and the number of large wildfires (7, 9, 44, 51). Here we show that fuel alteration from the introduction of nonnative, invasive grasses contributes to increased fire occurrence and frequency at regional scales. In the regions highlighted by this analysis, we suggest that fire and invasive species managers work together to create integrated management plans that account for invasive grass-fire interactions. Invasive species’ abundance and distribution will continue to increase (48, 52),

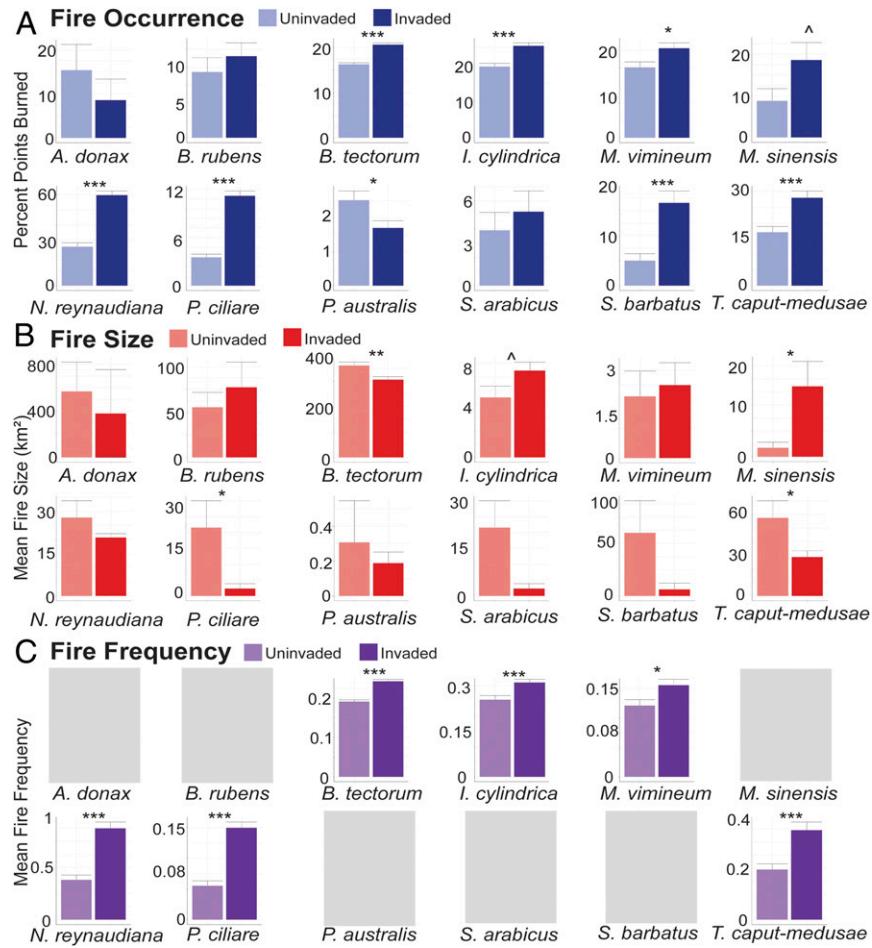


Fig. 2. Invasive grasses are significantly related to changes in fire regimes. Of the 12 species tested, 8 showed significant increases in fire occurrence (A), 2 showed a significant increase in mean fire size (B), and 6 showed significant increases in fire frequency (C). Six species were not tested for changes in fire frequency because their pixels rarely burned more than once. Each bar plot shows mean and SE. Significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^ $P < 0.1$.

and unabated, climate, human, and invasive species interactions will continue to promote wildfires across the United States.

Materials and Methods

Invasive Grass Data. We used the Invasive Plant Atlas of the United States (53) to identify invasive grass species in the United States. For each species ($n = 176$; *SI Appendix*, Table S1), we conducted a literature search on Web of Science (search terms: TS = ["Scientific name" OR "common name"] AND TS = [fire] AND TS = [increase OR promote OR cycle]). We also reviewed species summaries on the Fire Effects Information System (3) to determine if the species is reported to promote fire (Table 1). For species associated with altered fire regimes ($n = 18$; *SI Appendix*, Table S1), we downloaded spatial occurrence data compiled from 33 local, state, and national databases (54, 55).

Importantly, the presence of nonnative grasses at low-abundance seems unlikely to influence fire (6), but invasive plant occurrence data tend to be skewed toward low-abundance records because they are collected for early detection and rapid response (56). Therefore, we focused on occurrence data that included abundance estimates (percent cover, stem count, or density). We excluded points with very low abundance reported as either <1% (percent cover), a single plant (stem count), or as trace/rare (density). However, data with very low abundance as well as data lacking abundance information (presence only) were retained to inform the selection of pseudoabsence pixels (see below). For each species, we aggregated points to a 500 × 500-m-square spatial resolution (hereafter, pixel). We identified pixels as "invaded" for those with any reported abundant infestation, and "present" for pixels containing only points with very low or unknown abundance.

For each selected species, we determined a study region by identifying areas where each species was reported to have invaded and by assessing

ecoregions where the literature reported a fire effect. Most invaded pixels were within geographic regions with reported grass-fire impacts, with the exception of *A. donax*, which had the majority of invaded pixels in Texas but was linked to altered fire regimes in California. We used a convex hull polygon to identify invaded landscapes for each grass species based on the invaded pixels that fell within US Environmental Protection Agency (EPA) level III ecoregions (57) that encompassed the geographic regions identified in the literature (Fig. 1). We created a set of random "pseudoabsence" pixels to represent the nearby uninvaded landscape for each invasive grass species (58). Pseudoabsence pixels, hereafter referred to as uninvaded pixels, were randomly located within the invaded landscape, but were not within 500 m of a presence or invaded-pixel centroid. However, they were constrained within 5 km from an invaded-pixel centroid to increase the likelihood that they represent generally similar habitats and land use conditions as invaded pixels (e.g., elevation, climate; ref. 59).

Fire Data. We used US fire records from 2000 to 2015 from the Fire Program Analysis fire-occurrence database (FPA fod; ref. 60) and Monitoring Trends in Burn Severity (MTBS; ref. 61) from 2000 to 2015, based on years with the most consistent fire-data availability (62), to assess relationships between nonnative invasive grasses and regional fire regimes. The FPA fod is a spatial database of federal, state, and local wildfires and excludes agricultural fires and prescribed burns (60). The FPA fod records are point data and contain attributes such as fire year, final fire size, and, in some cases, an identifier that links the record to the MTBS database. The MTBS database is a compilation of US fires that reached a final fire size of at least 404 ha in the western United States or 202 ha in the eastern United States and includes a final perimeter polygon of the fire event. For each point in the FPA fod database that could be linked to a fire in the MTBS database, the fire perimeter from the MTBS database was retained (1.18% of fire records, 88% of

Table 2. Generalized linear models show significant relationships between invaded areas and fire occurrence and frequency

Grass	Fire-Occurrence Model	Fire-Size Model	Fire-Frequency Model
<i>B. tectorum</i>	Invaded***, Road***, BPS***, Ecorg***, Dev*** 7.1 (0.58) 20	BPS^, Ecorg*** 12	Invaded***, Road^, BPS***, Ecorg***, Dev*** 9.3 (0.59) 81
<i>I. cylindrica</i>	Invaded**, Road***, BPS**, Ecorg*** 5.9 (0.20) 8.1	BPS***, Ecorg***, Dev*** 21.3	Invaded^, Road***, BPS**, Ecorg*** 7 (0.08) 1.3
<i>M. sinensis</i>	Invaded*, Road** 10 (3.0) 2.3	Ecorg*** 39.2	n/a n/a
<i>M. vimineum</i>	Invaded*, Road**, Ecorg*** 2.3 (0.19) 2.5	n/a n/a	Invaded*, Road***, Ecorg*** 3.9 (0.27) 3.6
<i>N. reynaudiana</i>	Invaded***, Dev*** 13.8 (5.93) 44.9	n/a n/a	Invaded***, BPS*** 11.3 (5.91) 40.8
<i>P. ciliare</i>	Invaded***, Road***, BPS*, Ecorg**, Dev** 7.4 (2.56) [†] 60.9	Dev* 10.0	Invaded***, Road***, Ecorg***, Dev* 10.8 (2.18) ^{‡,†} 30.0
<i>P. australis</i>	Road**, BPS***, Ecorg***, Dev^ 9.8	n/a n/a	n/a n/a
<i>S. barbatus</i>	Invaded*, Road**, BPS* 11 (2.03) 4.6	n/a n/a	n/a n/a
<i>T. caput-medusae</i>	Invaded***, Ecorg***, Dev 10.1 (2.66) 20.3	Ecorg***, Dev** 15.8	Invaded***, Ecorg***, Dev^ 14.8 (3.44) 20.6

Percent deviance explained refers to the top-ranked model, with the percent explained by grass invasion in parentheses. ΔAIC is reported for the model if "Invaded" is dropped. Road, distance to road; BPS, biophysical setting; Ecorg, EPA level III ecoregion; Dev, percent development; Invaded, grass-invaded pixel; Dev. Explain, %, percent deviance explained. [†] $P < 0.1$ [‡] $P < 0.05$ ^{**} $P < 0.01$ ^{***} $P < 0.001$.

[†]Spatial autocorrelation was present in the full model.

[‡]A negative binomial model was used because of overdispersion in the Poisson model.

total burned area). For the remainder of fire events in the FPA fod database, we estimated fire perimeters as a circular buffer based on final fire size. The MTBS records provide the precise spatial pattern of the burned area extents, while the circular buffers are an approximation. The resulting yearly fire files were converted into 500-m spatial grid (Albers equal-area conic projection to cover the extents of the contiguous United States), and a pixel was considered burned if it overlapped any part of the fire perimeter. Yearly fire rasters were combined over the study period to create 3 fire datasets for the 16-y study period: fire occurrence (whether or not a pixel burned), fire size (maximum fire size associated with each pixel), and fire frequency (how many times a pixel burned; ref. 63).

Modeling. The modeling analysis consisted of 2 parts: First, we determined whether fire-regime parameters were significantly different on invaded vs. uninvaded pixels. Second, we modeled only those grasses that demonstrated significant differences as a function of grass invasion and additional ecological and anthropogenic covariates. This 2-step framework allowed us to narrow our scope for the second part of analysis.

To determine whether invasive grass significantly alters fire regimes, we estimated differences in fire occurrence, size, and frequency on invaded vs. uninvaded pixels. To ensure that fire occurrence did not drive results for size and frequency, fire size was only compared for pixels that burned, and frequency was only compared when at least 10% of pixels (and >20 individual pixels) burned more than once (see *SI Appendix*, Fig. S1 for fire-frequency histograms). We checked for significant differences in fire occurrence of invaded and uninvaded pixels using Pearson's χ^2 tests, fire size using Welch's t tests, and fire frequencies using Mann-Whitney U tests. All statistical analyses were performed in R version 3.3.2 (64).

For grasses that showed a significant difference in fire occurrence, size, or frequency, we extracted additional ecological and anthropogenic covariates to test whether grass presence remained a significant predictor of the altered fire regime. Cases where invasive grasses remained significant predictors of

observed alteration in fire regime, while considering ecological and anthropogenic factors, provide further evidence that the observed alteration in fire regime is influenced by the presence of the invasive grass. Ecological covariates included the ecoregion and the most common potential vegetation associated with the pixel centroid, while anthropogenic covariates included Euclidean distance to road and percent development per pixel (*SI Appendix*, Table S4). We created a GLM for each grass species using the ecological, anthropogenic, and grass invasion (invaded vs. uninvaded) variables as predictors of fire occurrence, size, or frequency using binomial, gamma, and Poisson distributions, respectively. We checked for correlation using the correlation variation inflation factor using the corvif function (65) and did not use any combination of variables with a variation inflation factor > 6 . We used backward selection and selected the best model for each grass and fire characteristic (occurrence, size, frequency) using the AIC. As a measure of variable importance, for each model that included invasive grass, we calculated the delta AIC (66) if the "invaded" covariate was dropped. We also calculated the deviance explained for each best model and subtracted the deviance explained from each model without the "invaded" covariate to determine the percent deviance explained by the invasive grass. To more directly compare the importance of invasive grass with other covariates, we completed these calculations for all predictor variables. We checked the models for spatial autocorrelation using a semivariogram. Cases where invaded pixels were significantly different from uninvaded pixels as well as significant predictors of fire in the GLM were interpreted as strong evidence that the invasive grass influenced the regional fire regime. Data are available at UMass Scholarworks (67).

ACKNOWLEDGMENTS. This work was funded by the NSF award BCS 1740267. We thank J. Allen, E. Beaury, and B. Ryan for contributing to grass data and grass data processing and N. Mietkiewicz for contributing to fire-data processing. P. Warren, J. Bellemare, two reviewers, and the editor provided helpful comments and insight, which improved this manuscript.

1. C. M. D'Antonio, P. M. Vitousek, Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23**, 63–87 (1992).
2. M. L. Brooks *et al.*, Effects of invasive alien plants on fire regimes. *Bioscience* **54**, 677–688 (2004).
3. U.S. Department of Agriculture, FEIS. Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Fire Effects Information System, [Online]. <https://www.feis-crs.org/feis/>. Accessed 20 June 2018.
4. P. A. Knapp, Spatio-temporal patterns of large grassland fires in the intermountain west, U.S.A. *Glob. Ecol. Biogeogr. Lett.* **7**, 259–272 (1998).
5. J. K. Balch, B. A. Bradley, C. M. D'Antonio, J. Gómez-Dans, Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Glob. Change Biol.* **19**, 173–183 (2013).
6. B. A. Bradley *et al.*, Cheatgrass (*Bromus tectorum*) distribution in the intermountain western United States and its relationship to fire frequency, seasonality, and ignitions. *Biol. Invasions* **20**, 1493–1506 (2018).
7. A. L. Westerling, H. G. Hildago, D. R. Cayan, T. W. Swetnam, Warming and earlier spring increase western U.S. Forest wildfire activity. *Science* **313**, 940–944 (2006).
8. P. E. Dennison, S. C. Brewer, J. D. Arnold, M. A. Moritz, Large wildfire trends in the western United States, 1984–2011. *Geophys. Res. Lett.* **41**, 2928–2933 (2014).
9. J. K. Balch *et al.*, Human-started wildfires expand the fire niche across the United States. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2946–2951 (2017).
10. J. B. Kauffman, C. Uhl, Interactions of anthropogenic activities, fire, and rain forests in the Amazon Basin. *Fire Trop. Biota* **84**, 117–134 (1990).
11. C. L. Lippincott, Effects of *Imperata cylindrica* (L.) Beauv. (Cogongrass) invasion on fire regime in Florida. *Nat. Areas J.* **20**, 140–149 (2000).
12. W. J. Platt, R. M. Gottschalk, Effects of exotic grasses on potential fine fuel loads in the groundcover of south Florida slash pine savannas. *Int. J. Wildland Fire* **10**, 155–159 (2001).
13. C. J. McDonald, G. R. Mcpherson, Creating hotter fires in the Sonoran Desert: Buffelgrass produces copious fuels and high fire temperatures. *Fire Ecol.* **9**, 26–39 (2013).
14. S. G. Whisenant, "Changing fire frequencies on Idaho's Snake River plains: Ecological and management implications" in *Symposium Cheatgrass Invasion, Shrub Dieoff, Other Aspects Shrub Biology Management* Las Vegas, NV, E. D. McArthur, E. M. Romney, S. D. Smith, P. T. Tueller, Eds. (US Department of Agriculture, Ogden, Utah, 1990), General Technical Report INT 276, pp. 4–10.
15. G. C. Coffman, R. F. Ambrose, P. W. Rundel, Wildfire promotes dominance of invasive giant reed (*Arundo donax*) in riparian ecosystems. *Biol. Invasions* **12**, 2723–2734 (2010).
16. S. L. Flory, K. Clay, S. M. Emery, J. R. Robb, B. Winters, Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. *J. Appl. Ecol.* **52**, 992–1000 (2015).
17. C. L. Gucker, *Phragmites australis*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/phraus/all.html>. Accessed 25 June 2018.
18. M. L. Brooks, Alien annual grasses and fire in the Mojave Desert. *Madroño* **46**, 13–19 (1999).
19. T. A. Fairman, L. T. Bennett, C. R. Nitschke, Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *J. Environ. Manage.* **231**, 59–65 (2019).
20. L. M. Porensky, D. M. Blumenthal, Historical wildfires do not promote cheatgrass invasion in a western Great Plains steppe. *Biol. Invasions* **18**, 3333–3349 (2016).
21. S. H. Reichard, P. White, Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* **51**, 103–113 (2001).
22. B. A. Bradley, R. Early, C. J. B. Sorte, Space to invade? Comparative range infilling and potential range of invasive and native plants. *Glob. Ecol. Biogeogr.* **24**, 348–359 (2015).
23. D. E. Calkin, K. M. Gebert, J. G. Jones, R. P. Neilson, Forest service large fire area burned and suppression expenditure trends, 1970–2002. *J. For.* **103**, 179–183 (2005).
24. D. M. J. S. Bowman *et al.*, Fire in the earth system. *Science* **324**, 481–484 (2009).
25. USDA NRCS, The PLANTS Database, (National Plant Data Team, Greensboro, NC). <http://plants.usda.gov>. Accessed 11 August 2019.
26. Global Invasive Species Database, Species profile: *Schismus barbatus*. <http://www.iucngisd.org/gisd/species.php?sc=552>. Accessed 11 August 2019.
27. J. McWilliams, *Arundo donax*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/arudon/all.html>. Accessed 25 June 2018.
28. A. M. Lambert, C. M. D'Antonio, T. L. Dudley, Invasive species and fire in California ecosystems. *Fremontia* **38**, 29–36 (2010).
29. K. A. Simonin, *Bromus madritensis*, *Bromus rubens*. In: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <http://fs.fed.us/database/feis/plants/graminoid/brospp/all.html>. Accessed 25 June 2018.
30. M. L. Brooks, J. R. Matchett, Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *J. Arid Environ.* **67**, 148–164 (2006).
31. K. Zouhar, *Bromus tectorum*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/brotec/all.html>. Accessed 25 June 2018.
32. J. L. Howard, *Imperata brasiliensis*, *I. cylindrica*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/impspp/all.html>. Accessed 25 June 2018.
33. J. L. Fryer, *Microstegium vimineum*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/micvim/all.html>. Accessed 25 June 2018.
34. M. A. Waggy, *Miscanthus sinensis*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/misssi/all.html>. Accessed 25 June 2018.
35. U. Jørgensen, Benefits versus risks of growing biofuel crops: The case of *Miscanthus*. *Curr. Opin. Environ. Sustain.* **3**, 24–30 (2011).
36. K. R. Stone, *Neyraudia reynaudiana*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/nereyre/all.html>. Accessed 25 June 2018.
37. A. S. Hauser, *Pennisetum ciliare*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/pencil/all.html>. Accessed 25 June 2018.
38. M. Marks, B. Lapin, J. Randall, *Phragmites australis* (*P. communis*): Threats, management, and monitoring. *Nat. Areas J.* **14**, 285–294 (1994).
39. P. J. Torell, L. C. Erikson, R. H. Haas, The Medusahead Problem in Idaho. *Weeds* **9**, 124–131 (1961).
40. A. J. Archer, *Taeniatherum caput-medusae*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/plants/graminoid/taecap/all.html>. Accessed 25 June 2018.
41. D. M. J. S. Bowman *et al.*, The human dimension of fire regimes on Earth. *J. Biogeogr.* **38**, 2223–2236 (2011).
42. A. D. Syphard *et al.*, Human influence on California fire regimes. *Ecol. Appl.* **17**, 1388–1402 (2007).
43. E. J. Fusco, J. T. Abatzoglou, J. K. Balch, J. T. Finn, B. A. Bradley, Quantifying the human influence on fire ignition across the western USA. *Ecol. Appl.* **26**, 2388–2399 (2016).
44. R. C. Nagy, E. Fusco, B. Bradley, J. T. Abatzoglou, J. Balch, Human-related ignitions increase the number of large wildfires across U.S. ecoregions. *Fire* **1**, 4 (2018).
45. A. L. Westerling, Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371**, 20150178 (2016). Correction in *Philos. Trans. R. Soc. Lond. B Biol. Sci.* (2016).
46. Y. Liu, J. Stanturf, S. Goodrick, Trends in global wildfire potential in a changing climate. *For. Ecol. Manage.* **259**, 685–697 (2010).
47. C. Trauernicht, Vegetation-Rainfall interactions reveal how climate variability and climate change alter spatial patterns of wildland fire probability on Big Island, Hawaii. *Sci. Total Environ.* **650**, 459–469 (2019).
48. J. S. Dukes, H. A. Mooney, Does global change increase the success of biological invaders? *Trends Ecol. Evol.* **14**, 135–139 (1999).
49. B. A. Bradley, D. M. Blumenthal, D. S. Wilcove, L. H. Ziska, Predicting plant invasions in an era of global change. *Trends Ecol. Evol.* **25**, 310–318 (2010).
50. B. A. Bradley *et al.*, Invasive species risk assessments need more consistent spatial abundance data. *Ecosphere* **9**, e02302 (2018).
51. M. D. Flannigan, M. A. Krawchuk, W. J. de Groot, B. M. Wotton, L. M. Gowman, Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* **18**, 483–507 (2009).
52. J. M. Diez *et al.*, Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* **10**, 249–257 (2012).
53. Invasive Plant Atlas of the United States, Invasive Plant Atlas of the United States - Database of Plants Invading Natural Areas. <https://www.invasiveplantatlas.org/>, <https://www.invasiveplantatlas.org/index.html>. Accessed June 2018.
54. J. M. Allen, B. A. Bradley, Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biol. Conserv.* **203**, 306–312 (2016).
55. EDDMapS, Early Detection and Distribution Mapping System, (The University of Georgia - Center for Invasive Species and Ecosystem Health, 2011). <http://www.eddmaps.org>. Accessed 9 July 2018.
56. T. Cross, J. T. Finn, B. A. Bradley, Frequency of invasive plant occurrence is not a suitable proxy for abundance in the northeast United States. *Ecosphere* **8**, e01800 (2017).
57. U.S. Environmental Protection Agency, Level III Ecoregions of the Conterminous United States. U.S. EPA Office of Research and Development (ORD) - National Health and Environmental Effects Research Laboratory (NHEERL). <https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>. Accessed 15 October 2018.
58. J. Franklin, *Mapping Species Distributions: Spatial Inference and Prediction* (Cambridge University Press, 2010).
59. J. VanDerWal, L. P. Shoo, C. Graham, S. E. Williams, Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecol. Model.* **220**, 589–594 (2009).
60. K. C. Short, *Spatial Wildfire Occurrence Data for the United States, 1992–2015* (Forest Service Research Data Archive, Fort Collins, CO, ed. 4, 2017).
61. J. Eidenshink *et al.*, A project for monitoring trends in burn severity. *Fire Ecol.* **3**, 3–21 (2007).
62. K. C. Short, Sources and implications of bias and uncertainty in a century of us wildfire activity data. *Int. J. Wildland Fire* **24**, 883–891 (2015).
63. W. H. Romme, "Fire history terminology: Report of the Ad Hoc committee. Proc Fire Hist Work USDA- Gen" (Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 1980), Tech. Rep. RM-81:135–137.
64. RStudio Team, RStudio: Integrated Development for R. <http://www.rstudio.com/>. Accessed 15 December 2018.
65. A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, G. M. Smith, "Mixed effects models and extensions in ecology with R" in *Statistics for Biology and Health* (Springer Science+Business Media, 2009).
66. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach* (Springer, ed. 2, 2002).
67. E. J. Fusco, J. T. Finn, J. K. Balch, R. C. Nagy, B. A. Bradley, Source data for "Invasive grasses increase fire occurrence and frequency across U.S. ecoregions." Scholarworks. <https://scholarworks.umass.edu/data/102>. Deposited 24 September 2019.