

# Non-native plants exert strong but under-studied influence on fire dynamics

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## Abstract

Altered fire regimes are among the most destructive consequences of anthropogenic environmental change. Fires have increased in frequency in some regions, and invasion by fire-adapted non-native species has been identified as a major driver of this change, which results in a feedback cycle promoting further spread by the non-native species and diminishing occurrence of natives. We notice, however, that non-native species are often invoked in passing as a primary cause of changing fire dynamics, but that data supporting this claim are rarely presented. We therefore performed a meta-analysis of published literature to determine whether a significant relationship exists between non-native species presence and increased fire effects and risk, examined via various fire metrics. Our analysis detected a strongly significant difference between fire metrics associated with non-native and native species, with non-native species linked to enhanced fire effects and risk. However, only 30 papers discussing this linkage provided data to support it, and those quantitative studies examined only eight regions, five biome types, and a total of 22 unique non-native taxa. It is clear that we are only beginning to understand the relationship between non-native species and fire and that results drawn from an extremely limited set of contexts have been broadly applied in the literature. It is important for ecologists to continue to investigate drivers of changing fire regimes as factors such as climate change and land use change alter native and non-native fuels alike.

## Keywords

fire extent, fire frequency, fire intensity, flammability, fuels, meta-analysis, native species

## Introduction

Anthropogenic global change has far-reaching consequences. Biodiversity is directly threatened by extinctions (Purvis et al. 2000; Barnosky et al. 2011). At the same time and perhaps more subtly, ecological processes are being altered as a result of both biotic and abiotic ecosystem transformation (Pausas 1999; Cramer et al. 2001; Grimm et al. 2013; Kraaij et al. 2018). These changes affect an increasing number of species and ecological communities – boosting some populations and reducing others (Clavel et al. 2010). Changing fire regimes exemplify such changes in process: fires are becoming more frequent in some contexts, more intense in others, and larger in extent in still others (Brooks et al. 2004; Rogers et al. 2011; Pausas and Fernández-Muñoz 2012; Balch et al. 2017; Schoennagel et al. 2017; Kelley et al. 2019). Each of these changes comes with significant potential to alter ecological systems and biodiversity as vulnerable species decline and other species replace them.

In places where fire has become more frequent in recent decades, fire regime changes are often the result of non-native species invasions increasing the local density of fine fuels, or of climate change bringing warmer temperatures and increasing the flammability of existing fuels (Wilson et al. 2010; Pyšek et al. 2012; Balch et al. 2013; Chambers et al. 2019). These drivers can also act synergistically (Bradley 2010). It can be difficult for native species in systems of low historical fire occurrence to recover after fire events, and decreases in native densities pave the way for increases in populations of non-native species that are adapted to frequent fires and capable of growing quickly following a burn event. This has occurred in, for example, the Sonoran Desert and the Great Basin of the western US, both of which have experienced invasion by Old World annual grasses bringing continuous fuels that recover readily after burning, replacing discontinuous and non-fire-adapted vegetation (Bradley and Mustard 2005; Balch et al. 2013; McDonald and McPherson 2013).

Such changes have been shown by multiple metrics to affect fire regimes (Brooks et al. 2004; Gill et al. 2013). Invasions have reduced the fire return interval at individual locations, impacting non-fire-adapted native plants and promoting still more invasion by non-natives (Van Wilgen and Richardson 1985; D'Antonio and Vitousek 1992; Le Maitre et al. 2014). Some non-native species also grow more quickly than natives because they lack the herbivores, competitors, and pathogens that would limit their growth in their regions of origin (Chun et al. 2010). Via these mechanisms, fires fueled by non-natives have been shown to hinder native species' regeneration, damage native soils, and otherwise result in ecosystem transformation and the replacement of native species with non-natives (Brooks et al. 2004). Where fires have become more intense (i.e., there has been an increase in heat at the fireline), this may be the result of fuels buildup following extended fire suppression or exclusion (Fulé et al. 1997) or of increased flammability of fuels as a result of climate change, or a combination of these factors. Additionally, introduced species may provide fuels that burn with higher intensity than native fuels, impacting seeds and soils and impeding recolonization by native plant species (Lippincott 2000; Brooks 2002; Esler et al. 2008; Le Maitre et al. 2014). Increases in fire extent caused by widespread invasions can also fundamentally alter vegetation communities. Recovery

after more extensive fire events can be delayed because seed or plant sources for such recovery are located a greater distance away (Cansler and McKenzie 2014). After severe fires, bare ground can persist for a longer period because of this distance, again promoting colonization by non-native weedy species that demonstrate disturbance-adapted traits enabling them to colonize sites with poor or eroded soils (Moles et al. 2008).

These changes in fire patterns can impact native biodiversity, ecological functions, and ecosystem resilience following disturbances (Johnstone et al. 2016). For example, non-native species that supply large quantities of flammable fine fuels may be promoted both by climate change and the fire cycle they perpetuate, generating feedback loops that can transform desert ecosystems into invasive grasslands (Abatzoglou and Kolden 2011). Heavily altered fire patterns can lead to degraded landscapes with reduced potential to support management objectives such as livestock grazing, conservation, recreation, and watershed maintenance (Allen et al. 2002). As a result, it is imperative for decision-makers and land managers to understand the key drivers of current changes in fire patterns so such changes can be better anticipated and prevented. This has led to increased focus on non-native species as sources of novel fuels and drivers of increased fire frequency and fire intensity (D'Antonio and Vitousek 1992; Brooks et al. 2004).

Although the link between non-native invasion and problematic shifts in fire is oft-cited in global change literature as an important invasion–fire cycle (e.g., D'Antonio and Vitousek 1992; Rossiter et al. 2003; Balch et al. 2013), that linkage depends on conditions that are not present in all systems at all times. Specifically, to alter fire regimes, invasion must alter fuels and/or flammability, thus altering fire frequency, intensity, or extent (Brooks et al. 2004; Bowman et al. 2011; Underwood et al. 2019; Bishop et al. 2020). Not all invasions result in such changes, which rely on characteristics of both the non-native species and the native communities. For any specific fire, for example, unusual precipitation and drought patterns associated with climate change may be as likely to result in increased biomass production and subsequent drying for native plant species as for non-native plant species (Liu and Wimberly 2016).

To understand how consistently non-natives have been quantitatively associated with increased fire effects and risk, we performed a meta-analysis of published quantitative studies examining the effect of non-native vs native plants on fire characteristics. Our goals were: (a) to determine whether non-native species, relative to functionally similar native species, quantitatively and consistently increase metrics of fire effects and risk in ecosystems, and (b) to gauge the range of contexts over which this has been quantitatively analyzed, in order to consider how broadly assumptions regarding these patterns can justifiably be applied. For this study, we define “fire metrics” as those quantifiable descriptors of fire patterns that can be compared across studies (i.e., fire frequency, fire intensity, flammability, fuels quantity, and fire spatial extent). Note that there have been previous meta-analyses that have examined related but different questions, contributing to our understanding of the link between fire and non-native species. Jauni et al. (2015) performed a meta-analysis examining the effect of disturbance on non-native species and found that fire events resulted in increased diversity of non-natives. Alba et al. (2015) found through meta-analysis that exotic species composition and performance were both enhanced following wildfires but not following prescribed burns.

## Methods

To perform our meta-analysis, we began by searching ISI Web of Science (with coverage of years 1900–present) to find records of studies that have quantitatively compared non-native and native species' effects on fire metrics. We used the search terms fire + each of the following: plant + (native\* OR exotic\* OR non-native\* OR alien\* OR invasive\*); plant + “functional group”; native + (tree\* OR shrub\* OR perennial grass\* OR annual grass\*); (severity OR frequency OR intensity OR extent) + (cause\* OR attribute\*), and applied them to all years inclusive. Additionally, we examined the Literature Cited sections of relevant papers to find additional studies – including from sources not referenced in Web of Science – that might contain relevant quantitative information. Searches were performed in summer 2020.

Although our search terms netted hundreds of references, only papers meeting the following criteria were useful in our meta-analysis: (1) they compared fire metrics stemming from native species (as a control group) with fire metrics stemming from non-native species; (2) they presented comparisons between the metrics of fire associated with native and non-native species from the same plant functional groups; (3) they included quantitative and original fire metrics. Many papers referenced fire effects in discussions of non-native species but did not include original quantitative information. Many other papers examined the effects of fire on non-native species (e.g., reporting experiments examining control measures for non-natives), but we sought the opposite metric: the effect of non-native species on fire. For each of the studies that suited our criteria, we derived from the reports treatment (effect of non-natives) and control (effect of natives) fire metrics as well as sample sizes and measures of variance for treatments and controls.

Across all of the studies we included in our analysis, fire metrics were the response variables of interest. However, there are many ways to measure the effect of a given factor (e.g., non-native fuels) on fire. We were able to include all of these in one common meta-analysis framework by using the ratio of means (ROM) to compare the treatment and control effects of all studies (Hedges et al. 1999; Schwartz et al. 2012). The ratio of means is calculated as the natural log of the quotient of the mean outcome from the experimental group divided by the mean outcome from the control group (Hedges et al. 1999). To parameterize the response ratio, we derived from each paper the average native vs. non-native plant effects on fire metrics; in the set of relevant studies we found, these metrics included fire frequency, fire intensity (i.e., heat at the fireline), fuels quantity (including biomass production, relative growth rate, and litter production), spatial extent, and flammability (including fuels moisture, heat of combustion, and volatility). We then calculated the natural log of the ratio of the experimental mean to the control mean fire metric within each study. The resulting set of ROMs, including ratios from all studies meeting our meta-analysis criteria, formed the set of values included in our analyses.

Categorical analysis can be used to further explore the population of studies included in the overall meta-analysis in order to ascertain whether significant treatment effects persist within certain limited contexts. As long as a given category is represented by at least two studies, it is possible to examine it separately from the other categories to measure the strength of the treatment effect within that categorical context. The categories

we examined as such included: biome type, geographic region, plant functional group, and fire effect metric. Because the total number of studies within each category was not always greater than 1, the total number of studies included in categorical analyses did not always equal the total number of studies included in the overall meta-analysis.

In meta-analyses, studies included in the calculation of effect sizes are weighted more heavily if they used a larger sample size in the original research. We included the variances and sample sizes of all studies in our response ratio meta-analysis by calculating fixed and random effects estimates and applying inverse variance weighting, thus allowing studies with larger sample sizes to carry greater influence on the effect estimates. We calculated heterogeneity Q statistics to evaluate whether effect sizes are homogeneous or, conversely, are suggestive of underlying unexplained structure in the data (Rosenberg et al. 2000). Using these models, we estimated effect size means and confidence intervals for the full meta-analysis as well as for categorical analyses of subgroups. As long as ROM means and confidence intervals exclude the value of 1, they can be considered significant effect sizes. We performed all calculations using the *meta* package in R version 3.6.3 (R Core Team 2020). For the overall model, significance was accepted at  $\alpha = 0.05$ .

An important consideration in meta-analysis is that researchers and journals may be less inclined to publish studies that fail to show the expected effect, either because the results were non-significant (in our case, finding no difference between native and non-native species and their effects on fire metrics) or because they were significant in the opposite direction from predicted (in our case, finding that native species enhanced fire metrics more than non-native species). To estimate the potential quantitative effect of this phenomenon, we calculated a fail-safe analysis, which we performed using the *trimfill* function in the *meta* R package. Results indicated whether the outcome of our overall meta-analysis was likely affected by a lack of publication or “file drawer” problem and also estimated the likely overall effect size after producing a correction for such a publication bias. Note that sample sizes were not sufficient to conduct a similar fail-safe analysis for subgroup categories.

## Results

Our search terms yielded 612 unique sources. We examined each of these for methodology and found only 30 papers, reporting results of 41 distinct studies, that included a usable quantitative comparison of the effects of native vs non-native species on fire metrics. This final sample of relevant papers displayed the following breakdown by subgroup categories: by region, nine studies took place in the Southwestern US, three in mediterranean California, five in the Western US more broadly, eight in Australia, six in the Eastern US, one in Europe, three in South Africa, and six in South America. By biome, six studies were performed in deciduous forest, 10 in desert, 16 in mediterranean systems, eight in savanna, and one in mixed shrubland/woodland. Functional groups included annual grasses (9 studies), forbs (1 study), perennial grasses (20 studies), shrubs (3 studies), and trees (6 studies). A total of five usable studies combined data from multiple species to report fire metrics of non-native vs native species, making it impossible to extract the contributions of individual species but allowing comparison between those two groups.

**Table 1.** The 16 species examined at the species level in quantitative comparisons of fire metrics stemming from native vs. non-native fuels, and key traits related to effects. Five analyzed studies compared groups of native vs non-native species and thus effects could not be ascribed to individual species, and these studies are excluded from this table.

Species	Traits related to fire effects in meta-analysis	Citation
<i>Ampelodesmos mauritanica</i>	Resprouts quickly after fire; produces flammable biomass more rapidly than native species	Grigulis et al. 2005
<i>Andropogon gayanus</i>	High growth potential relative to native species	Bilbao and Medina 1990
<i>Bromus hordeaceus</i>	Low quality litter decomposed less than native litter, contributing to regional fuels for a longer period of time; compared with native species, sustains dry biomass for a larger portion of the year	Hernández et al. 2019
<i>Bromus rubens</i>	Winter annuals that escape extreme summer heat, generating high fuel load production relative to native species	Brown and Minnich 1986
<i>Bromus tectorum</i>	Exploits soil water following fire, outcompeting natives in regeneration	Melgoza et al. 1990
<i>Cenchrus ciliaris</i>	Increases fuel loads relative to native species	Miller et al. 2010
<i>Cytisus scoparius</i>	Higher relative growth rate than native species	Fogarty and Facelli 1999
<i>Eragrostis lehmanniana</i>	Much faster biomass production than native species	Anable et al. 1992
<i>Hakea sericea</i>	Increased fuel loads relative to native species	Van Wilgen and Richardson 1985
<i>Hyparrhenia rufa</i>	Higher growth rates in fertile sites, relative to native species	Baruch et al. 1985
<i>Imperata cylindrica</i>	Increased fuel loads and fuel continuity relative to native species	Lippincott 2000
<i>Melinis minutiflora</i>	Higher growth rates in fertile sites, relative to native species	Baruch et al. 1985
<i>Pennisetum setaceum</i>	Increased fuel loads relative to native species	Rahlao et al. 2009
<i>Pinus contorta</i>	Increased vertical fire continuity and increased flammability of fuels relative to comparison native species	Cóbar-Carranza et al. 2014
<i>Schinus terebinthifolius</i>	Reduces fire frequency ecosystem-wide	Stevens and Beckage 2009
<i>Tamarix</i> sp.	Rapid biomass accumulation and rapid regrowth after fire	Ellis et al. 1998

Overall, our meta-analysis detected a strong, statistically significant link between non-native species and increased fire effect (random-effects model  $ROM = 2.21$ ; 95% bias-corrected  $CI$  1.52 to 3.20;  $n = 41$ ;  $p < 0.0001$ ). Heterogeneity was also significant ( $Q_T = 5.68 \times 10^5$ ,  $df = 40$ ,  $p < 0.0001$ ), which highlights the large amount of unexplained data structure in the dataset. The many different approaches to comparing fire stemming from natives and non-natives that were employed by the various studies we examined likely contributed to this heterogeneity, emphasizing the importance of subgroup comparisons. The relevant studies found for this analysis contained clear evidence of a link between non-native species and enhanced fire metrics. However, the total number of species and the total number of contexts covered is extremely limited. The 41 studies reported species-level fire metrics reported for only 16 taxa (Table 1). Usable studies took place in only eight regions and four biome types (Table 2).

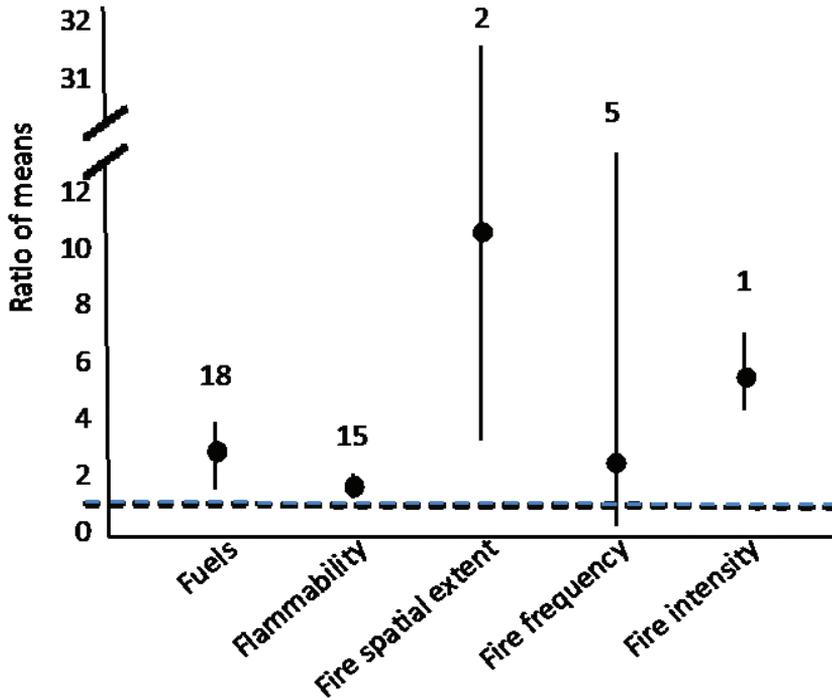
The significant response ratio of non-natives to natives held across almost all examined subgroups, as well. Among metrics of fire effects and risk, non-natives generated significantly higher fire metrics of flammability (random-effects model  $ROM = 1.50$ ; 95% bias-corrected  $CI$  1.39 to 1.62;  $n = 15$ ;  $Q_B = 1923.69$ ), fuels ( $ROM = 2.27$ ;  $CI$  1.30 to 3.97;  $n = 18$ ;  $Q_B = 6.48 \times 10^4$ ), and spatial extent ( $ROM = 10.02$ ;  $CI$  3.19 to

**Table 2.** Usable studies took place in eight regions and four biome types.

Region	Biome type	Study
Southwestern US	Savanna	Anable et al. 1992
		Brooks 1999
	Desert	Brown and Minnich 1986
		Busch 1995
		Eilts and Huxman 2013
		Ellis et al. 1998
Western US	Savanna	Stevens and Fehmi 2009
		Balch et al. 2013
		James and Drenovsky 2007
	Desert	Wilsey and Polley 2006
		Melgoza et al. 1989
		Whisenant 1990
Australia	Mediterranean	Fisher et al. 2009
		Fogarty and Facelli 1999
		Miller et al. 2010
		Rossiter et al. 2003
		Setterfield et al. 2010
Eastern US	Deciduous forest	Dibble et al. 2007
		Lippincott 2000
		Stevens and Beckage 2009
Europe	Mediterranean	Grigulis et al. 2005
California	Mediterranean	Keeley 2001
		Keeley and Brennan 2012
South Africa	Mediterranean	Rahlao et al. 2009
		Van Wilgen and Richardson 1985
South America	Savanna	Baruch et al. 1985
		Bilbao and Medina 1990

31.48;  $n = 2$ ;  $Q_B = 30.30$ ) (Fig. 1). Fire frequency did not differ significantly between native and non-native species ( $ROM = 2.22$ ;  $CI$  0.30 to 16.43;  $n = 5$ ;  $Q_B = 1544.80$ ) (Fig. 1). Among biomes, non-natives generated significantly higher fire metrics for deserts ( $ROM = 3.02$ ;  $CI$  2.17 to 4.20;  $n = 10$ ;  $Q_B = 1532.06$ ) and mediterranean biome ( $ROM = 2.82$ ;  $CI$  2.54 to 3.14;  $n = 16$ ;  $Q_B = 2376.90$ ), but not for savannas ( $ROM = 1.60$ ;  $CI$  0.48 to 5.28;  $n = 8$ ;  $Q_B = 2.26 \times 10^5$ ), or deciduous forests ( $ROM = 1.04$ ;  $CI$  0.90 to 1.19;  $n = 6$ ;  $Q_B = 26.76$ ) (Fig. 2).

Among functional groups, non-natives generated significantly higher fire metrics for perennial grasses ( $ROM = 2.53$ ;  $CI$  1.55 to 4.10;  $n = 20$ ;  $Q_B = 4.66 \times 10^4$ ), shrubs ( $ROM = 1.41$ ;  $CI$  1.34 to 1.49;  $n = 3$ ;  $Q_B = 0.27$ ), trees ( $ROM = 1.73$ ;  $CI$  1.51 to 1.99;  $n = 6$ ;  $Q_B = 1695.02$ ), and annual grasses ( $ROM = 2.39$ ;  $CI$  1.24 to 4.60;  $n = 9$ ;  $Q_B = 1. \times 10^4$ ) (Fig. 3). Finally, among regions, non-natives generated significantly higher fire metrics for the Southwestern US ( $ROM = 3.85$ ;  $CI$  1.80 to 8.21;  $n = 9$ ;  $Q_B = 2.10 \times 10^4$ ), Australia ( $ROM = 3.65$ ;  $CI$  2.77 to 4.81;  $n = 8$ ;  $Q_B = 132.71$ ), South Africa ( $ROM = 1.78$ ;  $CI$  1.14 to 2.78;  $n = 3$ ;  $Q_B = 29.49$ ), and South America ( $ROM = 1.59$ ;  $CI$  1.38 to 1.83;  $n = 6$ ;  $Q_B = 2515.47$ ), but not for the Eastern US ( $ROM = 1.04$ ;  $CI$  0.90 to 1.19;  $n = 6$ ;  $Q_B = 26.76$ ), California ( $ROM = 3.25$ ;  $CI$  0.66 to 15.94;  $n = 3$ ;  $Q_B = 460.80$ ), or Western US ( $ROM = 1.06$ ;  $CI$  0.40 to 2.80;  $n = 5$ ;  $Q_B = 1.01 \times 10^4$ ) (Fig. 4).

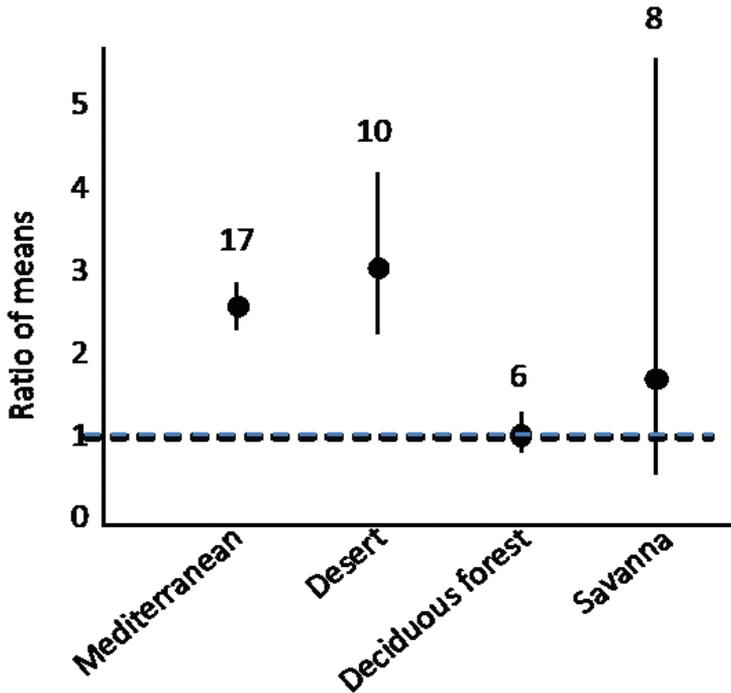


**Figure 1.** Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for fire metric subgroups analyzed using Hedges'  $d$  response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

The fail-safe analysis detected a significant file drawer problem ( $t = -2.49$ ;  $df = 39$ ;  $p = 0.017$ ). Upon correcting for this problem via an estimate of the effect size in the absence of a file-drawer problem, the *trimfill* recommended analysis assumed an addition of 19 non-significant studies but predicted that with such studies included the overall effect would remain significant ( $ROM = 5.46$ ;  $CI 3.83$  to  $7.77$ ;  $p < 0.0001$ ) and that the link between non-native species and increased fire metrics would persist.

## Discussion

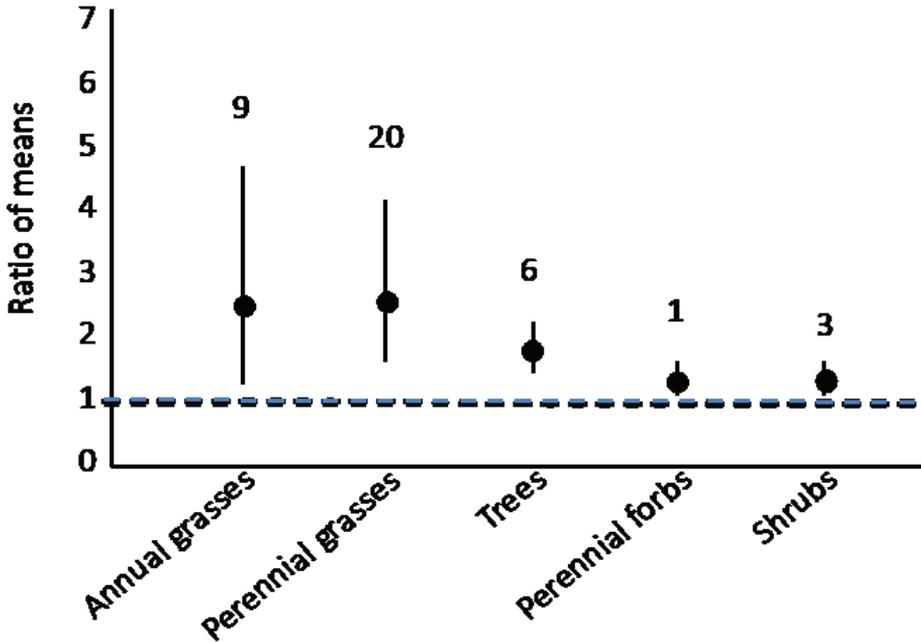
Our meta-analysis found a significant link between non-native plant species and fire metrics broadly, and specifically found that non-natives are associated with increased fuels, fire intensity, flammability, and fire extent, compared with native plant species, where the two have been contrasted. That is, quantitative research finds evidence that non-natives alter fire regimes by shifting the characteristics, quantity, and/or flammability of fuels. At the same time, our search terms netted a very small number



**Figure 2.** Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for biome subgroups analyzed using Hedges'  $d$  response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

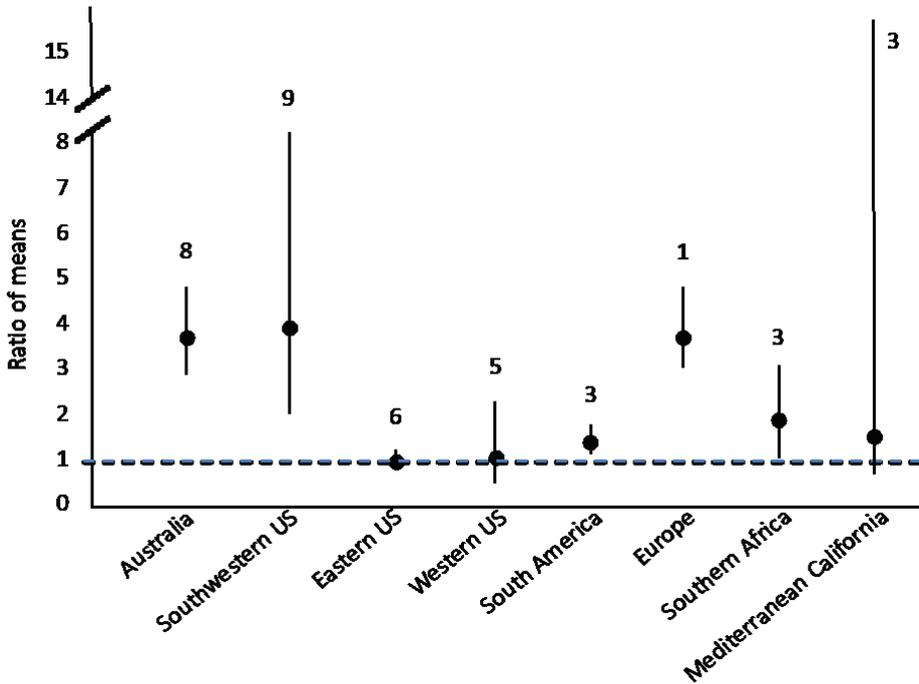
of quantitative studies examining an even smaller number of species. Approximately a twentieth of the studies that met our search criteria compared native and non-native plant species quantitatively; most of the others simply referenced the relationship between non-natives and fire.

Together, these results suggest that we are only beginning to understand the role of non-native species in fire regimes under environmental change, globally. Effects are quite strong where they have been quantitatively analyzed, but analyses have been limited to a few contexts. By one estimate, there are almost 17,000 species that have been established outside their native range (Seebens et al. 2017). As of 2016, just under 5,000 plant species were classified as “invasive,” suggesting that they exert a negative impact in the systems where they are introduced (Kew 2016). It is clear that the 16 taxa included in these studies are merely a fraction of all invasive species, and the effects of the remainder of those species on fire have not been examined with reference to native species. In most cases, the difference in fire conditions between sites before and after invasion is unknown. Since fire interacts with other environmental change drivers, in addition to biological invasion, the future consequences of many invasions remain uncertain or unpredictable.



**Figure 3.** Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for functional group subgroups analyzed using Hedges'  $d$  response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

The 16 taxa that were examined at a species level in these studies included annual and perennial grasses, trees, shrubs, and a forb. Nearly all of them contributed to increases in fire metrics; the sole exception was *Schinus terebinthifolius*, which is associated with decreased fire frequency that promotes further invasion by this non-native tree (Stevens and Beckage 2009). In the quantitative research reviewed here, higher biomass production relative to native species were associated with the grasses *Ampelodesmos mauritanica*, *Andropogon gayanus*, *Bromus rubens*, *B. tectorum*, *Cenchrus ciliaris*, *Eragrostis lehmanniana*, *Hyparrhenia rufa*, *Imperata cylindrica*, *Melinis minutiflora*, and *Pennisetum setaceum* (Table 1). Similarly, the shrubs *Cytisus scoparius* and *Hakea sericea* and trees in the genus *Tamarix* were associated with increased fuels production relative to native species (Table 1). Other important factors included continuity and flammability of fuels (for example, *Pinus contorta* exhibited greater vertical continuity and volatility of biomass than did comparison native species; Cóbar-Carranza et al. 2014), as well as phenological drivers; *B. rubens*, for example, accumulated biomass during the winter months and thereby escaped damage from extreme summer heat and produced higher total fuels than comparison natives (Brown and Minnich 1986) (Table 1). In each case where fire frequency was increased



**Figure 4.** Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for region subgroups analyzed using Hedges'  $d$  response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

by the presence of non-native species, the critical factor distinguishing invaded sites from non-invaded sites was the exceptional continuity (in space or over time) of fuels produced by the non-natives, increasing fire frequency and risk.

Non-native plants have led to novel fire disturbances in the studied systems. Our results demonstrated that fires in invaded sites recur with greater frequency, burn with higher fireline intensity, or burn over greater extent than in native-dominated sites. Such systems are subject to significant ecological transformation: when native species are non-fire-adapted or unable to recover from severe fires, a positive invasive species-fire feedback cycle emerges (D'Antonio and Vitousek 1992; Rossiter et al. 2003). This cycle can threaten native communities over very large areas, fundamentally reshaping ecosystems and ushering in alternative, non-native-dominated stable states (e.g., Brooks et al. 2003; Godfree et al. 2017).

Altered fire regimes are evidently a strong component of global change. Furthermore, they interact with other drivers of environmental change. Climate change alone can boost the growth rate (i.e., production and thus total quantity of fuels) and flammability of biomass both native and non-native (Myneni et al. 1997; Westerling et al. 2006; McGranahan et al. 2018). Unusual fire patterns stemming from climate change

may or may not depend on non-native species invasion, although system-specific characteristics (such as historical fire frequency, timing of precipitation, and fire adaptations among native species) may elevate the likelihood that non-native fuels carry particular significance during any given fire year. Land use changes and resulting increases in human footprints in natural areas can also transform fire regimes, increasing the rate of intentional and accidental ignitions (e.g., 95% of all annual ignitions in California are caused by humans; Syphard et al. 2008).

Disentangling the effects of climate change, land use, and non-native fuels will be important for spatially-explicit fire risk assessment and management and restoration decision-making (Gray et al. 2014; Westerling 2016; Balch et al. 2017; Syphard et al. 2017). Improved forecasting to guide such assessments will require continued and extended research of the quantitative fire metrics associated with non-native species across functional groups, regions, and biome types, as well as the response of those fire metrics to climate change and land use change. As conditions change in any given system, the relative fire risk driven by each of these factors is also likely to change (McWethy et al. 2013). Classic adaptive management requires sequential use of management activities to meet certain objectives, and also requires careful study of the effectiveness of each activity (Holling 1978; Gunderson 1999; Williams and Brown 2012), highlighting the importance of continued research in complex systems. Study of the relative roles of native vs non-native plants in fire regimes within any particular location will be necessary to facilitate effective management decisions over time.

## Conclusions

Global change today consists of multiple drivers operating both individually and in synergy. The combined influence of biological invasions, land use change, and climate change can result in dramatic changes in fire dynamics within particular systems, yet understanding how each driver contributes to fire regime change is essential for effective management decision-making in response. Our study identified a clear role of non-native species in increased fire metrics, but also highlighted the limited scope of our understanding – only a small number of species and systems have been quantitatively examined to this point. Both native and non-native fuels must be considered in light of changing climatic patterns and land uses, and increased empirical assessment of the respective roles of climate, land use, and invasion are necessary for appropriate responses.

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