Biol Invasions (2023) 25:693–711
https://doi.org/10.1007/s10530-022-02951-y

REVIEW

Research gaps limit understanding of invasion-fire cycles

Giovanna Tomat-Kelly · S. Luke Flory

Received: 28 February 2022 / Accepted: 20 October 2022 / Published online: 1 November 2022

Abstract Invasive plants can alter fuels and fire regimes in ways that facilitate their spread and dominance through a process known as the invasion-fire cycle. This phenomenon can result in considerable fire and ecosystem impacts, but mechanisms, habitat susceptibility, and prevalence of invasion-fire cycles are poorly understood. Here, we reviewed literature on invasion-fire cycles and describe how mechanisms by which and habitats in which invasion-fire cycles occur are influenced by invader growth form, including woody versus herbaceous and perennial versus annual species, among other factors, and highlight research needs to better understand invasion-fire cycles. We found evidence that annual herbaceous species facilitated more continuous and frequent fires in shrublands and deserts by increasing fine fuel continuity, while perennial grasses and woody invaders more often facilitated intense and vertically continuous fires in forest habitats by increasing fuel loads. There was some evidence woody invaders can suppress fires by decreasing fine fuels, and both woody invaders and perennial grasses and forbs can inhibit fires due to high fuel moisture and low flammability, but effects of fire suppression by invaders on native communities were ambiguous. Fire suppression and climate change may complicate effects of invasions on fire regimes directly, or indirectly through shifting abundances of fire prone or fire adapted native plant species. More research is needed to understand how propagule pressure, ignitions, climate, and resource availability affect invasion-fire cycles, and to determine relative importance of invasion-fire cycles in driving plant invasions and effects of invader driven changes to fire regimes on native communities.

Keywords Climate · Facilitation · Fire behavior · Fire regime · Fire suppression · Fuels · Growth form · Ignitions

Introduction

Non-native invasive plants can change fuel properties and alter fire-regimes in ways that facilitate invader dominance through a process known as the invasion-fire cycle (D’Antonio and Vitousek 1992). Invasion-fire cycles can have significant impacts on fires (e.g., flame heights, temperatures, duration), ecological communities (e.g., community composition, structure), and ecosystem functions (e.g., carbon and nutrient cycling, Mack and D’Antonio 1998, Simberloff 2011), and may even affect ecosystem provisioning services such as forage and timber production. Moreover, ecosystems

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-022-02951-y.

G. Tomat-Kelly · S. L. Flory (✉)
Agronomy Department, University of Florida, 3105 McCarty Hall B, Gainesville, FL 32611, USA
e-mail: flory@ufl.edu

subjected to invasion-fire cycles can be difficult to restore, making prevention an important management goal. However, multiple factors, including the ongoing introduction of non-native species globally (Seebens et al. 2021), climate change and its effects on fuels, fire regimes, and spread of invasive species (e.g., Prichard et al. 2021), and the suppression of natural fires and mesophication of ecosystems (e.g., Alexander et al. 2021), complicate predictions of invasion-fire cycles. Thus, identifying ecosystems vulnerable to invasion-fire cycles, and invasive species likely to drive alteration of fire regimes, remains a research priority (Gaertner et al. 2014; Chambers et al. 2019).

Determining conditions required for invasion-fire cycles to occur and understanding underlying mechanisms is necessary for: (1) predicting where invasion-fire cycles are likely to take place; (2) predicting how invasion-fire cycles may influence invasive species establishment and spread; and (3) developing informed management practices that both prevent development of future invasion-fire cycles and limit expansion of those that are already occurring (Zouhar et al. 2008). Generally, an invasive species is said to cause an invasion-fire cycle if: (1) it alters the flammability, continuity, bulk ratio, or amount of fuels within the invaded system; (2) it changes the frequency, extent, intensity, type, or seasonality of fire; (3) the new fire regime decreases abundance of native species; and (4) the new fire regime increases abundance of invasive fuels that drive the cycle (Brooks 2008). While these steps can be used to identify invaders with potential to initiate invasion-fire cycles, understanding drivers and mechanisms of invasion-fire cycles can further allow us to identify habitats most susceptible to their occurrence and impacts.

We conducted a systematic review of peer-reviewed literature to assess current knowledge about drivers and mechanisms of invasion-fire cycles. Our review provides a basis for assessment of how growth forms of invasive plant species determine underlying mechanisms of invasion-fire cycles and habitats where invasion-fire cycles might occur. We synthesize our findings from literature, discuss factors that influence whether plant invasions result in development of invasion-fire cycles, and highlight research needs to better understand causes and consequences of invasion-fire cycles.

Methods

We used the invasion-fire cycle (described above, Brooks 2008) as a basis to evaluate how and where non-native invasive plant species have the potential to initiate invasion-fire cycles by altering fuels and fire behavior, and to identify research gaps (James et al. 2016). Information was collected by conducting a systematic search across Web of Science and Google Scholar (Livoreil et al. 2017). We first searched Web of Science in February 2020 to locate literature on invasive plants with the potential to alter fuels or fire behavior by using the search query (TS = ((*fire* OR burn* OR fire regime OR fuel*) AND (plant invad* OR invasive plant* OR naturali* plant* OR establish* plant* OR alien plant* OR exotic plant* OR introduced plant* OR non-indigenous OR non-native OR casual OR weed*) NOT ant* NOT "power plant") AND (SU = Agriculture OR SU = Biodiversity & Conservation OR SU = Environmental Sciences & Ecology OR SU = Evolutionary Biology OR SU = Forestry OR SU = Plant Sciences)). We also scanned references of publications that met search criteria for additional literature. Finally, we searched Google Scholar using the search terms "fire, fire regime, OR fuel, OR fuel load, OR flammability, OR invasion, OR invasive, OR invaded, OR invader, OR alien, OR non-native, OR exotic, OR regime, OR cycle -ant, -powerplant" for additional papers. We focused our search on plant species that occurred outside their native range, excluding instances of encroachment by native species. In addition, our search was limited to the potential effects of invasive plants on fire, although invasive insects and pathogens can also impact fire regimes (e.g., Hood et al. 2018).

From these publications, we compiled a list of invasive plant species that could potentially initiate invasion-fire cycles by altering fuels and/or fire behavior, and compiled information on how each species has been observed to complete each step of the invasion-fire cycle. We also collected information on the fuel and fire characteristics each study investigated, and how they were evaluated. The complete data, including separate files organized by species and by paper, can be found at: https://doi.org/10.5061/dryad.qz612jmjz. Note that we initially sought to conduct a meta-analysis of invader effects on fuels and fire behavior across different invader growth habits and ecosystems, but there was insufficient data to do so.

Relationships between invader growth form and invasion-fire cycles

In our review of the literature, we identified 114 publications (Supplemental Table S1) with 78 species that were reported to affect fuels or fire behavior in ways that suggested they could lead to development of an invasion-fire cycle (Supplemental Table S2, Supplemental Information 3). These species included 13 annual grasses (five of which belong to the genus *Bromus*), 29 perennial grasses (including two species that exhibit both grass and shrub growth forms), eight forbs (three annual and five perennial species), and 28 woody species (including seven trees, six shrubs, two subshrubs, two vines, and eleven species with dual tree and shrub growth forms; Supplemental Table S1). Most reports of invasive species affecting fuels or fire behavior (anecdotal reports included) are of grass invasions in arid and semi-arid regions in the United States and Australia (Fig. 1). Available accounts of invasion-fire cycles could indicate that regional conditions dictate where invasion-fire cycles occur but research output could also suffer from geographic bias (Pyšek et al. 2008).

The location and reported mechanisms by which invasive species affected fire behavior and fire regimes differed among invader growth-forms (Supplemental Table S2, Figs. 2, 3). Qualitative and quantitative differences in fuels between pre- and post-invaded communities are largely responsible for determining how and to what extent fire regimes change (Brooks et al. 2004). Hence, evaluating relationships between invader functional groups and the habitats where invasive species have altered fuels and/or fire behavior can provide a first step to determining where invasive plants are most likely to initiate invasion-fire cycles (Gaertner et al. 2014). However, differences in traits of introduced invaders (Divíšek et al. 2018), the direct and indirect effects of climate change (Flory et al. 2022), and land use change may result in occurrence of invasion-fire cycles in regions or habitats where they were previously thought to be unlikely.

Based on available evidence, we identified five major types of invasion-fire cycles, all of which differ in underlying mechanisms. The different mechanisms may partially dictate habitat types where each invader, based on its growth form, is likely to cause invasion-fire cycles. These five types of invasion-fire cycles are: pyrogenic annual grasses and forbs that promote fires (Supplemental Fig. S1), perennial invasive grasses that promote fires (Supplemental Fig. S2, panel A), woody invaders that promote fires (Supplemental Fig. S3, panel A), perennial herbaceous invaders that suppress fires (Supplemental Fig. S2, panel B), and woody invaders that suppress fires (Supplemental Fig. S3, panel B).

Pyrogenic annual grasses and forbs

Our literature review suggested that invasive annual grasses and forbs primarily alter fire behavior in fuel-limited systems that experience infrequent fires. Overall, nine of 13 invasive annual grasses and two of three annual forbs identified were reported to increase fine fuel loads or fuel continuity or produce drier fuels than native vegetation in arid to semi-arid deserts or shrublands (Supplemental Table S2). Only one annual grass with potential to initiate an invasion-fire cycle was reported outside of the United States. Increased availability of fine fuels due to annual grass invasions is generally associated with greater fire frequency (e.g., Whisenant 1990; Billings 1994; Bradley et al. 2018; Fig. 2) and more continuous, fast-spreading, and extensive fires (e.g., Peters and Bunting 1994; Brooks 1999; Brooks and Matchett 2006; Fig. 2) that theoretically exclude native vegetation and lead to dominance of the annual invader via an invasive fire-cycle (Supplemental Fig. S1).

Within shrublands and desert communities, increased fire frequency can deplete reserves of non-structural carbohydrates in sprouting species (Keeley and Brennan 2012) and exclude native perennial obligate seeders by inhibiting plants from recovering or reaching reproductive maturity before the next fire (Zedler et al. 1983; Keeley and Brennan 2012). Seeds of annual invasive species can be killed by hot fires that occur under woody species of shrubland ecosystems. However, if native shrubs are excluded with frequent fire events, fire intensity may be reduced and, consequently, survival of invasive annual seeds and dominance of invaders driving the altered fire-regime can increase (Keeley 2000).

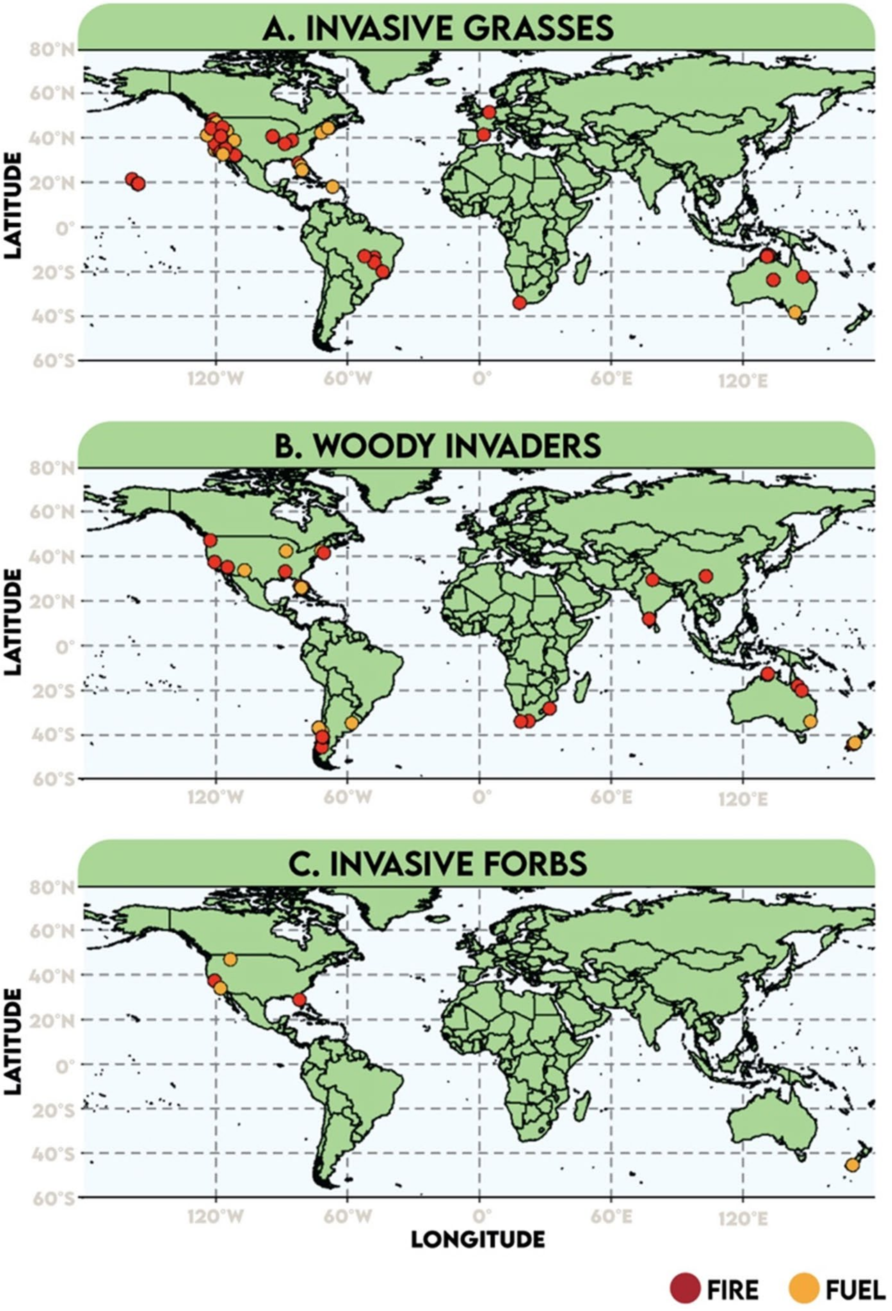

Fig. 1 Locations of anecdotal and empirical studies of invasive **A** grasses, **B** woody species (i.e., shrubs, trees, and woody vines), and **C** forbs that altered the fire regime (red points) or fuel bed (orange points) of the invaded ecosystem

Examples of annual-grass fire cycles transforming native communities to invasive-annual grasslands is primarily limited to *Bromus tectorum* in the western United States. In that ecosystem, invasive annuals infill spaces between native sagebrush, thereby creating continuous flammable fuel beds that persist late into the dry season (Davies and Nafus 2013). At a regional scale, areas invaded by *B. tectorum* experience more frequent fires (Whisenant 1990; Talluto and Suding 2008). Sagebrush communities can take 35–125 years to recover from fire events (Baker 2006), such that frequent fires can exclude native vegetation by preventing vegetation from recovering and reaching reproductive maturity before the next fire event (Zedler et al. 1983; Talluto and Suding 2008; Keeley et al. 2005). Fire can also increase spread rate

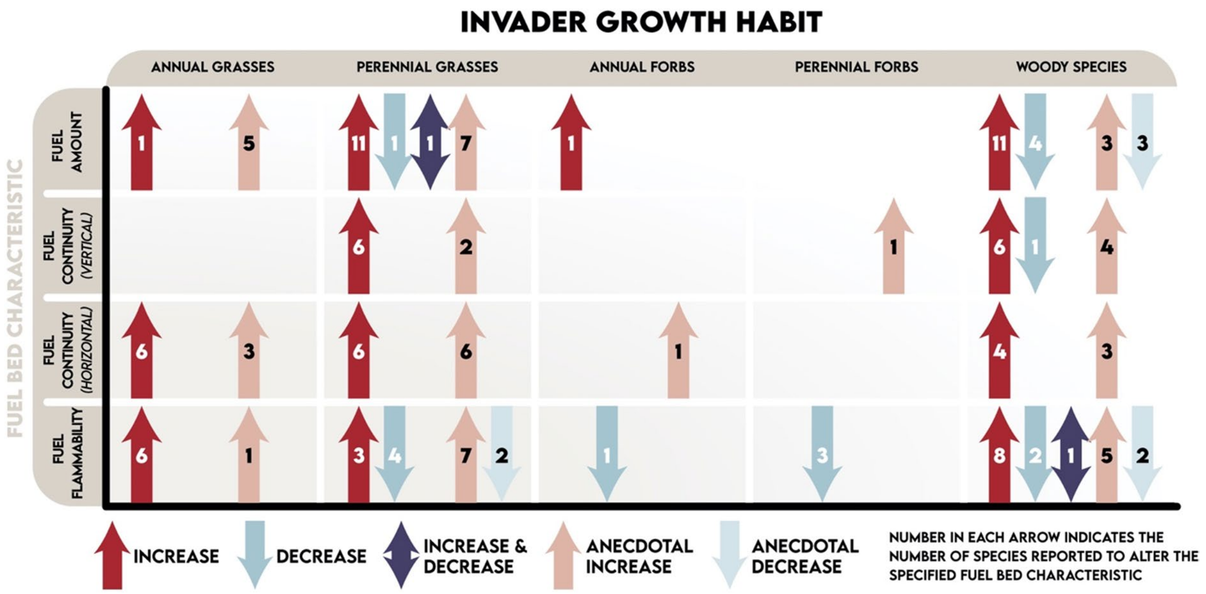

Fig. 2 Number of invasive plant species, organized by growth habit, with empirical (darker colored arrows) or anecdotal (lighter colored arrows) evidence of increasing (upward arrows), decreasing (downward arrows), or both increasing and decreasing (two sided arrows) fuel amount (fuel loads or combustible biomass), vertical or horizontal fuel continuity, or fuel flammability. Changes to fuel flammability include species reported likely to alter probability that fuels will ignite and carry fire based on evidence that the invader has lower or higher fuel moisture than native vegetation or increases the abundance of dead/ dry plant material

of *B. tectorum* invasions by increasing seed dispersal distances (Monty et al. 2013), and eventually *B. tectorum* can replace native vegetation lost to frequent fires via an annual-grass fire cycle (Supplemental Fig. S1).

Changes to fire regimes and native community composition may depend on density or abundance of the invader or characteristics of the invaded ecosystem. Non-native grasses at low abundances appear unlikely to alter fire regimes (Bradley et al. 2018), and loss of herbaceous perennial vegetation in response to annual invaders may not occur until the invader has reached more than 60% cover (Underwood et al. 2019). While two sequential fires in arid shrublands or deserts may be sufficient to reduce abundance of native woody vegetation (Zedler et al. 1983), the frequency of fires needed to exclude herbaceous vegetation is unclear.

We found only one annual species with potential to initiate an invasion-fire cycle within forests. *Microstegium vimineum* is a shade tolerant annual grass that invades the understory of deciduous forests and disturbed areas in the eastern United States. It is the only annual species we found that has been documented to produce hotter fires that reduce germination of native trees, but the mechanism by which it enhances fire temperature is unclear (Emery et al. 2011). The aerated fuel structure of *M. vimineum* may drive hotter fires in invaded forests, but it is also possible that it is invading forested habitats with particular characteristics, such as higher woody fuel loads that cause fires to burn more intensely and for longer (Wagner and Fraterrigo 2015). Fire can increase *M. vimineum* establishment, likely by producing greater light availability via litter removal (Schramm and Ehrenfeld 2010) and by reducing overstory canopy cover (Flory et al. 2017). However, effects of fire on *M. vimineum* vary. While *M. vimineum* biomass may increase after fires (Wagner and Fraterrigo 2015), fires also decrease *M. vimineum* soil seed banks (Emery et al. 2011; Wagner and Fraterrigo 2015). Additionally, fire effects of *M. vimineum* may primarily be a concern in regions where fire is used as a management tool. Fires are infrequent in much of the invaded range of *M. vimineum* (e.g., the northeast and parts of the Midwest and southeast US) because historical fire

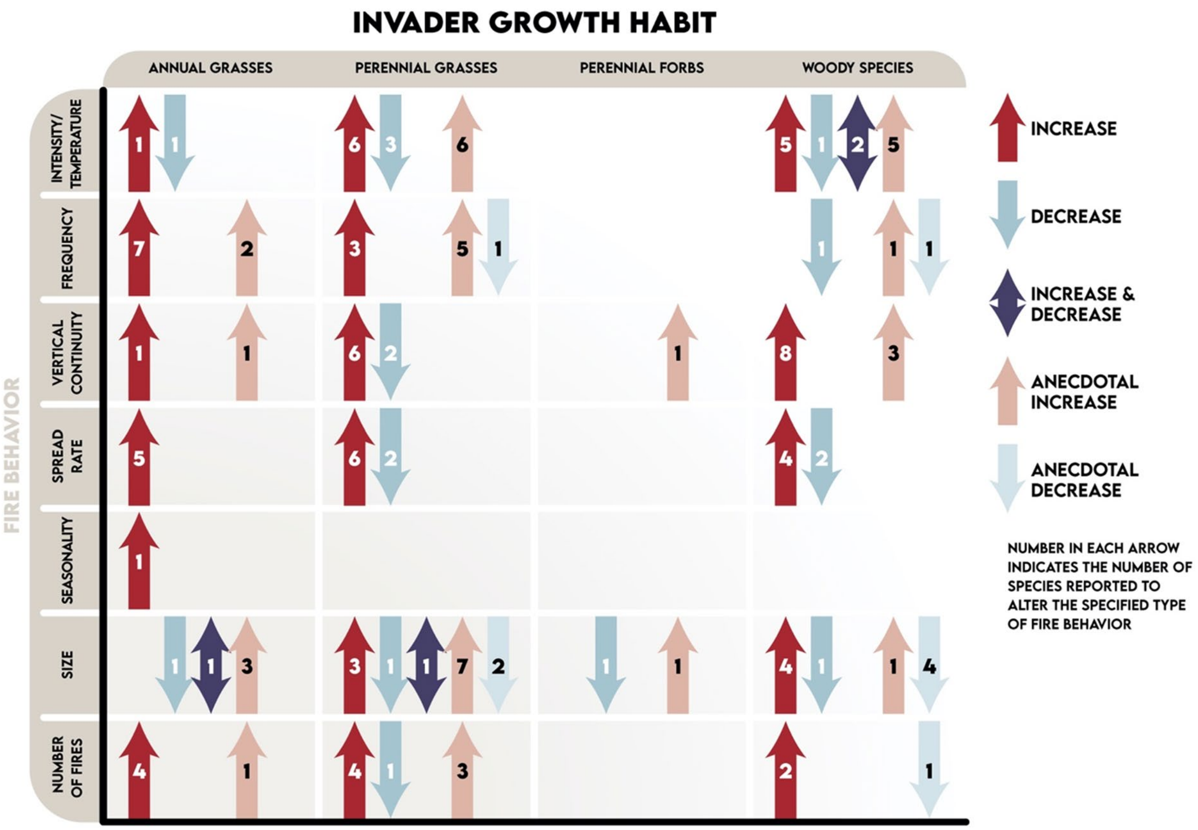

Fig. 3 Number of invasive plant species, organized by growth habit, with empirical (darker colored arrows) or anecdotal (lighter colored arrows) evidence of increasing (upward arrows), decreasing (downward arrows), or both increasing and decreasing (two sided arrows) "fire intensity" or temperature, fire frequency, vertical fire continuity, fire spread rate, fire seasonality, fire size, or the number of fires

suppression has led to "mesophication" (i.e., replacement of pyrogenic forest species with low-flammability, fire sensitive species, Nowacki and Abrams 2008) of forests in those regions. Conversely, in other *M. vimineum* invaded areas, prescribed fire use has been more consistent over time and effects of *M. vimineum* on fire regimes may be more prevalent. Moreover, fire suppression or frequent prescribed fire use may lead to shifting dominance of fire prone and fire adapted species, further complicating effects of invasions on fire regimes. Thus, interactions among land use, climate, ignition frequency, and native species may be limiting factors to initiation of invasion-fire cycles such that, while experimentally inducible (e.g., Flory et al. 2017), are less predictable in nature.

Overall, we found little evidence that annual species cause invasion-fire cycles in savannas, woodlands, or forests. Most current invasive species are shade-intolerant annuals (Sutherland 2004), hence site conditions, such as low light availability, could limit their establishment and survival in forests (Connolly et al. 2017). Additionally, established invasions of annuals might not alter forest fuel beds enough to alter the fire regime. For example, in California woodlands, the invasive annual grass *Cynosurus echinatus* was found to have lower fuel moisture than native herbaceous species (Livingston and Varner 2016), and *Bromus tectorum* has been observed in the understories of ponderosa pine forests (Keeley and McGinnis 2007; McGlone et al. 2009), but in neither case is there currently evidence that invasions have resulted in altered fire regimes. Regardless, climate change, shifting forest management practices, and the introduction of new annual grass and forb species with unique traits may result in future threats to forests and other ecosystems (Kerns et al. 2020).

Pyrogenic perennial grasses

We found 26 species of invasive perennial grasses with the potential to initiate invasion-fire cycles by promoting more intense and occasionally more frequent fires. The identified perennial grasses reportedly increased fuel loading or continuity (Fig. 2), primarily in shrublands, savannas, and woodlands (n = 20), and occasionally grasslands (n = 2) and more closed-canopy forests (n = 8) (Supplemental Table S2). Invasive perennial grasses were mostly associated with increased fire intensity and taller flames (e.g., Rossiter et al. 2003; Schlesinger et al. 2013; Rossi et al. 2014) and were occasionally reported to cause greater fire frequency (e.g., Smith and Tunison 1992; Fusco et al. 2019; Fig. 2). The greater fire intensities and flame heights caused by perennial grass invasions could result in mortality of native vegetation that is then rapidly replaced by the invader in a perennial grass-fire cycle (Supplemental Fig. S2 panel A).

Currently available evidence for perennial grasses affecting fire frequency is limited. Most examples of pyrogenic grasses that have increased fire frequency are from invasions of dry Hawaiian woodlands that seldom burned historically (e.g., Hughes et al. 1991; D'Antonio et al. 2000). All available empirical evidence that perennial grasses increase fire frequency was from a single study on invasive species effects on fire size, frequency, and occurrence across the entire range where each species was reported to occur in the continental United States (Fusco et al. 2019). The practical significance of this finding is very limited because information in the study were averages from across all habitats where each species had invaded. Thus, there is a critical need for additional studies to determine the effects of invasive perennial grasses on fire frequency in particular habitats.

Given the available evidence in the literature, it is unclear whether perennial grass invaders are appreciably affecting fire frequency in habitats where fires are already common. Many habitats where perennial grass-fire cycles are reported or studied are fire-adapted. For example, while *Imperata cylindrica* can increase fuel loads and fuel continuity in southern pine savannas of the United States (Lippincott 2000), fires in that ecosystem already occur every 3–7 years (Rother et al. 2020; Huffman 2006). Similarly, *Urochloa decumbens* and *Melinis minutiflora* reportedly increase fuel loads in Brazilian cerrado (Silvério et al. 2013; Rossi et al. 2014), where fires occur every 3–6 years (Júnior et al. 2014). However, fire return intervals in systems where fires are considered "common" vary widely, so invaders that increase fire from once every 5–10 years to once every year or two in those ecosystems could have profound impacts. Even when invasive species enhance fuel accumulation, fire frequency may still be limited by infrequency of lightning strikes and anthropogenic ignitions, both of which may change under future conditions with climate and land use change. Fire-prone communities may be resilient to increases in fire frequency, and frequent fires can limit fuel accumulation and modulate effects of fire intensity and limit fire frequency (Murphy and Russell-Smith 2010; Hart et al. 2019) but these same invaders can also suppress fire-dependent native species independent of fire frequency (e.g., Fahey et al. 2018). Notably, interactions among invasions, fire, and other global change drivers may have negative synergistic effects on species and ecosystems (Flory et al. 2022), but outcomes of such interactions have often been difficult to predict.

Based on available empirical evidence, increased fire intensity followed by post-fire shading appear to be the primary mechanisms by which perennial grass-fire cycles result in loss of native vegetation and dominance of an invasive grass. Even fire-adapted savanna species that typically survive frequent, low intensity fires can be killed by intense perennial grass-fueled fires (e.g., Lippincott 2000; Setterfield et al. 2010). Invasive perennial grasses often quickly resprout after fires, rapidly reaccumulate biomass, and shade-out native vegetation. *Imperata cylindrica*, for example, has been observed to re-accumulate aboveground biomass quickly post-fire (Lippincott 2000) and suppress growth of native pine tree saplings by reducing light availability (NeSmith et al. 2018). Similarly, *Andropogon virginicus*, *Hyparrhenia rufa*, and *Melinis minutiflora* can regenerate quickly post-fire (D'Antonio et al. 2000) and suppress growth of native woody species (D'Antonio et al. 1998). The large amount of biomass and litter produced by *M. minutiflora* is also known to decrease seedling emergence of native trees in neotropical savannas (Hoffmann and Haridasan 2008).

Evidence of perennial grasses transforming native communities to invasive species dominated grasslands is limited to invasions in Hawaii, although similar dynamics may occur elsewhere. Native species of submontane and lowland Hawaiian woodlands are not fire adapted and are hence vulnerable to fire-induced mortality (D'Antonio et al. 2011). Apart from the five species of perennial grasses that drive invasive grass-fire cycles in Hawaii (*H. rufa*, *A. virginicus*, *M. minutiflora*, *Pennisetum setaceum*, and *Schizachyrium condensatum*), five other species reportedly increase fire severity or increase mortality of native trees (Supplemental Table S2; *Ampelodesmos mauritanica*, *Arundo donax*, *Pennisetum ciliare*, *Imperata cylindrica*, and *Andropogon gayanus*). Nevertheless, evidence of these perennial grasses transforming native communities to invasive grasslands via invasion-fire cycles is lacking, which illustrates the need for studies on effects of invader-altered fire regimes on native community composition and structure over time.

Pyrogenic shrubs and trees

We found 21 woody invaders that, like perennial grasses, were reported to increase fuel loads and flammability (Fig. 2) and cause more intense fires (Fig. 3), mostly in forested habitats (i.e., forests, woodlands, and savannas, n = 16) and in shrublands (including fynbos and steppes; n = 10), but occasionally in grasslands (n = 3; Supplemental Table S2). Theoretically, woody species can increase fire intensity and severity, resulting in mortality of native vegetation and increased relative abundance of the invader in an invasion-fire cycle (Supplemental Figure S3, panel A), but evidence to support this dynamic is lacking.

Empirical reports of woody invaders increasing fire intensity are restricted to *Acacia cyclops* invasions in South African fynbos (Jayiya et al. 2004), *Eupatorium adenophorum* invasions in coniferous and broad leaf forests in China (Wang and Niu 2016), and three species of *Pinus* that invaded shrublands, steppes, and temperate forests in Argentina and Chile (Kraaij et al. 2018; Paritsis et al. 2018; Davis et al. 2019). These same species, excluding *A. cyclops*, were the only species whose effects on fire intensity were also reported to either increase fire severity or reduce vegetative cover of native species (Supplemental Table S2). Severe fires produced by *P. contorta* can increase soil heating (Taylor et al. 2017) and have the potential to sterilize the upper layers of soil seed banks. Additionally, the species *Tamarix ramosissima* and *Lantana camera* are reported to increase occurrence of fires (Busch 1995; Priyanka and Joshi 2013, respectively), and common gorse (*Ulex europaeus*) was highly flammable and increased flammability of species mixtures in a study of six native and four invasive species in New Zealand (Wyse et al. 2018). But like most instances of invader-altered fire regimes, evidence for consequences of altered fire behavior for native plant community composition and structure caused by woody invasive species are lacking. Moreover, current data is from a limited number of recipient ecosystems that could ultimately be affected, necessitating studies across more ecosystems before reliable conclusions can be drawn.

By promoting intense or frequent fires, woody invasive species may create conditions that favor their own establishment. Promoting occurrence of intense fires could increase light availability and contact of invasive seeds with mineral soils via removal of litter and overstory cover (Gentle and Duggin 1997) and free-up space and resources previously monopolized by native species (Bullock 2009). However, *Tamarix ramosissima* and *Pinus contorta* were the only two woody invaders reported to have greater abundance or density in response to the fires they facilitate via an invasion-fire cycle (Busch 1995; Taylor et al. 2017; Davis et al. 2019).

Initial invader density may determine how woody invaders respond to fire events. For instance, *P. contorta* was found to increase in abundance post fire only when its pre-fire abundance exceeded a density threshold. Below the threshold, vegetation of invaded areas responded to fire like that of uninvaded areas, and the density of *P. contorta* did not change (Taylor et al. 2017). Whether invasion-fire cycles are an important driver of woody plant invasions or, alternatively if altered fire regimes are simply a consequence of high invader abundance is unclear.

Fire suppressing herbaceous perennials

Despite grass-fire cycles traditionally being associated with greater fire frequency and sometimes higher fire intensity, we found papers suggesting that invasive perennial grasses and forbs occasionally decreased intensity and continuity of fires, which could lead to a fire-suppression cycle (Figs. 2, 3; Supplemental Fig. S2 panel B). Seven species of perennial grasses were found to have potential to suppress fires in pyrogenic habitats, including marshes (2), grasslands (2), annual grass-invaded desert (1), savannas (1), and coniferous forests (1). Likewise, four species of forbs were reported to decrease flammability of native grasslands in New Zealand, and one species, *Centaurea maculosa*, was reported to reduce fire extent in Montana grasslands (Supplemental Table S2).

In the papers we examined, fire suppression by perennial forbs and grasses was exclusively the result of reduced flammability due to either greater fuel moisture, or an increase in the ratio of live to dead fuels during the dry season when native-fueled fires typically occur (e.g., McGranahan et al. 2012; Padullés Cubino et al. 2018; Fig. 2). *Schedonorus arundinaceus*, for example, reduced fire extent in the tallgrass prairies of Missouri and Iowa, likely because this species remains green during the summer when native grasses have mostly senesced (McGranahan et al. 2012, 2013). The perennial grasses *Arundo donax* and *Phragmites australis* can decrease fire intensity and fire occurrence, respectively, in grassy riparian habitats, likely because of high fuel moisture (Guthrie 2007; Fusco et al. 2019). Interestingly, while *A. donax* decreased fire intensity in *Phragmites* floodplain habitats in South Africa (Guthrie 2007), it increased fire intensity in the shrubby riparian areas of California (Bell 1997). Likewise, while *Brachypodium sylvaticum* has been observed to decrease severity of spring fires in coniferous forests (Poulos and Roy 2015), it is suspected that it may increase fall fire intensities (Anzinger and Radosevich 2008). Both examples illustrate the habitat and seasonal context specificity of invasion-fire cycles and the need for additional research.

What fire suppression by moist perennial grasses and forbs might mean for the structure of native grasslands or floodplain communities is unclear (Supplemental Fig. S2 Panel B) but the most obvious implication is that fire suppression could complicate the use of prescribed fire as a management practice in invaded communities (McGranahan et al. 2012). In theory, fire suppression by invasive perennial grasses and forbs could allow for encroachment of native woody vegetation into grassland habitats or may alter community composition by favoring species that are more competitive but less fire tolerant than native vegetation. However, we were unable to find evidence in the literature for this dynamic.

Fire suppressing trees and shrubs

We found nine woody species with the potential to suppress fires in savannas (1), woodlands, (2), forests (4), grasslands or sedge meadows (4), and fynbos or shrublands (3). As fire-suppressing trees and shrubs invade, they shade-out native vegetation in the understory, reducing abundance of fine-flammable fuels (Fig. 2; Supplemental Fig. 3 panel B; e.g., Braithwaite et al. 1989; Heneghan et al. 2004). Like perennial grasses that suppress fire, flammability of some invasive trees and shrubs themselves are often exceptionally low, further inhibiting ability of fires to ignite and carry across invaded areas (Van Wilgen and Richardson 1985; Braithwaite et al. 1989). Theoretically, invasions of non-pyrogenic shrubs and trees could lead to complete fire exclusion and formation of a closed invasive plant canopy (Fig. 3 panel B), but such dynamics would depend on traits of the recipient ecosystem, including species composition and underlying abiotic conditions.

Invasions of fire-suppressing trees and shrubs have been associated with instances of anthropogenic fire suppression (Loope and Dunevitz 1981; Converse 1984). Species responsible for fire suppression are sometimes fire- sensitive such that their ability to initiate an invasion- fire suppression cycle may depend on extended fire-free periods during which the invader establishes and becomes abundant enough to survive subsequent fires (Stevens and Beckage 2009). Hence, whether some fire-suppressing invaders can establish and spread without the initial aid of anthropogenic fire suppression is unclear and requires further study.

Rather than decreasing fuel-loads, invasive species can also suppress fires by producing fuel-beds with high bulk densities and high fuel moistures. For example, in South Africa the Australian shrubby trees *Hakea sericea* and *Acacia saligna* both increased fuel loads, but the high moisture content of *A. salinga* and high-bulk density of *H. sericea* decreased the extent and intensity of fires in invaded fynbos (Van Wilgen and Richardson 1985). Under historical weather parameters, *H. sericea* and *A. saligna* suppress fire but under extreme weather conditions, such as predicted with climate change, abundant fuel beds of both species could increase fire intensity.

Factors affecting occurrence of invasion-fire cycles

Where and when a plant invasion induces an invasion-fire cycle depends on more than the flammability, abundance, and structure of fuels within invaded landscapes (Brooks 2008). Other factors that influence fire behavior, such as climate and ignitions, can play an important role in determining the probability that a fire event will occur (Keeley and Syphard 2018) and responses of invasive species to fire. Factors that independently are known to affect the distribution and abundance of invasive species, such as propagule pressure (Simberloff 2009) and resource availability (Mata et al. 2013), can also limit the effects of invasion-drive fires on invasive plant abundance and spread. To better predict where invasive species are likely to cause invasion-fire cycles, a better understanding of the relationships among invasive-fueled fires and climatic, anthropogenic, and environmental factors is needed. Here we provide a brief discussion of how ignitions, propagule pressure, and resources and climate may influence invasion-fire cycles.

Ignitions

Anthropogenic ignitions play a large role in occurrence of wildfires and may be an important driver of invasion-fire cycles. Throughout the United States, humans are responsible for starting more than 80% of wildfires, which accounts for nearly half of the total land area burned (Balch et al. 2017). As such, in many areas where there is substantial evidence of invasion-fire cycles, anthropogenic ignition sources are also prevalent. For example, in California, areas dominated by grasses, which may include invasive annual grasses in the genera *Bromus*, *Avena*, and *Schismus*, tend to burn more frequently than other landcover types (Syphard et al. 2017). However, most fires in California are caused by humans (Syphard et al. 2007), meaning that frequent fires in areas invaded by annual-invasive grasses are potentially dependent on prevalence of human ignitions. Similarly, Hawaii wildfires are most likely to occur in areas dominated by invasive grasses, but expansion of these grasses via an invasion-fire cycle is likely dependent on occurrence of anthropogenic ignitions that are responsible for nearly all wildfires in the state (Trauernicht et al. 2015). Although unburned native Hawaiian vegetation can still be invaded by invasive perennial grasses without fire (e.g., Goergen and Daehler 2001), reducing anthropogenic ignitions would likely also reduce occurrence of perennial grass-fire cycles and hence the rate of invader spread and loss of native canopy trees and shrubs. If ignition sources are limited, an invasion-fire cycle may be unlikely to develop. However, once an invasion-fire cycle is established, chances are higher that any ignition will result in a fire.

Propagule pressure

Whether an invasive species will increase or decrease in abundance post-fire may depend largely on propagule pressure of both the invader and co-occurring native species and hence any factors (such as resource availability) that limit seed production or propagule growth may influence post-fire plant community dynamics. Many invasive annual grasses and forbs that facilitate frequent and extensive fires produce small, light-weight seeds that can be killed by hot-burning fires. Hence, these species often depend on propagule dispersal into burned patches to colonize post-fire rather than establishment from the seed bank. Without sufficient availability of propagules, invaders may either decrease in abundance or be eliminated by fire events. For example, fires in chaparral communities in California burn hot, and invasive annual grasses and their seeds cannot survive those fires (Keeley 2000). However, if abundant invasive annual species are located outside of the burned area and disperse readily, invaders may quickly recolonize and lead to more fires by increasing availability of fine flammable fuels (Keeley 2000). When invasions of species with heat sensitive seeds are small and localized, prescribed burns may reduce or eradicate the invader if surrounding populations are not available to recolonize the burned area. More research is needed to determine how invader propagule pressure, fire tolerance, dispersal ability, and other traits contribute to invasion patterns across variable landscapes after fires.

Propagule pressure, rather than fire, may even be the primary driver of invader distribution and abundance. For example, *Pennisetum ciliare*, an invasive perennial grass, was found to increase fuel loading, and hence fire intensity in the regions it invades (Butler and Fairfax 2003). *Pennisetum ciliare* also has been reported to as much as double in abundance in burned areas (Butler and Fairfax 2003) and was reported to increase fire severity for native trees (Schlesinger et al. 2013). However, in a correlational analysis, researchers found that abundance of *P. ciliare* does not depend on fire but is instead driven by abundance of seed sources bordering burned patches (Fensham et al. 2013). Desert communities can also be transformed into invasive grasslands by *P. ciliare* without altering the overall fire regime (Olsson et al. 2012). Hence, while invasive species might alter fire regimes, propagule pressure rather than fire may be driving the invasion. Ultimately, invasive species that produce copious seeds may be more likely to alter fire behavior or be abundant after fire events. Native-seeding efforts after fire events can help restore areas degraded by invasive species but the success of restoration efforts depends on many factors, including tolerance of native and invasive species to fire, diversity and abundance of the native seedbank, and abiotic and biotic characteristics of the ecosystem (see e.g., D'Antonio and Meyerson 2002; Davies et al. 2019).

Resource availability and climate

Resource availability can prevent invasive species from gaining an advantage over native species through fire events fire due to its effects on propagule pressure, invader establishment, and competition with native flora. For example, in the western United States, *Avena barbata* has been observed to increase in abundance post-fire (Lambert et al. 2010) but low-nutrient availability in Western Australian mallee habitats seems to limit the ability of the species to benefit from fire events (Gosper et al. 2011), perhaps by limiting propagule availability or establishment of invasive seedlings. Across the Great Basin of the western United States, *B. tectorum* cover is highly correlated with preceding wet years (Pilliod et al. 2017). However, *B. tectorum* may not respond positively to fire in sagebrush communities that experience high rainfall during summer months, possibly because summer rainfall increases competitiveness of native perennials (Taylor et al. 2014). In the North American Great Plains, precipitation occurs predominantly during the summer (Lauenroth and Burke 1995) and fires do not increase *B. tectorum* abundance in this region (Porensky and Blumenthal 2016). Alternatively, *B. tectorum* does not respond positively to fire in very dry regions (Larson et al. 2017), illustrating that climatic conditions that limit resource availability and influence competitive outcomes may inhibit invaders benefiting from the fires they facilitate.

Anthropogenic climate change may also be contributing to occurrence of invasion-fire cycles by directly influencing patterns of precipitation and temperature that affect distribution of invasive species, as well as the flammability and abundance of fuels. Drought events and warmer temperatures resulting from climate change can increase fuel flammability and hence the risk of fires (Littell et al. 2016). Climate change is also predicted to increase frequency of lightning in parts of North America and Europe but decrease frequency of lightning in the tropics and across most of Africa (Finney et al. 2018), which may affect the probability of fire occurrences across the globe. Evaluating relationships among ranges of invasive species, climatic conditions, and resource availability across landscapes could help us better determine which factors are most influential to development of invasion-fire cycles and to identify vulnerable regions and habitats.

Research priorities

Here, we outlined some patterns and mechanisms of invasion-fire cycles based on the currently available literature, but overall, we found that empirical evidence for invasion-fire cycles is limited, especially given the potential scale of the problem across many ecosystems. Thus, although it is clear that invasive plants can initiate invasion-fire cycles that have profound effects, less well known is what factors determine where invasion-fire cycles occur, how climate change will alter effects of invaders on fire, and what their long-term effects on ecosystems will be. To better understand invasion-fire interactions and how they drive changes in native plant communities and ecosystems, and to take a precautionary approach against initiation of invasion-fire cycles, we highlight the following research needs:

1. Long-term effects of invader-driven fires on native communities

There are many examples of invasive species causing changes to fuels and fire behavior, but there is a dearth of evidence that these changes are sustained over time and eventually lead to transformation of native communities to alternative, invader-dominated states. Only 22 of the 79 invasive species we identified were reported to increase fire severity or generally reduce native species cover via their effects on fire behavior (Supplemental Table 2), and an additional four invasive species were associated with reduced native species cover. However, whether this pattern was caused by fire-effects is unclear. Surprisingly, only five studies reported on long-term impacts of an invasion-fire cycle on native community composition over a timespan longer than 3 years (i.e., Billings 1994; Talluto and Suding 2008; D'Antonio et al. 2011; Ellsworth et al. 2014; Underwood et al. 2019), although the dearth of research on longer-term impacts of invaders is known to be a general issue (D'Antonio and Flory 2017). Reported impacts of invader-fueled fires also tended to focus on only a few target native species opposed to overall community composition and structure. Likewise, only 22 of the 79 invasive species we identified were empirically reported to increase in cover, density, biomass, or their rate of spread in response to the fire conditions they facilitated (Supplemental Table 2). Three of the invasive species we identified are unlikely to cause invasion-fire cycles as they decreased in abundance post-fire (Tveten and Fonda 1999; Radford et al. 2008; McDonald and McPherson 2011b).

Short-term observations on effects of invader-altered fire behavior on native and invader abundance is problematic as these changes can be ephemeral (e.g., Vilà et al. 2001; Flory et al. 2017) and there may be time lags between fire events and invasion. Longer-term studies on how altered fire regimes driven by invasive species affect native communities can provide greater evidence that invasion-fire cycles occur and help us identify which communities are most vulnerable to being transformed by invasion-fire cycles. When historical data are available, retrospective studies can be used to detect long-term trends in cover types and fire regimes (e.g., Talluto and Suding 2008).

2. Testing steps of the invasion-fire cycle over invasion gradients and across invader genotypes

How invasive species change fuel properties and consequently fire behavior has been generally described (Brooks et al. 2004), but the extent by which fuels, and resultant fire behavior must be altered by invasive species to lead to loss of native vegetative cover and diversity is an unexplored topic. Low levels of invasion may be unlikely to alter fire regimes (Bradley et al. 2018), and a threshold of invader cover might need to be reached before native vegetation is lost (Underwood et al. 2019). Additionally, invasive species may not drastically alter fire regimes until they are already abundant (Taylor et al. 2017) at which point native vegetation may have already been lost to competitive exclusion. It is likely that studies of invasion-fire cycles are conducted where highly abundant invaders have already been observed to affect fire regimes, thus producing a bias towards positive results. Such practices also likely lead researchers to draw conclusions at the species level when in fact, abundance of many invaders can vary widely among sites, which can affect fuel loads and fire behavior (Dillon et al. 2021). Moreover, traits of invasive species that might affect invasion-fire cycles (e.g. biomass, Hiatt and Flory 2020) can vary among populations or genotypes of invasive species, but to our knowledge the role of invader intraspecific trait variation on fire effects has not been explored.

Field studies that evaluate the relationship between fuel properties, fire behavior, and native community composition over an invasion gradient and with different invader source populations or genotypes would help us understand mechanisms of invasion-fire cycles and could allow us to identify communities that are most vulnerable to their consequences. Such studies could also be used to improve fire behavior models used to predict potential impacts of invasive species and different invasive species genotypes on fire-regimes.

3. Relationships among factors affecting occurrence of invasion-fire cycles

Climate, ignitions, and other factors can drive and inhibit occurrence of invasion-fire cycles by modulating the probability that fuels will ignite, while propagule pressure, resource availability, and climate can modulate occurrence of invasion-fire cycles by affecting responses of invasive and native species to fire events. In some instances, anthropogenic fire suppression or anthropogenic ignitions may be the underlying driver of initial invader dominance and spread (e.g., Xanthopoulos 1986; Stevens and Beckage 2009), indicating that changes in fire management could help restore or prevent further loss of native communities affected by invasion-fire cycles. Understanding the relationship among these variables (and others) could also be used to identify where invasion-fire cycles are more likely to occur and how distribution of susceptible habitats and locations might be altered by climate change, land use change, and other anthropogenic influences.

4. Effects of altered fire-regimes on native plant communities

While intense fires caused by plant invasions can suppress seed and bud banks via increased soil heating (Tomat-Kelly et al. 2021), it is unknown whether this is a potential mechanism of invasion-fire cycles. Additionally, while greater fire frequency might exclude slow-to-recover native vegetation, and increased fire intensity can kill native vegetation (Flory et al. 2017), it is unclear how altered fire regimes influence competitive interactions between invasive and native species. Instead of altered-fire regimes directly excluding or killing native plant species, the altered fire regime may reduce competitive ability of native vegetation that would otherwise be able to compete with the invader. Understanding what factors determine if invasion-fire cycles lead to loss of native vegetation and greater dominance of the invader, be it via soil heating, post-fire competition, propagule pressure, or some other mechanism, would help managers formulate restoration plans by informing whether efforts such as broadcast seeding or fuel reduction would aid in restoring areas affected by invasion-fire cycles.

Conclusion

We found that the growth form of invasive species has influenced the mechanisms and locations where invasion-fire cycles have been documented to occur, but more research is needed to predict which species are most likely to cause invasion-fire cycles and to identify communities that are most vulnerable to their occurrence. Moreover, because many studies have focused on specific invaders suspected of causing invasion-fire cycles, the role of recipient ecosystem characteristics in invasion-fire cycles is not well understood. Management of invasive species that cause invasion-fire cycles is critical for preventing large-scale degradation of native ecosystems and reducing the need for costly restoration efforts, as is evident from the story of *Bromus tectorum* in the western United States and perennial grass invasions in Hawaii. Ultimately, focusing research efforts on identifying factors that affect the occurrence of invasion-fire cycles, and the mechanisms by which they occur, can help prevent large-scale consequences of invasion-fire cycles and improve understanding of biological invasions.

Author contributions GTK and SLF developed the underlying questions and approach. GTK collected and synthesized literature. GTK and SLF wrote and edited the paper.

Funding Florida Fish and Wildlife Conservation Commission, USDA/NIFA McIntire-Stennis (FLA-AGR- 005772) and the Strategic Environmental Research and Development Program (RC-2636).

Data availability All data is available within the article and supplementary data files, or at https://doi.org/10.5061/dryad.qz612jmjz.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent to participate Not applicable.

References

Agbalog RE (2010) Effects of fire on cheatgrass (*Bromus tectorum*): a case study of fire restoration in the Lake. Chelan National Recreation Area, Washington

Alexander HD, Siegert C, Brewer JS et al (2021) Mesophication of oak landscapes: evidence, knowledge gaps, and future research. Bioscience 71:531–542

Anable ME (1990) Alien plant invasion in relation to site characteristics and disturbance: *Eragrostic lehmanniana* on the Santa Rita Experimental Range. The University of Arizona, Arizona, pp 1937–1989

Anzinger D, Radosevich SR (2008) Fire and nonnative invasive plants in the Northwest Coastal bioregion. In: Zouhar K, Smith JK, Sutherland S, Brooks ML (eds) Wildland fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42-vol, vol 6. US Department of

Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp 197–224

Baker WL (2006) Fire and restoration of sagebrush ecosystems. Wildl Soc Bull 34:177–185

Balch JK, Bradley'BA, D'Antonio CM et al (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Change Biol 19:173–183

Balch JK, Bradley BA, Abatzoglou JT et al (2017) Human-started wildfires expand the fire niche across the United States. Proc Natl Acad Sci 114:2946–2951

Bell GP (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. In: Brock JH, Wade M, Pysek P, Green D (eds) Plant invasions: studies from North America and Europe. Blackhuys Publishers, Leiden, The Netherlands, pp 103–113

Berry Z, Wevill K, Curran T (2011) The invasive weed *Lantana camara* increases fire risk in dry rainforest by altering fuel beds. Weed Res 51:525–533

Bianchi LO, Oddi FJ, Muñoz M et al (2019) Comparison of leaf moisture content and ignition characteristics among native species and exotic conifers in northwestern Patagonia, Argentina. For Sci 65:375–386

Billings W (1994) Ecological impacts of cheatgrass and resultant fire on ecosystems in thewestern Great Basin. In: Monsen SB, Kitchen SG (eds) Proceedings–ecology and management of annual rangelands, pp 22–30

Blackhall M, Raffaele E (2019) Flammability of patagonian invaders and natives: when exotic plant species affect live fine fuel ignitability in wildland-urban interfaces. Landsc Urban Plann 189:1–10

Bossard CC, Randall JM, Hoshovsky MC (2000) Invasive plants of Cali'ornia's wildlands. Universiy of California Press

Bowman DM, MacDermott HJ, Nichols SC et al (2014) A grass–fire cycle eliminates an obligate-seeding tree in a tropical savanna. Ecol Evol 4:4185–4194

Bradley BA, Curtis CA, Fusco EJ et al (2018) Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biol Invasions 20:1493–1506

Braithwaite RW, Lonsdale W, Estbergs J (1989) Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. Biol Conserv 48:189–210

Brooks ML (1999) Alien annual grasses and fire in the Mojave Desert. Madroño 46:13–19

Brooks ML (2008) Plant invasions and fire regimes. In: Zouhar K, Smith JK, Sutherland S, Brooks ML (eds) Wildland fire in ecosystems: fire and nonnative invasive plants. General technical reports RMRS-GTR-42-vol, vol 6. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp 33–4642

Brooks ML, Matchett J (2006) Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. J Arid Environ 67:148–164

Brooks ML, D'antonio CM, Richardson DM et al (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Bullock JM (2009) A long-term study of the roles of competition and facilitation in the establishment of an invasive pine following heathland fires. J Ecol 97:646–656

Busch DE (1995) Effects of fire on southwestern riparian plant community structure. Southwest Nat 40:259–267

Busch DE, Smith SD (1993) Effects of fire on water and salinity relations of riparian woody taxa. Oecologia 94:186–194

Butler BDW, Fairfax RJ (2003) Buffel grass and fire in a Gidgee and Brigalow woodland: a case study from central Queensland. Ecol Manage Restor 4:120–125

Chambers JC, Brooks ML, Germino MJ et al (2019) Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. Front Ecol Evol 7:185

Cóbar-Carranza AJ, García RA, Pauchard A et al (2014) Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *ArauXXXraucanaaucana* and *Nothofagus antarctica* forests. Biol Invasions 16:2273–2291

Coffman GC, Ambrose RF, Rundel PW (2010) Wildfire promotes dominance of invasive giant reed (*Arundo donax*) in riparian ecosystems. Biol Invasions 12:2723–2734

Connolly BM, Powers J, Mack RN (2017) Biotic constraints on the establishment and performance of native, naturalized, and invasive plants in Pacific Northwest (USA) steppe and forest. NeoBiota 34:21–40

Converse CK (1984) Element stewardship abstract for *Rhamnus cathartica*. *Rhamnus frangula* (syn. *Frangula alnus*. The Nature Conservancy, Arlington, VA

Cox JR, Ruyle GB, Roundy B (1990) Lehmann lovegrass in southeastern Arizona: biomass production and disappearance. Rangel Ecol Manag/J Range Manage Arch 43:367–372

D'Antonio CM, Flory SL (2017) Long-term dynamics and impacts of plant invasions. J Ecol 105:1459–1461

D'Antonio CM, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: synthesis. Restor Ecol 10:703–713

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

D'Antonio CM, Hughes RF, Mack M et al (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. J Veg Sci 9:699–712

D'Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecol 25:507–522

D'Antonio CM, Hughes R, Tunison J (2011) Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. Ecol Appl 21:1617–1628

Dascanio LM, Barrera MD, Frangi JL (1994) Biomass structure and dry matter dynamics of subtropical alluvial and exotic *Ligustrum* forests at the Río de la Plata. Argentina Vegetatio 115:61–76

Davies KW, Nafus AM (2013) Exotic annual grass invasion alters fuel amounts, continuity and moisture content. Int J Wildland Fire 22:353–358

Davies KW, Bates JD, Boyd CS (2019) Postwildfire seeding to restore native vegetation and limit exotic annuals: an evaluation in juniper-dominated sagebrush steppe. Restor Ecol 27:120–127

Davis KT, Maxwell BD, Caplat P et al (2019) Simulation model suggests that fire promotes lodgepole pine (*Pinus contorta*) invasion in Patagonia. Biol Invasions 21:2287–2300

Dibble AC, Rees CA (2005) Does the lack of reference ecosystems limit our science? A case study in nonnnative invasive plants as forest fuels. J Forest 103:329–338

Dillon WW, Hiatt D, Flory SL (2021) Experimental manipulation of fuel structure to evaluate the potential ecological effects of fire. For Ecol Manag 482:118884

Divíšek J, Chytrý M, Beckage B et al (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat Commun 9:1–10

Doren RF, Whiteaker LD (1990) Effects of fire on different size individuals of *Schinus terebinthifolius*. Nat Areas J 10:107–113

Douglas MM, Setterfield SA, Rossiter N et al (2004) Effects of mission grass (*Pennisetum polystachion* (L.) Schult.) invasion on fuel loads and nitrogen availability in a northern Australia tropical savanna. In: Sindel BM, Johnson SB (eds) Proceedings of the 14th Australian weeds conference, pp 179–181

Ellis LM, Crawford CS, Molles MC Jr (1998) Comparison of litter dynamics in native and exotic riparian vegetation along the Middle Rio Grande of central New Mexico, USA. J Arid Environ 38:283–296

Ellsworth LM, Litton CM, Dale AP et al (2014) Invasive grasses change landscape structure and fire behaviour in Hawaii. Appl Veg Sci 17:680–689

Emery SM, Uwimbabazi J, Flory SL (2011) Fire intensity effects on seed germination of native and invasive eastern deciduous forest understory plants. For Ecol Manag 261:1401–1408

Fahey C, Angelini C, Flory SL (2018) Grass invasion and drought interact to alter the diversity and structure of native plant communities. Ecology 99:2692–2702

Fensham R, Fairfax R, Cannell R (1994) The invasion of *Lantana camara* L. in forty mile scrub National Park, north Queensland. Aust J Ecol 19:297–305

Fensham RJ, Donald S, Dwyer JM (2013) Propagule pressure, not fire or cattle grazing, promotes invasion of buffel grass *Cenchrus ciliaris*. J Appl Ecol 50:138–146

Ferriter A, Bodle M, Goodyear C et al (2001) Exotic species in the Everglades. Environmental Consolidate Report

Finney DL, Doherty RM, Wild O et al (2018) A projected decrease in lightning under climate change. Nat Clim Change 8:210–213

Flory SL, Clay K, Emery SM et al (2015) Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. J Appl Ecol 52:992–1000

Flory SL, Bauer J, Phillips RP et al (2017) Effects of a non-native grass invasion decline over time. J Ecol 105:1475–1484

Flory SL, Dillon W, Hiatt D (2022) Interacting global change drivers suppress a foundation tree species. Ecol Lett 25:971–980

Flowers JD (1991) Subtropical fire suppression in *Melaleuca quinquenervia*. In: Proceedings of the Symposium on Exotic Pest Plants. USDI. National Park Service, pp 151–158

Franzese J, Raffaele E, Blackhall M et al (2020) Changes in land cover resulting from the introduction of non-native pine modifies litter traits of temperate forests in Patagonia. J Veg Sci 31:223–233

Fuentes-Ramirez A, Veldman JW, Holzapfel C et al (2016) Spreaders, igniters, and burning shrubs: plant flammability explains novel fire dynamics in grass-invaded deserts. Ecol Appl 26:2311–2322

Fusco EJ, Finn JT, Balch JK et al (2019) Invasive grasses increase fire occurrence and frequency across US ecoregions. Proc Natl Acad Sci 116:23594–23599

Gaertner M, Biggs R, Te Beest M et al (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Divers Distrib 20:733–744

García RA, Engler ML, Peña E et al (2015) Fuel characteristics of the invasive shrub *Teline monspessulana* (L.) K. Koch. Int J Wildland Fire 24:372–379

Gentle C, Duggin J (1997) Lantana camara L. invasions in dry rainforest-open forest ecotones: the role of disturbances associated with fire and cattle grazing. Aust J Ecol 22:298–306

Goergen E, Daehler CC (2001) Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae). Int J Plant Sci 162:317–326

Gorgone-Barbosa E, Pivello VR, Bautista S et al (2015) How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. Biol Invasions 17:423–431

Gosper CR, Yates CJ, Prober SM et al (2011) Fire does not facilitate invasion by alien annual grasses in an infertile Australian agricultural landscape. Biol Invasions 13:533–544

Grace JB, Smith MD, Grace SL et al (2000) Interactions between fire and invasive plants in temperate grasslands of North America. In: Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference, pp 40–65

Grigulis K, Lavorel S, Davies ID et al (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands. Glob Change Biol 11:1042–1053

Guthrie G (2007) Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level. Master's Thesis, University of the Western Cape

Hart SJ, Henkelman J, McLoughlin PD et al (2019) Examining forest resilience to changing fire frequency in a fire-prone region of boreal forest. Glob Change Biol 25:869–884

Heneghan L, Rauschenberg C, Fatemi F et al (2004) European buckthorn (*Rhamnus cathartica*) and its effects on some ecosystem properties in an urban woodland. Ecol Restor 22:275–280

Hiatt D, Flory SL (2020) Populations of a widespread invader and co-occurring native species vary in phenotypic plasticity. New Phytol 225:584–594

Hiremath AJ, Sundaram B (2005) The fire-lantana cycle hypothesis in Indian forests. Conserv Soc 3:26–42

Hoffmann WA, Haridasan M (2008) The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. Austral Ecol 33:29–36

Hoffmann WA, Lucatelli VM, Silva FJ et al (2004) Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. Divers Distrib 10:99–103

Hood SM, Varner JM, Van Mantgem P, Cansler CA (2018) Fire and tree death: understanding and improving modeling of fire-induced tree mortality. Environ Res Lett 13(11):113004

Huffman JM (2006) Historical fire regimes in southeastern pine savannas. Dissertation, Louisiana State University and Agricultural and Mechanical College

Hughes F, Vitousek PM, Tunison T (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. Ecology 72:743–747

Jacquemyn H, Brys R, Neubert MG (2005) Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. Ecol Appl 15:2097–2108

James KL, Randall NP, Haddaway NR (2016) A methodology for systematic mapping in environmental sciences. Environ Evid 5:1–13

Jayiya AT, Moses AG, van Wilgen AGFB (2004) The effects of invasion by alien shrubs and trees on the fuel properties of ecosystems in the Western Cape, South Africa. CSIR report to Working for Water. http://www.dwaf.gov.za/wfw/docs/Jayiyaetal

Keeley JE (2000) Fire and invasive species in Mediterranean-climate ecosystems of California. In: Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference. pp 81–94

Keeley JE, Brennan TJ (2012) Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia 169:1043–1052

Keeley JE, McGinnis TW (2007) Impact of prescribed fire and other factors on cheatgrass persistence in a Sierra Nevada ponderosa pine forest. Int J Wildland Fire 16:96–106

Keeley JE, Syphard AD (2018) Historical patterns of wildfire ignition sources in California ecosystems. Int J wildland fire 27:781–799

Keeley JE, Fotheringham C, Baer-Keeley M (2005) Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. Ecol Appl 15:1515–1534

Kerns BK, Tortorelli C, Day MA et al (2020) Invasive grasses: a new perfect storm for forested ecosystems? For Ecol Manag 463:117985

Kraaij T, Baard JA, Arndt J et al (2018) An assessment of climate, weather, and fuel factors influencing a large, destructive wildfire in the Knysna region, South Africa. Fire Ecol 14:1–12

Lambert AM, D'Antonio CM, Dudley TL (2010) Invasive species and fire in California ecosystems. Fremontia 38:29–36

Larson CD, Lehnhoff EA, Rew LJ (2017) A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. Oecologia 185:763–774

Lauenroth W, Burke I (1995) Great plains, climate variability. Encyclopedia of Environmental Biology 2:237–249

Link SO, Keeler CW, Hill RW et al (2006) *Bromus tectorum* cover mapping and fire risk. Int J Wildland Fire 15:113–119

Lippincott CL (2000) Effects of *Imperata cylindrica* (L.) Beauv. (cogongrass) invasion on fire regime in Florida sandhill (USA). Nat Areas J 20:140–149

Littell JS, Peterson DL, Riley KL et al (2016) A review of the relationships between drought and forest fire in the United States. Glob Change Biol 22:2353–2369

Livingston AC, Varner JM (2016) Fuel moisture differences in a mixed native and non-native grassland: implications for fire regimes. Fire Ecol 12:73–87

Livoreil B, Glanville J, Haddaway NR et al (2017) Systematic searching for environmental evidence using multiple tools and sources. Environ Evid 6:1–14

Lonsdale W, Miller I (1993) Fire as a management tool for a tropical woody weed: *Mimosa pigra* in Northern Australia. J Environ Manag 39:77–87

Loope LL, Dunevitz HL (1981) Impact of fire exclusion and invasion of *Schinus terebinthifolius* on limestone rockland pine forests of southeastern Florida. National Park Service, South Florida Research Center, Everglades National Park

Macdonald I (1983) Alien trees, shrubs and creepers invading indigenous vegetation in the Hluhluwe-Umfolozi Game Reserve Complex in Natal. Bothalia 14:949–959

Macdonald I, Frame G (1988) The invasion of introduced species into nature reserves in tropical savannas and dry woodlands. Biol Conserv 44:67–93

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends Ecol Evol 13:195–198

Mata TM, Haddad NM, Holyoak M (2013) How invader traits interact with resident communities and resource availability to determine invasion success. Oikos 122:149–160

McDonald C, McPherson G (2011a) Fire behavior characteristics of buffelgrass-fueled fires and native plant community composition in invaded patches. J Arid Environ 75:1147–1154

McDonald CJ, McPherson GR (2011b) Absence of a grass/fire cycle in a semiarid grassland: response to prescribed fire and grazing. Rangel Ecol Manage 64:384–393

McDonald CJ, McPherson GR (2013) Creating hotter fires in the Sonoran Desert: buffelgrass produces copious fuels and high fire temperatures. Fire Ecol 9:26–39

McGlone CM, Springer JD, Covington WW (2009) Cheatgrass encroachment on a ponderosa pine forest ecological restoration project in northern Arizona. Ecol Restor 27:37–46

McGranahan DA, Engle DM, Fuhlendorf SD et al (2012) An invasive cool-season grass complicates prescribed fire management in a native warm-season grassland. Nat Areas J 32:208–214

McGranahan DA, Engle DM, Miller JR et al (2013) An invasive grass increases live fuel proportion and reduces fire spread in a simulated grassland. Ecosystems 16:158–169

Miller G, Friedel M, Adam P et al (2010) Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central

Australia–does field evidence support a fire-invasion feedback? Rangel J 32:353–365

Mistry J, Berardi A (2005) Assessing fire potential in a Brazilian savanna nature reserve. Biotropica 37:439–451

Monsen SB (1994) Selection of plants for fire suppression on semiarid sites. SB Monsen and SG Kitchen (compilers). In: Proceedings—ecology and management of annual rangelands. General technical report INTGTR-313, US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, pp 363–373

Monty A, Brown CS, Johnston DB (2013) Fire promotes downy brome (*Bromus tectorum* L.) seed dispersal. Biol Invasions 15:1113–1123

Murphy BP, Russell-Smith J (2010) Fire severity in a northern Australian savanna landscape: the importance of time since previous fire. Int J Wildland Fire 19:46–51

NeSmith JE, Alba C, Flory SL (2018) Experimental drought and plant invasion additively suppress primary pine species of southeastern US forests. For Ecol Manag 411:158–165

Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58:123–138

O'Brien JJ, Mordecai KA, Wolcott L (2010) Fire managers field guide: hazardous fuels management in subtropical pine flatwoods and tropical pine rocklands. General technical reports SRS-123. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station, vol 55, no. 123, pp 1–55

Olsson AD, Betancourt J, McClaran MP et al (2012) Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. Divers Distrib 18:10–21

Padullés Cubino J, Buckley HL, Day NJ et al (2018) Community-level flammability declines over 25 years of plant invasion in grasslands. J Ecol 106:1582–1594

Paolini JJ, Quon LH, Questad EJ (2014) The impact of invasive forbs on fine fuel loads in degraded coastal sage scrub. Crossosoma 40:9–21

Paritsis J, Landesmann JB, Kitzberger T et al (2018) Pine plantations and invasion alter fuel structure and potential fire behavior in a Patagonian forest-steppe ecotone. Forests 9:1–117

Pauchard A, Garcia RA, Pena E et al (2008) Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. Biol Invasions 10:547–553

Pereira Júnior AC, Oliveira SL, Pereira JM, Turkman MAA (2014) Modelling fire frequency in a Cerrado savanna protected area. PloS one 9(7):e102380

Peters EF, Bunting SC (1994) Fire conditions pre-and post-occurrence of annual grasses on the Snake River Plain. Proceedings—ecology and management of annual rangelands. General Technical report INT-GTR-313. Intermountain Research Station, USDA Forest Service, Ogden, UT:31–36

Pickford G (1932) The influence of continued heavy grazing and of promiscuous burning on spring–fall ranges in Utah. Ecology 13:159–171

Piemeisel RL (1951) Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32:53–72

Pilliod DS, Welty JL, Arkle RS (2017) Refining the cheatgrass–fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. Ecol Evol 7:8126–8151

Platt WJ, Gottschalk RM (2001) 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

Porensky LM, Blumenthal DM (2016) Historical wildfires do not promote cheatgrass invasion in a western Great Plains steppe. Biol Invasions 18:3333–3349

Poulos LP, Roy BA (2015) Fire and false brome: How do prescribed fire and invasive *Brachypodium sylvaticum* affect each other? Invasive Plant Sci Manag 8:122–130

Prichard SJ, Hessburg PF, Hagmann RK et al (2021) Adapting western North American forests to climate change and wildfires: 10 common questions. Ecol Appl 31:e02433

Priyanka N, Joshi P (2013) Assessment of plant invasion and forest fires linkage-a case study of *Lantana camara*. Int J Sci Technol Res 2:40–46

Pyšek P, Richardson DM, Pergl J et al (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

Radford IJ, Grice AC, Abbott BN et al (2008) Impacts of changed fire regimes on tropical riparian vegetation invaded by an exotic vine. Austral Ecol 33:151–167

Richburg J, Patterson W III, Ohman M (2004) Fire management options for controlling woody invasive plants in the Northeastern and Mid-Atlantic US. Department of Natural Resources Conservation, University of Massachusetts, Amherst

Rossi RD, Martins CR, Viana PL et al (2014) Impact of invasion by molasses grass (*Melinis minutiflora* P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil. Acta Bot Brasilica 28:631–637

Rossiter NA, Setterfield SA, Douglas MM et al (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Divers Distrib 9:169–176

Rother MT, Huffman JM, Guiterman CH et al (2020) A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA. For Ecol Manag 475:118406

Salvo Aires F (2015) Effects of woody weeds on fuels and fire behaviour in Eastern Australian forests and woodlands. Dissertation, University of Sydney

Schlesinger C, White S, Muldoon S (2013) Spatial pattern and severity of fire in areas with and without buffel grass (*Cenchrus ciliaris)* and effects on native vegetation in central Australia. Austral Ecol 38:831–840

Schramm JW, Ehrenfeld JG (2010) Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. Biol Invasions 12:3195–3204

Seebens H, Bacher S, Blackburn TM et al (2021) Projecting the continental accumulation of alien species through to 2050. Glob Change Biol 27:970–982

Setterfield SA, Rossiter-Rachor NA, Hutley LB et al (2010) Biodiversity research: turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Divers Distrib 16:854–861

Setterfield SA, Rossiter-Rachor NA, Douglas MM et al (2013) Adding fuel to the fire: the impacts of non-native grass invasion on fire management at a regional scale. PLoS One 8(5):e59144. https://doi.org/10.1371/journal.pone.0059144

Silvério DV, Brando PM, Balch JK et al (2013) Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. Philos Trans R Soc B Biol Sci 368:20120427

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

Simberloff D (2011) How common are invasion-induced ecosystem impacts? Biol Invasions 13:1255–1268

Smith CW, Tunison JT (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. Alien plant invasions in native ecosystems of Hawaii: management and research. Cooperative National Park Resources Studies Unit, Honolulu, pp 394–408

St. Clair SB, Bishop TB (2019) Loss of biotic resistance and high propagule pressure promote invasive grass–fire cycles. J Ecol 107:1995–2005

Stevens JT, Beckage B (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytol 184:365–375

Stoner JR, Adams R, Simmons D (2004) Management implications of increased fuel loads following exotic grass invasion. Ecol Manag Restor 5:68–70

Sutherland S (2004) What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia 141:24–39

Syphard AD, Radeloff VC, Keeley JE et al (2007) Human influence on California fire regimes. Ecol Appl 17:1388–1402

Syphard AD, Keeley JE, Abatzoglou JT (2017) Trends and drivers of fire activity vary across California aridland ecosystems. J Arid Environ 144:110–122

Talluto MV, Suding KN (2008) Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. Landscape Ecol 23:803–815

Taylor K, Brummer T, Rew LJ et al (2014) *Bromus tectorum* response to fire varies with climate conditions. Ecosystems 17:960–973

Taylor KT, Maxwell BD, McWethy DB et al (2017) *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. Ecology 98:678–687

Thaxton JM, Van Bloem SJ, Whitmire S (2012) Fuel conditions associated with native and exotic grasses in a subtropical dry forest in Puerto Rico. Fire Ecol 8:9–17

Tomat-Kelly G, Dillon WW, Flory SL (2021) Invasive grass fuel loads suppress native species by increasing fire intensity and soil heating. J Appl Ecol 58:2220–2230

Trauernicht C, Pickett E, Giardina CP et al (2015) The contemporary scale and context of wildfire in Hawaii. Pac Sci 69:427–444

Tunison JT, Loh R, Leialoha J (1995) Fire effects in the submontane seasonal zone. Hawai'i Volcanoes National Park

Tunison J, D'Antonio C, Loh R (2000) Fire and invasive plants in Hawai'i Volcanoes National Park. In: Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference. pp 122–131

Tveten RK, Fonda R (1999) Fire effects on prairies and oak woodlands on Fort Lewis. Wash Northwest Sci 73:145–158

Underwood EC, Klinger RC, Brooks ML (2019) Effects of invasive plants on fire regimes and postfire vegetation diversity in an arid ecosystem. Ecol Evol 9:12421–12435

Van Wilgen B, Richardson D (1985) The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. J Appl Ecol 22:955–966

Veblen TT, Kitzberger T, Raffaele E et al (2003) Fire history and vegetation changes in northern Patagonia, Argentina. In: Fire and climatic change in temperate ecosystems of the western Americas. Springer, pp 265–295

Vilà M, Lloret F, Ogheri E et al (2001) Positive fire–grass feedback in Mediterranean Basin woodlands. For Ecol Manag 147:3–14

Wade D, Ewel J, Hofstetter R (1980) Fire in south Florida ecosystems. General technical reports SE-17. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC, p 125

Wagner SA, Fraterrigo JM (2015) Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. For Ecol Manag 354:170–176

Wang S, Niu S (2016) Do biological invasions by *Eupatorium adenophorum* increase forest fire severity? Biol Invasions 18:717–729

Wang H-H, Wonkka CL, Grant WE et al (2016) Range expansion of invasive shrubs: implication for crown fire risk in forestlands of the southern USA. AoB Plants 8

Watt M, Kriticos D, Manning L (2009) The current and future potential distribution of *Melaleuca quinquenervia*. Weed Res 49:381–390

Whisenant SG (1990) Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur ED, Romney EM, Smith SD, Tueller PT (eds) Proceeding-symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management, USDA Forest Service Intermountain Research Station General Technical Report INT-276, pp 4–10

Wyse SV, Perry GL, Curran TJ (2018) Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation-fire feedbacks favouring invasive species. Ecosystems 21:886–900

Xanthopoulos G (1986) A fuel model for fire behavior prediction in spotted knapweed (*Centaurea maculosa* L.) grasslands in western Montana. Master's Thesis, University of Montana

Young JA (1992) Ecology and management of medusahead (*Taeniatherum caput-medusae* ssp. asperum [Simk.] Melderis). The Great Basin Naturalist:245–252

Zedler PH, Gautier CR, McMaster GS (1983) Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64:809–818

Zouhar K, Smith JK, Sutherland S (2008) Effects of fire on nonnative invasive plants and invasibility of wildland ecosystems. In: Zouhar K, Smith JK, Sutherland S, Brooks ML (eds) Wildland fire in ecosystems: fire and nonnative invasive plants. General technical reports RMRS-GTR-42-vol,

vol 6. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp 7–3242