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Invasive grasses: A new perfect storm for forested ecosystems?

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ABSTRACT

Exotic grasses are a widespread set of invasive species that are notable for their ability to significantly alter key aspects of ecosystem function. Understanding the role and importance of these invaders in forested landscapes has been limited but is now rising, as grasses from Eurasia and Africa continue to spread through ecosystems of the Americas, Australia, and many Pacific islands, where they threaten biodiversity and alter various aspects of the fire regime. The ecological, social and economic impacts of the grass-fire cycle associated with species such as cheatgrass (*Bromus tectorum*) have been long recognized in aridlands such as the iconic sagebrush ecosystems of the western US. However, the damaging impacts of invasive grasses in forestlands have received considerably less attention. We review literature, conceptual models, model output, and empirical evidence that indicate grass invasion in forest ecosystems may be an important yet largely under-recognized phenomenon. In combination with climate change, wildfire, and overstory management, invasive grasses could create a "perfect storm" that threatens forest resilience. Invasive grasses can be successful in forested environments or develop strongholds within forested mosaics and could provide the literal seeds for rapid change and vegetation type conversion catalyzed by wildfire or changes in climate. Although invasive grass populations may now be on the edge of forests or consist of relatively rare populations with limited spatial extent, these species may disrupt stabilizing feedbacks and disturbance regimes if a grass-fire cycle takes hold, forcing large portions of forests into alternative nonforested states. In addition, forest management actions such as thinning, prescribed fire, and fuel reduction may actually exacerbate invasive grass populations and increase the potential for further invasion, as well as broader landscape level changes through increased fire spread and frequency. Lack of understanding regarding the ecological consequences and importance of managing invasive grasses as a fuel may lead to unintended consequences and outcomes as we enter an age of novel and rapid ecological changes. This paper focuses on the contributory factors, mechanisms, and interactions that may set the stage for unexpected forest change and loss, in an effort to raise awareness about the potential damaging impact of grass invasion in forested ecosystems.

1. Introduction

Almost three decades ago D'Antonio and Vitousek (1992) published a landmark paper cautioning that invasive grasses may become widespread and effective enough to alter regional and global aspects of ecosystem function. There is ample evidence to suggest that we are now living in that future. Grasses from Eurasia and Africa have spread throughout many ecosystems of the Americas, Australia, and the Pacific islands, where they threaten native biodiversity and alter various aspects of the fire regime. These grasses are now recognized as some of the most important ecosystem-altering species on the planet. Notorious examples include buffelgrass (*Cenchrus ciliaris*) in Australia, the US Southwest, and Mexico (Schlesinger et al., 1990; Burquez-Montijo et al., 2002; McDonald and McPherson, 2013); gamba grass (*Andropogon gayanus*) in Australia (Setterfield et al., 2010; Setterfield et al., 2013); and cheatgrass (*Bromus tectorum*) and cogongrass (*Imperata cylindrical*) in the US (Knapp, 1996; Lippincott, 2000). Loss of native biodiversity, reduced carbon storage, and habitat degradation are just some of the impacts these species can have (Godfree et al., 2017). Of potentially even greater consequence is that these grasses can also alter fundamental ecosystem processes such as disturbance regimes through the development of a grass-fire cycle, which can initiate a cascade of

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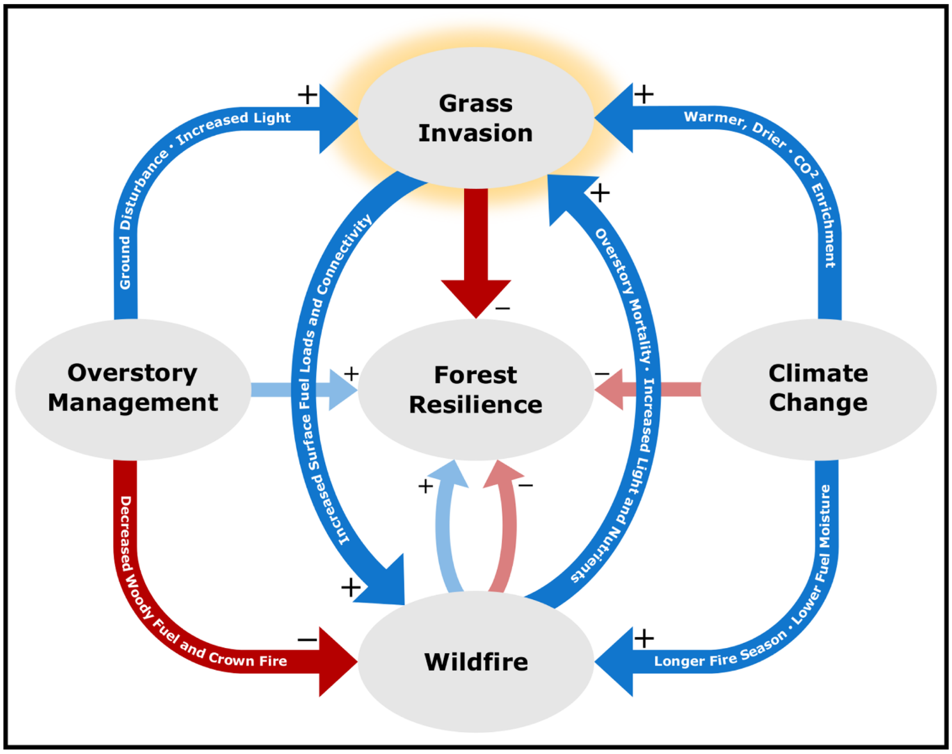

Fig. 1. Grass invasion (presumed exotic) in forested landscapes can strongly influence woody and other native plant establishment and reduce forest resilience. Grass invasion combined and interacting with climate change, wildfire, and overstory management may be a perfect storm that threatens forest resilience. Bold blue "+" arrows indicate positive interactions while bold red "−" arrows indicate negative interactions. Important example mechanisms discussed in the text that drive each interaction are listed within each arrow, but not all potential mechanisms could be included. Smaller arrows that are not bold acknowledge other important interactions that are only touched upon briefly in this paper. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

related changes and ecological, social, and economic impacts that may be irreversible. These impacts have long been recognized in arid and semiarid ecosystems such as the iconic sagebrush ecosystems of the western US due to species such as cheatgrass, an invasion that has prompted substantial focus, action, and commitment of resources. But are exotic invasive grasses a major threat to forested ecosystems?

Grass invasion (hereinafter presumed exotic) may be an important and largely under-recognized phenomenon that in combination with other processes and practices could create a "perfect storm" that reduces forest resilience owing to concurring novel disturbances, stressors, and unintended management consequences in forested ecosystems (Fig. 1). While there are many definitions in the literature, we adopt the definition that forest resilience is 'the ability of a forest to absorb disturbances and reorganize under change to maintain similar functioning and structure' (Scheffer, 2009). This definition recognizes that most forests will not recover exactly to pre-disturbance conditions, but that they will reside within the same ecosystem type or state (Scheffer, 2009; Reyer et al., 2015). We consider a perfect storm a critical or catastrophic situation created by a powerful combination of factors. Together, the factors result in impacts that may not have ensued if individual elements occurred separately. The perfect storm factors we will focus on and review here include: (1) grass invasion, (2) climate change, (3) wildfire, and (4) overstory management (Fig. 1).

Globalization is constantly exposing forests to a pipeline of new invasive grasses that may perform well, despite historically low rates of forest invasion (McDougall et al., 2011). We emphasize that invasive grasses are a common component of many forests around the globe (Martin et al., 2009), yet little is known about the extent to which these species could provide the literal seeds for rapid and novel change and reduced resilience in forested ecosystems worldwide. Continued global warming and concomitant increases in wildfire activity in the 21st century (Barbero et al., 2015) are virtually certain if greenhouse gas emissions continue unabated (Collins et al., 2013). Climate change may directly increase invasion exposure in forests as favorable climate conditions allow invaders to expand into new ranges (Bradley et al., 2010). In addition, many invasive species are well adapted to take advantage of fluctuating resources after disturbances such as wildfire (Davis et al., 2000). We review increasing evidence suggesting that drier fire-prone forests and woodlands are already prone to climate- and fire-driven state changes or tipping to nonforested vegetation types. These state changes may be persistent or "sticky" due to exotic grass invasion, particularly if a destabilizing grass-fire cycle develops. Management actions such as thinning and prescribed fire, often designed to alleviate threats related to wildfires, may also exacerbate grass invasion and increase fine fuels, with potential landscape scale consequences that are largely under-recognized.

We explore these four perfect storm components (grass invasion, climate change, wildfire, overstory management) for forest ecosystems and their interactions in greater detail, reviewing and synthesizing relevant examples from the literature and simulation modeling. We also highlight an on-the-ground example from our collaborative research from the Inland Northwest that may represent an alarming canary in the coal mine. First, we provide background information regarding grass invasion in forests and challenge the notion that forests are inherently resistant or resilient to these invasions. We then describe how grass invasion can potentially interact with other perfect storm components to decrease forest resilience, focusing on three key topics: (1) climate change and invasion risk, (2) wildfire and grass-fire cycles, and (3) overstory management and unintended consequences. Lastly, we discuss strategies that could potentially mitigate the perfect storm. This paper is an attempt to focus on the contributory factors, mechanisms, and patterns that may set the stage for unexpected forestland conversion to nonforested states, and raise awareness about the potential damaging impact of grass invasion in forested ecosystems. Ecology and management of nonwoody species generally receive less attention and study in forested ecosystems, which may translate into a lack of effective management, policies and funding for control and mitigation.

2. Grass invasion and forest resilience

The twenty-first century threat of emerging invasive exotic species is extensive and distributed globally (Early et al., 2016). However,

Fig. 2. Above: A mosaic of forest and nonforest in the Umatilla National Forest, Oregon. The yellow outline is a 728 ha fuel reduction prescribed fire project area. The area includes western juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and other tree species interspersed with open herbaceous areas, many that are largely stable features of the landscape maintained by soil and topography. Below: Open areas within this landscape are characterized by a suite of native and nonnative herbaceous species. Many of the interspaces between larger perennial bunchgrasses and forbs have been filled in by the invasive exotic annual grass *Ventenata dubia*. Photo credit: Becky Kerns. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

forests, and in particular temperate forests, are often considered to be resistant (no or few invaders) and resilient (invaders do not change the ecosystem state) to exotic grass invasion. Succinctly summarized by Martin et al. (2009), the rationale for this assumption is that dense forest canopies limit understory light availability (Rejmánek et al., 2013), cooler temperatures and relatively short growing seasons act as an environmental filter to grass invasion (McDougall et al., 2011), and human activity and propagule pressure are generally lower (Parks et al., 2005). Other factors, such as characteristics of the litter layer and throughfall water quantity and chemistry may also play a role (Barbier et al., 2008). However, there are notable invaders that challenge these assumptions. Despite the focus in invasion ecology on early successional species, shade tolerant invasive species are actually common in forests, including grasses (Martin et al., 2009). Shade tolerant invasive grasses include Japanese stiltgrass (*Microstegium vimineum*) and Chinese silvergrass (*Miscanthis sinensis*) in eastern US deciduous forests, and it is well documented that Japanese stiltgrass is negatively impacting the natural regeneration of woody and herbaceous species (Flory and Clay, 2010; Quinn et al., 2012). Competition between herbaceous vegetation and woody seedlings for soil water and other nutrients can strongly influence woody plant establishment (Davis et al., 1998). Shade tolerant false brome (*Brachypodium sylvaticum*) has invaded understories and replaced native vegetation in western US coniferous forests (Holmes et al., 2010; Poulos and Roy, 2017).

The notion that cooler temperatures may constrain grass invasion in forests and mountainous areas can also be challenged, especially as these areas are increasingly exposed to a pipeline of exotic grass species as global trade increases and human communities, roads, and other development expand into forested areas. Most grasses are easily dispersed and can produce vegetative shoots in the same growing season in which they emerge, thus their likelihood of becoming a successful plant invader, even in very cold ecosystems, may be increased over nonnative plants without this ability. Poaceae (grass family) species are actually the most common non-native plants found globally in the alpine zone (Alexander et al., 2016). The concept that cooler (and shadier) forested environments may constrain grass invasion may simply reflect the traits and performance of early seral, light-loving species that were often intentionally introduced and have been historically problematic invaders in warmer, low elevation nonforested ecosystems (e.g. cheatgrass, buffelgrass; Martin et al., 2009). However, shade-intolerant grasses also threaten forested landscapes, as forests are not continuous stands of trees, but rather "patchwork hierarchies" (sensu Hessburg et al., 2015) composed of complex mosaics of vegetation types and seral stages, including agro-pastoral areas that differ in size from small forest canopy gaps to larger openings such as meadows and other nonforested plant communities (Fig. 2).

Cheatgrass in the arid Great Basin of the western US provides a salient example of a historically problematic shade intolerant invader in nonforested ecosystems that has shaped much of our understanding about invasive grasses. Ecosystem resistance and resilience to cheatgrass invasion across elevational gradients appears to be related to temperature at higher elevations and soil water availability at lower elevations (Chambers et al., 2014). Maps and other tools (e.g. soil surveys) depicting environmental and soil factors associated with cheatgrass occurrence and abundance, and ecosystem resistance to invasion, are used to help decision makers and managers assess risk and prioritize allocation of resources to weed management (Maestas et al., 2016; Chambers et al., 2019). While these tools are highly valuable and relevant for cheatgrass invasion in shrub-steppe ecosystems, it is unclear the extent to which these concepts are transferable to forested environments and to other invasive annual grasses that are more problematic in forests.

The intrinsic vulnerability of an area to invasion can change dramatically with new invaders that have different traits and environmental filters, as the role of species traits and invasion success is complex and context-specific (Pyšek and Richardson, 2008; Hui et al., 2016). One emerging example is *Ventenata dubia* (ventenata), a winter annual grass (germinates in the fall) similar to cheatgrass. It has been highly problematic at elevations similar to those occupied by cheatgrass (Wallace et al., 2015) in the northwestern US. However, ventenata is also invading nonforest and areas of low tree cover intermixed throughout ponderosa pine and mixed conifer forests (Panel 1) (Averett et al., 2016; Pekin et al., 2016), communities historically not highly impacted by annual grasses. While both cheatgrass and ventenata are winter annual C3 grasses, their invasion dynamics appear to be somewhat different, most likely due to varied ecological niches (Tortorelli et al., in review). Characterizing forest resilience to grass invasion will require information about invasion levels, propagule pressure and dispersal vectors, and characteristics of the newly introduced species, as well as complex relationships between the invading species and the biotic and abiotic environment of the recipient ecosystem (Pyšek et al., 2010; Catford et al., 2012; Hui et al., 2016).

3. Climate change and invasion risk

Climate change can directly increase invasion risk in forests as favorable climate conditions allow invaders to expand into new ranges. Climate change alters the abiotic and biotic conditions under which plant species establish, survive, reproduce, and spread. Invasive grasses may be directly enhanced by warmer temperatures, earlier springs and snowmelt, reduced snowpack, and elevated nitrogen and CO_2 concentrations. Increased productivity in response to elevated CO_2, and increased nutrient and water use efficiency are typical plant responses that have been documented for a number of invasive grasses (Ziska and George, 2004; Runion et al., 2015). Invasive C4 grasses are well equipped to spread into areas where conditions become drier and warmer, while C3 grasses flourish under higher CO_2 concentrations (Sage and Kubien, 2003). Biomass and seed production of invasive annual grasses have been found to benefit from elevated CO_2 concentrations more than neighboring native species (Nagel et al., 2004; Smith et al., 2000). Grasses, particularly annual grasses, are well adapted to quickly disperse, and initiate growth and reproduction as soon as resources become available.

Climate change can also increase grass invasion by stressing existing native species, altering ecosystem dynamics such as competition and disturbance regimes, and providing new invasion opportunities. Evidence is accumulating that some forests may not be sustained in the future due to increased drought and disturbance-related tree mortality (Allen et al., 2010; McDowell and Allen, 2015). Warming temperatures have already resulted in many species shifting poleward and upward in elevation, a pattern that has been observed globally (Parmesan and Yohe, 2003; Chen et al., 2011). Many simulation models also project that climate change alone will shift forests to nonforest states around the world (Kashian et al., 2006; Malhi et al., 2009; Gonzalez et al., 2010; Hurteau and Brooks, 2011; Kim et al., 2017, 2018). The velocity of these shifts is projected to be rapid in many places under most climate change scenarios (Loarie et al., 2009; Corlett and Westcott, 2013; Kerns et al., 2016), with many areas/regions projected to enter climates without recent analogs (Williams et al., 2007). Invasive plants may also be better able to adjust to these rapid changes in abiotic conditions by tracking seasonal temperature trends and shifting their phenology (Willis et al., 2010). Under many climate change scenarios, climate is not projected to stabilize for centuries (Meinshausen et al., 2011). The extensive duration and intensity of climate change has the potential to leave long-lived, slow-dispersing plant species such as trees vulnerable while creating more niches for short-lived, fast-dispersing species such as invasive grasses (Abatzoglou and Kolden, 2011; Walck et al., 2011).

Various combinations of rapid climate change, long-term climate instability, insect and disease outbreaks (Anderegg et al., 2015), herbivore pressure, increased fire activity (Barbero et al., 2015), and the influx of competitive invasive grasses may lead to large scale forest die-offs (Solomon and Kirilenko, 1997; Allen et al., 2010; Parks et al., 2018), disrupt tree regeneration dynamics, and ultimately tip many forests into nonforest states (Anderson-Teixeira et al., 2013; Savage et al., 2013; Bowman et al., 2014; Petrie et al., 2017; Stevens-Rumann et al., 2018). Tipping points refer to critical thresholds where small changes can dramatically alter the state or development of a system (Lenton et al., 2008). Trailing edge forests (forests at the contracting margins of their climate tolerance zone) may already be “tipsy” as they are particularly at risk for conversion to nonforest. Forest biogeography in many parts of the world is not at equilibrium with the current climate (Prentice et al., 1991; Araújo and Pearson, 2005). In addition, evidence increasingly suggests ecosystem states can be self-reinforcing across multiple scales, and transitions between forested and grassland states are nonlinear, governed by localized feedbacks such as fire and grazing (Mayer and Khalyani, 2011; Staver et al., 2011; de L. Dantas et al., 2013; Donato et al., 2016; Charles-Dominique et al., 2018; Parks et al., 2019) that can tip forest and nonforest states. Thus forest and nonforest areas can be alternative stable states in many landscapes (Wood and Bowman, 2012; Fletcher et al., 2014), maintained by climate (including seasonality) and strong feedbacks between fire and flammable species such as grasses (Bond and Keeley, 2005; Mayer and Khalyani, 2011).

4. Wildfire and grass-fire cycles

While the ecological benefits of wildfire are well known, we may be entering a global era of megafires and megadisturbances when negative consequences of fire rise in impact. Megafires are driven by hotter and longer fire seasons, increased fuel accumulation due to decades of fire suppression, intense insect and pathogen outbreaks, increased anthropogenic ignitions, and other human disturbances (Dennison et al., 2014; Stephens et al., 2014; Jolly et al., 2015; Jones et al., 2016; Westerling, 2016; Balch et al., 2017; Stephens et al., 2018). For some forests that historically experienced lower severity frequent fire, megafires represent a substantial departure in the fire regime: the long-term pattern in fire frequency, seasonality, size, extent and severity across a given landscape driven by fuels, topography, and climate (Agee, 1993; Archibald et al., 2013). These large, severe fires often result in significant, uncharacteristic overstory tree mortality and large, open patches with little remaining overstory cover (Miller et al., 2012; Lydersen et al., 2014; Reilly et al., 2017). Therefore, there is increased potential for rapid landscape change driven by large patches of early successional plant communities that can dominate post-disturbance landscapes (Mallek et al., 2013; Hessburg et al., 2015).

Open patches in forests generated from higher severity disturbances are highly vulnerable to invasion by exotic grasses (Griffis et al., 2001; Holzmueller and Jose, 2012; Keeley and Brennan, 2012; Peeler and Smithwick, 2018). While early-successional species and open forest patches are important components of landscape diversity and historically were more extensive (Hessburg et al., 2000; Swanson et al., 2011), they are also excellent habitat for invasive, shade intolerant grasses. Invasive grasses, particularly annual grasses, may also compete for moisture during the early growing season with regenerating conifers, limiting forest regeneration. Even in cases where wildfire does not initially catalyze a grass invasion, there is evidence that short interval wildfire reburning may do so (Reilly et al., in press), substantially altering the historically positive effects of frequent fire. Therefore, the contemporary and future function of these early successional patches may be quite different than the past.

Whether disturbance mediated or not, grass invasion can facilitate dramatic ecosystem change by altering fire regimes. A recent analysis encompassing multiple ecoregions in the US indicated that invasive grasses can increase fire occurrence up to 230% and fire frequency up to 150% (Fusco et al., 2019). Changes in fire regimes due to grass invasion are driven by fundamental alterations in the spatial and temporal fuel structure on the landscape. Invasive grasses often increase fine fuel biomass through higher productivity; extend horizontal and vertical fuel connectivity through novel structures, such as a continuous horizontal spatial pattern in infilled gaps and monocultures; and increase flammability due to their high surface area to volume ratio and seasonal phenology distinct from native species (Brooks et al., 2004). A shift in any one of these elements can alter fire regimes, consequently impacting ecosystem function. Many invasive grasses exhibit rapid postfire recovery rates which increase post-burn fuel loads and often reduce fire return intervals within a community, creating a positive grass-fire feedback loop, or a grass-fire cycle (D'Antonio and Vitousek, 1992; Brooks et al., 2004; Pilliod et al., 2017) that may be difficult to reverse. These fuel changes can increase fire spread rate, severity, and frequency, which often leads to state shifts from shrub-steppe or woodland communities to grasslands. Less commonly, invasion by a high moisture grass can decrease fire spread and activity when it leads to increased understory fuel moisture (McGranahan et al., 2013).

Grass-fire cycles are notable for their pronounced ecosystem impacts in semiarid ecosystems that had historically low fuel connectivity and patchy fire occurrence, such as sagebrush ecosystems of the western US, and desert ecosystems of the southwest and Mexico (Esque and Schwalbe, 2002). In these ecosystems, slight shifts of the fire regime can have severe effects on native plant communities. These communities evolved under pressure from mixed severity fire regimes burning in patchy mosaics at moderate return intervals, and lack the adaptations to recover quickly after fire (Whisenant and Uresk, 1990; D'Antonio and Vitousek, 1992). As a result, even low levels of invasion, when coupled with fire, can lead to the creation of spatially extensive and temporally persistent, or "sticky" invasive grass monocultures across the landscape. Recent work across the Great Basin of the western US indicates that cheatgrass invaded landscapes are much more likely to ignite and burn earlier in the fire season, and burn more frequently, extensively and homogeneously than uninvaded sites (Balch et al., 2013; Bradley et al., 2018b). In some sagebrush ecosystems, cheatgrass cover as low as 5% has been associated with increased fire risk (Bradley et al., 2018b), and significant losses to native biodiversity have been found in sagebrush ecosystems after only one fire with invasive annual grasses present (Knapp, 1996; Davies et al., 2012). The impact of even limited amounts of cheatgrass cover on fire risk may be related to the species' flammability, as flammability has been shown to be more important for fire behavior than amount of biomass for grass species in some ecosystems (Cardoso et al., 2018).

While much focus in the literature on invasive grass-fire cycles has been on aridlands such as the sagebrush steppe, there are many examples demonstrating how this cycle can tip ecosystem states in tropical and temperate woodlands and forests, including converting treed communities into invasive grasslands that might be sticky (Table 1). Forest ecotones that border woodland, shrub and grassland ecosystems harboring invasive grasses may be particularly at risk for annual grass induced fire regime and state shifts as fires that ignite in grass-invaded areas often carry across and into adjacent forests (Balch et al., 2013; Kunst et al., 2015). Invasions into open areas (existing or created from high severity fire or other disturbance) within a forested mosaic are also problematic, because invasion could initiate an uncharacteristic positive grass-fire feedback with the potential to propagate into forests, creating larger invasive grass-dominated sticky patches in previously forested areas (Fig. 3). Wildfire ignited in invaded open patches could allow more rapid and extensive fire spread into the adjacent forest stands, resulting in tree mortality. It is well known that tree torching (individual tree burning) and forest crown fire initiation generally requires a substantial surface fire (Wagner, 1977; Scott and Reinhardt, 2001). Tree mortality, in turn, may then exacerbate annual grass expansion along the edge of stands and lead to the development of larger open patches that may be maintained or stuck in a nonforested state. The potential for a grass-fire cycle and these processes to unfold in interior Pacific Northwest dry forests due to the invasion of *Ventenata dubia* is particularly worrisome, and the subject of ongoing research (Panel 1).

In forests that evolved with frequent fire regimes that have been subject to fire suppression, dense forest development, and subsequent fuel accumulation (e.g. Hessburg et al., 2005; Fule et al., 1997), more frequent burning and tree mortality may be desired. However, large patches of high severity fire coupled with grass invasion could preclude the reestablishment of a more historically characteristic, open and fine-grained forest mosaic with native understories (Fig. 3). Invasive grass could competitively exclude tree and other native plant establishment, and rapid fire spread with reburning could kill native perennials, tree seedlings and saplings.

5. Overstory management and unintended consequences

The escalation in wildfire activity, fuel accumulation, and fire suppression costs over the past several decades have ushered in a new era of forest management and ongoing calls to action (Covington, 2000; Hessburg et al., 2015; McWethy, 2019; North et al., 2015; Schoennagel et al., 2017; USDA-USDI, 2013). In the US, this new era of wildfire-risk focused policy and management has largely focused on restoration and resilience concepts, managing woody fuels through actions such as forest thinning and prescribed fire use, overstory manipulation, and delivery of timber goods and services (USDA Forest Service, 2012, 2018). In 2018 alone, the USDA Forest Service was directed to treat over 1.4 million ha to reduce hazardous fuels through prescribed fire, thinning, and timber sales (U.S. Executive Office of the President, 2018). However, forest management practices that result in gap-formation and ground disturbance (e.g. thinning, creation of multi-layered structured canopies, brush clearing, prescribed fire use, slash burning, fuel break creation) can introduce, spread, or exacerbate invasive grasses (Keeley, 2006; Keeley and McGinnis, 2007; Merriam et al., 2006; McGlone et al., 2009; Ross et al., 2012; Kerns and Day, 2017), and increase the potential for further invasion, fire risk, and broader landscape-level changes.

Lack of recognition of the importance of managing invasive grasses in concert with other forest management practices may lead to unintended consequences and tradeoffs that could considerably alter restoration, fuel reduction, and other outcomes. If annual grasses invade after overstory treatments, outcomes related to native plant recovery, forage production, and old-growth tree protection, which are common land management goals associated with fuel reduction and restoration actions, may be reduced or negated. Of particular concern is that grass invasion after fuel treatment may result in a fuel *tradeoff* rather than a fuel *reduction*. A shift from hazardous woody fuels to hazardous herbaceous fuels may actually increase wildfire ignitions and fire spread rates, with more extensive fires burning across invaded areas and spreading into the surrounding landscape or adjacent developments such as the wildland urban interface. Examination of standard fire behavior fuel models demonstrates that even small changes in fine fuels can dramatically increase fire rates of spread and flame length (e.g. see GR1 compared to GR2, Scott and Burgan, 2005). Possible tradeoffs between woody versus fine fuel for surface fire potential, fire intensity, flame length, and spread rates are illustrated in Fig. 4 using a simple simulation model of different fuelbeds (inherent physical characteristics of fuel that contribute to fire behavior and effects) from the Fuel Classification Characterization System (Prichard et al., 2013). This comparison demonstrates how grass invasion may lead to undesirable and unintended outcomes, depending on post-treatment understory composition and structure and grass invasion.

A deeper and more nuanced understanding of the potential impacts of invasive grasses as a wildland fuel in forested landscapes is critically important. Grass invasion and conversion to higher surface fire potentials may rapidly tip forests to sticky nonforest states if a grass-fire cycle develops, potentially increasing landscape scale fire risk, compromising ecosystem services, and diminishing restoration or other management objectives and associated outcomes for the landscape. Even in areas where overstory treatments may be motivated by recent woody encroachment and state changes, and where increasing fire on the landscape is a goal, grass invasion and the subsequent undermining of restoration objectives remains a risk (Bates and Davies, 2016). The potential unintended consequences from overstory management approaches for wildfire regimes and social-ecological resilience are largely unknown, but deserve further attention, especially as forest exposure to grass invasion increases.

6. Heading off the storm

Heading off a perfect storm of grass invasion, climate change, wildfire, and overstory management and potentially catastrophic ecosystem effects in forestlands will be facilitated by new thinking about invasive grasses and forest resilience using multidisciplinary, integrated and collaborative research and management efforts. We highlight the following points and challenges for researchers, managers, and decision makers to consider.

Recognize and communicate that invasive grasses can be high impact species in forest ecosystems and take early action to mitigate and monitor such invasions. Because invasive grasses may not be fully recognized as

Table 1
Invasive grass species in forested and woodland systems that demonstrate evidence of a grass-fire cycle, grass-fire feedbacks or conversion to grassland.

Species	Life history	Origin	Invaded Ecosystem	Region	Example Citation	Major Findings
Buffelgrass (*Cenchrus ciliaris* = *Pennisetum ciliare*)	Perennial C4 bunchgrass	Africa, India, western Asia	Semi-arid woodland	Australia	Miller et al. (2010) and Fusco et al. (2019)	Invasion was significantly correlated with increased fuel loads and burn severity, and burn severity was correlated with woodland overstory mortality
Cheatgrass (*Bromus tectorum*)	Annual C3	Europe, SW Asia, N Africa	Temperate forest	Western US	Peeler and Smithwick (2018)	High-severity fire increased invasion extent into areas unsuitable without fire
Cogongrass (*Imperata cylindrica*)	Perennial C4 rhizomatous	SE Asia, India, Polynesia, Australia	Temperate coniferous forest	Eastern US	Fusco et al. (2019), Lippincott (2000) and Platt and Gottschalk (2001)	Increases regional fire frequency; Invasive grass areas had higher fine-fuel loads and continuity; Changes in fire could lead to type conversion
Fountaingrass (*Pennisetum setaceum*)	Perennial C4 bunchgrass	Africa, Middle East and SW Asia	Tropical dry forest	Hawaii	Litton et al. (2006)	Grass invaded forest had 7x the understory biomass than uninvaded forest, dramatically changing aboveground carbon sequestration following widespread grass invasion and conversion of Hawaiian dry forests to grasslands
Gamba grass (*Andropogon gayanus*)	Perennial C4 bunchgrass	Africa	Tropical savanna	Australia	Setterfield et al. (2013) and Bowman et al. (2014)	Increased fuel loads and increased fire management costs; grass-fire cycle associated with invasion resulted in tree “recruitment bottleneck”
Guinea grass (*Megathyrsus maximus* = *Panicum maximum*)	Perennial C4 bunchgrass	Africa	Tropical forest and grassland	Hawaii	Ellsworth et al. (2014)	Evidence of type conversion from forest to grassland and subsequent fire due to exotic grass invasion
Japanese stiltgrass (*Microstegium vimineum*)	Annual C4	Asia	Temperate deciduous forest	Eastern US	Fusco et al. (2019), Wagner and Fraterrigo (2015) and Flory et al. (2015)	Increases regional fire frequency; prescribed fire facilitated invasion, more in wetter than drier sites; no difference in fuel loads in invaded habitats but increased flame lengths, fire intensity and duration, reducing tree seedling survival and recruitment
Mauritanian grass [1] (*Ampelodesmos mauritanica*)	Perennial C3 bunchgrass	Mediterranean	Mediterrean forest/ woodland	Catalonia, Spain	Grigulis et al. (2005) and Vilà et al. (2001)	Invasive grass increased horizontal fuel continuity and flammability through persistent litter; evidence of positive feedback between fire and grass invasion
Molasses grass (*Melinis minutiflora*)	Perennial C4 rhizomatous	Africa	Tropical savanna	Brazil	Hoffmann et al. (2004) and Rossi et al. (2014)	Higher fuel loads where present, associated with forest edges; increase in fine fuel biomass, fire spread, and intensity
			Subtropical woodland	Hawaii	D'Antonio et al. (2017)	Short and long-term woody plant composition and structure dramatically altered following exotic grass invasion and fire
Natal grass (*Melinis repens*)	Annual to perennial C4	Africa	Subtropical dry forest	Argentina	Kowaljow et al. (2019)	Associated with high frequency fire environments
Palisade signalgrass (*Urochloa brizantha* = *Brachiaria brizantha*)	Perennial C4 rhizomatous	Africa	Tropical savanna	Brazil	Gorgone-Barbosa et al. (2015) and Balch et al. (2009)	Higher flame length, but lower fire intensity and efficiency in invaded areas at both the community and individual plant levels; fire increased probability of grass incursion into forest edges
Signalgrass (*Urochloa decumbens* = *Brachiaria decumbens*)	Perennial C4 rhizomatous	Africa	Tropical forest/ savanna	Brazil	Silvério et al. (2013)	Fires decreased canopy cover and increased grass invasion into forest edges, increasing fine fuel load and increasing fire intensity
Silkreed (*Neyraudia reynaudiana*)	Perennial C4 rhizomatous	SE Asia, India, Polynesia, Australia	Temperate coniferous forest	Eastern US	Platt and Gottschalk (2001) and Fusco et al. (2019)	Highly flammable, exotic grass increased fine fuels, litter biomass, total biomass; increased regional fire frequency
Slender false brome (*Brachypodium sylvaticum)*	Perennial C3 bunchgrass	Eurasia and North Africa	Temperate coniferous forest	NorthwestUS	Poulos and Roy (2017)	Low-severity fires increased cover, suggesting invasion might instigate a grass–fire cycle, but areas of high grass cover burned at lower severity

[1] Nonnative status unclear.

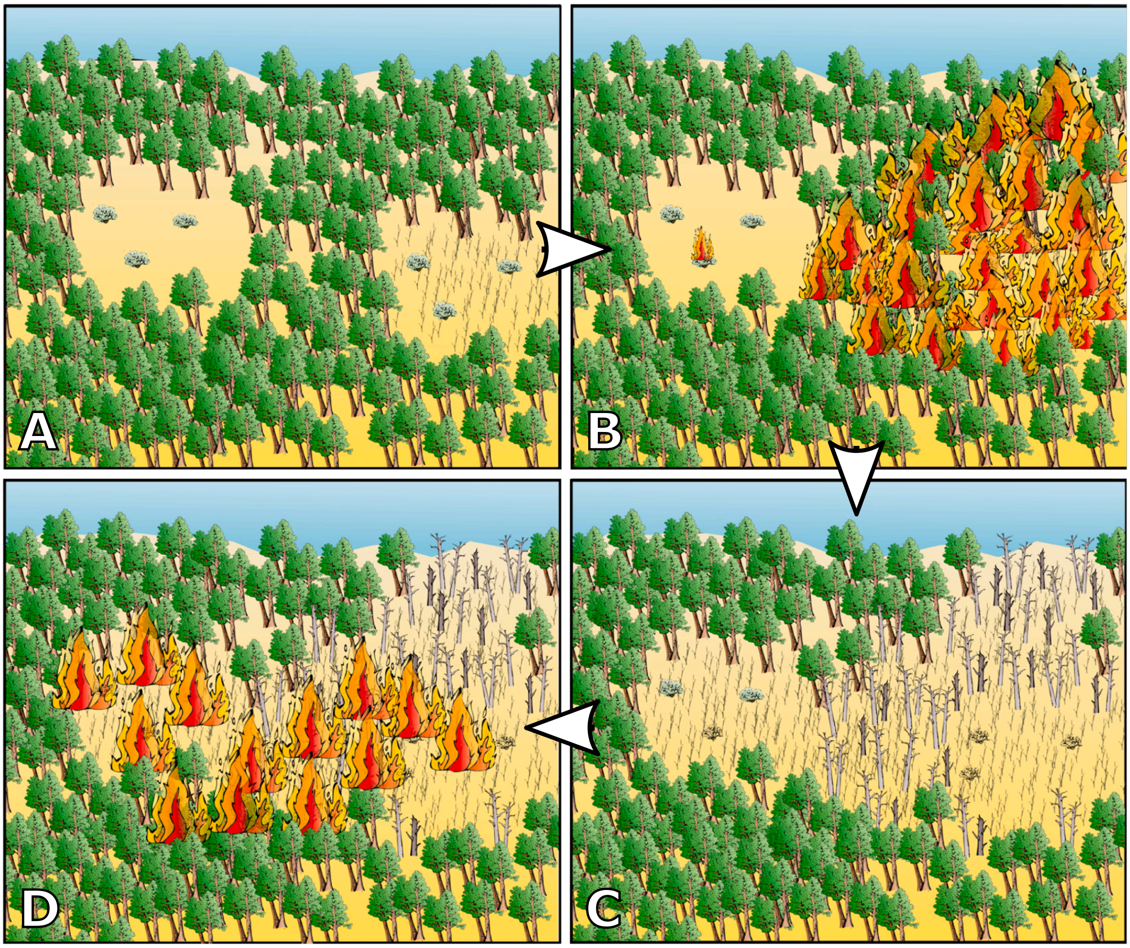

Fig. 3. Schematic depicting the hypothetical expansion and propagation of positive grass-fire feedbacks in a forest mosaic due to invasion and wildfire. Panel A depicts a forest mosaic with two open patches that are stable topoedaphic features of the landscape. The patch on the left is uninvaded and has very low and sparse fuel, and the patch on the right is similar, but invaded by an exotic grass. Wildfire is ignited in both patches in panel B, but the uninvaded patch contains the fire while the invasive grass in the patch on the right allows the fire to spread into the adjacent forest resulting in substantial tree mortality shown in panel C. The post fire invasion spread shown in panel D will increase fine fuels in these patches, increasing ignitability in recently burned areas, and potentially initiating a grass-fire cycle. This grass-fire feedback could prevent the reestablishment of tree seedlings, ultimately creating much larger invaded nonforested areas and relatively temporally stable larger or "sticky" nonforested areas once occupied by trees. A similar process could unfold in a closed canopy forest if a high severity wildfire or other disturbance creates suitable open patches for grass invasion.

important drivers of forest change, initial introductions may go undetected or be ignored, and even basic information about their location and extent may be limited or nonexistent. This can translate into less effective procedures, policies, and funding to detect, respond and eradicate the invading species. It is prudent to flag and monitor any new and existing exotic grass species in forests, nonforest patches, roads, and adjacent ecotones as sources for potentially high impact species. Many forests and mountainous areas are currently not highly invaded or highly disturbed, therefore proactive approaches may still be possible, although it can be a challenge to convince decision makers and commit resources at early invasion stages (McDougall et al., 2011).

Basic communication about the potential threat that invasive grasses may pose for forested ecosystems is key. One potential challenge might be that forest managers, practitioners, and decision makers (particularly outside of botany, range, or wildlife disciplines) are typically not trained to recognize and identify invasive grasses and their potential impacts. Our experience conducting workshops and holding conversations with managers and staff in the northwestern US revealed that invasive grass issues are often not "on the radar" for many forest managers, or are only considered aridland or rangeland issues. This is starting to change as invasive grasses are becoming increasingly problematic in many forests and woodlands, although investments in staff training about grass species and their identification, and communicating the issues we raise in this paper are still needed.

Develop treatment options based on individual species biology, ecology and invasion drivers. The ability to estimate the potential impacts of invasive grasses in forested ecosystems and develop treatment options to ameliorate them will be facilitated by a better understanding of the mechanisms of invasion, species response to disturbances such as wildfire, and forest vulnerability and resilience. Primary research is a vital means of building a knowledge base. While considerable knowledge has accrued regarding some invasive grasses (e.g. Germino et al., 2016), simply transposing this knowledge, often developed in nonforested aridlands, to a new but similar species in forested areas may not be effective. In the absence of basic information, fundamental theories regarding invasion ecology and information gleaned from similar species could be used as an initial management approach. As knowledge is developed and control and mitigation treatments emerge that are specific to the new species, forest management can be adapted. Tackling grass-fire-weed issues and developing treatment options will

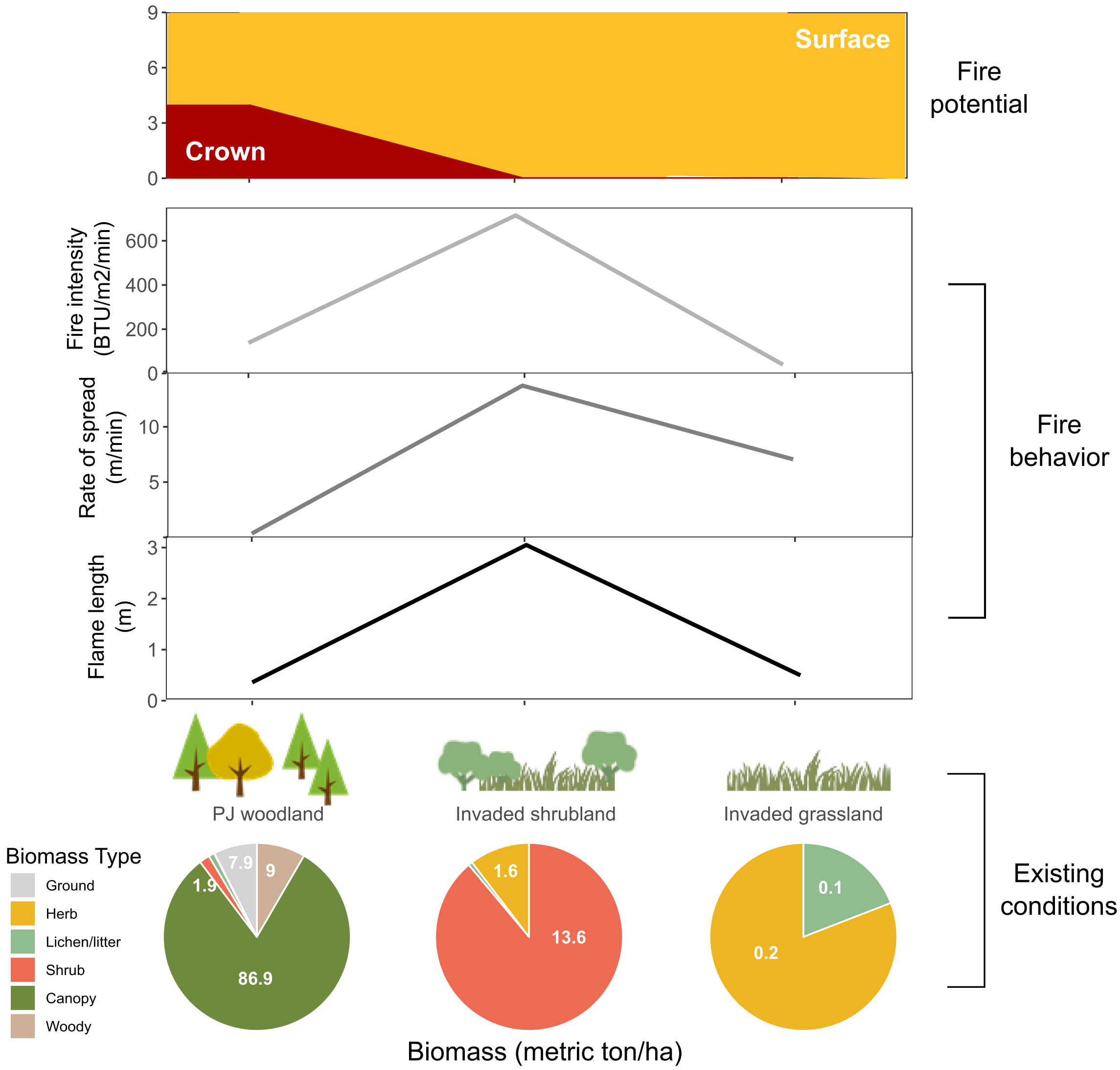

Fig. 4. Model output (FCCS, Fuel Classification and Characterization System, version 2.0.1020, Prichard et al., 2013) illustrates potential fuel and fire behavior tradeoffs among PJ (Pinyon-juniper) woodland and invaded shrubland and grassland communities. Dense PJ woodlands may be targeted for restoration to reduce tree crown fire risk, but they may also be at risk for heavy grass invasion. Biomass type and existing conditions are shown for each community in the bottom panel. Fire behavior (flame length, rate of spread, fire intensity) and fire potential (surface, crown) are plotted for each community type. Based on the different existing conditions shown and benchmark environmental variables, FCCS predicts that PJ woodlands have relatively low crown fire potential (given the conditions used), flame length, spread rate, and fire intensity. In contrast, invaded shrublands and grasslands (approximately 70% exotic annual grass) have no tree crown fire potential, but increased surface fire behavior (flame length and spread rate). Invaded shrublands also have increased fire intensity compared to PJ woodlands. Data were simulated from unedited existing conditions for fuelbeds 25, 56 and 57 in FCCS.

entail challenging dialogue across disciplines that acknowledges tensions and tradeoffs around the important role that overstory management and fire may play as potential invasion drivers in forests.

The development of effective management and restoration approaches for new grass species and invaded forest ecosystems is likely to be a time consuming and complex process. Initially, information about life-history, origin, and habitat conditions of the new species' native range may offer important clues regarding mitigation strategies that do not require years or decades to develop. But environmental constraints on invasion may not be temporally stable due to species adaptation, climate change, and changes in disturbance regimes (Clements and Ditommaso, 2011; Keeley and Brennan, 2012; Colautti and Barrett, 2013; Vandepitte et al., 2014), and short-lived grass species may quickly adapt and spread to novel habitats, so native range information may decline in relevance over time (Colautti and Barrett, 2013; Ackerly, 2003). Much research on invasive grass control focuses on reducing abundance, rather than ecosystem restoration, the latter of which addresses underlying processes responsible for invasive species persistence (Germino et al., 2016; Monaco et al., 2016). The Ecologically Based Invasive Management Plan is an example of a framework that integrates ecosystem health assessment, knowledge of ecological processes, and adaptive management into a successional management model (James et al., 2017).

Map and monitor invasive grass populations. Early detection and mapping of invasive grasses remains a challenge for forest managers. Yet, this information is vital for the effective development and deployment of treatment options in a diverse, forested matrix of land ownerships and plant communities. As mentioned previously, both shade tolerant and shade intolerant species can pose a threat to forests. The presence of these species in any component of the forest matrix can potentially have impacts on the forest patches dispersed across the landscape. Thus, continuous maps of invasive grass populations are key components of a decision support system.

An estimate of both abundance and locale of infested areas provides the most robust and relevant information for risk assessments and spatial investigations (Bradley et al., 2018a). Collection and use of spatially explicit data on invasive grasses has become more common with citizen science initiatives and programs such as EDDMaps (https://www.eddmaps.org/) that collect and archive millions of unique observations of invasive plant species in the US and Canada (Bargeron and Moorhead, 2007; Bradley et al., 2018b; Fusco et al., 2019). However, these databases cannot capture the full spatial extent of invasions. Thus species distribution modeling has assisted in providing predictions of potential locations of invasive grasses (Arriaga et al., 2004).

Recently, remote sensing data have been recognized as a potentially useful source of information for the detection and mapping of invasive plants (Bradley, 2014; He et al., 2015). One of the major benefits of using remote sensing data is that characteristics of the species of interest can be more directly observed as opposed to using indirect associations with environmental variables. However, effectively differentiating an exotic grass from surrounding species requires some type of unique spectral, temporal, structural, or spatial characteristic associated with the species that the sensing method can detect (Bradley, 2014). Successful detection of invasive grass species has been achieved with spectral and temporal indicators (Schmidt and Skidmore, 2001; Peterson, 2005; Irisarri et al., 2009; Clinton et al., 2010; Olsson et al., 2011; Boyte and Wylie, 2016). Spectral differences resulting from unique pigmentation, leaf chemistry, and leaf water content have been used to help in distinguishing exotic plant species from their surroundings (Ustin et al., 2002; Galvão et al., 2005; Andrew and Ustin, 2008; Asner et al., 2008; Huang and Asner, 2009; Große-Stoltenberg et al., 2016). Additionally, satellite image time series have been used to identify phenological patterns associated with grass species like cheatgrass (Clinton et al., 2010; Bradley et al., 2018b).

While these methodologies have been successful in nonforested and low canopy areas, the presence of high tree canopy cover may preclude the detection of invasive grasses located in forest understories. In deciduous forests, this challenge may be circumvented by detecting invasive plants during times before bud burst or after senescence (Kimothi and Dasari, 2010). Even in forested conditions with persistent canopy cover, high spatial resolution imagery may help to detect populations of invasive grasses in canopy gaps. Perroy et al. (2017) found that detection of an invasive plant was possible in conditions with as little as 10% canopy openness. However, additional research is needed into cost-effective methods for detecting, mapping and monitoring invasive grasses across ecosystems and canopy conditions.

Identify potential tradeoffs of management actions and integrate overstory, woody fuel, fire, and weed management approaches. Management approaches will increasingly need to recognize current vulnerabilities to novel disturbances and tradeoffs associated with other ecological processes (Merschel et al., 2014; Stine et al., 2014; Seidl et al., 2016). It will be critical to gain a better understanding of the potential landscape-scale effects and tradeoffs of management practices such as hazardous fuel reduction in forests. While overstory management tradeoffs can be assessed and discussed in planning stages as a conceptual process, landscape simulation modeling can provide novel insights into how exotic grass invasion following overstory treatments may alter potential wildfire behavior, ecosystem services such as wildlife and livestock forage, and human exposure to wildfire. Such modeling and analysis can also help support decision making by explicitly demonstrating tradeoffs between different management actions and the potential for long-term loss of resource values due to increased invasion (e.g. Spies et al., 2017; Barros et al., 2019).

Modelling tradeoffs will require more accurate information and model parameters for invasive grasses, such as the quantification of grass fuel loads and their spatial arrangement across landscapes. Spatial fuels databases and accurate fuel maps can also be used in tactical wildfire situations, and for strategic planning by a variety of stakeholders and landowners. Over the past decade significant agency resources in the US and other countries have been devoted to collecting fuel information during field inventories and developing adequate fuel maps (Krasnow et al., 2009). However tools for predicting herbaceous fuel components are often quite limited (Reeves and Frid, 2016), and it is unclear if fire simulation models adequately include fuel dynamics associated with invasive grasses given their dynamic nature and high flammability that may not be strongly related to standing crop (Cardoso et al., 2018).

Going forward, it will be increasingly important to integrate invasive grass management into all aspects of forest resource management. For example, additional investment in treatments and protocols to reduce the introduction, abundance, and extent of invasive weeds may also be an effective way to lower fuels and decrease areas of fire spread associated with invasive grass populations. Additionally, locations of invasive grass populations could be explicitly incorporated into decisions about where on the landscape to conduct overstory manipulations. We are aware that such conversations and considerations are ongoing, although understanding the spatial distribution of invasive grass populations remains a critical challenge. If fuel treatments or replanting efforts introduce or spread invasive grasses, adequate funding for post-treatment invasive mitigation is also key to reducing the potential for unintended negative outcomes. Successful integration of weed, fuel and fire management, and forest restoration programs could result in treatments that are more likely to restore ecosystem services as well as treating fuels.

7. Conclusion

We propose that forests may be surprisingly more vulnerable to grass invasion than conventional wisdom might suggest, and climate change and wildfire may increase invasion risk for forests. However, knowledge is only now emerging about the extent to which these species could catalyze rapid and novel change and reduce resilience in forested ecosystems worldwide. Increasing evidence suggests that drier forests and woodlands may be "tipsy" already, vulnerable to climate and wildfire driven state changes and vegetation type conversion due to inherently unstable states between grass and tree dominated ecosystems. The effects of both climate change and a century of fire suppression and uncharacteristic fuel loads have ushered in an era of megafires with the potential to create large highly invadable early seral patches that may exacerbate ecosystem state changes. There is considerable risk that these state changes may be persistent or "sticky" due to exotic grass invasion, particularly if a destabilizing grass-fire cycle develops. The interactions between grass invasion, climate change, and wildfire and the increasing potential for grass-fire cycles are sufficient cause for concern for forest managers, but overstory management may represent a fourth critical factor in this potential perfect storm. Forest management actions designed to manipulate forest structure or alleviate threats related to wildfires almost exclusively focus on trees and woody fuel targets and treatments. However, these treatments can actually exacerbate invasive grass populations, increase invasion risk, and then substitute highly flammable and easily ignitable fine fuels for less ignitable woody fuels. We acknowledge that the evidence, examples, and models presented in this paper may not be relevant for all forest systems, particularly wetter and colder forests with reduced fire risk, or in less common circumstances where grass invasion increases fuel moisture and reduces fire spread.

As we continue forward in this era of novel and rapid ecological change, failure to fully recognize the importance of managing invasive grasses as an important threat to forest resilience may lead to increased exposure of forested ecosystems to these invaders, unintended consequences such as higher wildfire risk and severity, and more frequent or rapid conversion of forests into nonforest ecosystems. Mitigating this new perfect storm may be facilitated by greater recognition and increased communication regarding invasive grass threats in forests, primary research to develop species-specific treatment and mitigation options, reliable mapping and monitoring tools, explicit identification of fuels and invasive grass management tradeoffs, and more seamless integration of weed, fire, and overstory treatment approaches.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Panel 1: Ventenata dubia Invasion: A new perfect storm for interior forests of the US?

Ventenata dubia (ventenata) is a recently introduced Eurasian annual gras s (Fig. 5) that has been documented in eight western states (Fryer, 2017) and has expanded rapidly into grasslands and pasturelands, where its economic and ecological impacts are already becoming evident (Prather and Steele, 2009; Pavek et al., 2011). Introduced in the early 1950s near Spokane, Washington, ventenata was spreading at a rate of 1.2 million ha yr^{-1} in the Pacific Northwest by 2001 (Novak et al., 2015). This species is also invading shrublands, woodlands and forest mosaics across the Pacific Northwest (Noone et al., 2013; Averett et al., 2016; Pekin et al., 2016; Jones et al., 2018), raising alarms with forest and woodland managers who note that the species increase over the past decade has been dramatic (Fig. 6). The species is of concern on at least six national forests in the Pacific Northwest Region of Oregon and Washington based on our site visits and listening sessions, and was recently listed as a noxious weed in Oregon. Unpublished data from national forestlands in the Blue Mountains Ecoregion of eastern Oregon revealed that ventenata is widely disseminated across many forested areas and can be dominant in open and low canopy sites (up to about 40% overstory canopy cover).

Fig. 5. *Ventenata dubia* in a western juniper (*Juniperus occidentalis*) and sagebrush (*Artemesia* spp.) community. Photo credit: Michelle Day.

Fig. 6. Thousands of hectares of open and low overstory canopy cover areas in the Ochoco National Forest have been invaded with *Ventenata dubia* in central Oregon. Above: This dry, rocky (basalt derived), low biomass meadow or "scabland" burned in a wildfire in 2015, due to invasion prior to the fire according to local managers. Fire fighters reported that ventenata carried the wildfire across this historically pyroresistant area, creating unexpected wildfire behavior. Scattered juniper trees and sagebrush shrubs within the opening were killed. Below: Ponderosa pine stands at the edge of the scabland were also killed, reportedly due to fire fueled by the ventenata invasion in the area. This early seral plant community is now dominated by ventenata (and to a lesser extent *Bromus tectorum*), setting it up for a grass-fire cycle that could preclude the return to a forest condition. Photo credits: Claire Tortorelli.

Despite concern about ventenata in forested mosaics of the Northwest, documentation of the extent and spread of the species and research concerning abiotic and biotic drivers has just begun. Observations from fire fighters on the ground suggest the species may be promoting fire, although Fusco et al. (2019) note there is no literature suggesting that ventenata promotes fire. However, the spread of ventenata into relatively undisturbed historically sparsely vegetated and pyroresistant dry meadows is of increasing concern to land managers in the region (Figs. 6 and 7). These dry meadow sites historically had very low biomass and have been largely uninvaded despite being exposed for decades to other exotic grasses such as annual bromes. The invasion of these areas may allow fire to spread into the adjacent forests, leading to more frequent fires or larger, more potentially severe fires and broader landscape level changes. Ventenata has also been observed to spread into previously forested and closed canopy dominated areas after fire, highlighting the potential for the species to tip forested areas to annual grasslands and homogenize landscape structure (Fig. 6, bottom). The temporal persistence or stickiness of such states is largely unknown. Research to assess the extent of ventenata invasion in the Blue Mountains Ecoregion of Oregon, examine how the invasion has changed through time, and what environmental (climate, soil, light) and disturbance (fire and grazing) factors influence and/or exacerbate populations is currently underway (http://www.nwfirescience.org/ventenata).

Fig. 7. Uninvaded, low biomass, dry rocky meadows or "scablands" in the Blue Mountains Ecoregion of Oregon. These areas are at risk for invasion by ventenata. Historical plant cover in these areas is not well known, but these areas did not historically burn, and today given their low biomass and plant cover they would resist fire unless they become invaded. The area above already has a small population of ventenata encroaching and the area below is adjacent to propagule sources. Photo credits: Becky Kerns.

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