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Review paper

Cogongrass (*Imperata cylindrica*) invasions in the US: Mechanisms, impacts, and threats to biodiversity

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ABSTRACT

Invasions of non-native species can suppress biodiversity and alter ecosystem functions, but for many of the most widespread invasive species the mechanisms underlying their invasive success and effects on native species are poorly understood. Here we evaluated the peer-reviewed literature on causes and impacts of invasion by cogongrass (*Imperata cylindrica*), one of the most problematic invasive plant species in the southeast US. We assess what is known about why cogongrass is particularly invasive and how it affects native communities and ecosystems, review patterns in research methods employed, and provide a roadmap for future research on cogongrass. Although many studies have focused on the basic biology and management of cogongrass, we found surprisingly few (30) studies that have directly tested mechanisms or impacts of cogongrass invasions. The most commonly tested mechanisms, disturbance and allelopathy, were evaluated 4 and 12 times, respectively, and studies on invasion impacts were limited to five studies total: native plant diversity (2 studies), nitrogen cycling (2), decomposition (1), and fine fuel loads (1). Excluding laboratory studies on allelopathy, 75% (6/8) of impact studies used observational methods, raising questions about cause and effect. Given the paucity of studies on the ecology of cogongrass invasions, and the need to protect conservation areas from invasions, we urge that research efforts focus on: (1) environmental correlates of distribution and performance, (2) the role of propagule pressure in invasion success, (3) enemy release and post-introduction evolution as mechanisms of invasion, and (4) experimental tests of community and ecosystem impacts of invasions.

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1. Introduction

Ecologists generally recognize that invasive plants can alter the diversity and composition of ecological communities (Powell et al., 2013; Pyšek et al., 2012), and invasions are often considered one of the primary drivers of ecosystem change (Brooker, 2006; Ehrenfeld, 2010; Liao et al., 2008; Mack et al., 2000; Simberloff, 2011). However, for many invasive plants the mechanisms underlying their invasive success (Levine et al., 2003) and effects on plant populations and communities (Hulme et al., 2013) are poorly understood. Furthermore, understanding the impacts of invasions can be hindered by use of observational research methods that cannot disentangle cause and effect, raising questions about underlying drivers of invasion. For example, invasive species that appear to negatively impact native communities may instead benefit from anthropogenic disturbances that simultaneously inhibit native plants (Bauer, 2012; MacDougall and Turkington, 2005). Improving knowledge of what drives invasions of the most widespread and damaging species, and how they affect communities, ecosystems, and biodiversity, will inform invasion risk of non-native species and improve natural areas management and conservation strategies.

Cogongrass (*Imperata cylindrica*, (L.) P. Beauv., hereafter cogongrass), is a non-native, perennial C4 grass found in the southeastern US from Texas to Florida and as far north as Virginia (Fig. 1, USDA and NRCS, 2005). It is considered a primary threat to biodiversity and ecosystem functions (Brewer, 2008; Daneshgar and Jose, 2009a; MacDonald, 2004) and is predicted to spread north to Oklahoma and Tennessee, and east to coastal North Carolina, encroaching on numerous conservation areas (Fig. 1, Bradley et al., 2010). It is native to Asia and was accidentally introduced to Alabama in 1912 via packing materials and intentionally imported for forage in Texas, Mississippi, Alabama, and Florida during the 1920s (Dozier et al., 1998; Hubbard, 1944).

Cogongrass invasions can occur in diverse habitats from relatively undisturbed natural areas to pine plantations (Fig. 2(A)) and managed pastures (Dozier et al., 1998). There are a wide variety of possible explanations for the invasive success of cogongrass. For example, the ability of the species to establish and persist in highly variable habitats has been attributed to dense rhizome formation (Dozier et al., 1998; MacDonald, 2004), allelopathy (Cerdeira et al., 2012; Hagan et al., 2013b), high rates of reproduction through both seeds and rhizomes (Holly and Ervin, 2007), exceptional phenotypic plasticity (Patterson, 1980), and tolerance of diverse growing conditions including shade, drought, and poor soil quality (Bryson et al., 2010; Patterson, 1980). In addition, fire, cultivation, or other anthropogenic disturbances are also thought to promote cogongrass invasions (Fig. 2(B), Holzmueller and Jose, 2012; Lippincott, 2000).

The putative impacts of cogongrass invasions include community-level effects on native plant diversity and performance (Brewer, 2008) and ecosystem-level impacts on nutrient cycling (Daneshgar and Jose, 2009a), disturbance regimes (Platt and Gottschalk, 2001), and decomposition (Holly et al., 2009). Because cogongrass is a federally listed noxious weed (USDA and NRCS, 2005), and appears to spread rapidly and significantly impact communities (reviewed by MacDonald, 2004), establishing management strategies based on reliable data is a critical step toward conserving vulnerable habitats and native biodiversity. In addition, with a cost of $400 per hectare for a single herbicide application (Van Loan et al., 2002), an estimated 500 million invaded hectares worldwide (Dozier et al., 1998), and over 100,000 ha infested in Florida, Alabama, and Mississippi (Schmitz and Brown, 1994), significant economic resources are spent each year on the control and management of cogongrass. However, it is unclear why cogongrass appears to invade so frequently, which types of habitats are most susceptible to colonization, and how invasions affect native plant communities and ecosystems. Previous reviews have provided discussions of possible invasion mechanisms (Holzmueller and Jose, 2011) and biological characteristics and management options for cogongrass (Dozier et al., 1998; MacDonald, 2004), but no study has systematically reviewed the literature on the causes and effects of cogongrass invasions.

Here we compiled a comprehensive database of all publications from peer-reviewed journals that have addressed either mechanisms or impacts of cogongrass invasions. We identified the hypothesis or type of effect examined, and the research method (observational or experimental), spatial scale, and setting (natural area, common garden, greenhouse) of each study. A formal meta-analysis (e.g. Kettenring and Adams, 2011; van Hengstum et al., 2014; Vila et al., 2011) or data mining (e.g. Pyšek et al., 2012) was not possible due to the low number of studies identified. Finally, we outline the types of studies, such as field surveys or removal or addition experiments that should be used to evaluate the mechanisms and impacts of invasions, and discuss their advantages and disadvantages. Our overarching goals were to determine what is known about the mechanisms underlying the invasive success of cogongrass and its impacts on native systems, establish if predictions and management efforts are based on experimental evidence or observational studies, and provide a roadmap for future research.

2. Materials and methods

To compile our database on the mechanisms and impacts of cogongrass invasions, we searched the peer-reviewed literature using a combination of two predominant online search engines: ISI Web of Knowledge (http://wokinfo.com) and Google Scholar (http://scholar.google.com). We searched titles, abstracts, and keywords of articles using all possible

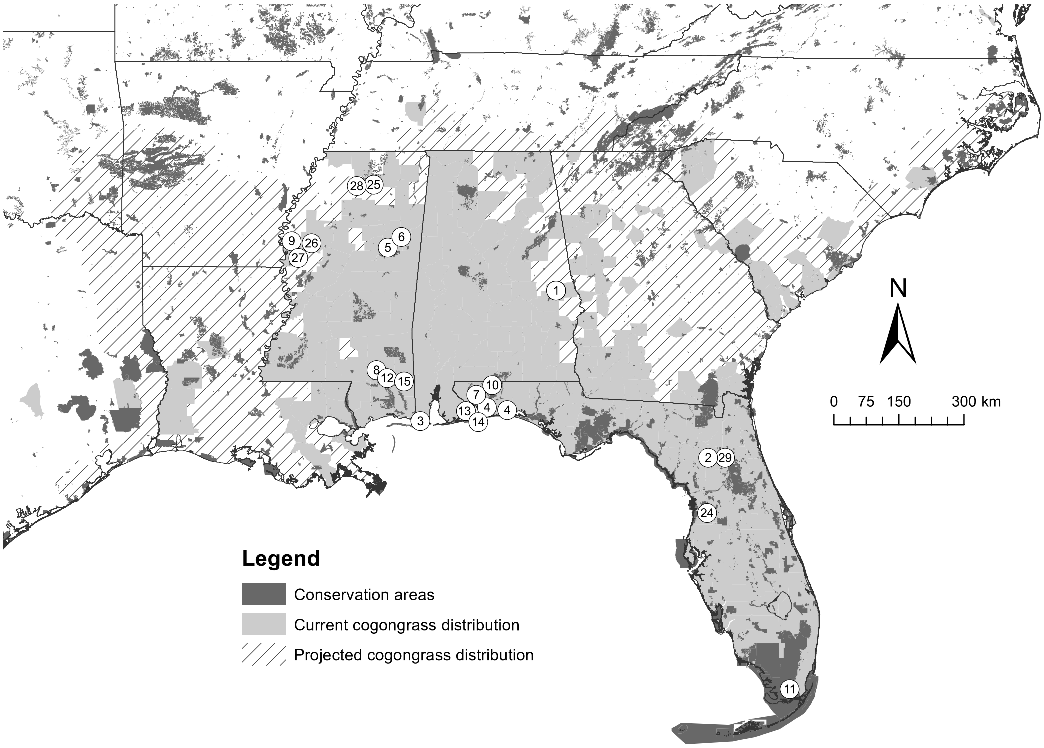

Fig. 1. Map displaying county level distribution of cogongrass in the US, projected distribution based on bioclimatic envelope modeling from Bradley et al. (2010), conservation areas, and locations for US studies. Numbers correspond to Study #'s presented in Table 1. Current distribution data obtained from EDDMapS (http://www.eddmaps.org).

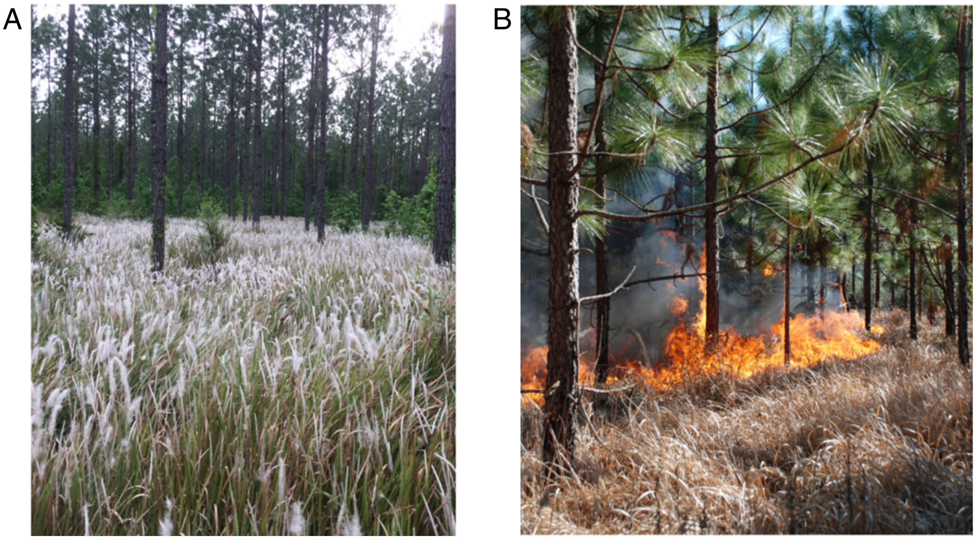

Fig. 2. An extensive cogongrass invasion flowering in Marion County, Florida (A) and a prescribed fire in an invaded area in Alabama (B). Photo credits: A. S. Luke Flory, B. Nancy Loewenstein.

combinations of the following words: *Imperata cylindrica*, cogongrass, mechanisms, impacts, and invasion (e.g. "*Imperata cylindrica* invasion", "cogongrass invasion mechanism", "cogongrass impacts", etc.). To identify additional studies that addressed mechanisms or impacts of cogongrass invasions, we then searched citations within articles and "searched forward" by looking for articles that had cited studies found in our original search. We conducted the searches in July and August 2013 and examined all papers found with the search engines up to that time.

Table 1
Summary of studies investigating mechanisms (M) and impacts (I) of cogongrass invasion. For location, GH = greenhouse, GC = growth chamber, NA = natural area, OM = outdoor microcosm, DA = disturbed area. Study # corresponds to the numbers in Fig. 1.

Study #	M/I	Hypothesis or impact	Evidence for M/I	Method	Scale	Location	Reference
1	M	Competition	Yes	exp	1.6 L, 1.0 m^2	GH, GC, NA	Wilcut et al. (1988)
2	M	Competition	Yes	exp	2.8 L	GH, GC, NA	Willard and Shilling (1990)
3	M	Disturbance	Yes	exp	0.8–78.5 m^2	NA	King and Grace (2000)
4	M	Biodiversity–invasibility	No	obs	4.0 m^2	NA	Collins et al. (2007)
5	M	Mechanical inhibition	No	obs	0.06 m^2	NA	Holly and Ervin (2006)
6	M	Propagule-pressure	No	exp	0.8–1.1 m^2	GH, GC	Holly and Ervin (2007)
7	M	Biodiversity–invasibility	No	exp	117 L	OM	Daneshgar and Jose (2009b)
8	M	Disturbance	No	obs	None reported	DA	Yager et al. (2009)
9	M	Ideal weed	Yes	obs	<1 L	NA	Bryson et al. (2010)
10	M	Disturbance	Yes	obs	84,000 ha	NA	Holzmueller and Jose (2012)
11	I	Fine fuel loads	Yes	obs	4.8 m^2	NA	Platt and Gottschalk (2001)
12	I	Native plant diversity	Yes	obs	0.5 m^2	NA	Brewer (2008)
13	I	Native plant diversity	Yes	obs	86.1 m^2	NA	Daneshgar et al. (2008)
14	I	N cycling	Yes	exp	86.1 m^2	NA	Daneshgar and Jose (2009a)
15	I	N & P cycling	No	obs	736 ha	NA	Hagan et al. (2013a)
16	I	Decomposition	Yes	exp	9.0 m^2	NA	Holly et al. (2009)
17	M & I	Allelopathy	Yes	exp	Unknown	Lab, GH	Eussen and Wirjahardja (1973)
18	M & I	Allelopathy	Yes	exp	Unknown	GH	Eussen et al. (1976)
19	M & I	Allelopathy	Yes	exp	Unknown	Lab	Eussen and Soerjani (1975)
20	M & I	Allelopathy	Yes	exp	Unknown	Lab	Eussen (1977)
21	M & I	Allelopathy	Yes	exp	Unknown	GH	Eussen (1978)
22	M & I	Allelopathy	Yes	exp	Unknown	Lab	Inderjit and Dakshini (1991)
23	M & I	Allelopathy	Yes	exp	0.05 m^3	GH	Tominaga and Watanabe (1997)
24	M & I	Allelopathy	Yes	exp	0.02 m^2	Lab	Casini et al. (1998)
25	M & I	Disturbance	Yes	obs	1225–5075 m^2	NA	Lippincott (2000)
26	M & I	Superior competitor	Yes	obs	0.3 m^2	NA	Brewer and Cralle (2003)
27	M & I	Allelopathy	Yes	exp	0.9 m^2	GH	Koger et al. (2004)
28	M & I	Allelopathy	Yes	exp	0.6 m^2	GH	Koger and Bryson (2009)
29	M & I	Allelopathy	No	exp	None reported	Lab	Cerdeira et al. (2012)
30	M & I	Allelopathy	Yes	exp	0.2 L	GH	Hagan et al. (2013b)

There have been many studies that have examined the specific biological characteristics (e.g., morphology), economic impacts, management, and pasture/crop production effects of cogongrass, but we did not include those studies in our database because we were specifically focused on what is known about ecological interactions of invasions in natural areas. However, we do use such studies in our discussion of mechanisms and impacts below. Studies that we included in our database were classified by whether they tested mechanisms or impacts of invasions, the specific hypothesis or impact tested, whether there was evidence to support the mechanism or impact, and if the methods employed were experimental or observational. We also determined the spatial scale and setting (e.g., greenhouse, natural area, laboratory) of each study.

3. Results

A search for the term "*Imperata cylindrica*" in ISI Web of Knowledge (http://wokinfo.com) yielded 2303 results (search conducted in July 2013) but only 30 publications focused specifically on invasion mechanisms or impacts and applied their findings to understanding ecological interactions (Table 1). Many studies have investigated management approaches for cogongrass invasions (1054), such as herbicide trials (477), as well as evaluation of basic biological characteristics such as growth and reproduction, environmental tolerance, or distribution. Of the studies that we included in our database, 10 described potential mechanisms of invasion, six examined community or ecosystem impacts, and 14 investigated both mechanisms and impacts (Table 1). Experimental settings included laboratories, greenhouses and growth chambers, and natural and disturbed field sites with spatial scales ranging from 0.02 m^2 to 84,000 ha (Table 1).

Overall, allelopathy and disturbance were the most often tested hypotheses for invasion mechanisms and impacts, with 12 studies focused on allelopathy and four that investigated the effect of disturbance on establishment (Table 1). All allelopathy studies were either greenhouse or laboratory experiments, while the disturbance studies were conducted in unmanaged natural habitats. Of the 12 studies that investigated allelopathy, 11 used either pulverized tissues or leachate and only one utilized soils from an established cogongrass population. Most allelopathy trials were conducted on crop species (e.g., cucumber, tomato, rice), and all but one study (Cerdeira et al., 2012) reported negative effects on germination and/or growth rates of test species.

Disturbance was the second most studied mechanism to explain cogongrass invasions. We found multiple studies suggesting that cogongrass initially establishes in highly disturbed habitats, such as along trails, roadsides, and riparian areas (e.g. Willard et al., 1990; Yager et al., 2009). Fire has also been found to increase the abundance and dominance of cogongrass within native communities. For example, Lippincott (2000) found higher fuel loads, greater fire intensities, and increased tree mortality, and hypothesized that fire-invasion interactions could result in greater dominance of cogongrass. Holzmueller and Jose (2012) evaluated the history of sites following hurricanes and reported that invasions were more widespread in areas that were burned more frequently or had been salvage logged. However, there is also evidence that cogongrass can thrive in relatively undisturbed habitats (King and Grace, 2000). Overall, although disturbance has been associated with the establishment and spread of cogongrass, there is a distinct lack of experimental evidence that quantifies the role of disturbance in invasions.

Our search also identified eight studies that focused on how competition might influence the invasion success of cogongrass and impacts on native biodiversity. In experimental trials, cogongrass was shown to out-compete and displace bahiagrass (*Paspalum notatum*) seedlings, but was not able to colonize established bahiagrass stands (Willard and Shilling, 1990). Additionally, it has been demonstrated that cogongrass inhibits bermudagrass (*Cynodon dactylon*) growth, but was less competitive than Johnsongrass (*Sorghum halepense*) (Wilcut et al., 1988). Competition studies utilized a combination of greenhouse, growth chamber, and natural areas settings (Table 1). In observational studies in forest systems, cogongrass invasion has been correlated with significant reductions in light levels, decreased native plant diversity, and reduced productivity and growth of native pine seedlings (Brewer, 2008; Daneshgar et al., 2008). Fertilization studies also suggest that cogongrass may outcompete native species for both phosphorous and nitrogen (Brewer and Cralle, 2003; Daneshgar and Jose, 2009a). Finally, two studies (Collins et al., 2007; Daneshgar and Jose, 2009b) have specifically evaluated the ability of diverse native plant communities to resist invasion by cogongrass (i.e., the Biodiversity–Invasibility Hypothesis Elton, 1958; Kennedy et al., 2002; Levine, 2000), with both studies finding that native plant diversity did not inhibit cogongrass establishment success or the rate of spread. However, Daneshgar and Jose (2009b) found that *Andropogon virginicus* may have higher resistance to cogongrass invasion than other species, suggesting that species composition could be an important factor in limiting invasion success.

4. Discussion

4.1. Current trends in cogongrass literature

Although there has been an abundance of research on the biological characteristics and management of cogongrass (reviewed by Dozier et al., 1998; MacDonald, 2004), we found surprisingly few studies that directly tested mechanisms or impacts of cogongrass invasions. Disturbance and allelopathy were the most often tested mechanisms, and while disturbance appears to enhance cogongrass spread, considerable uncertainty remains regarding the relative importance of allelopathy due to limited evidence of below-ground chemical transfer and a lack of trials on native plant species. Observational studies have suggested that cogongrass invasions impact native plant diversity and fine fuel loads (Brewer, 2008; Platt and Gottschalk, 2001), and experimental evidence indicates that cogongrass can alter nitrogen cycling and decomposition rates (Daneshgar and Jose, 2009a; Hagan et al., 2013a; Holly et al., 2009). However, we found no studies on how cogongrass invasions impact arthropod diversity, soil microbial communities, carbon cycling, or hydrology, which are all possible effects of plant invasions (Powell et al., 2013; Pyšek et al., 2012; van Hengstum et al., 2014). Outside of laboratory studies on allelopathy, most of the remaining studies we reviewed (10/17 overall, 4/6 impact studies) used observational methods. Although observational studies can provide broad correlative patterns on characteristics of invaded areas, it is often difficult to discern whether the observed changes in the native communities were actually due to the cogongrass invasion. For example, anthropogenic disturbances such as fire or cultivation may both inhibit native species and promote invasions (Hill et al., 2005; Lake and Leishman, 2004).

Multiple studies on the potential allelopathic effects of cogongrass have demonstrated negative impacts on the performance of test species, but it is important to distinguish between allelopathy and phytotoxicity. Phytotoxicity refers to chemicals from one plant affecting the growth and germination of another (e.g., through leaf litter), while allelopathy is the effect of a chemical(s) that is released into the soil by one plant and absorbed by another (Romeo, 2000). This distinction is critical because it is not known whether cogongrass litter negatively impacts native plant species performance, or whether chemical doses that were applied in studies utilizing pulverized tissues or leachates were ecologically realistic. Given these definitions, only four studies in our database met the criteria for allelopathy. Of these, only Hagan et al. (2013b) found a reduction in performance of co-occurring natives (wiregrass, *Aristida stricta*, and slash pine, *Pinus elliottii*). Therefore, although "allelopathy" is the most common invasion mechanism addressed in the cogongrass literature, additional studies aimed at evaluating soil-mediated inhibition of native species under realistic natural conditions are needed to determine if allelopathy is driving invasion success in ecologically relevant settings.

There is evidence that disturbance generally facilitates cogongrass invasion but it is less clear how various types of disturbance (e.g., fire, flooding, road grading) may differentially affect establishment (Burke and Grime, 1996; Maron et al., 2013) or whether disturbance and environmental factors (e.g., light, soil moisture) might interact to alter establishment success (Davis and Pelsor, 2001; Parendes and Jones, 2000). Disturbed areas may also simply be the sites with the highest introduction rates (i.e., propagule pressure Colautti et al., 2006; Levine, 2000; Von Holle and Simberloff, 2005), and it is unclear if sufficient propagule pressure can overwhelm environmental resistance (e.g., shade) in undisturbed or less-disturbed habitats (e.g. Von Holle and Simberloff, 2005).

Overall, our synthesis of the peer-reviewed literature has shown that allelopathy and disturbance may be contributing to invasion success but has also revealed multiple areas where additional research on cogongrass invasions is needed. In the following sections we outline our recommendations for research on patterns of invasions, potential mechanisms, and invasion impacts, including suggestions for effective experimental methodologies.

4.2. Environmental correlates of distribution and abundance

Despite the rapid expansion of cogongrass throughout the southeastern US and its ability to colonize a wide range of habitats, we are not aware of any study that has comprehensively quantified the ecological requirements of cogongrass within the invasive range. While studies have provided information on the basic environmental conditions associated with cogongrass invasions, their limited scope does not permit us to quantify patterns of performance across variable habitats. Bryson et al. (2010) showed that cogongrass invasions are able to persist in a wide variety of soil types in Mississippi, and Brewer and Cralle (2003) found that phosphorus enriched sites in Mississippi were less susceptible to invasion, but it is unclear if these findings can be extrapolated to invasions in other habitats or conditions. In a related study, Bradley et al. (2010) used bioclimatic envelope modeling to identify susceptible geographic regions, but the large scale of the study plots (36 km^2) required the use of data from environmental monitoring stations rather than the direct measurement of environmental parameters (e.g., light or soil moisture availability, soil characteristics) at individual invasion sites. Furthermore, the use of second party abundance estimates to determine regional distributions of cogongrass makes it difficult to relate cogongrass performance (e.g., biomass, density, height) to environmental variables. A comprehensive investigation into the distribution and performance of invasions across a wide range of environmental conditions and habitats would help identify abiotic or biotic factors that influence cogongrass abundance, inform future research, and aid in the development of models to predict invasions and identify vulnerable habitats (e.g. Cole and Weltzin, 2004). We recommend a landscape-level survey of populations throughout the US invasive range with objectives to: (1) characterize invaded habitats in terms of topography, native plant composition, land use history, management history, soil characteristics, and light and moisture availability, and (2) quantify attributes of invasive populations with regard to invasion area, tiller height, density, above and below ground biomass, and, if possible, reproduction.

4.3. Propagule pressure and establishment

Propagule pressure is thought to be a primary factor regulating the establishment of non-native species (Levine, 2000; Von Holle and Simberloff, 2005) and may determine habitat susceptibility to invasion (Colautti et al., 2006). For cogongrass, a single plant can produce as many as 3000 seeds (Dozier et al., 1998; MacDonald, 2004) and germination rates may be as high as 98% (Schilling et al., 1997). There is also evidence that relatively small numbers of cogongrass seed (e.g., 10 seeds/12 cm diameter pots) can result in establishment (Holly and Ervin, 2007). Cogongrass also produces prolific rhizomes and rhizome fragments as small as 0.1 g may produce new plants (Ayeni and Duke, 1985). However, there has been only one study (Holly and Ervin, 2007) that experimentally manipulated propagule pressure to examine invasion success, and they focused exclusively on seed propagules. Therefore, while we have ample information on general reproductive biology of the species, more information is needed on how environmental and habitat conditions and disturbance might interact with propagule pressure to determine invasion success. For example, the amount of propagule pressure needed to establish a viable population in natural settings may depend on light, soil moisture, or nutrient availability. Moreover, studies are needed to investigate propagule pressure with rhizome fragments, which is a frequent means of unintentional introduction (e.g., fill dirt or machinery) throughout the invaded range (Willard et al., 1990). Cogongrass must outcross to produce viable seed, thus studies on propagule pressure with rhizomes are needed in areas such as Florida where few if any seeds are produced (MacDonald, 2004). Although early studies suggested that the size of the rhizome fragment affected initial emergence (Ayeni and Duke, 1985), the studies were conducted in greenhouses where ideal environmental conditions may have greatly enhanced the success of smaller rhizome segments. Since larger rhizome fragments would contain more nodes and carbon reserves to allocate toward shoot growth, it is plausible that larger propagules may have a greater likelihood of successful establishment, particularly in low-resource environments. Therefore, both propagule size (number of seeds or rhizomes introduced) and quality (i.e., size) could affect the establishment and spread of new populations (Lockwood et al., 2009; Simberloff, 2009), and determining their role in invasions should be a research priority.

Multiple experimental designs could be used to test propagule pressure effects for cogongrass invasions. While the most ecologically relevant means is through propagule addition studies, there are often ethical concerns with the introduction of non-native material into established native plant communities. Pot or mesocosm studies, introductions into "quarantined" semi-natural areas, and the use of common gardens can effectively limit these concerns. Common garden experiments in particular would allow for the controlled introduction of propagules into experimental communities, providing a more realistic view of the interaction between invasion pressure and native plant species without risking invasions into natural areas. However, to conduct such studies the appropriate state and federal permits must be obtained, protocols must be in place to monitor and treat escaped individuals, and all experimental plants would need to be removed at the conclusion of the study. Finally, to avoid introducing non-native species into novel areas, we recommend conducting experimental introductions at sites with existing invasions.

4.4. Enemy release

One of the most commonly cited hypotheses to explain non-native plant invasions is the enemy release hypothesis (ERH) (e.g. Colautti et al., 2004; Liu and Stiling, 2006). The ERH states that species introduced to a new range may experience a decrease in top-down regulation by specialist herbivores and other natural enemies, resulting in an increase in distribution and abundance (Colautti et al., 2004; Keane and Crawley, 2002; Mitchell et al., 2006). Early reports identified a variety of insects and pathogens associated with cogongrass in the native range (Mangoendihardjo, 1980; Soerjani, 1970; Syed, 1970) but the extent to which they control or limit population growth is not clear. Quantifying herbivory effects within native populations has been further complicated by a lack of agreement on clear boundaries for the native range (Holzmueller and Jose, 2011). In the US, multiple insects and fungi have been identified on invasive cogongrass populations (Van Loan et al., 2002), however none have been reported to cause substantial damage (Holzmueller and Jose, 2011) and it is not known if the limited damaged is due to generalist or specialist herbivores. To our knowledge, a comprehensive survey of herbivore regulation in either the native or invasive range has not been conducted but would represent a critical first step in evaluating the role of ERH in cogongrass invasion success.

Evaluating the relevance of complex ecological theories, including the ERH, is often problematic (Heger and Jeschke, 2014). The ERH is particularly difficult to examine due to complications associated with cross-continental experiments and obtaining samples from the invasive species native range (Keane and Crawley, 2002). However, the specific assumptions of the hypothesis can be more readily evaluated (Heger and Jeschke, 2014). For example, surveys of invasive cogongrass populations could determine if specialist enemies are absent or limited in the US or if cogongrass receives less damage than competing resident species (e.g. Halbritter et al., 2012; Lieurance and Cipollini, 2013). Furthermore, to inform biocontrol development efforts, it is important to know if invasive cogongrass populations experience less herbivore or pathogen damage than native range populations and if reduced damage significantly alters competitive interactions.

4.5. Evolution

Evolution of cogongrass populations may also promote invasions. For example, Japanese knotweed (*Fallopia japonica*) has hybridized with giant knotweed (*Fallopia sachalinensis*) (Bailey et al., 2009), greatly increasing its invasiveness, and purple loosestrife (*Lithrum salicaria*) (Colautti and Barrett, 2013) and stiltgrass (*Microstegium vimineum*) (Novy et al., 2013) have rapidly evolved across latitudinal gradients. The northward spread of cogongrass (USDA and NRCS, 2005) could be similarly influenced by evolutionary adaptations associated with cold tolerance. Lucardi et al. (2014) evaluated interspecific hybridization of cogongrass with Brazilian sandtail (*Imperata brasiliensis*) using amplified fragment length polymorphisms (AFLP) but found no genetic differentiation or evidence of hybridization. Thus, they concluded it is unlikely that cogongrass expansion in Florida is due to increased fitness through hybridization. However, analysis of neutral markers (e.g., AFLP) may not reveal genetic changes important for invasion success. Thus, a more general understanding of the population genetic structure of cogongrass, in particular determining whether introduced populations are genetically different than native range populations, is needed. Common garden (Colautti and Barrett, 2013), and preferably cross-continental biogeographic comparisons (Adams et al., 2009; Hierro et al., 2005), of invasive and native range populations could determine if there has been selection for introduced cogongrass populations with increased competitive ability or greater environmental tolerance, and invasion success.

4.6. Biodiversity impacts of invasions

Despite the widespread belief that cogongrass invasions threaten native plant diversity we found only two studies that documented the impacts of cogongrass invasion on native systems, and both used observational methods. Daneshgar et al. (2008) planted 1-year old pine seedlings alone, in naturally occurring stands of predominantly native species, and in areas invaded by cogongrass, and found that seedlings were significantly less productive in invaded areas. However, it is unclear if reductions in tree performance were due to the cogongrass invasion or poor environmental conditions in the invaded area independent of the invasion. Brewer (2008) detailed post-invasion changes in species composition during an invasion over a five-year period in longleaf savannas in Mississippi and concluded that native herbaceous plants were less abundant and had lower diversity after invasion. By following an advancing invasion front over time, it was concluded that the invasion caused declines in native species abundance, but again it is difficult to discern whether cogongrass is the driver of the changing plant communities. Instead, it might be possible that shifting environmental parameters (e.g., disturbance or soil chemistry) negatively impacted native species and promoted cogongrass spread. While both studies suggested that cogongrass was suppressing native plant abundance and performance, experimental studies are needed to confirm that changes in native communities can be attributed to the invasion rather than confounding factors. In addition, given the ability of cogongrass to thrive in various habitats across the southeastern US, including conservation areas, additional studies in other habitats and geographic locations are needed.

Coupling field surveys of invaded and uninvaded habitats with experimental removal or addition studies (e.g. Hagan et al., 2013a) might provide the most powerful and reliable test of invasion impacts (Alvarez and Cushman, 2002). Field surveys are informative because they quantify differences in invaded and uninvaded habitats and incorporate the environmental heterogeneity of diverse sites across broad landscapes. However, experiments that include plots where invasions are removed, plots with the invasion left intact, and nearby uninvaded plots with similar environmental conditions can be used to infer both the impacts of the invasion and also to measure any legacy effects of the invasion (Marchante et al., 2009). Ideally, field removal studies would be conducted across environmental gradients so as to gauge the legacy effects and community and ecosystem responses among variable habitat conditions, and over relatively long time frames (Kettenring and Adams, 2011). Separately, common garden and greenhouse introduction studies may be logistically more tractable and provide more precise and direct measures of impacts (Flory and Clay, 2010; Simao et al., 2010), but lack some of the realism of field studies. Clearly, a variety of research approaches must be employed in order to understand the full range of cogongrass impacts on communities and ecosystem processes.

5. Conclusions and research priorities

While our search identified a large body of literature on the basic biology and management of cogongrass, we found very little peer-reviewed information on the mechanisms driving invasions and their impacts on native communities and ecosystems. Given the large amounts of time and funds spent on invasive plant management, and the relative paucity of studies that have examined causes of invasions (Table 1, Fig. 1), we urge that future research efforts be focused on the following priorities:

- A landscape-level survey of invasive populations throughout the introduced range to relate the density, distribution, and performance of invasive populations to environmental characteristics.
- Experimental studies on the roles of propagule size and quality in invasion success and seed and rhizome dispersal into various habitats.
- A survey of specialist enemies (both herbivores and pathogens) and damage on invasive and co-occurring native species, and the relative amount of damage on populations in the native and introduced ranges.
- Studies to determine if introduced populations are genetically different than native range populations and whether evolutionary changes in introduced populations have contributed to increased performance and invasion success.
- Addition and removal experiments to more explicitly quantify the impacts of invasions on native communities and ecosystems, including alterations in plant, animal, and arthropod diversity, soil microbial communities, hydrology, fire regimes, and nutrient and carbon cycling processes.

In summation, while it is widely recognized that cogongrass invasions are problematic, the dearth of information on invasion mechanisms and impacts on native systems may be hampering management efforts and limiting policy development. Identifying the mechanisms and impacts associated with cogongrass and other invasive plant species can aid in predicting vulnerable habitats and rates of spread, provide more reliable data for effective management, and may help to prevent future introductions of ecologically similar species.

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