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Invasive grass fuel loads suppress native species by increasing fire intensity and soil heating

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Abstract

1. Non-native invasive grasses are driving intense fires across the globe but the impacts of native versus invader-fuelled fires on community assemblages are poorly understood. By increasing fire intensity, grass invasions might increase belowground mortality of heat-sensitive seeds and buds, thereby shifting community composition.
2. We compared fuel loads in native and non-native invasive (cogongrass, *Imperata cylindrica*) plant-dominated areas of pine savannas in Florida. Then, we conducted a field experiment to examine how fuel loads and native and invasive fuel types affected soil heating and seedling emergence or resprouting of native and invasive plant species.
3. Average fuel loads in invaded communities were 152% greater than that in native communities. Soil heating, including heating duration >60°C, maximum temperature and heat flux >60°C, increased, and seedling emergence and resprouting decreased with greater fuel loads; these relationships were similar across the overlapping range of native and invasive fuel loads. However, longer durations of soil heating at the higher average fuel loads of invaded communities resulted in 23% lower predicted probability of seedling emergence compared to average fuel loads of native communities.
4. Invasive cogongrass resprouting was not affected by fuel loads, indicating that cogongrass tolerates the intense fires it generates. In contrast, seedling emergence and resprouting of most other species was reduced by greater fuel loads.
5. *Synthesis and applications*. By increasing fuel loading and soil heating, grass invasions may alter post-fire community assemblages and facilitate invasive grass dominance at the expense of native species via an invasion-fire cycle. Fuel loads can be used to predict soil heating duration and depth, and these data, combined with information on species tolerances to heating, can be used to forecast the impacts of invasions on post-fire community composition. To maintain fire regimes that promote native communities and resist invader dominance, it is critical to manage invasive species that increase fuel loads.

KEYWORDS
fuel loads, grass-fire cycle, *Imperata cylindrica*, invasive species, pine savanna, soil heating

1 | INTRODUCTION

Non-native naturalized invasive (sensu Richardson et al., 2000) grasses are driving changes in fire regimes across the globe by altering flammability, fuel structure and fuel loading (Brooks et al., 2004). The grass-fire cycle hypothesis postulates that changes in fire regimes induced by invasive grasses alter the community composition and facilitate the dominance and spread of the invasive species (Brooks, 2008; D'Antonio & Vitousek, 1992). Invader-driven changes in fire regimes can negatively affect native species via reduced post-fire regeneration if fires are more frequent (Balch et al., 2013; Grigulis et al., 2005) or more severe and cause greater native species mortality (Flory et al., 2015; Miller et al., 2010). Fire has clear above-ground effects of reducing canopy and understorey vegetation cover (Miller et al., 2010; Setterfield et al., 2010), but it is less clear how invader-fuelled fires affect the below-ground seed and bud banks. While fire enhances the germination of some species (Auld & O'Connel, 1991; Bradstock & Auld, 1995; Williams et al., 2004), intense fires can reduce seedling emergence and prevent resprouting (Auld, 1986; Choczynska & Johnson, 2009; Lee, 2004; Wright & Clarke, 2007).

Many plant species in pyrogenic communities have traits that make them fire tolerant (Lamont et al., 2011; Pellegrini et al., 2017) and soil can insulate seeds and buds from heat (Hartford & Frandsen, 1992). Below-ground, buds may contain thick sheaths that allow them to survive and resprout post-fire (Clarke et al., 2013). While hard seed coats may protect seeds from heating (Wiggers et al., 2017), they may also depend on fire to facilitate germination (Keeley & Fotheringham, 2000). Thus, it is unclear whether greater fire intensity due to grass invasions affects seedling emergence and resprouting in pyrogenic ecosystems sufficiently to establish a grass-fire cycle. Fundamentally, the invader must tolerate the fire temperatures better than native species to become more dominant.

Prescribed fire is a crucial management tool for promoting and maintaining desirable species while reducing fuel hazards to prevent wildfires (Brennan & Keeley, 2017; McIver et al., 2013). Because invasive plants can affect prescribed fire intensity, their presence may complicate management by affecting the response of native vegetation to fire. Quantifying the effects of invasive grass fuels on soil heating and seedling emergence and resprouting of native and invasive species could help managers predict fire effects on plant colonization and regeneration (Dickinson & Ryan, 2010) and assist in setting priorities for invasive species management. Such information could be used to determine when prescribed fires can be applied to meet management goals or if invader removal is necessary before prescribed fires are implemented (Zouhar et al., 2008).

Here, we used longleaf pine *Pinus palustris*-dominated savanna communities in Florida, USA as a model system to test the relationship between fuel load (amount) and fuel type (native vs. invasive) on soil heating and seedling emergence or resprouting of native and invasive species. Invasive species are defined here as naturalized non-native species that spread in natural habitats (Richardson et al., 2000). While pine savanna communities are adapted to frequent, low-intensity fires, invasions by the perennial rhizomatous cogongrass *Imperata cylindrica* can increase fuel loading and continuity (Platt & Gottschalk, 2001), and produce more intense fires to those in native vegetation (Lippincott, 2000). Many savanna species (e.g. *Aristida* spp., *Andropogon* spp., *Pityopsis graminifolia*, *Quercus* spp.) are fire adapted and resprout readily following low-intensity fires (Menges & Kohfeldt, 1995), but they may not tolerate more intense invader-fuelled fires that increase soil heating. Using small-scale experimental fires, we tested the hypotheses that (a) greater fuel loads in invaded than native communities result in greater soil heating during fires and (b) greater fuel loads reduce post-fire seedling emergence and resprouting of native and invasive species, except for the invader producing the high fuel loads.

2 | MATERIALS AND METHODS

2.1 | Study system

Longleaf pine savanna understorey communities in Florida are composed of bunchgrasses (e.g. *Aristida stricta*, *Andropogon virginicus* and *Schizachyrium scoparium*), diverse forbs (e.g. *P. graminifolia*, *Liatris* spp.) and woody species (e.g. *Quercus laevis*, *Licania michauxii*) (Myers, 1985; Rodgers & Provencher, 1999). Soils are sandy, well-drained and contain little organic matter. Fire regimes are characterized by frequent, patchy low-intensity fires (Myers, 1990) that limit fuel accumulation.

Cogongrass is native to Asia and invasive throughout the Southeast USA, including more than 500,000 ha in Florida, especially around disturbed sites (e.g. roadsides, fire-break lines; MacDonald, 2004). It is considered a pyrogenic species (Holm et al., 1977) that principally propagates vegetatively by rhizomes (Dozier et al., 1998). Cogongrass spreads rapidly and threatens native communities by suppressing tree seedling growth (NeSmith et al., 2018), reducing community diversity, altering community composition (Fahey et al., 2018) and reducing longleaf pine survival (Alba et al., 2019).

2.2 | Fuel load measurements

To compare fuel loads in native and cogongrass-invaded locations, we sampled fine fuel loads in six native-dominated pine savannas, eight cogongrass-dominated pine savannas and two cogongrass-dominated pine plantations (see Table S1 and Figure S1). Due to cogongrass management, we could not always collect data from invaded sites paired with nearby native-dominated sites. To capture the smaller scale variation of litter and standing fuels within invaded and native communities, samples within communities were treated as replicates. We collected 77 samples from the six native locations and 40 samples from the 10 invaded locations (Table S1). Fine fuels (1-hr fuels, 0–6.4 mm diameter) were collected from 25 cm × 25 cm quadrats and separated into standing biomass and litter. Fresh fuels were weighed in the field and then dried to constant mass to determine dry weights and moisture contents.

2.3 | Seedling emergence and resprouting experiment

We established a field experiment in April 2019 at the Biven Arms Research Site in Gainesville, Florida (29.629982 N, −82.353814 W) to test the effects of fuel load (amount) and fuel type (native vs. invasive) on seedling emergence or resprouting of seven native and five non-native invasive plant species (Table S2). Native and invasive species were selected based on their commonness in Florida pine savannas and availability. Forty 1.5 m × 1.5 m plots were established in a fallow field and the top 10 cm of soil in each plot was replaced with a 50:50 mix of seed-free topsoil and sand. The location of each species was randomized across 16 subplots within the inner square metre of each plot, leaving an unplanted 0.5 m buffer surrounding the planted area. Seeds were sown the day before experimental fires at soil depths recommended by seed distributors (within top 1 cm of soil, Table S2). Two species, *A. stricta* and *P. graminifolia*, were planted as plugs (i.e. seedlings grown in plastic tubes) 2.5 weeks before the experimental fires (Southern Habitats, LLC) because these species often resprout from below-ground buds after fires. Cogongrass rhizome fragments, each with three nodes (Estrada et al., 2016), were planted the day before fires. The number of seeds sown ranged from 13 to 40 seeds for species with larger seeds and 175 to 350 seeds for species with smaller seeds (Table S2). All seeds were scarified and stratified according to literature and distributor recommendations to maximize the potential that seeds would germinate (Table S2). We scarified the seeds because our goal was to evaluate the effects of soil heating on seedling emergence given ideal seed germination conditions.

2.4 | Experimental fires

Experimental fires were conducted over 3 days in May 2019. Plots were randomly assigned fuel treatments of native, invasive or unburned controls. Six unburned controls had no fuels and were used to determine baseline seedling emergence and resprouting of species. The above-ground biomass of *A. stricta* and *P. graminifolia* plugs was clipped at ground level in each control plot. Each native (n = 17) and invasive (n = 17) fuel plot was assigned a unique fuel load within the ranges of fuel loads observed at the native and invaded sites. To test for effects of native and invasive fuel type on soil heating, we increased the overlap of fuel loads between fuel types by including native fuel loads that exceeded the maximum we observed in native sites (i.e. 980 g/m^2; Figure 1). Experimental native fuel loads ranged from 100 to 1,695 g/m^2 and varied by increments of 100 g/m^2. Invasive fuel loads ranged from 63 to 2,510 g/m^2 and starting at 157 g/m^2 increased by increments of 157 g/m^2.

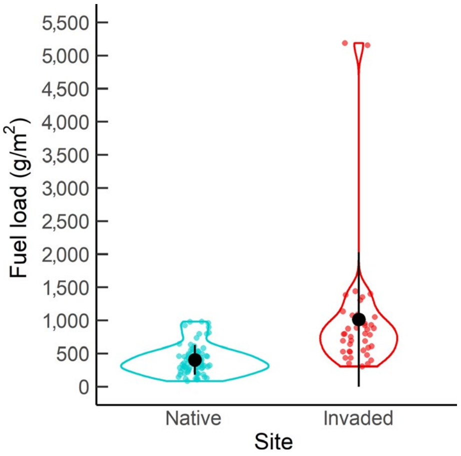

FIGURE 1 Violin plots (mean ± *SD*) of dry fuel loads showing average fuel loads 152% greater in invaded than native sites. Points show raw data

To simulate the observed fuel composition, invasive fuels were composed of 50% cogongrass litter and 50% standing live cogongrass, whereas native fuels were composed of 33% live standing fuels (50% *A. stricta* and 50% *A. virginicus*, by fresh weight) and 66% longleaf pine needle litter. Most fuels at field sites were herbaceous 1-hr fuels and invaded locations were dominated by cogongrass (woody fuels were infrequently observed), so we simulated field fuel conditions using only 1-hr fuels. The average moisture content of fuels used in the experimental fires was 37% for invasive fuels (65.5% ± *SE* 0.5 for live standing fuels and 9% ± *SE* 0.2 for litter fuels) and 17% for native fuels (25.4% ± *SE* 1.6 for live standing fuels and 12.6% ± *SE* 0.3 for litter fuels), meaning that native fuels used in the experiment were drier than those observed in field sites. There was no difference in fuel moisture between invaded and native sites (33% ± *SE* 1.31, $n = 40$ vs. 32.5% ± *SE* 0.88; $n = 77$; $p = 0.77$, $t = 0.29$).

Cogongrass and pine litter were collected 1 week prior to burns and standing biomass of native and invasive fuels were collected in the field after 3 days of no rain and 2 days before burns to approximate field fuel conditions. To simulate natural fuel structures, a standing metal grid (Dillon et al., 2021) was used to vertically arrange fuels within the central 1-m^2 area of each plot. Head fires were ignited with a drip torch with a 50:50 mix of gasoline and diesel fuel. Air temperature, relative humidity and wind speed were also recorded (Kestrel Meters).

To measure relative soil heating across a depth gradient, two 100-cm long type-K model TP875 braided steel insulated wire thermocouples (Extech Instruments) with a 2-mm bead tip were placed in each plot at 0 cm (soil surface), and 1, 2 and 3 cm below the surface. Thermocouples were attached to HOBO UX100-014M and HOBO U12 data loggers (Onset Computer Corporation) set to record temperature at 1-s intervals. While the temperature tolerances of seeds and buds of different species vary, 60°C is the most cited temperature threshold for plant cell death (Alexandrov, 1964). Our goal was not to test the specific temperature thresholds of each species but to evaluate the general response of species to fires across a range of fuel loads. Thus, we used 60°C as a threshold temperature to assess heating effects on seeds and buds as part of our measure of fire intensity.

Measures of soil heating included heating duration above 60°C (seconds), maximum temperature (°C) and heat flux (s · °C), and were calculated individually for each thermocouple. We calculated heat flux at each depth as the integrated area under the time–temperature curve above 60°C; heat flux values are therefore the summed products of time (seconds) and temperature (°C above 60°C) over the course of each experimental fire, producing the units of s · °C. Maximum temperature at each depth was the highest temperature recorded during each experimental fire.

2.5 | Seedling emergence and resprouting

After the fires, plots were watered daily, and emerging seedlings and resprouts were censused every 3 days by counting the number of individuals of each species in each plot. Plots were censused for 4 months by which time seedling emergence and resprouting of new plants had ceased. To prevent double counting, seedlings and resprouts were removed once they emerged.

2.6 | Analysis

To determine the effects of cogongrass invasion on fuel loads, average fuel loads in native and invaded sites were compared using one-tailed Welch's *t* tests. We tested the hypothesis that greater fuel loads in invaded than native communities would result in invader-fuelled fires with higher soil heating than native-fuelled fires using mixed-effects models. Effects of fuel type (native or invasive), fuel load (kg/m^2) and measurement depth (cm) on heating duration above 60°C (seconds) and heat flux (s · °C) were evaluated using GLMMs with a Poisson distribution. Effects on maximum temperature were evaluated using a linear mixed model with a Gaussian distribution. Maximum temperature was log transformed to correct for right skewness in the data. We also tested models for heating duration above 50 and 70°C and found the same qualitative patterns, so only report results of the model for heating duration above 60°C. Day of burn was included as a random effect in all models, and plot was included as a random effect in Poisson models to correct for overdispersion. Day of burn weather parameters did not improve models and were excluded (summarized in Table S3). All analyses were done in R (R Core Team, 2020).

We calculated marginal and conditional pseudo-R^2 values for each model using the rSquaredGLMM function in the MuMIn package (Barton, 2019). The marginal R^2 indicates variance explained by fixed effects in the model, whereas conditional R^2 indicates variance explained by the entire model. Hence, when discussing R^2 values, we are referring to the marginal values. Mixed-effects models were fit using the lme4 package (Bates et al., 2015) and diagnostics of model assumptions were conducted using the DHARMa package (Hartig, 2020).

To compare fire intensity in native and invaded communities, we plotted the predicted value for soil heating at the average fuel loads observed in each. Predicted values were calculated from the mixed models described above for heating duration, maximum temperature and heat flux, using the predict function in R. Standard errors for predicted values were generated using the bootMer function in the lme4 package. All figures show untransformed data with heating duration above 60°C converted from seconds to minutes for clarity.

We used GLMs (glm in R) with a quasibinomial distribution to test our hypotheses that seedling emergence and resprouting of all species, except cogongrass, decreased with increasing fuel loads, and to compare seedling emergence and resprouting of invasive species and native species across fuel loads. The quasibinomial distribution was used to account for overdispersion in the data (Zuur et al., 2009). To compare seedling emergence or resprouting of each species between native and invaded communities, we plotted predictions of seedling emergence or resprouting probability for each species at the average measured fuel loads. Predicted values and standard errors were calculated using the predict function.

3 | RESULTS

3.1 | Fuel load measurements

Average fine fuel loads were 152% greater in invaded (1,014 ± 160 g/m^2, mean ± *SE*; $n = 40$) than native sites (403 ± 26 g/m^2, mean ± *SE*; $n = 77$; $p < 0.001$, $t = 3.76$ Figure 1), but varied among sampling locations (Table S4). Litter fuel loads were 117% greater in invaded (410 ± 43 g/m^2, range 0–1,068 g/m^2) than native sites (189 ± 16 g/m^2; $t = 4.86$; $p < 0.001$; range 7–578 g/m^2), and standing fuel loads were 181% greater in invaded (604 ± 166 g/m^2, range 70–5185 g/m^2) than native sites (215 ± 17 g/m^2; $p = 0.02$, range 100–687 g/m^2).

3.2 | Experimental fires

Variation in heating duration, maximum temperature and heat flux was explained by fuel load and depth, but not fuel type (Table 1; panels a–d of Figure 2; Figures S2 and S3). Heat flux had the most variation explained by fuel loads ($R^2 = 0.73$), followed by maximum temperature ($R^2 = 0.66$) and heating duration ($R^2 = 0.63$; Table 1). Due to the similar trends across models and to simplify our discussion of fire intensity, we focus on interpreting the results for heating duration. The results for heat flux and maximum temperature are included as supplements (Figures S2 and S3; Table 1).

All measures of fire intensity were greatest at the soil surface and declined with soil depth (Table 1). For example, for every centimetre of depth, heating duration decreased by 49% (Figure 2) and maximum temperature (°C) decreased by 44% (Figure S2). Greater fuel loads produced greater fire intensity where, for every kg/m^2 of

TABLE 1 Mixed-effects model results for (a) heating duration >60°C (seconds), (b) log maximum temperature (°C) and (c) heat flux (s · °C), with depth (cm), fuel type (native vs. invasive) and fuel load (kg/m^2) as fixed effects

(a) Heating duration model. marginal $R^2 = 0.63$; conditional $R^2 = 0.99$

Parameter	Coefficient	*SE*	*Z* value	*p*-value
Intercept	4.53	0.41	11.05	<0.001
Fuel load	1.18	0.17	7.07	<0.001
Depth	−0.68	0.01	−123.77	<0.001
Fuel type—native	−0.05	0.22	−0.22	0.83

(b) Log maximum temperature model. marginal $R^2 = 0.66$; conditional $R^2 = 0.67$

Parameter	Coefficient	*SE*	*t* value	*p*-value
Intercept	5.07	0.12	43.27	<0.001
Fuel load	0.24	0.07	3.71	<0.001
Depth	−0.58	0.04	−15.47	<0.001
Fuel type—native	−0.02	0.08	−0.29	0.78

(c) Heat flux model. marginal $R^2 = 0.73$; conditional $R^2 = 0.99$

Parameter	Coefficient	*SE*	*Z* value	*p*-value
Intercept	9.16	0.37	24.6	<0.001
Fuel load	1.28	0.18	7.22	<0.001
Depth	−0.91	0.6e−4	−1450.84	<0.001
Fuel type—native	0.02	0.23	0.1	0.92

additional fuels, heating duration increased 225% (Table 1; Figure 2) and maximum temperature increased by 27% (Table 1; Figure S2). Predicted heating duration was 116% longer (Figure 2e–h), predicted maximum temperature (°C) was 19% greater (Figure S2e–h) and predicted heat flux was 110% greater (Figure S3e–h) at average fuel loads of invaded than native pine savannas.

3.3 | Seedling emergence and resprouting

Overall, resprouting was high (63%) and emergence from seeds was relatively low (22%) within control plots and varied widely among species (Table 2). Greater fuel loads corresponded with lower seedling emergence and resprouting but variance among species was high. On average, the probability of seedling emergence was 3% lower for each additional 100 g/m^2 of fuels ($p = 0.02$; odds ratio = 0.97; Figure S4, Table S5). Seedling emergence across all seeded species did not differ between native ($n = 5$) and invasive ($n = 4$) species ($p = 0.76$; Figure S4, Table S5). Overall, predicted seedling emergence of seeded invasive and native species together was 23% lower under average fuel loads of invaded (9.9% emergence ± *SE* 0.69) than native pine savannas (12.2% emergence ± *SE* 0.89).

Seedling emergence and resprouting of all species except cogongrass, the native *Sorghastrum nutans*, and the invasive *Melinis repens* significantly decreased with increasing fuel loads but there was variation within and between native and invasive species (Table 2; Figure 3). Of the invasive species, the odds of *Leucaena leucocephala* seedling emergence declined most rapidly with increasing fuel loads (8% decrease for every additional 100 g/m^2 of fuels). In contrast, the odds of native *P. graminifolia* resprouting declined 21% for every additional 100 g/m^2 of fuels. Predicted values of seedling emergence and resprouting for each species tended to be lower at the mean fuel loads measured in invaded compared to native communities (Figure 4).

4 | DISCUSSION

Additional fuel loading from a non-native grass invasion caused more soil heating during fires and less post-fire seedling emergence and resprouting of native species. Seedling emergence and resprouting of native and invasive species varied widely across the range of fuel loads in our experiment, suggesting that post-fire assemblages of invaded communities could change due to invasive fuels and variable tolerances of species to soil heating. We also found that cogongrass rhizomes were tolerant of intense invader-fuelled fires, suggesting that invasion-induced changes to fire intensity could accelerate the dominance by this invader by more strongly suppressing the seedling emergence or resprouting of less fire-tolerant native species.

The observation of greater fuel loads in cogongrass-invaded communities is consistent with previous studies in longleaf and slash pine savannas (Lippincott, 2000; Platt & Gottschalk, 2001) and is characteristic of some other invasive grasses (Rossi et al., 2014; Setterfield et al., 2010). As expected, heating duration increased with greater fuel loads but did not meaningfully differ between fuel types, indicating that the invasive and native fuels have similar heats

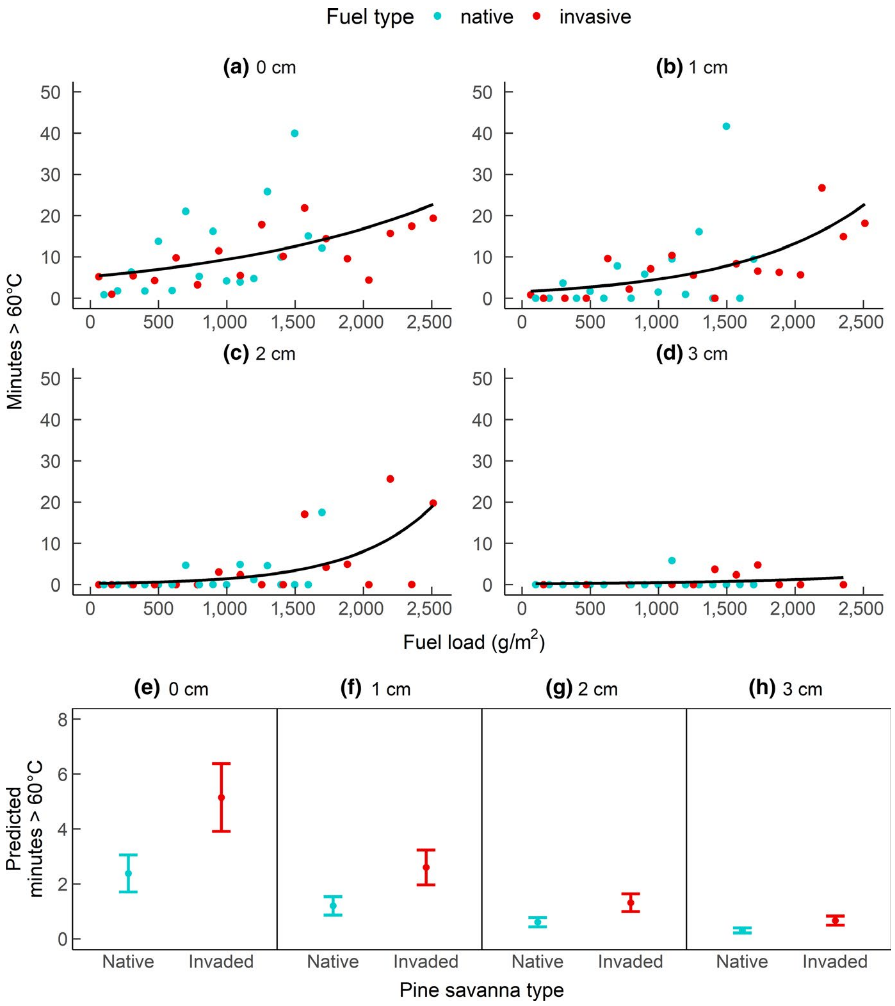

FIGURE 2 Heating duration (>60°C) at the soil surface (a), 1 cm (b), 2 cm (c) and 3 cm (d) below-ground was longer with greater fuel loads. Heating duration as a function of fuel loads did not differ between native (blue points) and invasive (red points) fuel types. Predicted lines are from Poisson regression. Predicted mean heating duration (±*SE*) was generally longer for the average fuel load observed in invaded than native pine savanna at all depths (e)–(h)

of combustion (Lippincott, 2000). More soil heating from greater invader fuel loads occurred despite the higher moisture of experimental cogongrass fuels, likely because the high surface to volume ratio of grasses can enhance drying, and abundant dry litter fuels aided in the ignition of moist standing fuels (Parsons et al., 2015; Simpson et al., 2016). Other invasive grasses can increase fire intensity or carry fire despite having higher fuel moistures than native species (Hughes et al., 1991; Setterfield et al., 2010).

We found that seedling emergence and resprouting of species, except for cogongrass, *M. repens* and *S. nutans*, decreased as fuel loads and soil heating increased, but sensitivity varied among species. The responses of species to soil heating can be due to differences in seed moisture, size or coat hardness (Tangney et al., 2019; Wiggers et al., 2017) and, in our study, may have been affected by scarification treatments. For example, soaking the seeds of *P. elliottii*, *P. palustris*, *Chamaecrista fasciculata* and *L. leucocephala* in water could have increased their moisture content and increased the likelihood of lethality due to soil heating (Tangney et al., 2019). Alternatively, species with harder seed coats are less sensitive to soil heating than species with softer seed coats (Wiggers et al., 2017), which may explain why seedling emergence of invasive *Mimosa pigra*, invasive *Indigofera hirsuta* and native *Rhus copallinum* were less sensitive to greater fuel loads and heating compared to most other seeded species. However, chemical and mechanical scarification altered the seed coats of these species, possibly reducing the threshold temperature or heating duration that lowers seed viability. Without scarification, short (1 min) pulses of heating between 60 and 100°C can increase the germination of *Mimosa* species but pulses above 100 or 200°C result in decreased seed viability and decreased germination (Zirondi et al., 2019). Germination of *R. copallinum* exposed to 10 min of heating is greatest at 90°C but rapidly declines at temperatures >90°C (Bolin, 2009), potentially explaining the jump in seedling emergence observed for *R. copallinum* at fuel loads around 1,000 g/m^2. Without scarification, the higher temperatures and durations of soil heating we observed under high cogongrass fuel loads would likely still result in lower emergence of scarified species in our study, but perhaps to a lesser degree.

Post-fire resprouting from below-ground buds, however, may ultimately be of greater importance than seedling emergence for persistence of long-lived perennial species in savanna communities (Clarke et al., 2013; Hoffmann, 1998; Pausas & Keeley, 2014). For example, Fabaceae species may maintain long-term seed banks, while dominant Poaceae species tend to have short-lived seed banks that limit their ability to recolonize post-fire (Coffey & Kirkman, 2006). Additionally, seed banks of intact and disturbed pine savannas can contain abundant weedy and ruderal herbaceous species but few

TABLE 2 Quasibinomial regression results for the probability of seedling emergence or resprouting of native and invasive species as a function of fuel loads. Odds ratio is the amount of change expected in the odds ratio of emergence or resprouting for every 100 g/m^2 increase in fuel loads. Odds ratio of 1 indicates that there is no change in the odds of emergence or resprouting as fuel loads increase. $n = 40$ for all species

Species	Growth habit	Type	Percent emergence in control plots	Odds ratio (per 100 g/m^2 of fuels)	Fuel load estimate	*SE*	*t*-Value	*p*-Value
Aristida stricta	Grass	Native plug	94%	0.87	−1.42	0.36	−3.90	<0.001
Chamaecrista fasciculata	Forb	Native seed	10%	0.90	−1.06	0.15	−7.06	<0.001
Pinus elliottii	Tree	Native seed	7%	0.87	−1.41	0.67	−2.12	0.04
Pinus palustris	Tree	Native seed	10%	0.88	−1.30	0.55	−2.36	0.02
Pityopsis graminifolia	Forb	Native plug	56%	0.79	−2.41	0.84	−2.87	0.01
Rhus copallinum	Tree/Shrub	Native seed	38%	0.96	−0.41	0.13	−3.05	0.01
Sorghastrum nutans	Grass	Native seed	5%	0.98	−0.21	0.14	−1.49	0.1
Imperata cylindrica	Grass	Invasive rhizome	40%	0.98	−0.25	0.35	−0.70	0.5
Indigofera hirsuta	Forb	Invasive seed	16%	0.97	−0.30	0.13	−2.33	0.03
Leucaena leucocephala	Tree	Invasive seed	33%	0.92	−0.84	0.23	−3.6	<0.001
Melinis repens	Grass	Invasive seed	4%	0.97	−0.29	0.17	−1.68	0.1
Mimosa pigra	Forb	Invasive seed	22%	0.94	−0.66	0.23	−2.8	0.01

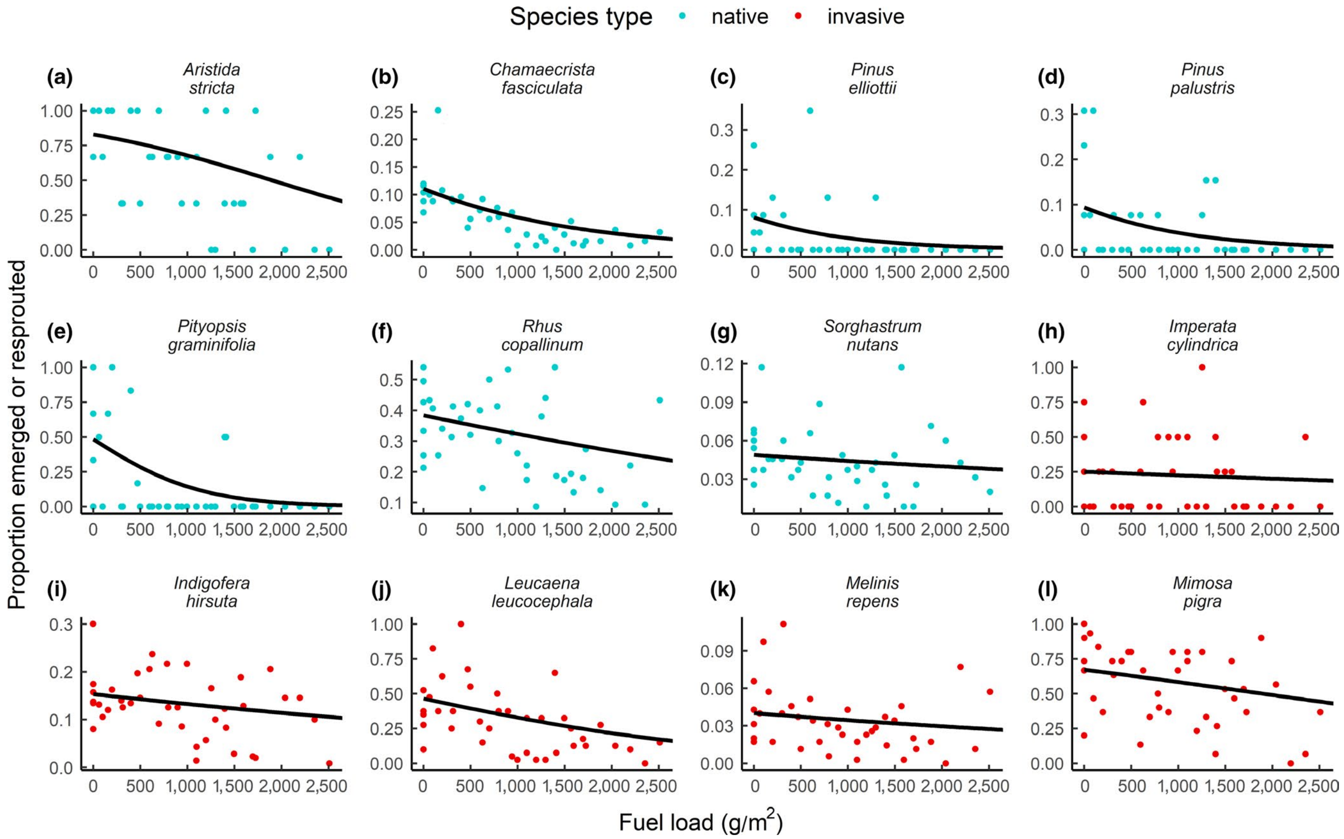

FIGURE 3 Resprouting (a, e and h) and seedling emergence (all other panels) of both native (a–g) and invasive (i–l) species decreased with greater fuel loads ($p < 0.05$), except for cogongrass (panel h; $p = 0.5$), *Sorghastrum nutans* (panel g, $p = 0.1$) and *Melinis repens* (panel k, $p = 0.1$). Points at fuel loads of 0 are proportion emerged in unburned control plots. Black lines are best fits from quasibinomial regressions. *Y*-axis scales differ among panels to show patterns for species with a low baseline emergence

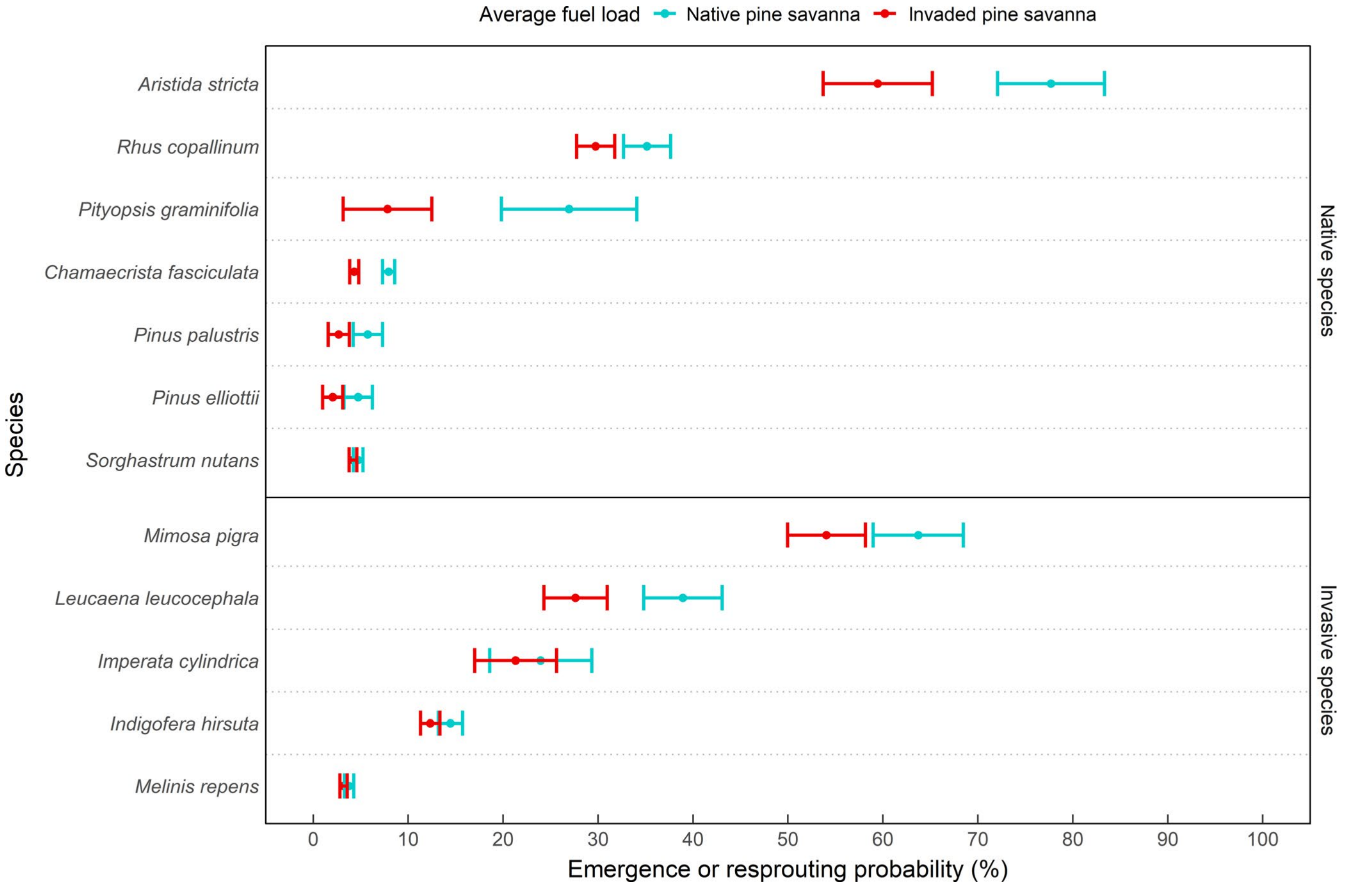

FIGURE 4 Predicted resprouting (*Aristida stricta*, *Pityopsis graminifolia* and *Imperata cylindrica*) or seedling emergence (all other species) probability (±*SE*) of native and invasive species was generally lower under the average fuel load of invaded (red) than the average fuel loads of native (blue) pine savannas

old-growth species that characteristically dominate these communities (Diaz-Toribio & Putz, 2017; Parks, 2007).

When invasive species are more tolerant to intense fires than native species, fire intensity will influence community assemblages (Gómez-González & Cavieres, 2009) such that the dominant invader driving the invasion-fire cycle may facilitate the establishment of secondary invaders. For example, the predicted seedling emergence probabilities of native *C. fasciculata* and *P. elliottii* were approximately 50% lower at the average fuel loads of invaded than native pine savannas, indicating that commonly observed invader fuel loads could reduce the abundance of these species. In contrast, predicted seedling emergence of the invasive species *I. hirsuta* and *M. pigra* was only 17% lower at average invaded fuel loads than native fuel loads, despite scarification potentially overestimating the decline in seedling emergence of both species. This result suggests that the relative abundance of *I. hirsuta* and *M. pigra* could increase post-fire compared to less fire-tolerant native species. Cogongrass was unaffected by the intense fires it generated, suggesting that its relative dominance could increase over time through an invasion-fire cycle.

Lethal soil temperatures during savanna fires seldom penetrate more than a few centimetres of soil and quickly decrease with depth (Bradstock & Auld, 1995; Choczynska & Johnson, 2009), suggesting that the impacts of soil heating on seedling emergence and resprouting of plants depend on the depth distribution of seeds and buds (Choczynska & Johnson, 2009; Flinn & Wein, 1977). Even under high invader fuel loads, we seldom recorded lethal temperatures (≥60°C) at depths of 3 cm, but this threshold was frequently exceeded at 2 and 1 cm depths. Species with buds concentrated near the soil surface may be most affected by shallow soil heating. In North Carolina pine savannas, up to 72% of *Andropogon gerardii*, *S. nutans* and *Panicum virgatum* buds were located within the top 2 cm of soils (Choczynska & Johnson, 2009) while *A. stricta* and *P. graminifolia* buds tend to occur at depths of 2–3 cm (Hartnett, 1987; Lemon, 1949). All these species could resprout less due to the longer heating duration from cogongrass-fuelled fires, or from fuel accumulation due to fire suppression. However, the extensive rhizomatous network of cogongrass tends to occur within the top 10–15 cm of soil (MacDonald, 2004), well below the depths where soil heating occurred.

Without management, grass invasions that increase fuel loading and soil heating may alter post-fire community assemblages and facilitate invader dominance at the expense of native species (Hughes et al., 1991; Lippincott, 2000; Setterfield et al., 2010). To reduce the impacts of invasive grass fuel loading, mechanical fuel removal could be employed (e.g. using a mower with sweeper attachment) and prescribed fires avoided during dry spells to reduce fire intensity. When information on additional parameters such as fuel and soil moisture are available, more precise estimates of soil heating could be forecasted (Reinhardt & Dickinson, 2010). However, collecting data on multiple soil and fuel parameters before conducting prescribed fires is logistically challenging. Our results demonstrate that fuel load, which is easily measured, can be used to assess potential below-ground effects of fires on plant communities and may therefore be used alone when deciding whether to conduct prescribed fires. For communities with few native buds or seeds remaining, soil heating might be less of a concern because reseeding or planting will likely be required (Coffey & Kirkman, 2006; Maliakal et al., 2000). Ultimately, the management of invasive species that increase fuel loading is critical for maintaining fire regimes that promote native communities and resist invader dominance.

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AUTHORS' CONTRIBUTIONS

S.L.F. and G.T.-K. conceived the study; G.T.-K. collected the data and led the writing; G.T.-K. and W.W.D. analysed the data. All the authors contributed to formulating methodology and contributed critically to the final manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.pc866t1np (Tomat-Kelly et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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