

Priority effects, not fire alone, determine the success of invasive alien plant species

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Research Article

Keywords: Fire Ecology, Climate change, Plant Fire Response, Disturbances, *Urochloa arrecta*, Biological Invasion, Wetlands

Posted Date: September 1st, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7208112/v1>

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Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Fire Ecology on June 25th, 2026. See the published version at <https://doi.org/10.1186/s42408-026-00534-z>.

Abstract

1. Fire is a key disturbance known to facilitate plant invasions, but the mechanisms driving competitive outcomes, especially how they are shaped by the pre-existing stage of invasion, remain unclear.
2. We experimentally assessed how fire and pre-disturbance dominance affect performance and competitive interactions between a widespread invasive alien plant species (IAPS, *Urochloa arrecta*) and a resident native plant species (NPS, *Hemarthria altissima*). We simulated fire across a gradient of IAPS dominance, hypothesizing that fire's impact would depend on the initial invasion stage.
3. The IAPS's advantage was driven by a superior regenerative strategy, not by consistently higher biomass production. Post-fire, the IAPS's sprout production was critically dependent on its own dominance, more than doubling when at high abundance. Crucially, this high IAPS dominance suppressed the number of NPS sprouts and prolonged their sprouting time. In contrast, at low abundance, the IAPS's regenerative capacity was credibly reduced.
4. *Synthesis.* Our findings reveal that fire facilitates plant invasion not simply by creating opportunity, but by amplifying the regenerative and suppressive traits of an already-dominant invader. This demonstrates that priority effects and propagule pressure are key mediators of post-disturbance success. Considering the increasing records of fire disturbances and plant invasion processes worldwide, these findings contribute to a more profound understanding of the rationale behind the IAPS dominance in fire-disturbed environments.

1 INTRODUCTION

Disturbances are fundamental components of ecosystems, shaping their structure and function (Sousa, 1984; Burton et al., 2020; Lázaro-Lobo et al., 2023). Wildland fires, in particular, are a critical disturbance whose frequency and intensity are increasing in many neotropical ecosystems due to climate change. While fires can create windows of opportunity for invasive alien plant species (IAPS), the fine-scale mechanisms that determine the success of invaders over native species remain understudied, especially in vulnerable wetland environments (Davis et al., 2000; Hobbs & Huenneke, 1992; Burton et al., 2020; Roy et al., 2024; Valliere et al., 2024). In post-fire environments, plant species with high resprouting capacity or adaptations for rapid growth during early successional stages are often the first to colonise these newly available niches (Pausas & Keeley, 2014; Kelly et al., 2020). Furthermore, the ashes produced by wildland fires are typically rich in organic and inorganic compounds (Sánchez-García et al., 2023; Araujo et al., 2025), which can further influence nutrient cycling and the process of plant establishment. Fire events thus create transient opportunities for the colonisation and establishment of species with diverse ecological strategies, particularly those adapted to exploit fluctuating resource availability (Supp & Ernest, 2014; Roy et al., 2024).

Evidence suggests that fires play a crucial role in maintaining plant diversity in certain ecosystems, such as open and non-forested landscapes (Sühs et al., 2020). However, the frequency and intensity of fires

have increased in many parts of the world in recent decades (Jones et al., 2024), primarily attributed to climate change, which induced warmer, prolonged, and more intense dry seasons (Mansoor et al., 2022). Numerous studies indicate that invasive alien plant species (IAPS) are increasingly taking advantage of altered disturbance regimes (Lembrechts et al., 2016; Jo et al., 2024), with higher IAPS dominance and diversity observed as disturbance intensity increases (Seabloom et al., 2003; Lake & Leishman, 2004; Roy et al., 2024). Disturbance facilitates the establishment of IAPS because they have faster recolonization rates after disturbance events (Michelan et al., 2013; Weiser et al., 2016; Fares et al., 2020; Cornwall, 2022; Roy et al., 2024). In addition, IAPS actively modify fire regimes by increasing fuel loads, leading to a positive invasion-fire feedback that further facilitates their establishment (Gaertner et al., 2014; Cornwall, 2022). Understanding how disturbances can facilitate the establishment of IAPS offers valuable insight into why some plant species can persistently invade areas outside their natural range after such disruptions, while others do not. This question represents a significant challenge for ecosystem management and biodiversity conservation.

Invasion is a serial process that involves overcoming biotic and abiotic filters, such as climatic and edaphic conditions, biotic interactions, and resource availability (Richardson & Pyšek, 2006; Dai et al., 2020; Tangney et al., 2022). Invasive alien species depend on their ability to survive and reproduce and must succeed through all stages of the invasion process to persist: colonisation, establishment, and spread (Theoharides & Dukes, 2007; Catford et al., 2009). The colonisation stage involves the survival of the introduced individuals, which usually starts with a few individuals. During the establishment stage, the species forms self-sustained populations that persist in time. Lastly, during the spread stage, the species undergoes explosive population growth and rapid expansion in the introduced region, causing negative effects on native biodiversity and ecosystem services (Elton, 1958; Williamson & Fitter, 1996; Blackburn, 2011; David et al., 2017; Wilsey et al., 2024). The interaction between disturbance events and the ongoing invasion process can significantly influence the performance and regenerative capacity of both IAPS and native plant species (NPS). If the disturbances occur when the IAPS are well-established, they may exacerbate their dominance. In contrast, disturbances at the early invasion stages might allow the NPS to withstand invasion (Omer et al., 2022).

The invasion stage at the time of disturbance, which inherently determines the invasive pre-disturbance dominance, can thus be critical. Indeed, pre-disturbance dominance can significantly influence the success of regrowth following environmental disturbances (Cowan et al., 2023), particularly in ecosystems where clonal growth is a primary regeneration strategy. A higher initial dominance of a particular species may lead to a greater belowground bud bank, thereby enhancing resprouting potential after disturbances such as flooding or mechanical damage (Klimešová & Klimeš, 2007). In temperate wetlands, species with extensive rhizome networks often show higher post-disturbance survival due to their ability to regenerate rapidly from belowground reserves (Middleton, 2009). Although such mechanisms are well documented in response to hydrological stress, it remains unclear whether similar patterns occur following fire. To isolate these mechanisms, this study uses a representative wetland system from Southern Brazil, where the globally successful IAPS *Urochloa arrecta* co-occurs with the widespread perennial grass *Hemarthria altissima*. While large-scale events, such as the 2020 wildfires

that burned nearly 30% of the Pantanal, highlight the continental urgency of this issue, understanding the plant-level interactions is critical for developing generalizable management principles (Damasceno-Junior et al., 2021).

Here, we experimentally evaluated the performance of IAPS and NPS, considering different invasion stages, before and after fire occurrence. We hypothesised that IAPS would exhibit superior performance (in terms of biomass production and allocation) compared to NPS, (i) regardless of fire occurrence, (ii) enhancing its competitive advantage after fire, and (iii), especially when IAPS dominate the plant community. The rationale of these hypotheses is that IAPS have faster recovery after disturbance than NPS (Michelan et al., 2013; Fares et al., 2020). Moreover, the higher IAPS dominance before the disturbance (pre-disturbance dominance) may improve the resprouting success (as demonstrated for other plant traits by Matula et al., 2019). However, this interaction across the invasion stages under fire disturbance remains to be fully elucidated for competitive wetland plants.

2 MATERIALS AND METHODS

2.1 Studied species and sampling

The experiment was conducted in a greenhouse from May to November 2023 (180 days), where plants grew in trays with water-saturated soil conditions typical of wetlands (water depth of ~ 2 cm aboveground). To assess the effect of fire on plant performance and interactions, considering different stages of invasion, we used the grass *Urochloa arrecta* as the IAPS because it is originally from South Africa and has become a successful invader of freshwater ecosystems in Brazil and other tropical and subtropical regions worldwide (Fares et al., 2020; Bando et al., 2023; GBIF, 2024). While the precise evolutionary origin of the grass species *Hemarthria altissima* remains debated, we used it as the NPS because it is widely naturalized and functions as a native component in many Brazilian wetlands, as evidenced by multiple reports (Ayala & Simon, 1914; Oliveira & Marquis, 2002; Nabinger et al., 2001; Kawakita et al., 2018). It frequently co-occurs with our target IAPS and there are no records of it causing negative ecosystem impacts. For the purposes of this study, which focuses on the interaction between a known aggressive invader and an established resident species, we considered them suitable for our comparative analysis. Furthermore, given that both species are perennial, emergent C4 herbaceous plants, which share similar morphology and architecture (Nabinger et al., 2001; Oliveira & Marquis, 2002; Kawakita et al., 2018), we considered them suitable for interaction and competition studies.

We sampled adult individuals of both species in the wetland areas adjacent to a stream at Ressacada Experimental Farm (27°41'06.28" S; 48°32'38.81" W), Florianópolis, Santa Catarina, Brazil. The sampled sites comprise fine, loamy sand soils with continuous herbaceous communities. The climate in this region is subtropical, characterized by an annual mean temperature of 19.5°C, a mean annual precipitation of 1,600 mm, and an annual mean humidity of 84% (Weather Spark, 2023). After sampling, we cut both species to produce vegetative propagules of similar lengths (17 cm, comprising a shoot of 15 cm and a root of 2 cm) and weights (mean = 1.12 g, standard deviation $\pm$ 0.37). This procedure

mitigates potential initial plant size differences, allowing for individual comparability (Parepa & Bossdorf, 2016; Bando et al., 2016).

2.2 Experimental design

We planted vegetative propagules in plastic trays (56 × 36.3 × 14.5 cm) filled with a 10 cm layer of sediment (~ 12 kg). The soil used was a 50:50 mixture of soil from the sample sites and sand. Non-target seedlings emerging from the soil seed bank were removed upon germination to prevent interference with experimental treatments. Each tray received 12 vegetative propagules, varying species proportions according to the treatment. Our experimental design simulated different invasion stage scenarios: non-invaded (only NPS), colonised (NPS dominance), established (IAPS dominance), and dominated (only IAPS) (Fig. 1). In the non-invaded treatment we used 12 NPS vegetative propagules, corresponding to NPS monoculture; in the colonised treatment we used 9 NPS and 3 IAPS vegetative propagules, simulating NPS dominance with IAPS colonisation as the early stage of the invasion process (75% NPS and 25% IAPS); in the established stage, we applied the opposite of the colonised treatment, corresponding to IAPS dominance with low abundance of NPS (75% IAPS and 25% NPS); and in the dominated treatment, we used 12 IAPS vegetative propagules, corresponding to IAPS monoculture. Each treatment consisted of 12 trays, totalling 48 trays.

Plants were grown for 90 days, including 20 days without a water supply, during which they produced dry, flammable biomass. Individuals reached lengths of up to 1 m, comparable to those of field-grown adult plants. On day 90, we randomly selected three trays per treatment for plant removal. Plant above- and below-ground components were measured, and the biomass was oven-dried (at 60°C until constant weight) and weighed (above-ground and below-ground). This approach enabled us to identify the pre-fire conditions without compromising the continuity of the experiment. After this stage, nine trays per treatment remained, which were subjected to a fire disturbance using a butane kitchen blowtorch (with a maximum flame temperature of ~ 1083°C). This before-after design with an intense burn method was chosen to simulate fast-moving surface fires typical of some wetland grasslands, focusing on the consumption of aboveground biomass and ash deposition, while minimising deep soil heating. The flame was applied by systematically moving it across each tray's entire aboveground dry biomass for three minutes to ensure relatively uniform exposure. Wildfires typically exceed 800°C (Michaletz & Johnson, 2007; Kutzer & Meincken, 2024). The simulated fire consumed only the aerial biomass, leaving ash dispersed on the substrate and mimicking post-wildfire conditions (e.g., García-Carmona et al., 2025). This controlled approach was prioritised over landscape-level burns to ensure treatment uniformity across replicates, thereby isolating the effects of dominance from the inherent heterogeneity of natural fire events.

After the fire disturbance on day 90, a 2-cm water layer was added in the trays, and soils remained moist throughout the subsequent 90-day growth period (days 90–180). At the end of this period, plants were harvested, washed, and separated into their above-ground and below-ground components (stems/leaves and roots, respectively). All material was oven-dried at 60°C to constant weight (~ 20 days), then

weighed using a semi-analytical balance (precision ± 0.01 g) to assess biomass allocation and performance.

2.3 Data collection

2.3.1 Effects of fire and pre-disturbance dominance on the regrowth of alien invasive and native plant species

Through routine daily monitoring, we determined the time to resprout (in days after the fire) for each plant species to assess the success of plant regrowth. On day 180 (90 days post-fire, during the growth period), we counted the total number of regenerated plants and the number of sprouts that emerged from each plant species. This monitoring allowed us to test the impact of fire and the gradient of IAPS dominance on the regenerative capacity of NPS and IAPS.

2.3.2 Effects of fire and pre-disturbance dominance on biomass production by alien invasive and native plant species

Stock biomass is a crucial indicator of ecosystem functioning (Su et al., 2023), representing the mass balance between production, respiration, and mortality. We quantified the biomass stock of each individual (from both IAPS and NPS), referred to as 'individual biomass'. To characterise the unburned individual biomass, we summed the above-ground and below-ground biomass of each individual on the 90th day before the fire event. Also, we summed the above-ground biomass of each individual per tray on the 180th day (as the initial above-ground biomass was zero due to the fire) and generated a measurement we termed 'net change in root biomass relative to unburned species average'. This net change was calculated by subtracting the average dry root biomass of individuals of each species on the 90th day (unburned) from the individual's dry root biomass on the 180th day (burned). This approach, using the unburned species average as a standardised baseline due to the destructive nature of the fire event for the regrowing sample, was intended to provide an exploratory estimate of how post-fire individual root systems differed from a typical pre-fire condition. This proxy relies on the assumption that the pre-fire biomass of burned individuals would have been reasonably close to the measured average of the unburned reference group. This simplification enables a comparative analysis of pre- and post-fire conditions. Therefore, the variable burned 'individual biomass' (post-fire) includes this calculated root biomass change and the new above-ground biomass, and does not include individuals who failed to regenerate after fire. Individuals that failed to regenerate after fire were assigned a total biomass of zero for subsequent analyses where appropriate. We calculated the shoot/root biomass ratio for each individual species to analyse whether there were any modifications in the biomass allocation between above-ground and below-ground tissues before and after fire occurrence (using actual post-fire above and below-ground biomass for the post-fire ratio).

2.3.3 Effects of fire and pre-disturbance dominance on the performance of alien invasive and native plant species

To evaluate the effects of fire and gradient of IAPS dominance on the competitive dynamics between NPS and IAPS, we calculated the biomass deviation for each species, a measure of relative productivity in mixtures compared to monocultures, calculated as:

$$RYT_i = (B_{i_{mix}} - B_{i_{mono}}) / B_{i_{mono}}$$

Where $B_{i_{mix}}$ represents the observed biomass production of species i in the mixture, and $B_{i_{mono}}$ represents the expected biomass of species i based on its monoculture performance. For simplicity, we only calculated the relative yield total (RYT_i; Follower, 1982) using the individual biomass of plant species. Values of RYT_i > 0 indicate overyielding, while RYT_i < 0 indicates underyielding.

To explore the interaction between IAPS and NPS in a gradient of IAPS dominance, we used the Relative Interaction Intensity index (RII), calculated for each individual plant in the mixture treatments (native and invasive dominance) (Armas et al., 2004). The RII was calculated as:

$$RII = (B_{individual_mix} - B_{mono_avg}) / (B_{individual_mix} + B_{mono_avg})$$

Where $B_{individual_mix}$ is the individual biomass of a plant of the target species growing in a mixture, and B_{mono_avg} is the average individual biomass of the same target species when grown in monoculture. RII values range from - 1 (maximum competition) to + 1 (maximum facilitation), with values around 0 indicating neutral interactions.

2.4 Data analysis

All statistical analyses were performed in R (version 4.4.2) using the GLMM structure and a Bayesian modelling framework implemented through the '*brms*' and '*rstanarm*' packages (Bürkner, 2017; Goodrich et al., 2024; R Core Team, 2024). These packages connect to STAN for Markov chain Monte Carlo (MCMC) sampling (Carpenter et al., 2017). Models were run for 2,000 iterations, with a 500-iteration warm-up across four chains. Weakly informative normal priors were used for all model parameters (e.g., Gelman et al., 2013; Lemoine, 2019). For the intercept, prior location values were set based on reference biomass estimates obtained from empirical data, log-transformed when necessary. Model convergence was assessed using trace plots, graphical posterior predictive checks, effective sample sizes, and the Gelman-Rubin diagnostic (R-hat), with values below 1.01 indicating satisfactory convergence (Gelman & Rubin, 1992; Brooks & Gelman, 1998; Gelman et al., 2013).

We tested the effects of fire and pre-disturbance dominance on three main groups of response variables: (1) regeneration capacity, (2) biomass production, and (3) competitive performance and species interactions.

To assess regeneration capacity, we modelled three response variables: (a) regrowth percentage (defined as the proportion of observed regenerated sprouts relative to planted propagules) with a Gaussian family, (b) the number of individuals that resprouted per species per tray with binomial negative family and (c) the resprouting time (days until the plants resprout) with binomial negative

family. Fixed effects included the gradient of IAPS dominance (four levels: non-invaded, colonised, established, dominated) and their interaction. Random intercepts were included for the experimental tray. For biomass production, we modelled individual biomass with the Gamma family (log link). This standardised baseline accounted for the gradient of IAPS dominance variation, allowing us to estimate deviations from typical biomass patterns. Shoot/root ratios were also analysed to assess allocation changes due to fire and the gradient of IAPS dominance treatments. These models included species identity, as Native Plant Species (NPS) vs. Invasive Alien Plant Species (IAPS), gradient of IAPS dominance, fire treatment, and their interactions, with nested random intercepts for tray.

To evaluate competitive performance and species interactions, we modelled three indices: the Invasive Alien Plant Species/Native Plant Species biomass ratio (for shoot, root, and individual biomass), the relative yield total (RYT_i), and the relative interaction intensity (RII) with a Gaussian family. These indices were modelled using similar fixed and random structures. The general model structure for most response variables follows:

Response variable ~ Explanatory factors + (1 | Tray)

For performance-related outcomes, interaction terms were included between fire and dominance treatments. Posterior distributions were used to extract means and 75% uncertainty intervals for all fixed effects. A priori hypotheses were tested using the *hypothesis()* function in *brms*, which computes the posterior probability (PP) and corresponding evidence ratio (ER = PP / (1 - PP)). We interpreted values close to 1 or 0 as strong evidence for or against a directional effect. Model diagnostics also included Pareto-smoothed importance sampling leave-one-out cross-validation (PSIS-LOO), with 98.7% of observations exhibiting satisfactory Pareto k values ($k \leq 0.7$) (Vehtari et al., 2017).

3 RESULTS

3.1 Fire and gradient of IAPS dominance effects on the resprouting of NPS and IAPS

The proportion of observed sprouts after fire relative to the planted propagules (hereafter regrowth) was influenced by the interaction between the origin of species and the gradient of dominance by Invasive Alien Plant Species (IAPS) (Figs. 2a and 2b). For native plants (NPS), the baseline regrowth in monoculture was approximately 5.54%, while it was higher (8.06%) under invasive dominance, and lower (-6.78%) under native dominance lower than in the monoculture - 6.78%, but this effect was not strongly supported as the CI included zero (Table 1). In contrast, IAPS exhibited a higher regrowth percentage (25.26%) in monoculture compared to NPS in monoculture, an increase of 19.72% (Table 1). Under native dominance, IAPS regrowth was lower compared to NPS monoculture, at -4.67%, although this negative effect was weak, as the CI broadly included zero (Table 1). Conversely, under invasive dominance, IAPS had a higher regrowth of 18.10% (Fig. 2a), although the CI also included zero (Table 1).

Regarding sprouting time, NPS in monoculture began sprouting approximately 2 days (2.25 days) after the fire; this sprouting time was credibly prolonged under invasive dominance by + 1.03 days. For IAPS in monoculture, the sprouting time was similar to that of NPS; no credible difference was detected (+ 0.08 days). Under native dominance, IAPS sprouting time showed a tendency to be delayed (+ 0.89 days, while under invasive dominance, it tended to be hastened (-0.88 days). However, these interaction effects for IAPS sprouting time were not strongly supported as their CIs included zero.

For the number of sprouts, NPS produced approximately 2 sprouts in monoculture 2.35 sprouts, and this number credibly decreased under invasive dominance - 1.19 sprouts). IAPS showed credibly established interactive effects on their number of sprouts: a reduction under native dominance - 1.37 sprouts, and an increase under invasive dominance + 1.21 sprouts; Fig. 2b).

Table 1

– Posterior summary statistics from a Bayesian model evaluating the effects of species identity (Native Plant Species vs. Invasive Alien Plant Species) and gradient of IAPS dominance (monoculture, native dominance, invasive dominance) on three response metrics on burned plants: regrowth percentage, sprouting time (days), and number of sprouts. For each metric, the Intercept represents the baseline response of the native plant in monoculture. Parameter estimates (posterior means) are reported, presented along with their Posterior Probability (PP), Evidence Ratio (ER), and 95% credible intervals (CI).

Parameter (Effect compared to reference conditions)	Estimate (Slope)	PP (Posterior Probability)	ER (Evidence Ratio)	CI 95% (Credible Interval)
Regrowth after fire (%)				
Intercept (Monoculture, Native Plant)	5.54	0.62	1.66	[-26.79, 37.64]
Native Dominance	-6.78	0.66	1.93	[-39.08, 24.77]
Invasive Dominance	8.06	0.69	2.20	[-24.52, 39.70]
Species	19.72	0.89	8.19	[-11.72, 51.19]
Native Dominance × Species	-4.67	0.61	1.53	[-39.38, 31.13]
Invasive Dominance × Species	18.10	0.85	5.65	[-16.88, 53.20]
Sprouting time (days)				
<i>Intercept (Monoculture, Native Plant)</i>	2.25	1.00*	599	[1.58, 2.93]
Native Dominance	0.54	0.87	6.63	[-0.41, 1.49]
<i>Invasive Dominance</i>	01.03	0.98*	63.52	[0.10, 1.96]
Species	0.08	0.56	1.29	[-0.80, 1.00]
Native Dominance × Species	0.89	0.93	13.46	[-0.30, 2.06]
Invasive Dominance × Species	-0.88	0.93	14.31	[-2.02, 0.28]
Regrowth (Number of sprouts)				
<i>Intercept (Monoculture, Native Plant)</i>	2.35	1.00*	599	[1.81, 2.93]
Native Dominance	-0.23	0.72	2.54	[-1.02, 0.58]
<i>Invasive Dominance</i>	-1.19	1.00*	284.71	[-2.05, -0.35]
Species	0.47	0.89	8.17	[-0.29, 1.23]
<i>Native Dominance × Species</i>	-1.37	0.99*	85.96	[-2.49, -0.22]
<i>Invasive Dominance × Species</i>	1.21	0.99*	67.97	[0.13, 2.30]

3.2 Fire and gradient of IAPS dominance effects on biomass production

Fire had a credibly positive effect on NPS biomass in monoculture, with an estimated increase of 1.1 g in burned conditions compared to unburned monoculture. For the main effect of species origin (IAPS vs. NPS) in unburned monoculture, IAPS biomass tended to be 0.4 g higher than NPS, although the 95% CI included zero, the posterior probability (PP = 0.91) suggested a positive effect. In contrast, for unburned NPS, biomass under native dominance 0.1 g or invasive dominance (0.2 g was not credibly different from that in monoculture, as indicated by CIs encompassing zero and lower PPs (Fig. 3). Regarding interactions for individual biomass, those detailed in Table 2 did not exert credibly non-zero effects.

For the shoot/root biomass ratio, the main effect of fire on NPS in monoculture indicated a tendency for reduction, -0.3; however, this effect was not credibly established as the CI included zero, despite a relatively high PP. The species effect (IAPS vs. NPS) in unburned monoculture showed that IAPS had a credibly lower shoot/root ratio (-0.8) compared to NPS. In contrast, for unburned NPS, neither native dominance - 0.1 nor invasive dominance - 0.3 showed effects on the shoot/root ratio that were credibly different from monoculture, as their CIs included zero. A credible two-way interaction ("Native Dominance × Species" in Table 2) was identified at 0.8, whereby IAPS under native dominance conditions exhibited a higher shoot/root ratio than would be predicted based on the main effects of species and native dominance alone. In contrast, other interaction terms for the shoot/root ratio did not demonstrate credibly non-zero effects (Fig. 4).

Table 2

— Posterior summary statistics from a Bayesian model evaluating the effects of species identity (NPS vs. IAPS) and gradient of IAPS dominance (monoculture, native dominance, invasive dominance) on two response metrics before and after the fire: individual biomass and shoot/root biomass ratio. For each metric, the intercept represents the baseline response of the native plant in an unburned monoculture. Parameter estimates (slopes) are reported as posterior means, accompanied by their Posterior Probability (PP), Evidence Ratio (ER), and 95% credible intervals (CI).

Parameter (Effect compared to reference conditions)	Estimate (Slope)	PP (Posterior Probability)	ER (Evidence Ratio)	CI 95% (Credible Interval)
Individual biomass (g)				
<i>Intercept (Unburned Monoculture, Native Plant)</i>	1.1	1.00*	5999	[0.65, 1.48]
Native Dominance	0.1	0.58	1.43	[-0.56, 0.64]
Invasive Dominance	0.2	0.71	2.45	[-0.48, 0.83]
Species	0.4	0.91	10.54	[-0.16, 0.88]
<i>Fire</i>	1.1	1.00*	5999	[0.56, 1.52]
Native Dominance × Species	-0.3	0.78	3.59	[-1.00, 0.44]
Invasive Dominance × Species	0.3	0.79	3.76	[-0.38, 0.97]
Native Dominance × Species × Fire	0.8	0.94	16.40	[-0.19, 1.83]
Invasive Dominance × Species × Fire	0.1	0.62	1.68	[-0.70, 0.97]
Shoot/root biomass ratio (g)				
Intercept (Unburned Monoculture, Native Plant)	0.4	0.96	25.67	[-0.04, 0.84]
Native Dominance	-0.1	0.57	1.36	[-0.73, 0.61]
Invasive Dominance	-0.3	0.76	3.20	[-0.96, 0.48]
<i>Species</i>	-0.8	0.99*	999	[-1.31, -0.27]
Fire	-0.3	0.87	07.06	[-0.90, 0.25]
<i>Native Dominance × Species</i>	0.8	0.98*	65.67	[0.09, 1.56]
Invasive Dominance × Species	-0.5	0.91	11.20	[-1.21, 0.19]
Native Dominance × Species × Fire	-0.3	0.71	2.53	[-1.30, 0.75]
Invasive Dominance × Species × Fire	0.1	0.56	1.32	[-0.79, 0.91]

3.3 Fire and IAPS abundance effects on the competitive performance of NPS

The Relative Interaction Index (RII) for NPS under unburned native dominance conditions (intercept) showed a credibly positive value of 0.19. Among the main effects investigated, neither the transition to invasive dominance 0.05 nor species type (IAPS vs. NPS; 0.10 credibly changed RII, as their respective CIs encompassed zero. Fire, however, showed a strong tendency to increase RII 0.20, although its 95% CI marginally included zero, thus not confirming a strictly credible effect despite the high posterior probability (Fig. 5).

Further analysis of interactive effects on RII did not reveal any credibly established influences. Specifically, the two-way interaction between invasive dominance and species type (0.22) and the species $\times$ fire interaction (0.23) suggested positive trends, particularly given their PPs (0.92 and 0.90, respectively); however, their CIs still included zero. The invasive dominance $\times$ fire interaction - 0.09 and the three-way invasive dominance $\times$ species $\times$ fire interaction - 0.25 also showed no clear impact on RII, with CIs for both broadly spanning zero (Table 3).

For Relative Yield Total (RYT), no main effect demonstrated a credibly non-zero influence. Specifically, the shift to invasive dominance (-0.08) did not result in a credible change. Similarly, the effect of species type (IAPS vs. NPS; 0.31 did not exert a credibly established effect, despite a PP of 0.78. The influence of fire (0.08) also showed no clear impact on RYT (Table 3).

Further analysis of interactive effects on RYT did not reveal any credibly established influences. The two-way interaction between the gradient of IAPS dominance levels and species identity (0.02) indicated no credible effect. Likewise, the interaction between the gradient of IAPS dominance levels and fire (-0.04), species identity and fire (0.16), and the three-way interaction involving the gradient of IAPS dominance levels, species identity, and fire (0.01) also did not credibly influence RYT (Fig. 6).

Table 3

— Posterior summary statistics from a Bayesian model evaluating the effects of species identity (NPS vs. IAPS) and gradient of IAPS dominance (monoculture, native dominance, invasive dominance) on two response metrics before and after the fire: Relative Interaction Index — RII and Relative Yield Total (RYT). For each metric, the intercept represents the baseline response of the native plant in unburned native dominance (25% of invasive alien plant — colonised stage). Parameter estimates (slopes) are reported as posterior means, accompanied by their Posterior Probability (PP), Evidence Ratio (ER), and 95% credible intervals (CI).

Parameter (Effect compared to reference conditions)	Estimate (Slope)	PP Posterior Probability	ER Evidence Ratio	IC 95% Credible Intervals
Relative Interaction Index — RII				
<i>Intercept (Unburned Native Dominance, Native Plant)</i>	0.19	0.97*	38.74	[0.00, 0.39]
Invasive Dominance	0.05	0.64	1.79	[-0.25, 0.34]
Species	0.10	0.80	3.90	[-0.13, 0.33]
<i>Fire</i>	0.20	0.95	20.82	[-0.04, 0.43]
Invasive Dominance × Species	0.22	0.92	11.05	[-0.10, 0.54]
Invasive Dominance × Fire	-0.09	0.69	2.19	[-0.44, 0.27]
Species × Fire	0.23	0.90	8.60	[-0.14, 0.58]
Invasive Dominance × Species × Fire	-0.25	0.87	6.97	[-0.69, 0.18]
Relative Yield Total (RYT)				
Intercept (Unburned Native Dominance, Native Plant)	0.29	0.71	2.43	[-0.75, 1.32]
Invasive Dominance	-0.08	0.58	1.39	[-0.90, 0.69]
Species	0.31	0.78	3.52	[-0.46, 1.10]
Fire	0.08	0.57	1.34	[-0.73, 0.89]
Invasive Dominance × Species	0.02	0.53	1.11	[-0.52, 0.57]
Invasive Dominance × Fire	-0.04	0.55	1.25	[-0.59, 0.49]
Species × Fire	0.16	0.72	2.59	[-0.39, 0.72]
Invasive Dominance × Species × Fire	0.01	0.52	01.08	[-0.38, 0.40]

4 DISCUSSION

Wildland fires have become more frequent and intense (Cunningham et al., 2024), resulting in increasingly larger burned areas in many natural regions worldwide (Burton et al., 2024). Although fire is a crucial ecological factor in many ecosystems (Pausas & Keeley, 2014), the increasing frequency and intensity of fires, largely attributed to climate change (Jones et al., 2024), have been associated with the spread of Invasive Alien Plant Species (IAPS) (Kerns et al., 2020; Roy et al., 2024). Our results reveal that the post-fire success of an invasive grass is not absolute but is critically contingent on its pre-disturbance dominance. We demonstrated that the competitive advantage of *Urochloa arrecta* was not driven by inherently superior biomass production, but by a more effective regenerative strategy that actively suppressed the native species' resprouting capacity. This effect, however, was only actualised when the IAPS was already dominant, highlighting that priority effects and propagule pressure—not fire alone—are the decisive drivers of post-disturbance community assembly in this system. Such interactions highlight how altered disturbance regimes can amplify the impact of biological invasions, with significant implications for ecosystem management and biodiversity conservation (Gaertner et al., 2014; Valliere et al., 2024).

Post-disturbance resprouting capacity is a key ecological trait that determines competitive success, enabling particular species to capture resources rapidly and occupy space (Kelly et al., 2020; Cornwall, 2022). Our analysis indicates that the IAPS *Urochloa arrecta* possesses a more effective post-fire regeneration strategy than the NPS *Hemarthria altissima*, albeit in a context-dependent manner. While the time to sprouting onset in monoculture was not credibly different, the presence of the IAPS imposed a significant burden on the NPS. Under invasive dominance, the NPS's sprouting time was credibly prolonged (Estimate: +1.03 days). The IAPS's advantage became even clearer in sprout production, where, under its dominance, it credibly increased its number of sprouts (Estimate: +1.21) while the NPS suffered a credible reduction (Estimate: -1.19). This superior regenerative success, a trait frequently associated with invasion success (Rosalem et al., 2024), confers a crucial advantage for post-disturbance recolonisation (Moore et al., 2019).

IAPS dominance is recognised as a critical factor influencing regeneration dynamics, partly due to its relationship with the below-ground bud bank that enhances resprouting (Klimešová & Klimeš, 2007; Cowan et al., 2023). Our results unequivocally demonstrate this principle. The regenerative advantage of the IAPS was most evident when comparing dominance scenarios: when the IAPS was dominant (in monoculture or at invasive dominance —75% of IAPS), its individuals produced, on average, more than double the number of sprouts (approximately 2.8) compared to when the native was dominant (approximately 1.2 sprouts under 25% of IAPS). This difference, supported by statistically credible interactions, suggests that the IAPS requires a dominance threshold to ensure its rapid recovery after fire. Such findings imply that if IAPS are not controlled before fire events, they can gain a disproportionate advantage, allowing them to dominate the regenerating community (Brooks et al., 2004; Slingsby et al., 2017).

Community assembly is strongly influenced by priority effects, wherein the arrival timing and establishment history of species determine their competitive success and shape subsequent community

structure (Fukami, 2015; Vannette & Fukami, 2014). Our findings provide a compelling illustration of this principle in a post-disturbance context. The gradient of IAPS dominance acted as a proxy for historical priority effects, and the post-fire regeneration outcomes were critically contingent upon this initial condition. The ability of the established dominant species—whether NPS or IAPS—to suppress the regenerative output of its competitor demonstrates that the system's resilience to disturbance is not an intrinsic property, but rather is driven by the pre-existing biotic context. For the IAPS, achieving dominance before the fire was fundamental to leveraging its regenerative traits, thereby reinforcing its incumbency and increasing the likelihood of locking the community into an invaded state.

Furthermore, the success of biological invasions is often directly linked to propagule pressure—the number of individuals introduced to a new environment (Lockwood et al., 2005; Simberloff, 2009). Our experimental design, by manipulating the initial dominance levels, effectively tested the role of varying propagule pressure in the face of disturbance. The results clearly indicate that the IAPS's ability to capitalise on the fire event was dependent on high initial propagule pressure. When established at high density (i.e., in the invasive dominance and monoculture treatments), the IAPS successfully translated the post-fire opportunity into enhanced regeneration. Conversely, at low propagule pressure (i.e., the native dominance treatment), its regenerative capacity was credibly suppressed. This suggests that while fire can create an invasion window (Davis et al., 2000), high propagule pressure is the necessary force for the IAPS to pass through it, overcome biotic resistance from the established native community, and ultimately achieve post-disturbance dominance.

The response of plant biomass to disturbances can be complex, reflecting both species' traits and changes in resource availability (Hobbs & Huenneke, 1992). Fire, for instance, can mineralise nutrients and increase productivity (Bodí et al., 2014; Araujo et al., 2025). Our results illustrate this complexity. The NPS, in isolation, responded well to fire, with a credible increase in biomass in monoculture (Estimate: +1.1 g). Analysing biomass production across different competition scenarios (without fire), a clear trend emerges: when the IAPS was dominant, it produced on average 35% more biomass than when the native was dominant. However, it is crucial to note that the interactions driving this difference were not statistically credible. Therefore, the competitive advantage of the IAPS appears to lie less in inherently superior biomass production and more in its ability to suppress NPS regeneration, thereby more effectively capitalising on post-fire resources, a key mechanism that facilitates IAPS persistence (Pausas & Keeley, 2014).

Biomass allocation is a fundamental adaptive strategy for survival in variable environments (Pausas et al., 2017). In our study, both species already prioritised root allocation before the fire, a common strategy in perennial grasses. Notably, the IAPS exhibited an even greater allocation to roots, with a credibly lower shoot/root ratio than the NPS. After the fire, a non-credible trend towards greater root investment was observed, consistent with the need to support regrowth. Interestingly, a credible interaction revealed that the IAPS plastically adjusted its strategy, increasing its shoot/root ratio under native dominance. This flexibility in allocation, combined with a substantial investment in below-ground reserve structures,

suggests a mechanism by which the IAPS optimises resource capture and resilience more effectively than the NPS (Klimešová & Klimeš, 2007; Pausas & Keeley, 2014; Pausas et al., 2018).

The nature of interspecific interactions can be profoundly altered by environmental disturbances (Holmgren & Scheffer, 2010). In our experiment, the analysis of the Relative Yield Total (RYT) revealed no credible effects, indicating that the productivity of mixed communities did not differ significantly from what was expected from the monocultures. The Relative Interaction Index (RII) revealed a fundamental and unexpected dynamic. Under native dominance and without fire, the NPS experienced credible facilitation (Intercept Estimate: 0.19). Under native dominance and without fire, the NPS experienced credible facilitation (Intercept Estimate: 0.19). Fire showed a strong tendency to intensify this positive interaction, although the effect was not fully credible. Therefore, the main narrative is not a shift from competition to facilitation induced by fire, but rather a baseline condition of facilitation for the NPS that fire tends to amplify. While the mechanisms underlying this facilitative interaction were not directly tested, we speculate that they may arise from non-competitive processes. For instance, the presence of IAPS, even at low abundance, may have improved soil structure or ameliorated microclimatic stressors, such as soil surface temperature, thereby indirectly benefiting the NPS. Such positive interactions, often overlooked in invasion studies, can be critical in shaping community dynamics, especially under the controlled, resource-abundant conditions of our experiment. Untangling the net effect of these simultaneous competitive and facilitative interactions presents a crucial avenue for future research.

Globally, it is well established that disturbances can weaken biotic resistance and create “invasion windows” (Davis et al., 2000), favouring species with rapid growth and high regenerative capacity (Pausas & Keeley, 2014). This synergy, where IAPS not only tolerate fire but are actively favoured by it, especially when already present, can lead to rapid increases in IAPS dominance, threatening native plant communities. In wetland ecosystems, such shifts are particularly alarming, as they can alter hydrological regimes, reduce habitat suitability for specialist fauna, and compromise vital ecosystem services, such as water purification and carbon sequestration (Zedler & Kercher, 2004), further underscoring the urgency for effective management strategies.

Although our findings are based on the interaction between *Urochloa arrecta* and *Hemarthria altissima*, and focus on early post-fire trajectories, they serve as a critical case study that elucidates a specific mechanism: the IAPS's advantage stems not necessarily from superior biomass production, but from its ability to regenerate rapidly and, crucially, to suppress the resprouting capacity of the NPS, especially when already dominant. While the precise direction and magnitude of the outcomes are inherently species-specific, the principle that pre-disturbance dominance dictates post-fire regenerative success by mediating priority effects is likely a key, and potentially generalizable, driver in other invaded systems susceptible to fire. This study contributes to the global understanding by demonstrating that even an NPS with some recovery capacity can be outpaced when an IAPS capitalises more effectively on post-disturbance conditions. Crucially, long-term monitoring programs in burned and unburned invaded wetlands are essential for tracking community changes over decadal timescales and assessing the ultimate persistence of fire-mediated shifts in dominance. Addressing these research avenues will

deepen our understanding of fire-invasion feedbacks and improve our capacity to manage these complex and increasingly prevalent challenges in a rapidly changing world.

Finally, our findings have critical implications in the context of global change. The increase in fire activity, driven by climate, is a reality in diverse biomes (IPCC, 2023). The regenerative advantage of IAPS, facilitated by fire, may represent a globally consistent mechanism that accelerates the loss of native biodiversity and the transition of ecosystems to invasive-dominated states (Brooks et al., 2004; Vilà et al., 2011). As fire regimes intensify, vulnerable ecosystems, such as those dominated by grasses, may be particularly susceptible to this dynamic, especially when the pre-disturbance dominance of IAPS is already substantial.

5 CONCLUSION

Understanding how climate-driven fire regimes accelerate the dominance of IAPS through competitive and facilitative interaction strategies is crucial. In conclusion, this study demonstrates that the interaction between fire and pre-existing dominance, rather than fire alone, is a critical driver of post-disturbance community assembly in invaded wetland ecosystems. Our findings reveal that the competitive advantage of the invasive alien grass *Urochloa arrecta* is not derived from inherently superior biomass production, but from a more effective regenerative strategy that is actualised only under conditions of high initial abundance. This mechanism, which involves suppressing the native species' resprouting capacity, underscores the pivotal roles of priority effects and propagule pressure in determining the outcome of disturbance. The discovery of baseline facilitation between the species further complicates simple competitive assumptions and underscores the context-dependent nature of plant interactions. In this instance, our findings reinforce the importance of controlling IAPS in advance of fire events; once an IAPS reaches high dominance, post-fire restoration may not be successful.

Declarations

AUTHOR CONTRIBUTIONS

Larissa Carrara, Amanda C. Stuermer, Roger P. Mormul and Bruno R. S. Figueiredo conceived the ideas and elaborated the experimental design and methods; Larissa Carrara, Amanda C. Stuermer and Bruno R. S. Figueiredo were involved in project administration; Larissa Carrara and Amanda C. Stuermer collected the data; Larissa Carrara and Dieison A. Moi curated the data; Larissa Carrara analysed the data; Larissa Carrara, Dieison A. Moi, Roger P. Mormul and Bruno R. S. Figueiredo interpreted the results; Larissa Carrara, Amanda C. Stuermer and Bruno R. S. Figueiredo wrote the original draft; all authors contributed to the writing, reviewing and editing of the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors acknowledge financial support for research provided by the Foundation for Research and Innovation of the State of Santa Catarina, FAPESC, Protocol n°: PJP2021321000109. We also thank the team from the Laboratory of Freshwater Biodiversity at UFSC (particularly Apolo A. Egeu, Luiz A. F. Fernandes, and Sabrina Suominsky) for their valuable assistance in the experiments. D.A.M. received a postdoctoral grant from FAPESP (Process Number 2022/13301-8).

FUNDING INFORMATION

The authors declare that they have no conflict of interest. The funders had no role in the design of the study, the collection, analysis, or interpretation of data, the writing of the manuscript, or the decision to publish the results.

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Figures

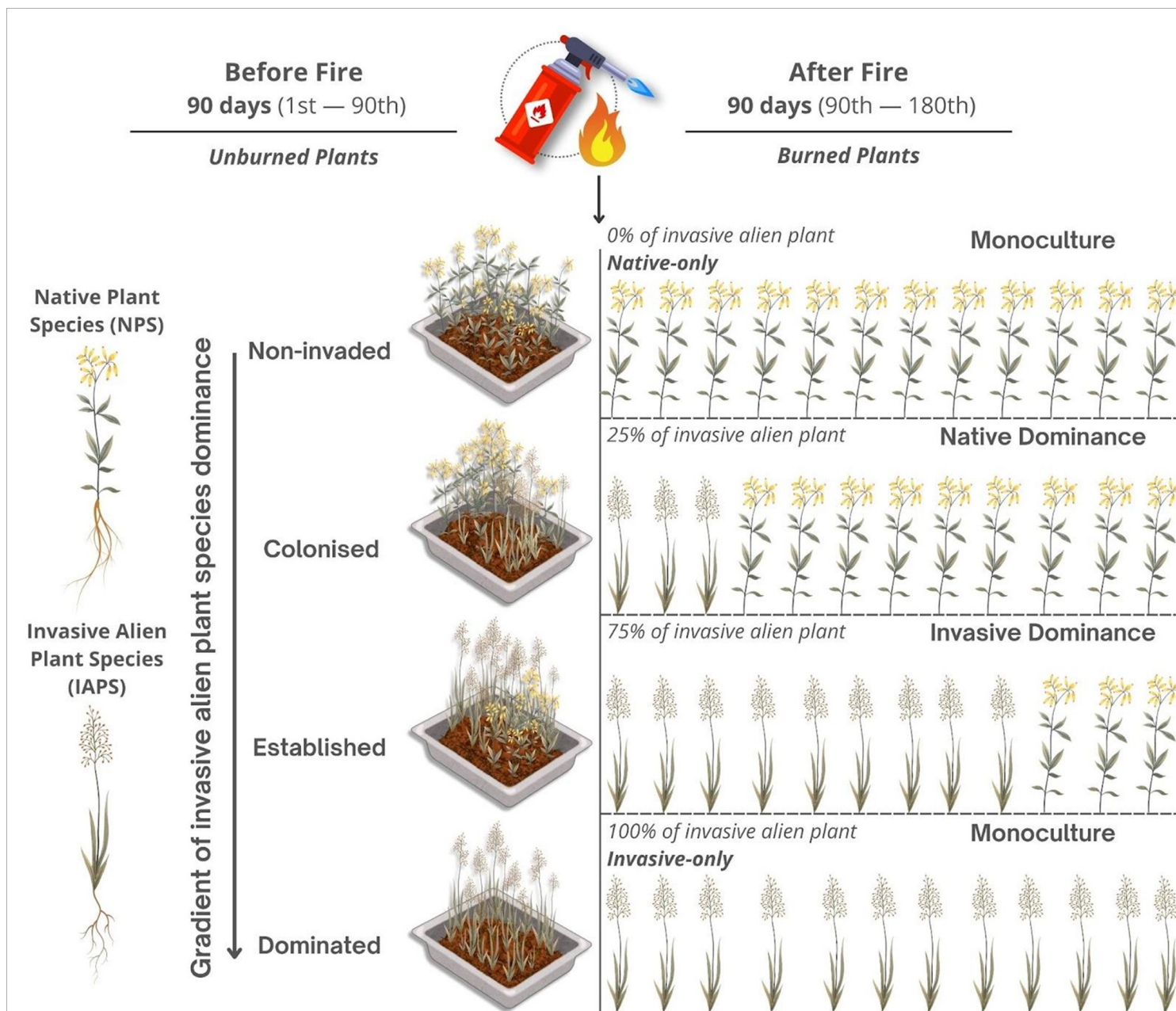


Figure 1

Schematic illustration of the experimental design assessing the performance of *Urochloa arrecta* (IAPS) and *Hemarthria altissima* (NPS) before and after a fire over a gradient of IAPS dominance and competition representing four key stages of invasion: ‘Non-invaded’ with 0% of invasive alien plant, ‘Colonised’ with 25% of invasive alien plant, ‘Established’ with 75% of invasive alien plant, and ‘Dominated’ with 100% of invasive alien plant. The experiment lasted 180 days and was divided into two phases of 90 days each: before (unburned plants) and after the fire (burned plants).

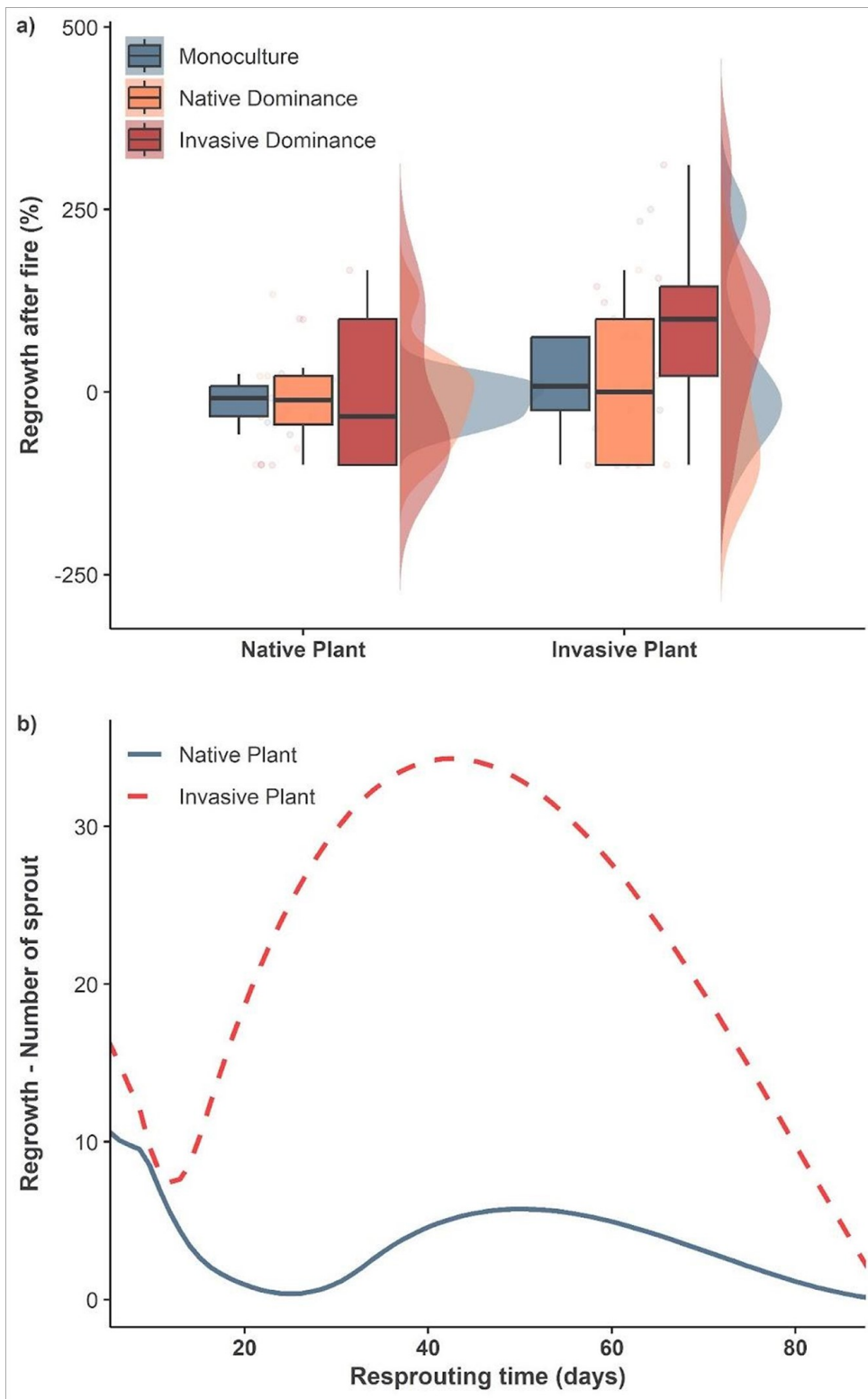


Figure 2

(a) Relationship between regrowth percentage after fire (proportion of observed sprouts relative to planted propagules, expressed as a percentage and the gradient of IAPS dominance: monoculture, native dominance, and invasive dominance. (b) Relationship between the number of sprouts and sprouting time for Invasive Alien Plant Species (IAPS; red dashed line) and Native Plant Species (NPS; blue solid line),

modelled by local polynomial regression under monoculture, native dominance, and invasive dominance conditions. NPS are shown in blue with a solid line, while IAPS are shown in red with a dashed line.

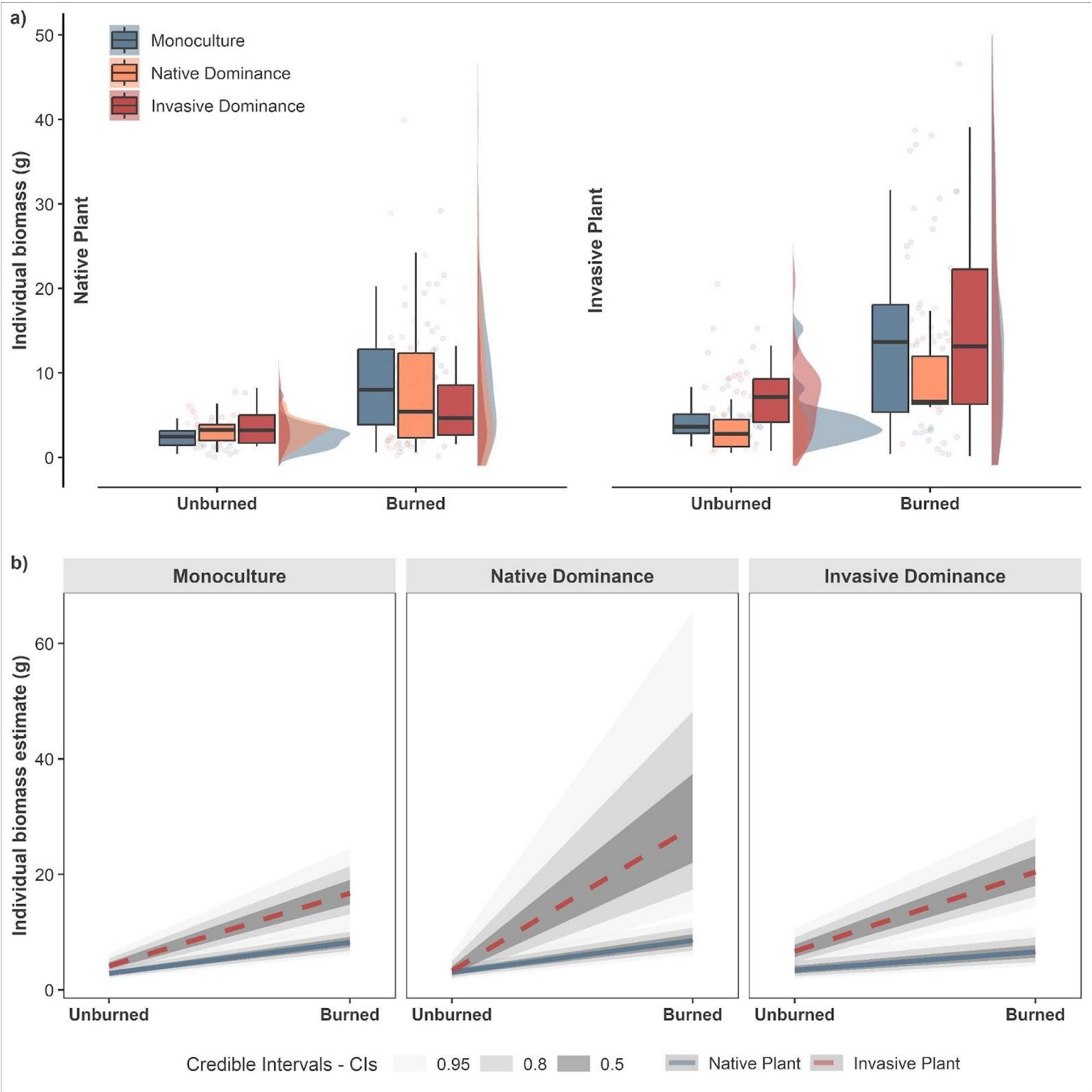


Figure 3

(a) Median individual biomass of *Urochloa arrecta* (IAPS) and *Hemarthria altissima* (NPS) is shown comparing unburned conditions before fire (left side of comparison) and burned conditions after fire (right side of comparison). These comparisons are made across a gradient of initial IAPS dominance levels (0%, 25%, 75%, and 100%). (b) Modelled estimates of individual biomass for *Hemarthria*

altissima(NPS; blue line) and *Urochloa arrecta*(IAPS; dashed red line). Estimates are presented for different experimental treatments (Monoculture, Native Dominance, Invasive Dominance) under both Unburned and Burned fire conditions. Lines indicate the central estimate, while shaded areas represent 50%, 80%, and 95% Credible Intervals (CIs).

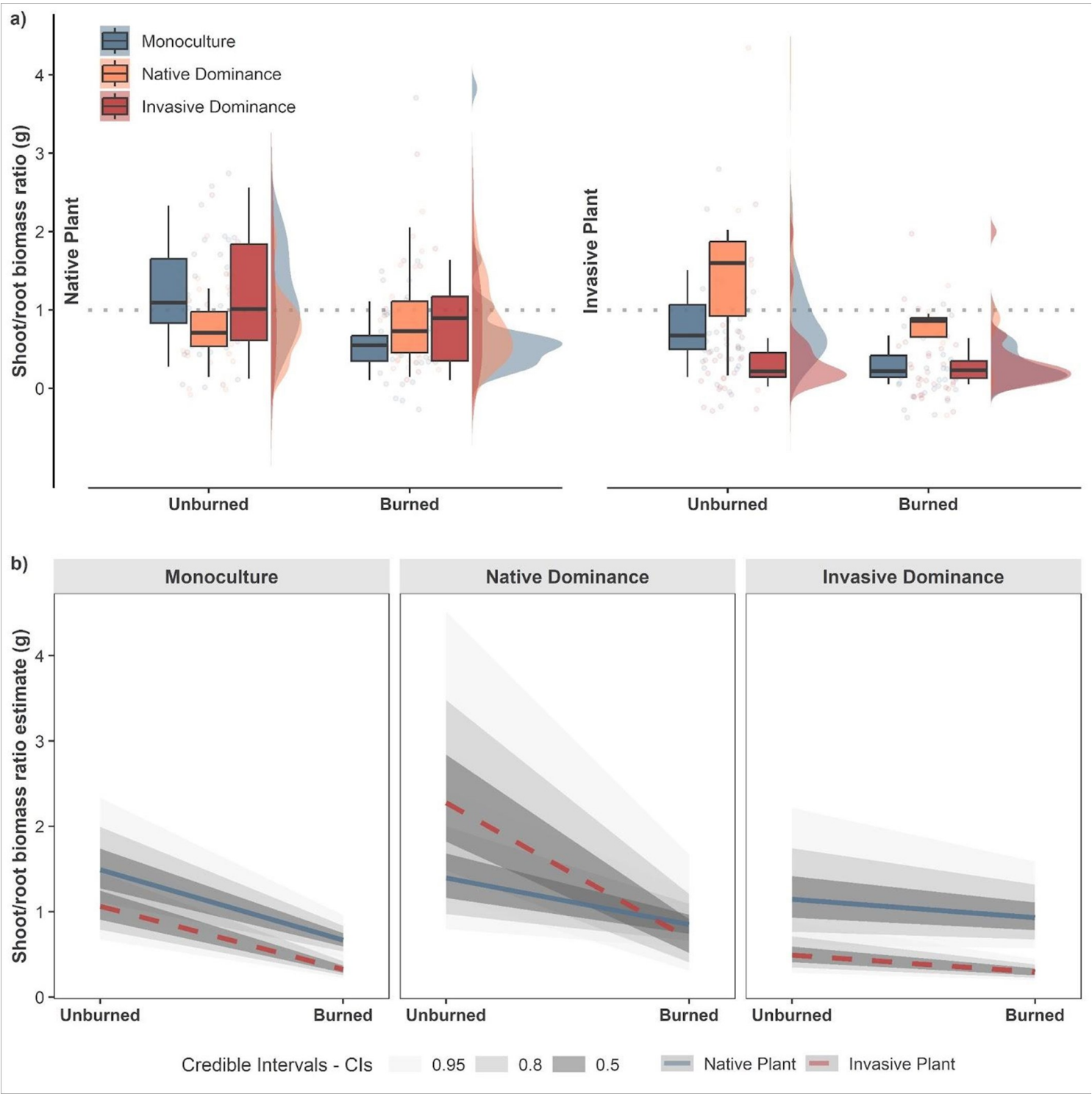


Figure 4

a) Median shoot/root biomass ratio of *Urochloa arrecta* (IAPS) and *Hemarthria altissima* (NPS) is shown comparing unburned conditions before fire (left side of comparison) and burned conditions after fire

(right side of comparison). These comparisons are made across a gradient of initial IAPS dominance levels (0%, 25%, 75%, and 100%). A horizontal line at $y=1$ indicates equal biomass allocation between shoots and roots; values above this line suggest greater allocation to shoots, while values below suggest greater allocation to roots. (b) Modelled estimates of shoot/root ratio for *Hemarthria altissima*(NPS; blue line) and *Urochloa arrecta*(IAPS; dashed red line). Estimates are presented for different experimental treatments (Monoculture, Native Dominance, Invasive Dominance) under both Unburned and Burned fire conditions. Lines indicate the central estimate, while shaded areas represent 50%, 80%, and 95% Credible Intervals (CIs).

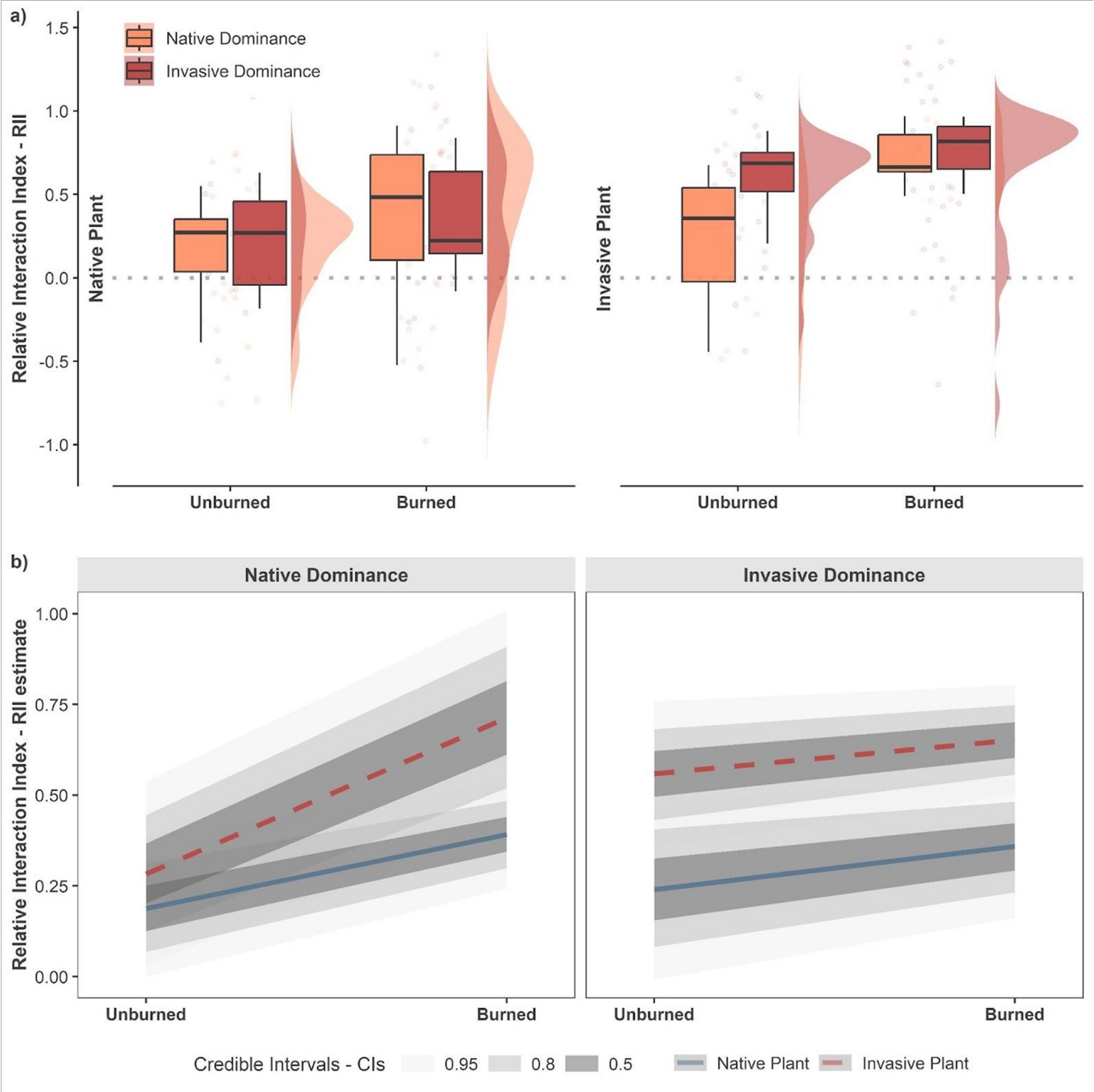


Figure 5

(a) Median of Relative Interaction Index (RII) of *Urochloa arrecta* (IAPS) and *Hemarthria altissima* (NPS) are shown comparing unburned conditions before fire (left side of comparison) and burned conditions after fire (right side of comparison). These comparisons are made across a gradient of initial IAPS dominance levels (25% – native dominance, and 75% – invasive dominance). A horizontal line at $y=0$ indicates neutral interactions; values above this line suggest maximum facilitation (+1), while values below suggest maximum competition (-1). (b) Modelled estimates of Relative Interaction Index (RII) for *Hemarthria altissima* (NPS; blue line) and *Urochloa arrecta* (IAPS; dashed red line). Estimates are presented for different experimental treatments (Native Dominance, Invasive Dominance) under both Unburned and Burned fire conditions. Lines indicate the central estimate, while shaded areas represent 50%, 80%, and 95% Credible Intervals (CIs).

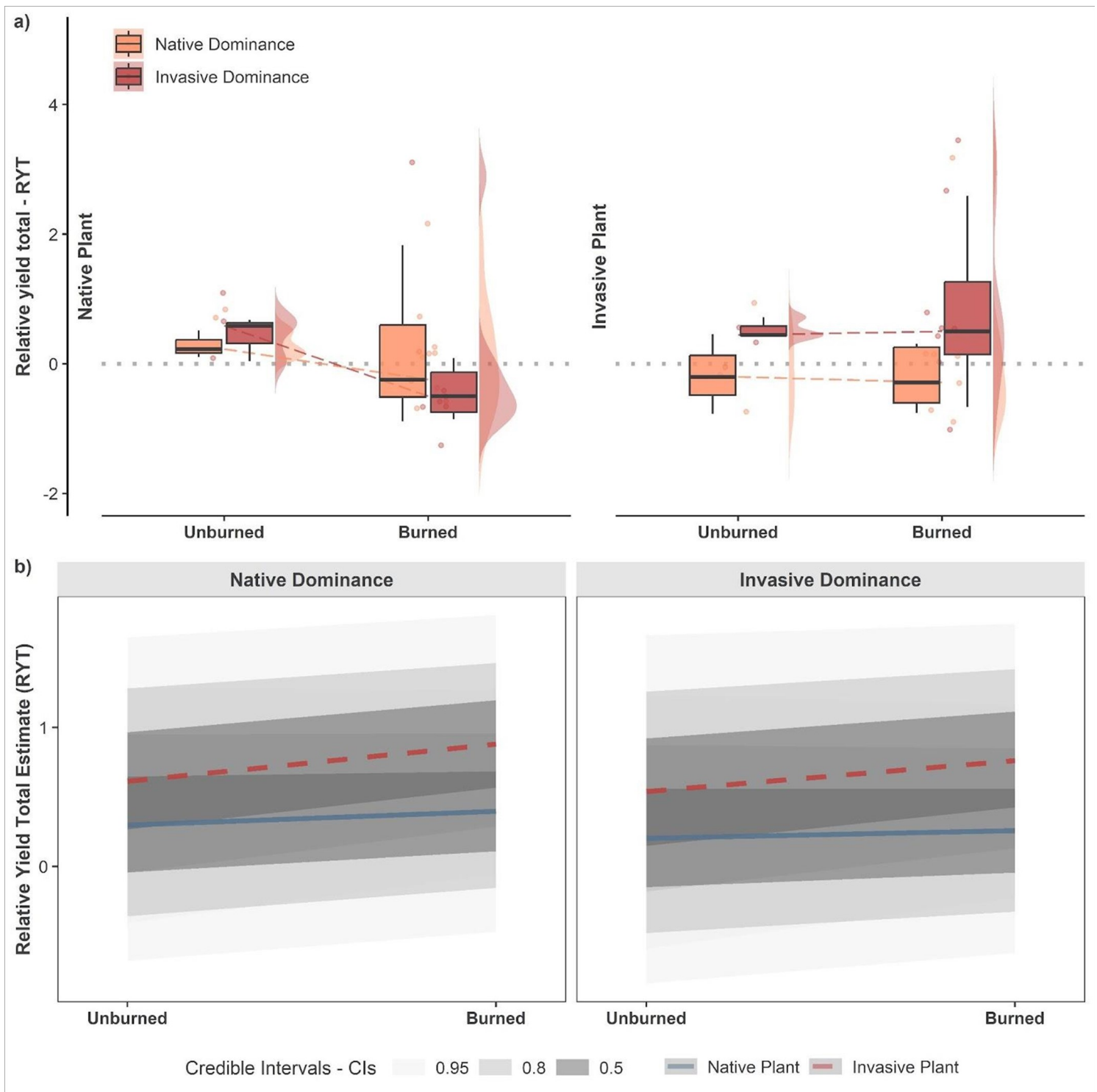


Figure 6

a) Median of Relative Yield Total (RYT) of *Urochloa arrecta* (IAPS) and *Hemarthria altissima* (NPS) are shown comparing unburned conditions before fire (left side of comparison) and burned conditions after fire (right side of comparison). These comparisons are made across a gradient of initial IAPS dominance levels (25% – native dominance, and 75% – invasive dominance). The horizontal dotted line ($y = 0$) indicates the threshold for overyielding (RYT > 0) and underyielding (RYT < 0). Values above this threshold indicate greater biomass production in mixed-species than monocultures, whereas values

below indicate reduced productivity under interspecific competition. (b) Modelled estimates of Relative Yield Total (RYT) for *Hemarthria altissima* (NPS; blue line) and *Urochloa arrecta* (IAPS; dashed red line). Estimates are presented for different experimental treatments (Native Dominance, Invasive Dominance) under both Unburned and Burned fire conditions. Lines indicate the central estimate, while shaded areas represent 50%, 80%, and 95% Credible Intervals (CIs).