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Pre-disturbance dominance, not fire alone, determines the success of an invasive alien plant species

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Abstract

Background Fire is a key ecological disturbance that can facilitate plant invasions, but the mechanisms driving post-disturbance competitive outcomes, especially the role of pre-existing species abundance, remain poorly understood. We conducted a greenhouse experiment using wetland plant species to test how fire and pre-disturbance dominance influence performance and competitive interactions between a widespread invasive alien grass (*Urochloa arrecta*) and a resident native grass (*Hemarthria altissima*). Fire was simulated across a gradient of invasive dominance, including native monoculture (0%), native dominance (25%), invasive dominance (75%), and invasive monoculture (100%), allowing us to assess whether post-fire competitive outcomes depend on initial community composition.

Results The competitive advantage of invasive alien plant species (IAPS) was driven by a superior regenerative strategy rather than by consistently greater biomass production. After fire, IAPS sprout production was critically dependent on its initial dominance, more than doubling under high-abundance conditions. Crucially, high IAPS dominance suppressed the number of native plant species (NPS) sprouts and delayed their emergence. In contrast, at low pre-disturbance abundance, the IAPS exhibited reduced regenerative performance.

Conclusions Our findings show that post-fire invasion success is density-dependent: only when already dominant does the invasive species gain a regenerative advantage by suppressing native sprout production and delaying the native emergence. These results demonstrate that pre-disturbance dominance and vegetative propagule pressure, particularly from the bud bank and clonal vegetative structures, are key mediators of post-disturbance success. Given the increasing global frequency of both fire disturbances and plant invasions, our study provides a mechanistic explanation for why fire promotes invasion under some dominance contexts but not others.

Keywords Biological invasion, Climate change, Disturbances, Fire ecology, Plant fire response, *Urochloa arrecta*, Wetlands

Resumen

Antecedentes El fuego es un disturbio clave que puede facilitar las invasiones de plantas, aunque los mecanismos involucrados y que resultan en relaciones de competencia en el post fuego, en especial el rol que tiene la abundancia de especies preexistentes, son aún muy pobremente comprendidos. Condujimos un experimento de vivero usando plantas de humedales para probar como el fuego y la dominancia de plantas en el pre-disturbio influyen

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la performance y las interacciones competitivas entre un pasto exótico ampliamente invasor (*Urochloa arrecta*) y uno nativo (*Hemarthria altissima*). El fuego fue simulado a través de un gradiente de dominancia invasora, incluyendo la monocultura del nativo (0%), dominancia del nativo (25%), dominancia de la invasora (75%), y monocultura de la invasora (100%), permitiéndonos determinar si los resultados de la competencia dependen de la composición inicial de la comunidad.

Resultados La ventaja competitiva de la planta invasora exótica (IAPS) fue dada por su estrategia regenerativa superior y no por su consistentemente mayor producción de biomasa. Luego del fuego, la producción de rebrotes de IAPS fue críticamente dependiente de su dominancia inicial, más que duplicándola bajo condiciones de alta abundancia. Crucialmente, la alta dominancia de IAPS suprimió el número de rebrotes de la planta nativa (NPS) y demoró su emergencia. En contraste, a baja abundancia en el pre-disturbio, la IAPS exhibió una performance regenerativa reducida.

Conclusiones Nuestros resultados muestran que el éxito de la invasión en el post fuego es densidad dependiente: solo cuando es dominante, la especie invasora gana una ventaja regenerativa mediante la supresión en la producción de rebrotes, demorando la emergencia de la nativa. Estos resultados demuestran que la dominancia en el pre disturbio y la presión de los propágulos vegetativos, particularmente del banco de brotes y estructuras clonales vegetativas, son mediadores claves en el éxito en el post disturbio. Dado el incremento en la frecuencia global de disturbios por fuego y las invasiones de plantas, nuestro estudio provee de una explicación mecanística por la cual el fuego promueve la invasión bajo algunos contextos de dominancia, pero no en otros.

Introduction

Disturbances are fundamental components of ecosystems, shaping their structure, composition, and functioning across spatial and temporal scales (Sousa 1984; Burton et al. 2020; Lázaro-Lobo et al. 2023). Among these disturbances, wildland fires play a particularly important ecological role by rapidly altering vegetation structure, resource availability, and competitive interactions among plant species (Pausas & Keeley 2014; Kelly et al. 2020). Fire events can open recruitment windows by removing aboveground biomass and modifying soil properties through the deposition of ashes rich in organic and inorganic compounds (Sánchez-García et al. 2023; Araujo et al. 2025), thereby creating transient conditions that favor species capable of rapid establishment or regeneration during early successional stages (Bengtsson et al. 2023; Jo et al. 2024). In fire-affected environments, invasive alien plant species (IAPS) may gain particular advantages when they possess traits such as fast growth or strong resprouting ability (Hobbs & Huenneke 1992; Davis et al. 2000; Burton et al. 2020; Tangney et al. 2022; Roy et al. 2024; Valliere et al. 2024). Such regeneration-mediated advantages may be especially pronounced in wetland ecosystems, where plant communities are often dominated by clonal aquatic macrophytes that rely heavily on vegetative propagation and rapid post-disturbance regrowth (Santamaria 2002; Thomaz 2022).

The interaction between fire and invasion dynamics has been extensively documented in fire-prone ecosystems. For instance, in North American semi-arid shrublands, invasive grasses can generate self-reinforcing fire cycles that facilitate their transition to dominance (Kerns et al. 2020). Similarly, in fire-dependent ecosystems such as the

Brazilian Cerrado, invasive African grasses exploit post-fire resource pulses to outcompete native flora (Pilon et al. 2021). These studies demonstrate that fire can act as a powerful driver of invasion by altering competitive balances and creating feedbacks that favor invasive species. However, whether similar mechanisms operate in fire-sensitive wetland ecosystems remains poorly understood, particularly in communities dominated by competitive clonal species. In these aquatic-terrestrial transition zones, where recovery relies heavily on vegetative regrowth from belowground bud banks and clonal fragments, the extent to which pre-disturbance dominance shapes post-fire recovery and competitive outcomes remains a key unresolved question.

Although disturbance can create opportunities for plant establishment, it does not necessarily determine which species ultimately dominate post-disturbance communities. Instead, invasion success after disturbance often depends on additional ecological factors, including vegetative propagule pressure (e.g., bud bank and clonal fragments), species-specific regenerative traits, and priority effects arising from differences in initial abundance (Seabloom et al. 2003; Lake & Leishman 2004; Lembrechts et al. 2016; Roy et al. 2024; Jo et al. 2024). Species capable of rapid vegetative regeneration may gain a competitive advantage during early post-disturbance succession (Michelan et al. 2013; Weiser et al. 2016; Fares et al. 2020; Cornwall 2022). In many cases, IAPS can also modify disturbance regimes themselves, for example, by increasing fuel loads and promoting more frequent or intense fires, thereby generating positive invasion–fire feedbacks that reinforce their dominance (Gaertner et al. 2014; Cornwall 2022).

Despite this growing body of evidence, it remains unclear whether post-fire invasion success in clonal wetland systems is driven primarily by disturbance effects per se or by pre-existing differences in species dominance and regenerative capacity that determine competitive recovery after fire.

Pre-disturbance species dominance may play a critical role in determining plant community recovery following disturbance. When IAPS are already abundant within a community, disturbances may reinforce their dominance by favoring rapid regrowth and resource capture during early post-disturbance succession. Conversely, disturbances occurring during the early stages of invasion, when IAPS remain at low abundance, may allow NPS to maintain competitive resistance (Omer et al. 2022). These dynamics are particularly relevant in ecosystems dominated by clonal plants, where regeneration frequently depends on belowground bud banks. In such systems, higher pre-disturbance abundance may correspond to a larger reservoir of dormant buds, enhancing resprouting potential after disturbances such as fire, flooding, or mechanical damage (Klimešová & Klimeš 2007; Cowan et al. 2023). Despite extensive research on fire disturbances and plant invasions (e.g., Brooks et al. 2004; Prev  y et al. 2024), little is known about how pre-disturbance dominance and fire interact to influence the regenerative capacity and competitive outcomes between native and invasive plant species. This gap is especially relevant in communities dominated by clonal plants, where recovery often depends on vegetative regeneration rather than seed recruitment, potentially leading to competitive outcomes that differ from those documented in seed-driven systems.

To investigate how pre-disturbance dominance shapes post-fire recovery dynamics, we used a representative wetland system from the Atlantic Forest in southern Brazil, where the globally invasive grass *Urochloa arrecta* co-occurs with the widespread perennial grass *Hemarthria altissima* (Kawakita et al. 2018). As both grass species reproduce clonally and can regenerate rapidly, this system provides a suitable framework for examining how initial abundance influences competitive recovery after disturbance. We experimentally tested how fire and pre-disturbance dominance interact to determine the performance of invasive and native species. We hypothesized that: (i) the invasive species exhibits a superior regenerative response after fire; (ii) this advantage is density-dependent, increasing with invader dominance; and (iii) native resistance occurs primarily when the invader is initially rare. These predictions are grounded in evidence that invasive species often recover more rapidly following disturbance and that greater pre-disturbance abundance can enhance resprouting capacity via larger belowground

bud banks (Michelan et al. 2013; Matula et al. 2019; Fares et al. 2020).

Materials and methods

Studied species and sampling

The experiment was conducted in a greenhouse from May to November 2023 (180 days), during which plants grew in trays with water-saturated soil conditions typical of wetlands (water depth of ~2 cm aboveground). We chose a before-and-after design with an intense burn method to simulate fast-moving surface fires typical of some wetland grasslands, focusing on the consumption of aboveground biomass and ash deposition while minimizing deep-soil heating. To assess the effect of fire on plant performance and interactions, considering different pre-disturbance dominance levels, 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.org 2024). We considered *Hemarthria altissima* as a native plant species (NPS) for the purposes of this study, reflecting its long-established, non-invasive role in natural plant communities of South American wetlands, where it contributes as a resident component without evidence of invasive behavior (Ayala & Simon 1914; Hirschhorn 1943; Nabinger et al. 2001; Oliveira & Marquis 2002; Kawakita et al. 2018). Although some taxonomic databases classify this species as introduced in the Americas, early records document its occurrence as part of natural wetland vegetation in South American wetlands prior to systematic forage grass introduction programs, and cytogenetic, molecular, and morpho-anatomical evidence indicates substantial differentiation between African and South American populations supporting the interpretation that South America may form part of its native range or at least reflects a long-standing, independent evolutionary history in the region (Tedesco et al. 1996; Huang et al. 2014; Zhang et al. 2016; see Supplementary Material). Whether these populations represent a native lineage, a very ancient introduction, or an independent evolutionary lineage remains unresolved. Regardless of its ultimate biogeographic origin, *H. altissima* functions, at the very least, as a long-established natural component of many Brazilian wetlands, including in non-managed systems, and we treat it as such throughout this study (Nabinger et al. 2001; Oliveira & Marquis 2002; Kawakita et al. 2016, 2018).

For 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. Both are stoloniferous and rhizomatous, emergent C4 perennial grasses that share similar

morphology and architecture. While *U. arrecta* is characterized by its capacity for rapid vegetative spread, *H. altissima* frequently functions as a dominant in wetland communities. Both act as early colonizers following disturbance and are typical of water-saturated soils along the shorelines of both lotic (lake and river margins) and lentic (floodplains) wetland systems (Nabinger et al. 2001; Oliveira & Marquis 2002; Kawakita et al. 2018); we considered them suitable for interaction and competition studies.

We collected adult individuals of both species from wetland areas adjacent to a stream at the Ressacada Experimental Farm (27°41′06.28″ S; 48°32′38.81″ W), Florianópolis, Santa Catarina, Brazil. The collection sites are characterized by fine, loamy to sandy soils with continuous herbaceous vegetation. The climate in this region is subtropical, with a mean annual temperature of 19.5 °C, annual precipitation sum of 1600 mm, and mean humidity of 84% (Weather Spark 2023). Propagules used in the experiment were obtained from multiple individuals within a natural population. We collected the plants by removing entire individuals from the soil, including the belowground biomass. The native and invasive populations were collected from nearby sites but did not co-occur within the same community; thus, the native population was not invader-experienced. After collection, we cut both species to produce vegetative propagules of similar lengths (17 cm, comprising a 15-cm shoot and a 2-cm root) and weights (mean = 1.12 g, standard deviation $\pm$ 0.37 g). Propagules were randomly assigned across all treatments to scatter any unknown variation and standardized by initial biomass in each tray to mitigate potential differences in parental investment. This procedure mitigates potential initial plant size, allowing for individual comparability (Parepa & Bossdorf 2016; Bando et al. 2016).

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, with species proportions varying according to treatment. Our experimental design simulated a gradient of pre-disturbance species dominance: native monoculture (0% IAPS), native dominance (25% IAPS), invasive dominance (75% IAPS), and invasive monoculture (100% IAPS) (Fig. 1). In the native monoculture treatment, each tray contained 12 NPS vegetative propagules. In the native dominance treatment, trays contained 9 NPS and 3 IAPS vegetative

propagules (75% NPS and 25% IAPS). In the invasive dominance treatment, trays contained 9 IAPS and 3 NPS propagules (75% IAPS and 25% NPS). In the invasive monoculture treatment, each tray contained 12 IAPS propagules. Each treatment consisted of 12 trays, totaling 48 trays, which were randomly arranged within the greenhouse.

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 belowground components were harvested, and the biomass was oven-dried (at 60 °C until constant weight) and weighed (aboveground and belowground). 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). The flame was applied by systematically moving it across each tray's entire aboveground dry biomass for 3 min 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 prioritized over landscape-level burns to ensure treatment uniformity across replicates, thereby isolating the effects of dominance from the inherent heterogeneity of natural fire events.

Following the fire disturbance on day 90, a 2-cm water layer was added to the trays, and the soil remained moist throughout the subsequent 90-day growth period (days 90–180). At the end of this period, plants were harvested, and the sediment was carefully washed away to allow manual disentanglement of individual root systems. Aboveground and belowground components (stems/leaves and roots, respectively) were then separated for each individual plant. All material was oven-dried at 60 °C for approximately 20 days and subsequently weighed using a semi-analytical balance (precision $\pm$ 0.01 g) to assess biomass allocation and performance.

Data collection

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 regrowth success. On day 180 (90 days post-fire,

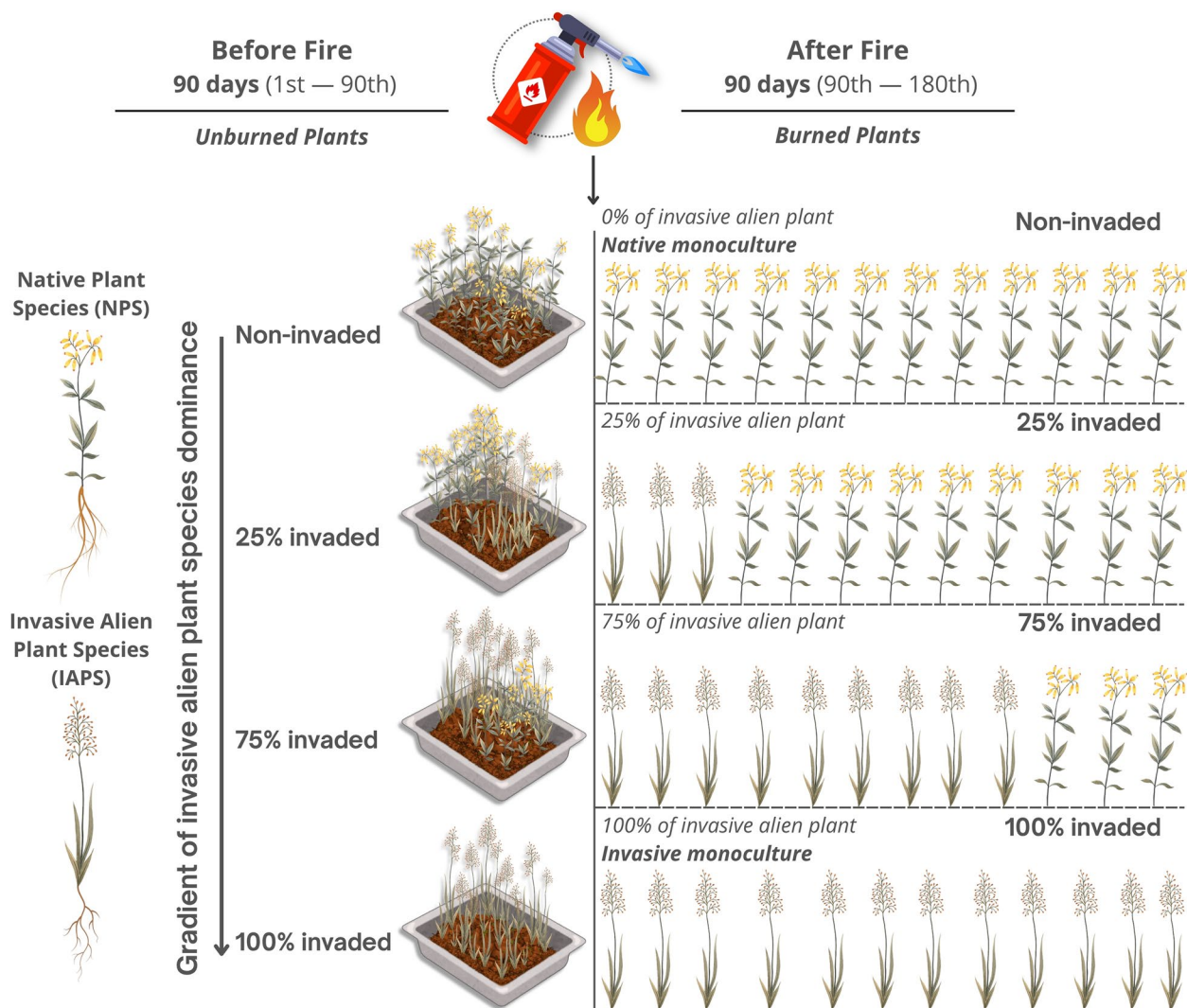


Fig. 1 Schematic representation of the experimental design used to assess the performance of *Urochloa arrecta* (invasive alien plant species, IAPS) and *Hemarthria altissima* (native plant species, NPS) across a gradient of IAPS dominance: native monoculture (0% IAPS), native dominance (25% IAPS), invasive dominance (75% IAPS), and invasive monoculture (100% IAPS), before and after fire. The experiment lasted 180 days and was divided into two 90-day phases: pre-fire (unburned plants) and post-fire (burned plants)

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.

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

We quantified the biomass of each individual (from both IAPS and NPS), which we refer to as “individual biomass.” To characterize the unburned individual biomass (IB_{UB}), we summed the aboveground (AGB_{UB}) and

belowground (BGB_{UB}) biomass of each individual on the 90th day before the fire event.

$$IB_{UB} = AGB_{UB} + BGB_{UB}$$

Also, we summed the aboveground biomass of each individual per tray on the 180th day (after burn, AGB_B) and generated a measurement we termed “net change in root biomass relative to unburned species average” (NCRB). This net change was calculated by subtracting the average dry root biomass of individuals of each species on the 90th day (unburned, BGB_{UB}) from the individual’s dry root biomass on the 180th day (after burn, BGB_B).

$$\text{NCRB} = \text{BGB}_B - \overline{\text{BGB}_{UB}}$$

This approach, using the unburned species average as a standardized baseline because of 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 typical pre-fire conditions. 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 (NCRB) and the above-ground biomass after fire (AGB_B), 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 analyze whether there were any modifications in the biomass allocation between aboveground and belowground tissues before and after fire occurrence (using actual post-fire above- and below-ground biomass for the post-fire ratio).

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

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

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

where $B_{\text{individual_mix}}$ is the individual biomass of a plant of the target species growing in a mixture, and $B_{\text{mono_avg}}$ 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.

Data analysis

All statistical analyses were performed in R (version 4.4.2) using the GLMM structure and a Bayesian modeling 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 2000 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 derived from empirical data and 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 modeled 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 a negative binomial family, and (c) the resprouting time (days until the plants resprout) with a negative binomial family. Fixed effects included the gradient of IAPS dominance (NPS monoculture, NPS dominance, IAPS dominance, and IAPS monoculture) and their interaction. Random intercepts were included for the experimental tray. For biomass production, we modeled individual biomass with the Gamma family (log link). This standardized baseline accounted for the gradient of IAPS dominance variation, allowing us to estimate deviations from typical biomass patterns. Shoot/root ratios were also analyzed to assess allocation changes due to fire and the gradient of IAPS dominance treatments. These models included species identity (NPS vs. IAPS), the IAPS dominance gradient, fire treatment, and their interactions, with nested random intercepts for trays.

To evaluate competitive performance and species interactions, we modeled three indices: the IAPS/NPS biomass ratio (for shoot, root, and individual biomass) and the relative interaction intensity (RII), using a Gaussian family. These indices were modeled 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 between fire and dominance treatments were included. Posterior distributions were used to extract means and 75% uncertainty intervals for all fixed effects. We interpreted effects as significant when the 95% credible interval (CI) did not include zero. A priori hypotheses were tested using the *hypothesis()* function in *brms*, which computes the posterior probability (PP) and corresponding evidence ratio ($\text{ER} = \text{PP}/(1 - \text{PP})$). 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).

To interpret the Bayesian results, we focused on the posterior probability (PP), which represents the probability that an effect exists in the estimated direction. A $PP \geq 0.95$ indicates that there is at least a 95% probability that the effect is strictly positive or negative, which we use as our threshold for statistical significance. We also reported 95% credible intervals (CIs), which indicate the range within which the true parameter value lies with 95% probability. For completeness, the evidence ratio (ER) is provided as a measure of the strength of evidence for the hypothesis vs. the null.

Results

Fire and IAPS dominance effects on resprouting

In line with our first hypothesis, the proportion of sprouts produced per planted propagule after fire (i.e., regrowth) differed between the NPS and IAPS but showed no clear response to dominance treatments alone (Fig. 2). Regrowth of the NPS in monoculture (baseline) was low (5.54%) and showed no consistent change across dominance treatments (+8.06% under invasive dominance; −6.78% under native dominance; credible intervals overlapping zero; Table 1). In contrast, the IAPS exhibited higher regrowth than the NPS, with an estimated increase of +19.72% relative to the baseline. This tendency was more pronounced under invasive dominance (+18.10%) and reduced under native dominance (−4.67%), although these interaction effects were not strongly supported by the model.

In accordance with our second hypothesis, sprouting time of the NPS in monoculture (baseline) began approximately 2.25 days after fire and was significantly delayed under invasive dominance (+1.03 days; 95% credible interval not overlapping zero). A similar delay was observed under native dominance (+0.54 days), although this effect was not strongly supported (95% credible interval overlapping zero). In contrast, sprouting time of the IAPS was comparable to that of NPS in monoculture

(+0.08 days) and showed no consistent response across dominance treatments (−0.88 to +0.89 days).

The number of sprouts revealed clearer differences between species. The NPS produced approximately 2.35 sprouts in monoculture (baseline) and showed a strong reduction under invasive dominance (−1.19; 95% credible interval not overlapping zero). A reduction was also observed under native dominance (−0.54), although this effect was not strongly supported (95% credible interval overlapping zero). In monoculture, the IAPS produced more sprouts than the NPS (+0.47). In addition, the number of sprouts produced by the IAPS showed a clear response to dominance treatments, with fewer sprouts under native dominance (−1.37) and more sprouts under invasive dominance (+1.21; Fig. 2b).

Fire and IAPS dominance effects on biomass production

Contrary to expectations, fire had a positive effect on NPS biomass in monoculture, with an estimated increase of +1.1 g relative to unburned conditions. In line with the predicted competitive potential of the invader, the biomass of the IAPS in unburned monoculture tended to be higher than that of the NPS (+0.4 g), although this effect was not strongly supported (95% credible interval overlapping zero; $PP = 0.91$). Biomass of the NPS under native dominance (+0.1 g) and invasive dominance (+0.2 g) did not differ consistently from monoculture, and no interaction effects on individual biomass were strongly supported (Fig. 3).

For the shoot/root ratio, fire tended to reduce allocation in NPS monoculture (−0.3), although this effect was not strongly supported. In contrast, the IAPS exhibited a significantly lower shoot/root ratio than the NPS in unburned monoculture (−0.8), indicating greater investment in belowground structures. Dominance treatments alone did not affect NPS allocation (−0.1 under native dominance; −0.3 under invasive dominance). However, the species × native dominance interaction was strongly supported (+0.8; Table 2), indicating that the IAPS under native dominance exhibited a higher shoot/root ratio than expected from the main effects alone. No other interaction terms were strongly supported (Fig. 4).

(See figure on next page.)

Fig. 2 **a** Regrowth percentage after fire (proportion of observed sprouts relative to planted propagules) along a gradient of invasive alien plant species (IAPS) dominance, ranging from native monoculture (0% IAPS) to invasive monoculture (100% IAPS), including native dominance (75% native and 25% IAPS propagules) and invasive dominance (75% IAPS and 25% native propagules). **b** Relationship between sprout number and sprouting time for invasive alien plant species (IAPS; red dashed line) and native plant species (NPS; blue solid line), based on linear regression models across the same dominance gradient

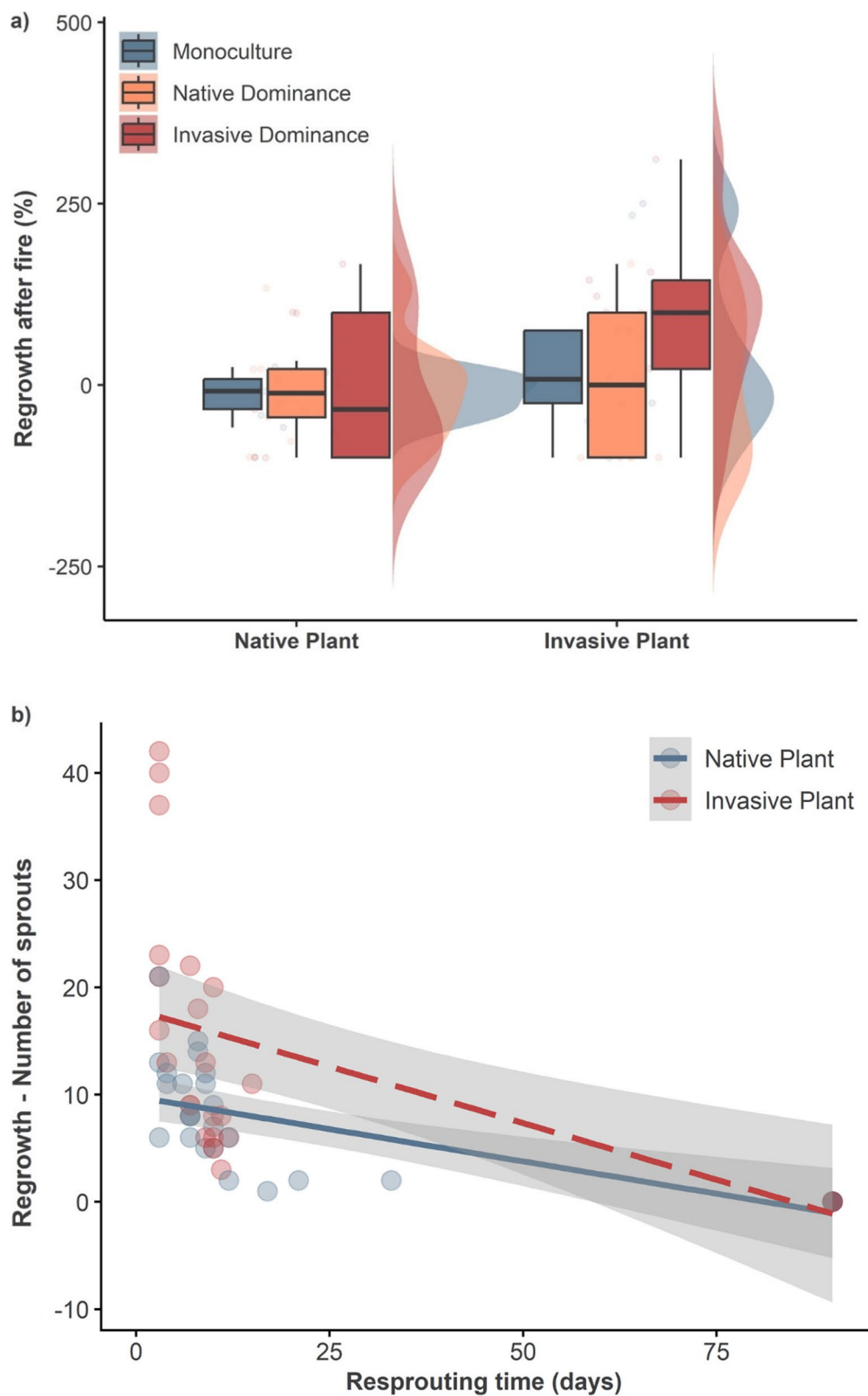


Fig. 2 (See legend on previous page.)

Table 1 Posterior summary statistics from a Bayesian model evaluating the effects of species identity (native plant species [NPS] vs. invasive alien plant species [IAPS]) and a gradient of IAPS dominance, ranging from native monoculture (0% IAPS) to invasive monoculture (100% IAPS), including native dominance (75% native and 25% IAPS propagules) and invasive dominance (75% IAPS and 25% native propagules), on three response variables in burned plants: regrowth (%), sprouting time (days), and number of sprouts. The intercept represents the reference baseline (NPS in monoculture), and parameter estimates correspond to effect sizes relative to this baseline (i.e., differences rather than raw means). Estimates (posterior means) are presented with their posterior probability (PP), evidence ratio (ER), and 95% credible intervals (CI). Effects are considered statistically credible when the 95% CI does not overlap zero and $PP \geq 0.95$ and are indicated by an asterisk (*)

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)				
Intercept (monoculture, native plant)	2.25	1.00*	599	[1.58, 2.93]
Native dominance	0.54	0.87	6.63	[−0.41, 1.49]
Invasive dominance	1.03	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)				
Intercept (monoculture, native plant)	2.35	1.00*	599	[1.81, 2.93]
Native dominance	−0.23	0.72	2.54	[−1.02, 0.58]
Invasive dominance	−1.19	1.00*	284.71	[−2.05, −0.35]
Species	0.47	0.89	8.17	[−0.29, 1.23]
Native dominance × species	−1.37	0.99*	85.96	[−2.49, −0.22]
Invasive dominance × species	1.21	0.99*	67.97	[0.13, 2.30]

Fire and IAPS dominance effects on the competitive performance of NPS

Supporting our third hypothesis regarding native resistance at low initial invader dominance, the relative interaction index (RII) under unburned native-dominance conditions (intercept) showed a positive value (0.19), with strong statistical support, indicating a positive competitive performance of the NPS under low IAPS abundance. Neither the shift to invasive dominance (+0.05) nor species identity (IAPS vs. NPS; +0.10) produced strongly supported changes in RII, as their 95% credible intervals overlapped zero.

In line with our first hypothesis that fire alters competitive outcomes, fire showed a strong tendency to increase RII (+0.20; Fig. 5). However, although the posterior probability was high, the 95% credible interval slightly overlapped zero, indicating that this effect was not strongly supported. Similarly, none of the interaction terms showed clear effects on RII. The two-way interactions between invasive dominance and species

identity (+0.22) and between species identity and fire (+0.23) suggested positive trends, but their 95% credible intervals also overlapped zero. Likewise, the invasive dominance × fire interaction (−0.09) and the three-way interaction among invasive dominance, species identity, and fire (−0.25) showed no consistent influence on RII (Table 3).

Discussion

Wildland fires have become more frequent and intense (Cunningham et al. 2025), resulting in increasingly large, burned areas across many natural regions worldwide (Burton et al. 2024). Although fire is a key ecological driver in numerous ecosystems (Pausas & Keeley 2014), its intensification, largely attributed to climate change (Jones et al. 2024), has been associated with the spread of invasive alien plant species (Kerns et al. 2020; Roy et al. 2024). Our results reveal that post-fire invasion success is not driven by disturbance alone; instead, it is critically contingent on pre-disturbance

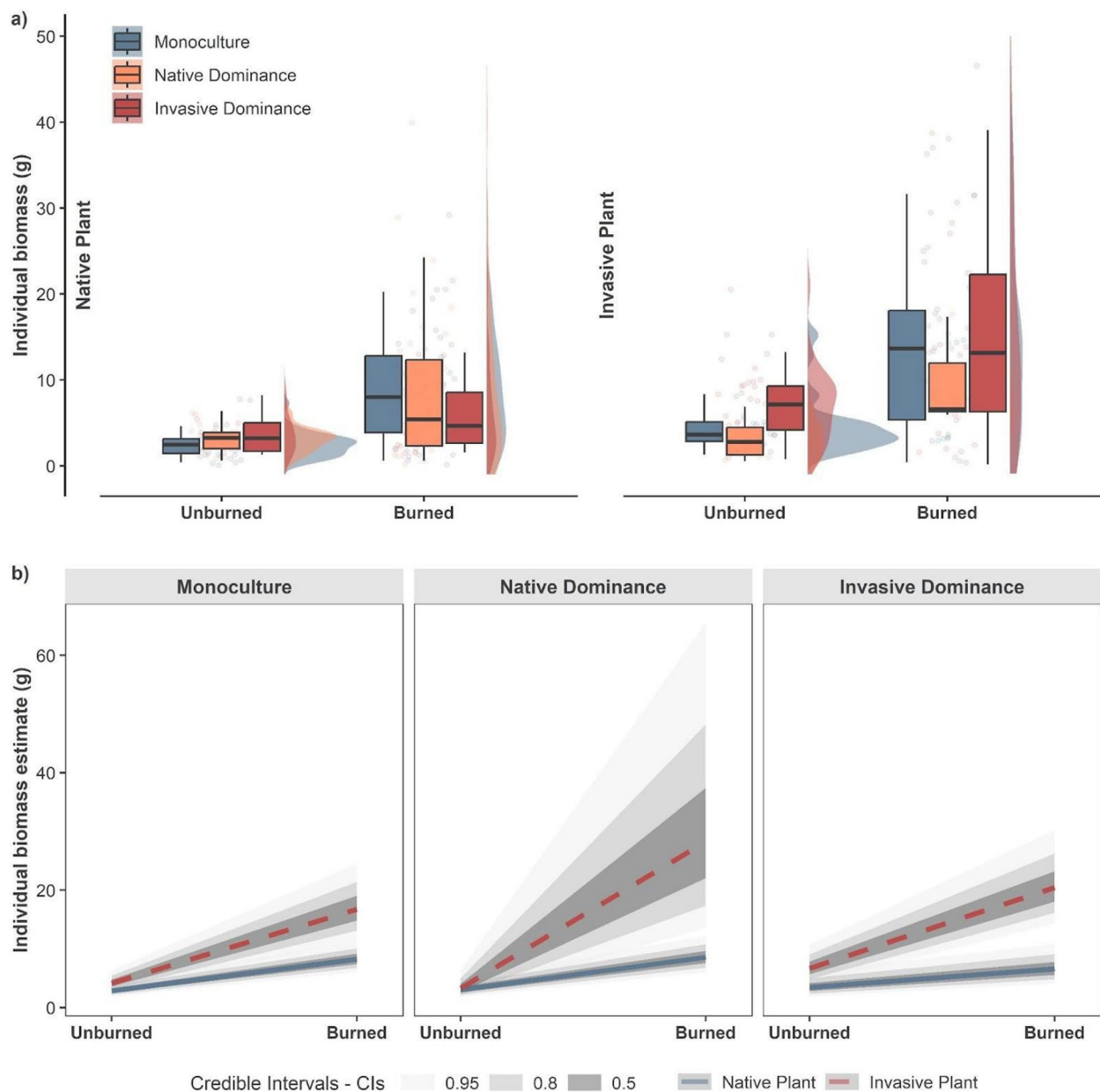


Fig. 3 **a** Median individual biomass of *Urochloa arrecta* (invasive alien plant species, IAPS) and *Hemarthria altissima* (native plant species, NPS) under unburned (pre-fire) and burned (post-fire) conditions across a gradient of initial IAPS dominance, ranging from native monoculture (0% IAPS) to invasive monoculture (100% IAPS), including native dominance (75% native and 25% IAPS propagules) and invasive dominance (75% IAPS and 25% native propagules). **b** Modeled estimates of individual biomass for *H. altissima* (NPS; blue line) and *U. arrecta* (IAPS; dashed red line) across the same dominance gradient under unburned and burned conditions. Lines represent posterior median estimates, and shaded areas indicate the 50%, 80%, and 95% credible intervals (CIs)

dominance. Specifically, the competitive advantage of *Urochloa arrecta* arises not from greater biomass production, but from a highly effective regenerative strategy that suppresses the resprouting capacity of the native species once the invader is dominant. This demonstrates that pre-disturbance dominance and vegetative propagule pressure are key drivers of

post-disturbance community assembly in this system (Gaertner et al. 2014; Valliere et al. 2024). By experimentally isolating the response of native and invasive plants to fire across a gradient of invasive dominance, our study provides a mechanistic explanation for why fire can promote invasion when the invader is already dominant, but not when it is initially rare.

Table 2 Posterior summary statistics from Bayesian models evaluating the effects of species identity (native plant species [NPS] vs. invasive alien plant species [IAPS]), pre-disturbance IAPS dominance (native monoculture, native dominance, invasive dominance, and invasive monoculture), and fire treatment (burned vs. unburned) on two response variables: individual biomass (g) and shoot/root biomass ratio. The intercept represents the reference condition (NPS in unburned monoculture), and all subsequent estimates correspond to effect sizes relative to this baseline rather than raw group means. Results are presented as posterior means (estimates), posterior probability (PP), evidence ratio (ER), and 95% credible intervals (CI). Effects were considered statistically credible when the 95% CI did not overlap zero and $PP \geq 0.95$, indicated by an asterisk (*)

Parameter (effect compared to reference conditions)	Estimate (slope)	PP (posterior probability)	ER (evidence ratio)	CI 95% (credible interval)
Individual biomass (g)				
Intercept (unburned monoculture, native plant)	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]
Fire	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]
Species	−0.8	0.99*	999	[−1.31, −0.27]
Fire	−0.3	0.87	07.06	[−0.90, 0.25]
Native dominance × species	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]

Post-disturbance resprouting capacity is a key ecological trait that influences competitive success, enabling species to rapidly capture resources and occupy space (Kelly et al. 2020; Tangney et al. 2022; Cornwall 2022). Both species in our study are rhizomatous C4 grasses, and the investment in belowground organs facilitates resprouting when fires are not intense enough to burn the soil layer (Clarke et al. 2013; Pausas et al. 2018). Other invasive grass species also show higher resprouting capacities after fire (Coffman et al. 2010), with traits such as rhizome-based clonal growth, rapid shoot emergence, and high post-fire shoot production being crucial for their success. Our analysis indicates that *U. arrecta* possesses a superior regeneration strategy compared to the native *Hemarthria altissima*, provided that a dominance threshold is reached. Under invasive dominance, the IAPS more than doubled its sprout production relative to scenarios in which the native species was dominant, while simultaneously prolonging the native's sprouting time and reducing its total sprout production. Such regenerative advantages

are frequently associated with invasion success (Moore et al. 2019; Rosalem et al. 2024). If IAPS are not controlled before fire events, they may leverage these historical priority effects to reinforce their dominance, potentially locking the community into an invaded state (Fukami 2015; Slingsby et al. 2017).

Community assembly after disturbance is strongly influenced by priority effects and vegetative propagule pressure, whereby the initial abundance and establishment history of species shape subsequent competitive outcomes (Lockwood et al. 2005; Fukami 2015). Our experimental manipulation of IAPS dominance provides a clear illustration of this mechanism in a post-fire context. The gradient of pre-disturbance dominance served as a proxy for historical dominance effects, and post-fire regeneration outcomes were strongly dependent on this initial condition. Notably, the invasive species was able to capitalize on fire only when established at high initial density, translating disturbance into enhanced regeneration, whereas its performance was suppressed when present at low abundance. These results indicate that

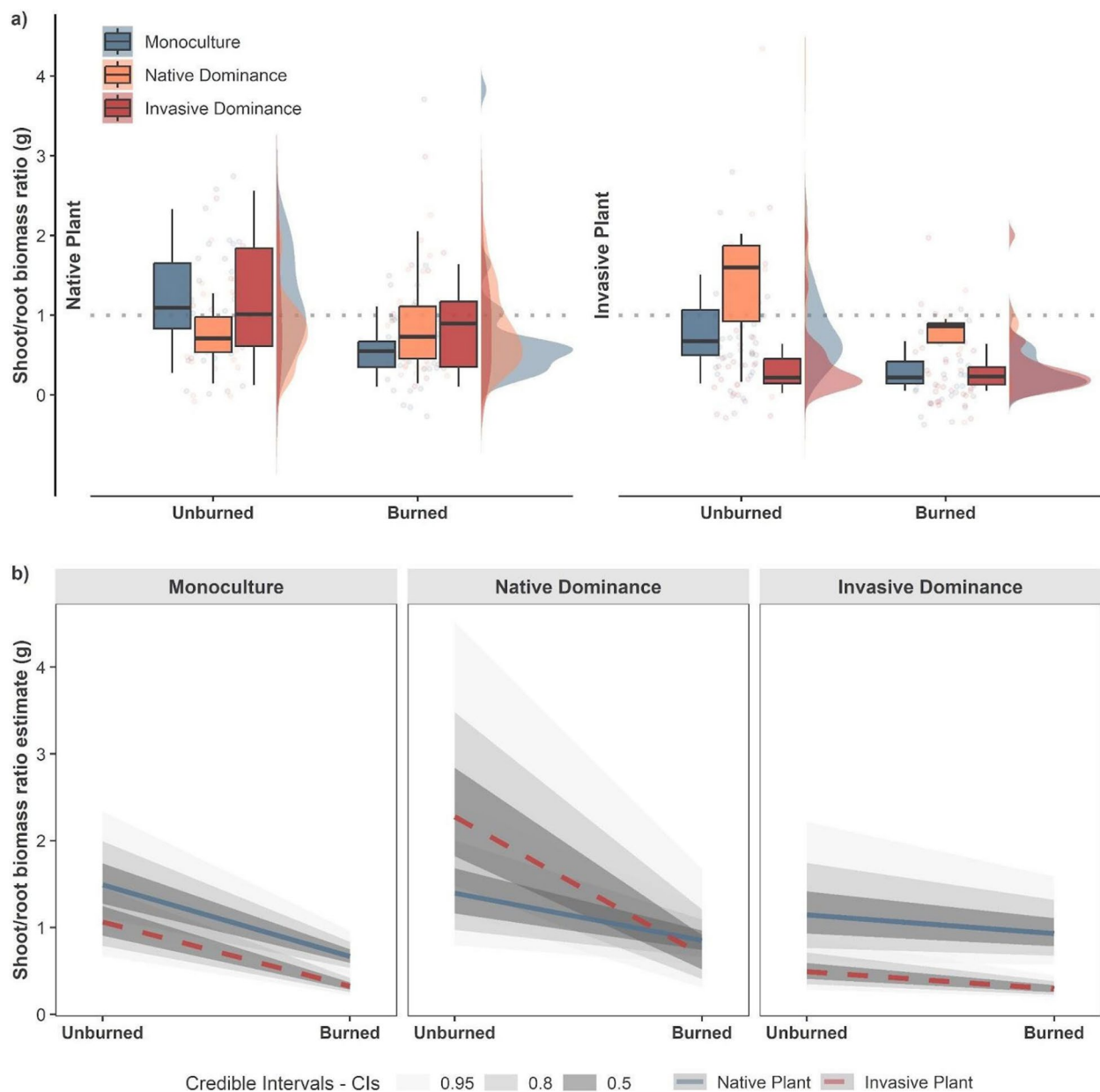


Fig. 4 **a** Median shoot/root biomass ratio of *Urochloa arrecta* (invasive alien plant species, IAPS) and *Hemarthria altissima* (native plant species, NPS) under unburned (pre-fire) and burned (post-fire) conditions across a gradient of initial IAPS dominance, ranging from native monoculture (0% IAPS) to invasive monoculture (100% IAPS), including native dominance (75% native and 25% IAPS propagules) and invasive dominance (75% IAPS and 25% native propagules). The horizontal line at $y=1$ indicates equal biomass allocation between shoots and roots; values above this line indicate greater allocation to shoots, whereas values below indicate greater allocation to roots. **b** Modeled estimates of shoot/root biomass ratio for *H. altissima* (NPS; blue line) and *U. arrecta* (IAPS; dashed red line) across the same dominance gradient under unburned and burned conditions. Lines represent posterior median estimates, and shaded areas indicate the 50%, 80%, and 95% credible intervals (CIs)

community resilience to disturbance is not an intrinsic property of the system but rather emerges from the pre-existing biotic context.

The response of plant biomass to disturbance can be complex, reflecting both species-specific traits and shifts in resource availability (Hobbs & Huenneke

1992; Wilsey et al. 2024). Fire can mineralize nutrients and increase productivity (Bodí et al. 2014; Araujo et al. 2025). In our study, the native species responded positively to fire when grown in isolation, showing an increase in biomass. However, the competitive advantage of the invasive species appears to lie less in

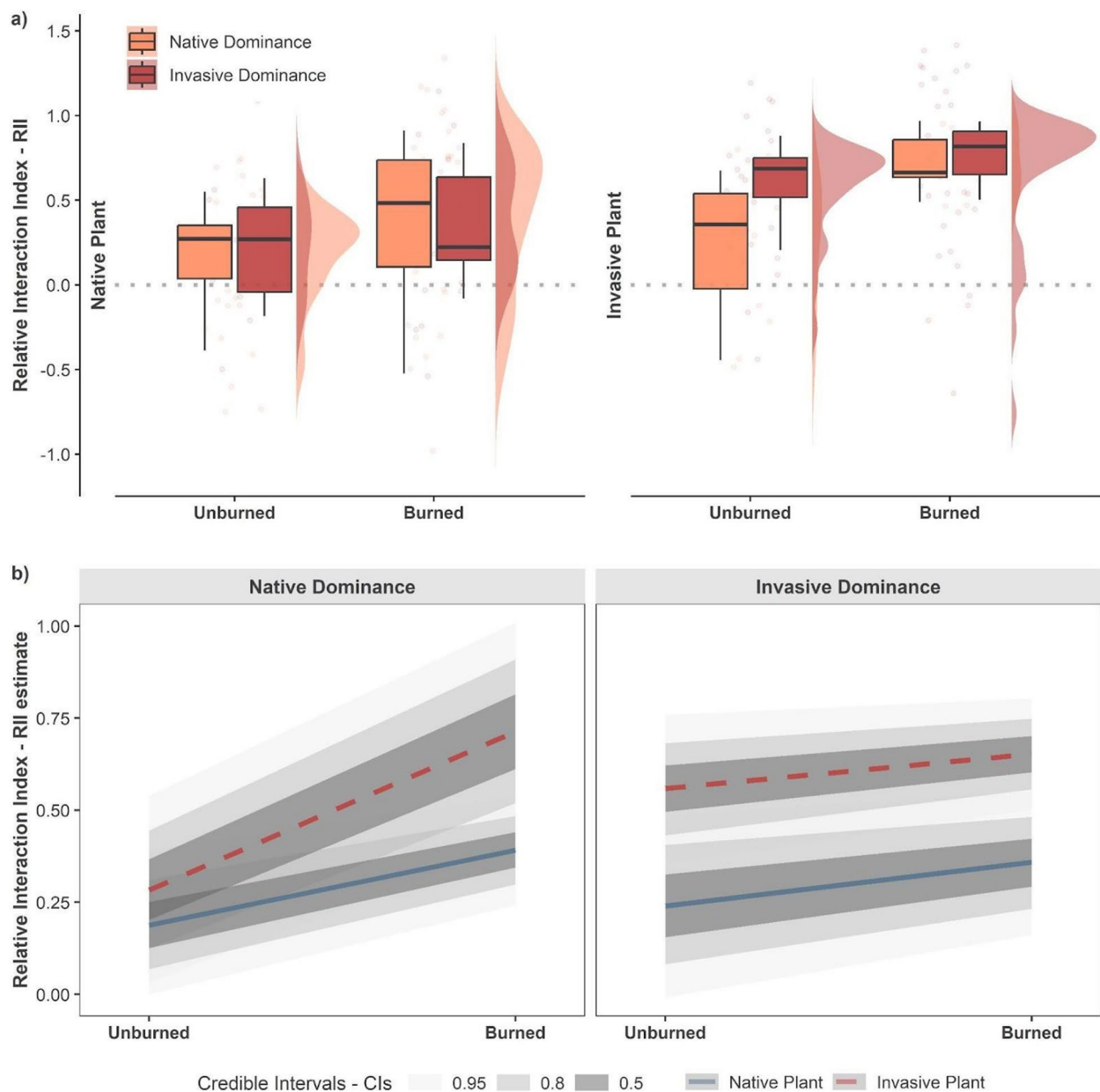


Fig. 5 **a** Median relative interaction index (RII) values for *Urochloa arrecta* (invasive alien plant species, IAPS) and *Hemarthria altissima* (native plant species, NPS) under unburned (left) and burned (right) conditions across a gradient of initial IAPS dominance, including native monoculture (0% IAPS), native dominance (25% IAPS), invasive dominance (75% IAPS), and invasive monoculture (100% IAPS). The horizontal line at $y=0$ indicates neutral interactions; positive values indicate facilitation (approaching +1), whereas negative values indicate competition (approaching -1). **b** Modeled estimates of RII for *H. altissima* (NPS; blue solid line) and *U. arrecta* (IAPS; red dashed line) under native- and invasive-dominance treatments in both unburned and burned conditions. Lines represent posterior mean estimates, and shaded areas indicate 50%, 80%, and 95% credible intervals (CIs)

superior biomass production and more in its capacity to suppress native regeneration. Biomass allocation patterns support this interpretation. The IAPS invested more strongly in belowground structures and displayed plastic adjustments in shoot–root allocation under competitive pressure. Such flexibility may enhance

resource capture and resilience after disturbance (Pausas et al. 2018).

Disturbance can also modify the nature of interspecific interactions (Holmgren & Scheffer 2010). The RII revealed an unexpected pattern: under native dominance and in the absence of fire, the native species showed a

Table 3 Posterior summary statistics from a Bayesian model evaluating the effects of species identity (native plant species [NPS] vs. invasive alien plant species [IAPS]), pre-disturbance IAPS dominance (native monoculture, native dominance, and invasive dominance), and fire treatment (burned vs. unburned) on the relative interaction index (RII). The intercept represents the reference condition (NPS under unburned native dominance), and all subsequent estimates correspond to effect sizes relative to this baseline rather than raw index values. Results are presented as posterior means (estimates), posterior probability (PP), evidence ratio (ER), and 95% credible intervals (CI). Effects were considered statistically credible when the 95% CI did not overlap zero and PP ≥ 0.95 , indicated by an asterisk (*)

Parameter (effect compared to reference conditions)	Estimate (slope)	PP (posterior probability)	ER (evidence ratio)	CI 95% (credible intervals)
Relative interaction index—RII				
Intercept (unburned native dominance, native plant)	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]
Fire	0.20	0.95	20.82	[−0.04, 0.43]
Invasive dominance $\times$ species	0.22	0.92	11.05	[−0.10, 0.54]
Invasive dominance $\times$ fire	−0.09	0.69	2.19	[−0.44, 0.27]
Species $\times$ fire	0.23	0.90	8.60	[−0.14, 0.58]
Invasive dominance $\times$ species $\times$ fire	−0.25	0.87	6.97	[−0.69, 0.18]

positive competitive performance in the presence of the invasive species, suggesting facilitation rather than pure competition. Fire showed a tendency to amplify this positive interaction, although the effect was not fully credible statistically. The mechanisms underlying this pattern were not tested here and remain unclear; possibilities include indirect effects of the invasive species on microhabitat conditions or resource availability. Such positive interactions between native and invasive species, when invader abundance is low, do not preclude negative outcomes as invasion progresses, competitive suppression, altered nutrient cycling, or broader ecosystem impacts may emerge once the invasive species reaches dominance.

Although our findings are based on the interaction between *U. arrecta* and *H. altissima* and focus on early post-fire trajectories, they provide a mechanistic case study of how invasive species can gain a competitive advantage following disturbance. Because our experiment included only one invasive and one native species under controlled greenhouse conditions, it should be interpreted as a baseline framework for understanding post-disturbance competitive dynamics. Caution is therefore required when extrapolating these results to field conditions, where fire intensity, return interval, soil moisture, and hydrological fluctuations may vary substantially. For example, under more intense fires or repeated burning events, buds located in the upper soil layer may experience heat damage, potentially reducing the regenerative advantage observed for the invasive species in our experiment (Clarke et al. 2013). In

contrast, species capable of resprouting are generally tolerant of a wider range of fire frequencies than those relying primarily on seed banks (Simpson et al. 2021). Likewise, it remains unclear to what extent other native wetland species possess traits that confer resilience to fire, such as persistent bud banks or rapid clonal regrowth. Because functional traits are key determinants of species persistence after fire (Clarke et al. 2013; Simpson et al. 2021), future research should expand this framework to a broader set of native species and disturbance scenarios, including different fire intensities and frequencies, to evaluate whether similar mechanisms operate at the community level. Beyond fire, it is also important to assess whether the dominance-dependent regeneration advantage observed here extends to other ecologically relevant disturbance regimes, such as sediment disturbance, grazing, and herbivory, which may similarly disrupt aboveground biomass while preserving clonal regenerative structures.

Unlike fire-dependent ecosystems, where species have evolved strategies to cope with recurrent burning, wetlands of the Atlantic Forest are generally considered fire-sensitive. Native species in these systems may therefore be less adapted to intense or frequent fires, potentially increasing their vulnerability to displacement by invasive grasses (Brando et al. 2020; Flores et al. 2021). As climate change continues to intensify fire activity (IPCC 2023), the regenerative advantage of invasive species following disturbance may represent a widespread mechanism that accelerates biodiversity loss and promotes transitions toward

invasive-dominated ecosystems (Brooks et al. 2004; Vilà et al. 2011; Wilsey et al. 2024). Globally, disturbances are known to weaken biotic resistance and create invasion windows that favor species with rapid growth and strong regenerative capacity (Davis et al. 2000; Pausas & Keeley 2014; Jo et al. 2024). These dynamics are particularly concerning in wetland ecosystems because shifts toward invasive dominance can alter hydrological processes, reduce habitat suitability for specialist fauna, and compromise ecosystem services such as water purification and carbon sequestration (Zedler & Kercher 2004).

Conclusion

Understanding how climate-driven fire regimes accelerate the dominance of IAPS through competitive and facilitative interaction strategies is crucial. 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 manifested only under conditions of high initial abundance. This mechanism, which involves suppressing the native species' resprouting capacity, underscores the pivotal roles of vegetative 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 before fire events, as once an IAPS reaches high dominance, post-fire restoration may not be successful.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-026-00534-z>.

Supplementary Material 1

Acknowledgements

The authors acknowledge financial support for research provided by the Foundation for Research and Innovation of the State of Santa Catarina, FAPESC, Protocol no. PJP2021321000109. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001. D.A.M. received a post-doctoral grant from the FAPESP (Process Number 2022/13301-8). We also thank the team from the Laboratory of Freshwater Biodiversity at UFSC (particularly Apolo A. Egeu, Luiz A. F. Fernandes, and Sabrina Suominisky) for their valuable assistance in the experiments. Finally, we thank N. Hanazaki and S. M. Thomaz for critically reading a previous version of this manuscript.

Code availability

Code is available upon request to the corresponding author.

Authors' 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.

Funding

This study was partially financed by the Foundation for Research and Innovation of the State of Santa Catarina, FAPESC, Protocol no. PJP2021321000109. 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.

Data availability

The data will be available to the corresponding author upon request.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 24 July 2025 Accepted: 8 June 2026

Published online: 25 June 2026

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