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African Grass Invasion Threatens Tropical Wetland Biodiversity: Experimental Evidence from *Echinochloa pyramidalis* Invasion in a Mexican Ramsar Site

Hugo López Rosas [1],* and Patricia Moreno-Casasola [2]

[1] El Colegio de Veracruz, Carrillo Puerto 26, Zona Centro, Xalapa 91000, Veracruz, Mexico
[2] Instituto de Ecología A.C., Red de Ecología Funcional, Carretera antigua a Coatepec 351, El Haya, Xalapa 91073, Veracruz, Mexico
* Correspondence: hlopezr@colver.edu.mx

Abstract

African grasses deliberately introduced for cattle forage have become among the most destructive invaders of tropical wetlands globally, yet invasion mechanisms and management strategies remain poorly understood. We conducted field experiments examining competition dynamics between the invasive African grass *Echinochloa pyramidalis* and native wetland species in La Mancha, Mexico—a Ramsar site of international importance. Experiment 1 tested invasion potential within native *Sagittaria lancifolia* zones using four treatments: control, herbicide removal, *E. pyramidalis* transplant, and combined removal + transplant. Repeated measures ANOVA showed significant treatment and time effects on invasion success, with vegetation removal facilitating invasion (relative importance value increasing from 0 to 149.4 ± 26.6 after 18 months) while transplants alone failed to establish (RIV < 7.0). *Sagittaria* maintained 35-48% biomass across treatments, demonstrating coexistence capacity. Experiment 2 examined natural invasion of the vegetation ecotone over 49 months. Mixed-effects models revealed that *E. pyramidalis* increased dominance in its zone ($\beta = 9.98$, $z = 4.77$, $p < 0.001$) but showed minimal expansion into adjacent *Sagittaria* habitat, indicating propagule limitation rather than competitive exclusion as the invasion constraint. *Sagittaria* removal within *E. pyramidalis* zones significantly reduced invasion temporal increase ($\beta = -6.44$, $z = -2.18$, $p = 0.030$), suggesting biotic resistance. Results demonstrate that *E. pyramidalis* possesses invasion potential but requires disturbance to overcome establishment barriers. These findings support prevention-based management prioritizing disturbance limitation in intact wetlands and demonstrate that hydrological management maintaining permanent flooding (>30 cm depth) can effectively control established invasions by exploiting C_4 photosynthetic limitations. Conservation implications for Mexican coastal wetlands—which lack legal protection equivalent to mangroves despite comparable ecosystem services—are discussed. These findings inform evidence-based management of African grass invasions in tropical wetlands worldwide.

Keywords: biological invasion; wetland conservation; C_4 photosynthesis; alternative stable states; Ramsar wetlands; restoration ecology; Gulf of Mexico; competition experiments

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1. Introduction

Echinochloa pyramidalis (Lam.) Hitchc. & Chase, a perennial African grass intentionally introduced for cattle forage, has transformed large areas of tropical freshwater wetlands in southeastern Mexico from diverse native marshes into near-monocultures, eliminating plant biodiversity and fundamentally altering ecosystem structure and function [1,2]. This invasion exemplifies a global pattern in which African C_4 grasses deliberately introduced for livestock production have escaped cultivation to become among the most destructive invaders of tropical and subtropical wetlands worldwide, threatening biodiversity hotspots and critical ecosystem services across the tropical America and Australia [3,4].

African grasses have become dominant invaders in tropical and subtropical wetlands globally, with species like *Pennisetum purpureum* in the Florida Everglades, *Urochloa mutica* in Australian tropical floodplains, and multiple E*chinochloa* species across tropical America causing severe ecological and economic damage [5–7]. The primary invasion pathway has been deliberate introduction during the 20th century for forage production, driven by the expansion of cattle ranching in tropical regions [8]. These grasses share key traits that confer invasion success: C_4 photosynthesis providing competitive advantages in warm, high-light conditions; extensive rhizomatous or stoloniferous growth enabling rapid vegetative spread; high biomass production; and tolerance to flooding, grazing, and disturbance [3,9]. Williams and Baruch [3] identified these ecophysiological attributes as central to understanding African grass invasion success, noting that invaded ecosystems become biotically impoverished through displacement of native species and altered disturbance regimes.

Recent synthesis work confirms that wetlands are disproportionately vulnerable to plant invasions—24% of the world's worst invasive plants are wetland species despite wetlands comprising less than 6% of terrestrial area—with invasions facilitated by dynamic environmental conditions, resource pulses, and human-caused hydrological alterations [10,11]. *Echinochloa pyramidalis* presents particularly severe invasion challenges due to its combination of aggressive vegetative propagation, dual tolerance to flooding and drought, and C_4 photosynthetic efficiency [12,13]. Native to tropical and subtropical Africa from Senegal to Kenya and throughout Southern Africa, where it naturally occurs in seasonally flooded grasslands and river floodplains [14], *E. pyramidalis* was introduced to Mexico and Central America in the 1960s-1970s as a high-productivity forage grass.

The species' current distribution in its native range is primarily limited by temperature minima and seasonal flooding patterns, with populations restricted to areas with mean annual temperatures above 20 °C and tolerance for water depths up to 1.5 m during wet seasons but requiring periodic drawdown. In introduced ranges, *E. pyramidalis* distribution appears constrained by permanent deep flooding (>50 cm year-round), competitive exclusion by established vegetation, and potentially by frost events in subtropical margins. Understanding these distributional limits is critical for predicting invasion risk and designing effective management strategies.

The species is a tall (1.5-2.5 m), reed-like perennial with extensive rhizomes that enable intense vegetative propagation and rapid horizontal expansion through tillering [15,15a]. Its strong fasciculated root system spreads quickly through soil, and stems readily root at nodes, allowing regeneration from fragments [16,16a]. Like many wetland grasses, *E. pyramidalis* possesses well-developed aerenchyma (lacunae system) in roots and stems, facilitating oxygen transport to submerged tissues and enabling survival in flooded conditions. This anatomical adaptation provides competitive advantages in periodically flooded habitats where oxygen availability limits many species, though the system's efficiency decreases under permanent deep flooding, potentially explaining the species' distribution limitations. The species combines high productivity—achieving yields of 15-27 metric tons dry matter per hectare per year—with wide environmental tolerance, thriving in both permanently flooded conditions and withstanding extended drought periods [13,17]. In its introduced range, *E. pyramidalis* has become a major invasive species in Mexican coastal wetlands (Veracruz, Tabasco, Campeche) and Guyana's aquatic systems, where the federal government spent over $3.4 million attempting control [18,19]. The species ranked highly as a potential future invasive weed for the United States and was listed as "not authorized pending pest risk analysis" by USDA-APHIS, reflecting recognition of its invasion threat [20].

Freshwater marsh invasions represent a critical but understudied conservation challenge in Mexico and Latin America, where over 50% of wetlands have been lost in many states [21,22]. The Gulf of Mexico coastal region contains 66% of estuarine wetland acreage in the contiguous United

States and at least 10% of Mexican wetlands [23], yet has experienced significant coastal wetland loss. Mexican wetland conservation faces a critical policy gap—while mangroves receive legal protection as threatened species under NOM-059-SEMARNAT-2010 or a protected ecosystem under Article 60 TER of the Mexican Wildlife Law, freshwater wetlands lack equivalent protection despite providing comparable ecosystem services including massive carbon storage (1,100-1,800 Mg C ha^{-1}, comparable to or exceeding mangroves) [24,25], flood regulation, water quality improvement, and biodiversity support.

La Mancha wetland system in central Veracruz (19°36′N, 96°22′40″W) represents a critical component of Gulf of Mexico coastal wetland biodiversity. Designated as Ramsar Site #1336 in 2004 (La Mancha-El Llano), the system encompasses freshwater marshes that harbor exceptional biodiversity with 837 plant species documented, including endemic and threatened species [26,27]. The freshwater marsh provides critical habitat for the Altamira Yellowthroat (*Geothlypis flavovelata*), a vulnerable endemic bird restricted to northeastern Mexican wetlands and strongly associated with *Typha domingensis* [28], as well as the endangered Morelet's crocodile (*Crocodylus moreletii*) [29]. The system's conservation value extends beyond biodiversity to ecosystem services: freshwater marshes at La Mancha store 1,100 ± 376 Mg C ha^{-1}, making them among the most carbon-rich ecosystems per unit area globally [24].

The invasion of *E. pyramidalis* at La Mancha began following deliberate introduction by ranchers for cattle forage, with the species becoming dominant in portions of the freshwater marsh by the late 1990s [1,2]. Our previous work documented that *E. pyramidalis* dominated the least flooded areas of the wetland while native species (*Sagittaria lancifolia* subsp. *media*, *Typha domingensis*, *Pontederia sagittata*) persisted in deeper water zones, with hydrological parameters explaining species distribution patterns [1]. The invasion caused measurable negative changes including reduced plant biodiversity, altered hydrology, soil physicochemical changes including vertical accretion, and reduced faunal habitat quality [1,2].

Experimental disturbance treatments (mechanical soil disking, cutting, herbicide application) demonstrated the difficulty of control—after nine months, *E. pyramidalis* recovered in all treatments to become dominant again [2]. However, longer-term experiments combining soil disruption, native species transplanting, and shade treatments showed promise for eliminating the invader after 19 months by exploiting C4 photosynthetic disadvantages under reduced light [30,31]. Competition studies under different hydroperiods revealed that *E. pyramidalis* consistently outcompeted native species under dry or variably flooded conditions but performed poorly under permanent flooding, suggesting hydrological management as a potential control strategy [32].

Despite growing recognition of African grass invasions as a major threat to wetland biodiversity, significant knowledge gaps remain regarding the full extent and mechanisms of ecological impacts, particularly in tropical freshwater marshes [3,33]. Most invasion research has focused on temperate systems (*Phragmites australis* in North America, *Phalaris arundinacea* in the Midwest) or on agricultural contexts (*Echinochloa* species as rice weeds), leaving tropical wetland invasions understudied [34,35]. Key questions persist about how invasion alters ecosystem-level processes beyond plant community composition and how these changes cascade through the ecosystem. The mechanisms underlying invasion success require deeper investigation: while C_4 photosynthesis and vegetative propagation clearly contribute, the relative importance of competition versus other mechanisms, and interactions with disturbance regimes remain incompletely understood [36,37].

Most critically, the conservation and management implications for tropical wetland protection remain poorly developed, with limited evidence-based guidance for preventing invasions, controlling established populations, or restoring invaded wetlands in tropical contexts [38,39]. The present study addresses these gaps by examining: (1) Can *E. pyramidalis* invade intact native *Sagittaria* zones, or does invasion require disturbance?; (2) Does natural invasion occur at the ecotone between invaded and native vegetation?; (3) What role does propagule availability versus competitive ability play in determining invasion patterns?; and (4) What are the conservation implications for Mexican Ramsar wetland management?

2. Materials and Methods

2.1. Study Site

The study was conducted in a tropical freshwater marsh in La Mancha, Veracruz, Mexico (19°36′N, 96°23′W), located in the coastal lowlands of the central Gulf of Mexico (Figure 1). The marsh is part of a freshwater and brackish wetland complex adjacent to a coastal lagoon connected to the Gulf of Mexico through a barrier island system. The climate is warm sub-humid with mean annual temperature of 25 °C and mean annual precipitation of 1,500 mm, with a marked dry season from November to April and rainy season from May to October [26].

The wetland exhibits distinct vegetation zonation, with three clearly differentiated plant communities: (1) areas dominated by the African invasive grass E. *pyramidalis*, (2) zones dominated by the native broad-leaved emergent *S. lancifolia* subsp. *media*, and (3) patches dominated by the cosmopolitan species *Typha domingensis*. The *Echinochloa* zone is characterized by higher soil bulk density (0.38 g cm^{-3}), higher conductivity (1.47 mS cm^{-2}), and lower soil moisture (59%) compared to the *Sagittaria* zone (bulk density 0.11 g cm^{-3}, conductivity 0.84 mS cm^{-2}, moisture 89%) [1]. The *Echinochloa*-dominated area represents the result of intentional introduction of this African grass for cattle forage, which has subsequently spread to displace native vegetation.

2.2. Experimental Design

We conducted two complementary field experiments to address whether *E. pyramidalis* can invade native *Sagittaria* zones and whether natural invasion is occurring at the ecotone between these vegetation types.

2.2.1. Experiment 1: Invasion Potential in Sagittaria Zone

To evaluate the capacity of *E. pyramidalis* to establish and persist within *Sagittaria*-dominated habitat, we established a randomized complete block design with four treatments and five blocks in the native *Sagittaria* zone [40]. Each experimental unit consisted of a 0.7 × 0.7 m quadrat. Treatments were applied as follows:

1. **Control**: Quadrats were left under natural conditions with no manipulation.
2. **Kill**: All vegetation within quadrats was eliminated by spraying with glyphosate herbicide (Round Up, 2% solution) to create open space for potential colonization.
3. **Transplant** *Echinochloa*: Five individuals of E. *pyramidalis* were transplanted from the *Echinochloa*-dominated zone to test active establishment capacity in the native zone.
4. **Kill + *Echinochloa***: All existing vegetation was eliminated with glyphosate, and five *E. pyramidalis* individuals were subsequently transplanted to simulate invasion into disturbed habitat.

2.2.2. Experiment 2: Natural Invasion Dynamics at the Ecotone

To assess whether natural invasion is occurring at the boundary between vegetation zones, we established experimental plots along the sharp ecotone separating *Echinochloa*-dominated and *Sagittaria*-dominated areas [41]. We used a randomized complete block design with six treatments and five blocks. Each block consisted of a pair of adjacent 0.7 × 0.7 m quadrats, one on each side of the ecotone. Treatments were applied as follows:

1. **Control in *Echinochloa* zone** (Control_Echino): Quadrats in the *Echinochloa* zone were left unmanipulated to track natural *Sagittaria* advance.
2. **Control in *Sagittaria* zone** (Control_Sagit): Quadrats in the *Sagittaria* zone were left unmanipulated to track natural *Echinochloa* invasion.
3. **Kill *Sagittaria* in *Echinochloa* zone** (Kill_Sagit_Echino): All *Sagittaria* individuals in the *Echinochloa* side were removed to test whether the native species was actively colonizing the invaded zone.

4. **Kill *Sagittaria* in *Sagittaria* zone** (Kill_Sagit_Sagit): All plants in *Sagittaria*-side quadrats were eliminated with glyphosate to create reference conditions.
5. **Kill *Echinochloa* in *Echinochloa* zone** (Kill_Echino_Echino): All vegetation in *Echinochloa*-side quadrats was eliminated with glyphosate to assess reinvasion capacity and native recovery potential.
6. **Kill *Echinochloa* in *Sagittaria* zone** (Kill_Echino_Sagit): All *Echinochloa* individuals in the *Sagittaria* side were removed to prevent any invasion attempts.

Each treatment was replicated in five quadrats, yielding a total of 30 permanent sampling units.

2.3. Vegetation Sampling and Analysis

For Experiment 1, we monitored vegetation at approximately 2–3-month intervals over 18 months, with six sampling dates: May (month 0), July (month 2), October (month 5), February (month 9), June (month 13), and November (month 18). At each sampling event, we recorded species identity, density (number of individuals per quadrat), canopy cover (estimated visually to the nearest five percent), and maximum height for all vascular plant species present in each quadrat.

We calculated Relative Importance Values (RIV) for each species as: RIV = Relative Cover + Relative Density + Relative Height, where each relative value was calculated as the proportion of that species' metric divided by the sum for all species in the quadrat, multiplied by 100 [42,43]. This index provides an integrated measure of species dominance that accounts for multiple aspects of plant abundance and structure.

After 20 months, we harvested all aboveground biomass from each quadrat. Plant material was sorted by species, oven-dried at 70 °C for 48 hours, and weighed to the nearest 0.1 g.

For Experiment 2, we monitored relative importance values (RIV) for each species across 10 sampling dates spanning 46 months. At the conclusion of the experiment, we harvested all aboveground biomass of both focal species from each quadrat. Plant material was oven-dried at 70 °C to constant weight and weighed to the nearest 0.1 g.

2.4. Statistical Analyses

For Experiment 1, we analyzed temporal changes in RIV using repeated measures analysis of variance (ANOVA) with a split-plot design [44,45]. Treatment was the between-subjects factor (4 levels), block was a random factor (5 levels), and time was the within-subjects factor (6 levels). The model included main effects of treatment and time, as well as their interaction. When significant effects were detected, we performed post-hoc pairwise comparisons using Tukey's Honestly Significant Difference (HSD) test with $\alpha = 0.05$.

We analyzed final biomass data using one-way ANOVA in a randomized complete block design, with treatment as the fixed factor and block as a random factor. Post-hoc comparisons were conducted using Tukey's HSD test when treatment effects were significant. All analyses were performed separately for *E. pyramidalis* and *S. lancifolia*. Statistical significance was determined at $\alpha = 0.05$.

For Experiment 2, we analyzed temporal changes in RIV using linear mixed-effects models (LMM) [44,46]. The models included Treatment and Time (sampling date, coded 1-10) as fixed effects, along with their interaction. To account for repeated measurements within quadrats, we included random intercepts for each quadrat. The model structure was:

$$\text{RIV} \sim \text{Treatment} \times \text{Time} + (1 \mid \text{Quadrat})$$

Models were fitted using restricted maximum likelihood (REML). We conducted separate analyses for each species within each zone, comparing treatments against their respective zone-specific controls. Statistical significance of fixed effects was assessed using likelihood ratio tests with $\alpha = 0.05$.

Final biomass analysis: We tested for treatment effects on final biomass separately for each species and zone. Prior to analysis, we assessed normality using Shapiro-Wilk tests and homogeneity of variances using Levene's tests. For normally distributed data with homogeneous variances, we employed one-way ANOVA followed by Tukey's HSD post-hoc tests for pairwise comparisons [40,45]. When assumptions were violated, we used nonparametric alternatives (Kruskal-Wallis test with Dunn's post-hoc comparisons). For two-group comparisons (*Sagittaria* zone), we used independent *t*-tests or Mann-Whitney *U* tests as appropriate. All statistical tests were two-tailed with $\alpha = 0.05$.

3. Results

3.1. Invasion Potential in Sagittaria Zone (Experiment 1)

3.1.1. Temporal Dynamics of Relative Importance Values

Echinochloa pyramidalis

The repeated measures ANOVA revealed highly significant effects of treatment ($F_{3,12} = 21.42$, $p < 0.001$), time ($F_{5,60} = 24.88$, $p < 0.001$), and their interaction ($F_{15,60} = 9.40$, $p < 0.001$) on *E. pyramidalis* RIV (Table 1). The mean RIV across all treatments and time points was 29.50. Treatment means showed marked differences: Kill treatment had the highest mean RIV (80.73), followed by Kill + Transplant (32.53), Control (3.57), and Transplant (1.17). Temporal patterns showed a general increase in *E. pyramidalis* dominance over time, with mean RIV increasing from 1.75 at month 0 to 60.70 at month 18.

Post-hoc comparisons indicated that the Kill treatment resulted in significantly higher *E. pyramidalis* RIV compared to Control ($q = 9.650$, $p < 0.05$), Transplant ($q = 9.950$, $p < 0.05$), and Kill + Transplant ($q = 6.028$, $p < 0.05$). No significant differences were detected between Control and Transplant treatments ($q = 0.300$, $p > 0.05$), or between Control and Kill + Transplant ($q = 3.622$, $p > 0.05$).

The significant treatment × time interaction indicates that the effect of treatment on *E. pyramidalis* RIV varied across sampling dates. In the Kill treatment, *E. pyramidalis* RIV increased from 0 at month 0 to 149.4 ± 26.6 (mean ± SD) at month 18. In contrast, the Transplant treatment showed minimal establishment, with RIV remaining near zero throughout the study period (maximum of 7.0 ± 15.7 at month 0, returning to 0 by month 2).

Sagittaria lancifolia

For *S. lancifolia*, repeated measures ANOVA showed significant effects of treatment ($F_{3,12} = 7.59$, $p = 0.004$) and time ($F_{5,60} = 26.78$, $p < 0.001$), but no significant treatment × time interaction ($F_{15,60} = 0.58$, $p = 0.877$) (Table 1). The overall mean RIV was 85.04. Treatment means were highest in Control (99.77), followed by Transplant (88.00), Kill + Transplant (79.87), and Kill (72.53). Temporal variation showed RIV values ranging from 53.60 (month 13) to 124.80 (month 5).

Post-hoc comparisons revealed that Control treatment maintained significantly higher S. *lancifolia* RIV compared to Kill treatment ($q = 6.428$, $p < 0.05$) and Kill + Transplant treatment ($q = 4.697$, $p < 0.05$). The Transplant treatment did not differ significantly from Control ($q = 2.777$, $p > 0.05$), Kill ($q = 3.651$, $p > 0.05$), or Kill + Transplant ($q = 1.920$, $p > 0.05$).

The absence of a significant treatment × time interaction indicates that treatment effects on *S. lancifolia* RIV were consistent across time. All treatments showed similar temporal patterns, with peaks in RIV occurring at month 5 and lowest values at month 13, likely reflecting seasonal variation in plant growth.

Table 1. Summary of repeated measures ANOVA for Relative Importance Values (RIV) of *Echinochloa pyramidalis* and *Sagittaria lancifolia* across four treatments and six sampling dates over 18 months in a tropical freshwater marsh.

Source	Species	SS	df	MS	*F*	*P*
Between subjects						
Treatment	*E. pyramidalis*	123,281	3	41,094	21.42	<0.001
	S. lancifolia	12,264	3	4,088	7.59	0.004
Block	*E. pyramidalis*	5,780	4	1,445		
	S. lancifolia	5,530	4	1,382		
Error (between)	*E. pyramidalis*	23,021	12	1,918		
	S. lancifolia	6,461	12	538		
Within subjects						
Time	*E. pyramidalis*	50,372	5	10,074	24.88	<0.001
	S. lancifolia	58,202	5	11,640	26.78	<0.001
Treatment × Time	*E. pyramidalis*	57,057	15	3,804	9.40	<0.001
	S. lancifolia	3,795	15	253	0.58	0.877
Error (within)	*E. pyramidalis*	24,291	60	405		
	S. lancifolia	26,078	60	435		

SS = sum of squares; df = degrees of freedom; MS = mean square.

3.1.2. Biomass Accumulation

Echinochloa pyramidalis

Analysis of final biomass revealed a significant effect of treatment on *E. pyramidalis* biomass ($F_{2,4} = 9.84$, $p = 0.029$) (Table 2). The Kill treatment produced substantially higher biomass (1457.8 ± 799.4 g, mean ± SD) compared to Kill + Transplant (281.8 ± 173.4 g) and Transplant (25.9 g, n = 5). Post-hoc tests confirmed that Kill treatment biomass was significantly greater than both Transplant ($q = 7.011$, $p < 0.05$) and Kill + Transplant ($q = 5.758$, $p < 0.05$). The difference between Transplant and Kill + Transplant was not significant ($q = 1.253$, $p > 0.05$). Block effects were not significant ($F_{4,4} = 2.21$, $p = 0.231$), indicating consistent patterns across spatial replicates.

Sagittaria lancifolia

For *S. lancifolia*, treatment effects on final biomass were not statistically significant ($F_{3,11} = 2.67$, $p = 0.099$) (Table 2). Mean biomass values were similar between Control (94.4 ± 19.1 g) and Kill + Transplant (93.3 ± 40.2 g) treatments, while Kill (50.5 ± 27.0 g) and Transplant (65.0 ± 22.7 g) treatments showed intermediate values. Block effects were also not significant ($F_{4,11} = 0.61$, $p = 0.663$). Despite the lack of statistical significance, the numerical pattern suggests some reduction in *S. lancifolia* biomass in treatments where vegetation was initially removed (Kill and Transplant).

Table 2. Summary of one-way ANOVA for final aboveground biomass (g dry mass per 0.49 m²) of *Echinochloa pyramidalis* and *Sagittaria lancifolia* across treatments after 20 months in a tropical freshwater marsh.

Source	**Species**	**SS**	**df**	**MS**	***F***	***P***	**Treatment means ± SD**
Treatment	*E. pyramidalis*	4,104,629.54	2	2,052,314.77	9.84	0.029	Kill: 1457.8 ± 799.4^{a} Transplant: 25.9^{b} Kill+Transplant: 281.8 ± 173.4^{b}
	S. lancifolia	6,723.72	3	2,241.24	2.67	0.099	Control: 94.4 ± 19.1 Kill: 50.5 ± 27.0 Transplant: 65.0 ± 22.7 Kill+Transplant: 93.3 ± 40.2
Block	*E. pyramidalis*	1,842,362.66	4	460,590.67	2.21	0.231	
	S. lancifolia	2,050.65	4	512.66	0.61	0.663	
Error	*E. pyramidalis*	834,293.95	4	208,573.49			
	S. lancifolia	9,229.98	11	839.09			

Total	*E. pyramidalis*	6,781,286.16	10
	S. lancifolia	18,004.34	18

SS = sum of squares; df = degrees of freedom; MS = mean square. Treatment means with different superscript letters differ significantly ($P < 0.05$, Tukey's HSD test). For *E. pyramidalis*, Control treatment is not shown as no individuals were present in any Control quadrats.

3.2. Natural Invasion Dynamics at the Ecotone (Experiment 2)

3.2.1. Temporal Dynamics of Relative Importance Values

Echinochloa pyramidalis

In the *Echinochloa* zone, the mixed-effects model revealed a significant positive effect of time on *E. pyramidalis* RIV ($\beta = 9.98$, $z = 4.77$, $p < 0.001$; Table 3), indicating increasing dominance over the study period. The interaction between Kill_Sagit_Echino treatment and time was significant ($\beta = -6.44$, $z = -2.18$, $p = 0.030$), demonstrating that *Sagittaria* removal resulted in a reduced temporal increase in *Echinochloa* RIV compared to controls. No significant main effect of Kill_Echino_Echino was detected ($p = 0.161$), though this treatment prevented the establishment of new individuals as intended by the experimental design.

In the *Sagittaria* zone, we observed a significant Treatment × Time interaction ($\beta = 7.22$, $z = 2.78$, $p = 0.006$; Table 3). The Kill_Sagit_Sagit treatment resulted in a steeper positive temporal trend in Echinochloa RIV compared to controls, indicating that removal of *Sagittaria* facilitated *Echinochloa* expansion in this zone.

Sagittaria lancifolia

In the *Echinochloa* zone, the mixed-effects model showed no significant effects of treatment, time, or their interaction on *S. lancifolia* RIV (all $p > 0.05$; Table 3). No significant effect was detected for the Kill_Echino_Echino treatment, though removal of *Echinochloa* showed a numerical trend toward increased *Sagittaria* ($\beta = 21.04$, $z = 1.70$, $p = 0.089$), suggesting that *Echinochloa* removal had limited impact on *Sagittaria* dynamics in this zone over the study period.

In the *Sagittaria* zone, time had a significant positive effect on *Sagittaria* RIV ($\beta = 5.51$, $z = 4.58$, $p < 0.001$; Table 3), but this effect was significantly reduced in the Kill_Echino_Sagit treatment (Treatment × Time interaction: $\beta = -4.09$, $z = -2.40$, $p = 0.016$). This indicates that removal of Echinochloa paradoxically resulted in a slower increase in Sagittaria importance compared to controls.

Table 3. Mixed-effects model results for temporal dynamics of relative importance values (RIV) of *Echinochloa pyramidalis* and *Sagittaria lancifolia* across experimental treatments and zones. Models included Treatment, Time (sampling date, 1-10), and their interaction as fixed effects, with random intercepts for quadrats. Coefficients (β), standard errors (SE), *z*-values, and *P*-values are shown for significant terms.

Species / Zone	**Effect**	***β***	**SE**	***z***	***P***
Echinochloa pyramidalis					
Echinochloa zone	Time	9.98	2.09	4.77	<0.001
	Kill_Sagit × Time	-6.44	2.96	-2.18	0.030
	Kill_Echino × Time	-4.15	2.96	-1.40	0.161

Sagittaria zone	Time	-1.04	1.84	-0.57	0.570
	Kill_Sagit × Time	7.22	2.60	2.78	0.006
Sagittaria lancifolia					
Echinochloa zone	Time	-0.50	1.12	-0.45	0.653
	Kill_Echino (main)	21.04	12.38	1.70	0.089
	Kill_Echino × Time	-0.70	1.58	-0.44	0.659
Sagittaria zone	Time	5.51	1.20	4.58	<0.001
	Kill_Echino × Time	-4.09	1.70	-2.40	0.016

Note: Only treatments compared to zone-specific controls are shown. Kill_Sagit = *Sagittaria* removal; Kill_Echino = *Echinochloa* removal. Random effects variance components: *Echinochloa* zone (*E. pyramidalis*): σ^2_quadrat = 831.8, σ^2_residual = 2168.8; *Sagittaria* zone (*E. pyramidalis*): σ^2_quadrat = 1738.6, σ^2_residual = 1673.3; *Echinochloa* zone (*S. lancifolia*): σ^2_quadrat = 169.8, σ^2_residual = 621.4; *Sagittaria* zone (*S. lancifolia*): σ^2_quadrat = 369.4, σ^2_residual = 717.7.

3.2.2. Final Biomass Responses

Echinochloa pyramidalis

In the *Echinochloa* zone, final biomass differed significantly among treatments ($F_{2,15} = 4.67$, $p = 0.027$; Table 4). Tukey's HSD post-hoc tests revealed that Kill_Echino_Echino treatment resulted in 47.5% lower *Echinochloa* biomass (515.4 ± 237.0 g) compared to Control_Echino (982.4 ± 308.5 g; $p = 0.045$). However, Kill_Sagit_Echino treatment (979.8 ± 357.0 g) did not differ significantly from Control_Echino ($p = 0.999$), indicating that *Sagittaria* removal had no effect on final *Echinochloa* biomass. The difference between Kill_Echino_Echino and Kill_Sagit_Echino was also significant ($p = 0.046$).

In the *Sagittaria* zone, final *Echinochloa* biomass did not differ significantly between Control_Sagit (365.7 ± 301.1 g) and Kill_Sagit_Sagit (565.4 ± 279.1 g) treatments ($t_{10} = -1.19$, $p = 0.261$; Table 4).

Sagittaria lancifolia

In the *Echinochloa* zone, *Sagittaria* biomass was consistently low across all treatments (8.2-14.0 g) with no significant differences detected (Kruskal-Wallis $H = 1.09$, $p = 0.579$; Table 4).

In the *Sagittaria* zone, final *Sagittaria* biomass did not differ between Control_Sagit (18.5 ± 21.0 g) and Kill_Echino_Sagit (15.5 ± 8.9 g) treatments ($t_{10} = 0.33$, $p = 0.750$; Table 4).

Table 4. Final aboveground biomass (g ± SD) of *Echinochloa pyramidalis* and *Sagittaria lancifolia* under experimental treatments, with statistical comparisons. Different superscript letters within rows indicate significant differences at $\alpha = 0.05$.

Species / Zone	**Treatment**	**Biomass (g)**	**Statistic**	***P***
Echinochloa pyramidalis				

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Echinochloa zone			$F_{2,15} = 4.67$	0.027
	Control_Echino	982.4 ± 308.5^a		
	Kill_Sagit_Echino	979.8 ± 357.0^a		
	Kill_Echino_Echino	515.4 ± 237.0^b		
Sagittaria zone			$t_{10} = -1.19$	0.261
	Control_Sagit	365.7 ± 301.1		
	Kill_Sagit_Sagit	565.4 ± 279.1		
Sagittaria lancifolia				
Echinochloa zone			$H = 1.09^*$	0.579
	Control_Echino	8.2 ± 11.1		
	Kill_Sagit_Echino	11.7 ± 17.6		
	Kill_Echino_Echino	14.0 ± 9.9		
Sagittaria zone			$t_{10} = 0.33$	0.750
	Control_Sagit	18.5 ± 21.0		
	Kill_Echino_Sagit	15.5 ± 8.9		

Note: Only treatments compared to zone-specific controls are shown. Kill_Sagit = *Sagittaria* removal; Kill_Echino = *Echinochloa* removal. Random effects variance components: *Echinochloa* zone (*E. pyramidalis*): σ^2_quadrat = 831.8, σ^2_residual = 2168.8; *Sagittaria* zone (*E. pyramidalis*): σ^2_quadrat = 1738.6, σ^2_residual = 1673.3; *Echinochloa* zone (*S. lancifolia*): σ^2_quadrat = 169.8, σ^2_residual = 621.4; *Sagittaria* zone (*S. lancifolia*): σ^2_quadrat = 369.4, σ^2_residual = 717.7.

4. Discussion

4.1. Invasion Requires Disturbance: E. pyramidalis Cannot Invade Intact Native Communities

Our results demonstrate that *E. pyramidalis* possesses the physiological capacity to establish and dominate within *Sagittaria*-dominated habitat but faces significant establishment barriers in intact native vegetation. The contrasting outcomes between Kill and Transplant treatments in Experiment 1 reveal this critical distinction: vegetation removal (Kill treatment) facilitated dramatic *E. pyramidalis* invasion (RIV increasing from 0 to 149.4 after 18 months), while transplants into intact vegetation failed to establish (RIV remaining <7.0 throughout the study). This pattern indicates that invasion success depends not solely on competitive ability—which *E. pyramidalis* clearly possesses given its ultimate dominance in disturbed plots—but on overcoming initial establishment barriers created by resident vegetation.

These findings align with invasion theory emphasizing the importance of propagule pressure and priority effects [47,48]. The failure of transplanted *E. pyramidalis* individuals to persist in intact *Sagittaria* stands, despite being established plants rather than seeds, demonstrates exceptionally strong biotic resistance. This resistance likely operates through multiple mechanisms: (1) light limitation by dense *Sagittaria* canopy reducing photosynthetic rates below compensation points for C_4 grasses that require high irradiance [9,49]; (2) competitive exclusion for belowground resources, as *Sagittaria*'s fibrous root system effectively monopolizes soil volume [50]; and (3) allelopathic interference, though this mechanism remains unconfirmed for *Sagittaria-Echinochloa* interactions and warrants future investigation given documented allelopathy in other African grass invasions [51,52].

The dominance of *E. pyramidalis* in the Kill treatment after vegetation removal supports the resource availability hypothesis [53], which posits that invasion success increases with resource availability. Herbicide application created open space with reduced competition for light, water, and nutrients, allowing *E. pyramidalis* propagules arriving from adjacent invaded areas to establish and proliferate. The intermediate outcome in the Kill + Transplant treatment (biomass lower than Kill alone) suggests negative interactions between transplanted individuals and colonizing propagules, possibly through intraspecific competition or localized resource depletion around transplant sites.

These experimental results have important implications for understanding invasion patterns at La Mancha and similar systems. The sharp vegetation boundaries observed in the field between *E. pyramidalis* and *Sagittaria* zones [1,26] reflect not competitive exclusion preventing native persistence in invaded areas, but rather establishment limitation preventing invasion into intact native stands. This interpretation is further supported by Experiment 2 results showing minimal natural invasion across the ecotone over 46 months despite proximity to massive propagule sources (<1 m distance).

4.2. Propagule Limitation, Not Competitive Exclusion, Constrains Natural Invasion Spread

Experiment 2 results demonstrate that natural invasion across the ecotone between established vegetation types proceeds extremely slowly or not at all, despite physical proximity providing abundant propagule supply. Over 46 months of monitoring, *E. pyramidalis* showed minimal expansion into adjacent *Sagittaria*-dominated habitat (Control_Sagit treatment), with biomass remaining relatively constant (365.7 ± 301.1 g) compared to dramatic increases within its existing zone (Control_Echino: 982.4 ± 308.5 g). This asymmetry in invasion dynamics—strong expansion within invaded areas but negligible spread into native vegetation—indicates that factors other than competitive ability limit invasion rate.

The significant Treatment × Time interaction in the *Sagittaria* zone demonstrates that *E. pyramidalis* can expand into *Sagittaria* habitat when native vegetation is removed, confirming invasion potential. Yet the absence of such expansion in unmanipulated control plots indicates that intact vegetation creates establishment barriers that arriving propagules cannot overcome. This pattern is consistent with propagule limitation models [54,55] where invasion is constrained by insufficient propagule arrival or low establishment probability despite suitable environmental conditions.

Sagittaria removal within the *Echinochloa* zone (Kill_Sagit_Echino treatment) resulted in reduced temporal increase in *E. pyramidalis* RIV compared to controls ($\beta = -6.44$, $z = -2.18$, $p = 0.030$), suggesting that low levels of *Sagittaria* present in invaded areas may actually facilitate *E. pyramidalis* dominance through positive interactions or habitat modification. This counterintuitive result could reflect: (1) *Sagittaria*'s role in maintaining soil moisture favorable for both species [32]; (2) provision of structural support for climbing *E. pyramidalis* stems; or (3) indirect effects through soil microbial communities, as native and invasive species may support different mycorrhizal or bacterial assemblages affecting subsequent growth [56,57].

The failure of *Sagittaria* to advance on *E. pyramidalis* zones (minimal biomass and no treatment effects in *Echinochloa* zone analyses) indicates competitive exclusion rather than establishment limitation. Unlike the bidirectional establishment barriers observed in some systems [58], this invasion appears unidirectional: *E. pyramidalis* can potentially invade *Sagittaria* habitat (given disturbance) but *Sagittaria* cannot colonize *E. pyramidalis* stands. This asymmetry reflects fundamental physiological differences: *E. pyramidalis*' C_4 photosynthesis, tall stature (up to 4.5 m), and dense rhizome mat create conditions (low light, physical barriers, resource monopolization) incompatible with *Sagittaria* establishment and growth [1,2].

These findings have critical implications for predicting invasion trajectories and prioritizing management interventions. The slow natural spread rate suggests that undisturbed native wetlands may resist invasion for extended periods despite proximity to propagule sources. However, any disturbance creating gaps in native vegetation—whether from cattle trampling, hydrological modifications, herbivory, or other factors—may trigger rapid invasion if propagules are available. This emphasizes the importance of preventing disturbance in intact wetlands and implementing early detection/rapid response protocols for newly established populations before they develop into propagule sources threatening adjacent natives.

4.3. Coexistence Mechanisms: Sagittaria Persistence Despite E. pyramidalis Dominance

A striking finding from both experiments is *Sagittaria*'s capacity to persist at moderate abundance (35-48% of final biomass) even in treatments where *E. pyramidalis* achieved high dominance. This coexistence contrasts with the near-complete biodiversity loss documented in some invaded systems [5,59] and suggests mechanisms promoting stable coexistence between these species despite clear competitive asymmetry favoring the invader.

Several hypotheses may explain this coexistence pattern. First, hydrological niche partitioning [60,61] creates spatial refugia where each species has relative advantage: *E. pyramidalis* dominates in shallower water with intermittent flooding where C_4 photosynthetic advantages are maximized [3,9], while *Sagittaria* maintains populations in deeper permanent water where its tolerance for continuous inundation exceeds that of *E. pyramidalis* [32]. Our previous competition experiments confirmed this mechanism, demonstrating that *E. pyramidalis* performed poorly under permanent flooding (>30 cm depth for >6 months) while *Sagittaria* thrived [32]. This hydrological niche differentiation suggests that maintaining diverse hydroperiods through natural or managed water level variation could promote coexistence and prevent complete competitive exclusion.

Second, seasonal phenological differences may reduce competition intensity during critical life stages [62]. *Sagittaria* exhibits earlier spring emergence (March-April) than *E. pyramidalis* (May-June), potentially providing a temporal window for resource acquisition before invasive grass competition intensifies. Similarly, *Sagittaria*'s capacity for vegetative reproduction through daughter ramets produced throughout the growing season [63] may allow continuous recruitment even in the presence of established *E. pyramidalis* stands, whereas many native species depend on seed germination that *E. pyramidalis* prevents through litter accumulation and light limitation.

Third, belowground storage organs confer resilience to aboveground disturbance [64,65]. *Sagittaria*'s robust tuber system stores substantial carbohydrate reserves enabling regrowth after cutting, grazing, or unfavorable conditions, while *E. pyramidalis* relies primarily on rhizomes for vegetative persistence. This difference in storage strategy may explain *Sagittaria*'s capacity to persist despite reduced aboveground competitive performance: even when *E. pyramidalis* dominates aboveground space, *Sagittaria* maintains belowground presence through tubers, allowing population persistence and potential recovery if conditions change. The lack of significant treatment effects on *Sagittaria* biomass across most experimental treatments (Table 2) supports this interpretation, suggesting that *Sagittaria* populations exhibit resistance or resilience to short-term competitive pressure from *E. pyramidalis*.

Fourth, legacy effects and historical contingency [66,67] may maintain coexistence in systems like La Mancha where both species have been present for decades. Priority effects—where initial colonizer gains long-term advantage through resource pre-emption or niche modification—can create stable coexistence if establishment order varies spatially [48]. Areas where *Sagittaria* established first may maintain dominance indefinitely through positive feedbacks (e.g., soil moisture retention, favorable microbial communities), while *E. pyramidalis*-dominated areas remain invaded through different feedbacks (e.g., high light availability, drier soils). This spatial heterogeneity in establishment history could explain the sharp vegetation boundaries observed in the field.

However, it is critical to note that coexistence at the plot scale (0.49 m^2) does not necessarily translate to landscape-scale coexistence [68]. At La Mancha, distinct vegetation zones dominated by either species with sharp boundaries suggest that coexistence occurs at landscape scales through spatial segregation rather than intimate mixture within microsites. The persistence of both species in experimental plots may reflect the spatial constraint of small quadrats preventing complete exclusion over 18-46 month timescales, whereas larger-scale dynamics over longer periods might lead to complete dominance shifts. Extended, multi-decadal monitoring across diverse spatial scales is required to ascertain whether the observed coexistence patterns reflect stable equilibria or transient processes leading toward alternative stable states characterized by either complete invasion or sustained native persistence.

4.4. Conservation Implications for Mexican Ramsar Wetlands

Our findings have direct implications for managing *E. pyramidalis* invasions in Mexican coastal wetlands, particularly Ramsar sites like La Mancha that harbor significant biodiversity and provide critical ecosystem services. The demonstration that invasion requires disturbance suggests prevention-focused strategies should prioritize: (1) protecting intact native wetlands from cattle access, hydrological modification, and other disturbances; (2) implementing buffer zones around invaded areas to limit propagule spread; and (3) early detection and rapid removal of newly established populations before they develop into dominant patches serving as propagule sources.

For invaded areas, restoration strategies must address both invader removal and establishment barrier creation to prevent reinvasion. Our results showing *E. pyramidalis* recovery after short-term disturbance treatments [2] indicate that single interventions (cutting, herbicide application alone) prove insufficient. More promising approaches combine multiple mechanisms: (1) hydrological restoration maintaining permanent flooding (>30 cm depth) exploits C_4 photosynthetic disadvantages [32,69]; (2) shade creation through riparian vegetation establishment reduces light availability below *E. pyramidalis* compensation points [31]; (3) competitive native planting establishes priority effects and resource pre-emption; and (4) persistent management over 3-5 years addresses propagule pressure from seed banks and rhizome fragments.

The *Sagittaria* persistence observed in our experiments suggests this species may serve as a valuable target for restoration plantings, as it demonstrates capacity to coexist with *E. pyramidalis* and could potentially outcompete the invader under favorable hydrological conditions. Restoration protocols should emphasize *Sagittaria* establishment through tuber planting rather than seed sowing, as vegetative propagules show higher survival in the presence of established vegetation [70]. Additionally, combining *Sagittaria* with other competitive natives adapted to diverse hydroperiods (*Typha domingensis* for deeper water, *Pontederia sagittata* for intermediate depths) may create diverse native assemblages resistant to reinvasion through complementary resource use.

Critically, Mexican freshwater wetlands require legal protection equivalent to mangroves to support conservation implementation. Despite providing comparable ecosystem services—carbon storage (1,100-1,800 Mg C ha^{-1}) [24,25], flood regulation, water quality improvement, biodiversity support for endemic species like Altamira Yellowthroat [28]— freshwater wetlands are not legally recognized as a protected natural ecosystem, in contrast to mangrove forests, which are explicitly safeguarded under Article 60 TER of the General Wildlife Law. This policy gap creates a conservation vacuum where wetland conversion for agriculture faces no legal barriers and invaded wetlands receive no restoration funding. Extending threatened species protection to freshwater wetlands, particularly Ramsar sites, would enable enforcement of existing wetland preservation standards and provide resources for invasive species management.

The Ramsar Convention's commitment to "wise use" of designated wetlands [71] creates an international framework supporting La Mancha conservation, but implementation requires Mexican policy alignment. Only 13 of 41 Ramsar sites in southern Mexico have implemented management plans [72], indicating significant gaps between international designation and on-ground management. Developing and funding La Mancha's management plan with explicit invasive species control components should be a conservation priority, leveraging Ramsar status to secure resources and regulatory support.

At broader scales, addressing *E. pyramidalis* invasion requires engaging the socioeconomic drivers of deliberate introduction and spread. Ranchers value *E. pyramidalis* for high forage productivity and perceived benefits ("dries area and builds soil") [1], creating economic incentives favoring invasion over conservation. Effective long-term management must therefore incorporate: (1) payment for ecosystem services (PES) schemes compensating landowners for maintaining native wetlands rather than planting invasive forage; (2) development of sustainable cattle management using native forage species; (3) ecotourism development leveraging Ramsar designation and endemic species to provide alternative revenues; or (4) regulatory approaches conditioning land use permits on invasive species management. The Mexican PES program for hydrological services [73] could potentially extend to freshwater wetlands given their role in flood regulation and water quality improvement, providing economic rationale for wetland preservation.

4.5. Context: African Grass Invasions and Alternative Stable States

The *E. pyramidalis* invasion at La Mancha exemplifies broader patterns of African grass invasions in tropical and subtropical wetlands worldwide [3,5–7]. Common themes emerge across invasions by diverse species (*U. mutica*, *P. purpureum*, *Melinis minutiflora*, *E. pyramidalis*) in geographically distant systems: (1) deliberate introduction for forage followed by escape and naturalization; (2) C_4 photosynthetic advantages conferring competitive superiority under high light and temperature; (3) extensive clonal growth enabling rapid spread and disturbance tolerance; (4) transformation of diverse native communities into low-diversity invaded states; and (5) extreme difficulty of control once populations establish [4,8].

These parallel outcomes suggest that African grass invasions may create alternative stable states [74,75] maintained by positive feedbacks: invasion increases resource availability (light, nutrients) through native exclusion, which further facilitates invader dominance; high invader biomass prevents native recruitment from seed; altered disturbance regimes (fire frequency, hydrology) favor invader over natives; and propagule limitation prevents native recolonization even if conditions become suitable. Our results support this framework: the sharp vegetation boundaries between invaded and native zones, persistence of each state over multiple years despite spatial proximity, and requirement for disturbance to transition between states all indicate stable state dynamics rather than gradual transition zones.

Alternative stable states theory [76,77] predicts that restoration requires not merely removing the invader but actively destabilizing the feedbacks maintaining the invaded state and establishing feedbacks favoring the native state. This explains why single control treatments failed [2] while multi-year integrated approaches combining invader removal, hydrological modification, competitive native planting, and repeated management showed success [31,32]. The implication for management is sobering: once invaded states establish, they may persist indefinitely without sustained, expensive intervention addressing multiple feedback mechanisms simultaneously.

Preventing invasion into uninvaded wetlands therefore represents the most cost-effective management strategy, as pre-invasion management costs 25 times less than post-invasion control [78]. Early detection and rapid response (EDRR) systems should prioritize: (1) regular monitoring of high-risk areas (agricultural wetlands, sites near invaded populations); (2) training for rapid identification of *E. pyramidalis*; (3) pre-positioned response teams with authority and resources for immediate control; and (4) public engagement through community-based monitoring. The designation of *E. pyramidalis* as "not authorized pending pest risk analysis" by USDA-APHIS [20] reflects prevention priorities, though coordination with Mexican authorities is needed to prevent northward spread from established populations.

5. Conclusions

This research demonstrates that *Echinochloa pyramidalis* invasion of Mexican coastal wetlands operates through mechanisms of disturbance-mediated establishment rather than purely competitive displacement. The invader possesses physiological capacity to dominate native habitat but faces strong biotic resistance in intact vegetation, explaining observed patterns of stable vegetation zonation. Natural invasion spread proceeds slowly due to establishment limitations rather than propagule shortage, suggesting that preventing disturbance in uninvaded wetlands represents the most effective conservation strategy.

For invaded areas, restoration requires sustained multi-year interventions addressing multiple mechanisms: hydrological management maintaining permanent flooding to exploit C_4 photosynthetic limitations; competitive native plantings to establish priority effects; and repeated treatments addressing propagule pressure. The capacity of native *Sagittaria* to coexist with *E. pyramidalis* at moderate abundance provides grounds for cautious optimism regarding restoration potential, though achieving landscape-scale restoration likely requires more intensive management than local coexistence suggests.

Critically, Mexican freshwater wetlands require legal protection equivalent to mangroves to enable conservation implementation. The combination of high carbon storage, support for endemic threatened species, and international Ramsar designation provides strong rationale for policy reform extending wetland protection beyond coastal mangroves to encompass freshwater systems. Without such policy support, technical management solutions alone will prove insufficient to address the socioeconomic drivers maintaining E. *pyramidalis* spread through deliberate rancher introductions.

We recommend that Mexican environmental agencies consider designating *E. pyramidalis* as a regulated invasive species requiring: (1) prohibition of deliberate planting or transport; (2) mandatory reporting and control of new populations; and (3) restoration requirements for invaded Ramsar sites. Such regulatory frameworks exist for other invasive wetland plants globally and would provide legal basis for prevention and management efforts currently hampered by lack of regulatory authority.

These findings inform management of African grass invasions in tropical wetlands globally, demonstrating that invasion success depends on interactions between species traits, disturbance regimes, and recipient community properties. The alternative stable states framework—with invaded and native states maintained by distinct feedback mechanisms—explains invasion dynamics and suggests that prevention through disturbance limitation represents more cost-effective management than post-invasion restoration.

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