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Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem

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Summary

1. Interactions between resident and exotic species have been shown to control the biotic resistance of communities to invasion. With different life stages of the exotic species, each sequential interaction may dampen or strengthen previous ones, thereby influencing invasion success.

2. We assessed the effects of resident vegetation type on the arrival and performance of *Triadica sebifera* (Chinese tallow), a widespread invader in freshwater floating marshes, using a combination of field studies and glasshouse experiments.

3. Our results indicated that *Triadica* abundance was positively associated with native woody species, particularly the native actinorhizal shrub *Morella cerifera* (wax myrtle). Seed dispersal and germination of *Triadica* were generally low but suggestive that *Morella* has weak, facilitative effects on the spread of *Triadica* by channelling its dispersal by birds into shrub thickets and promoting germination upon arrival. *Triadica* seedling growth was greatest where light and total inorganic N were higher. Growth of *Triadica* trees was greater in marsh sites without *Morella* and did not exhibit any detectable responses to elevated N levels in substrates from *Morella* thickets.

4. *Morella* may facilitate the spread of *Triadica* in floating shrub communities, yet inhibit its growth once established. The few individuals that establish in herbaceous marshes grow faster and may therefore reach maturity sooner than in *Morella* shrub thickets.

5. *Synthesis*. Our work suggests that the net effects of facilitation and inhibition by native, resident species on exotics can influence invasion success. In this case, weak, facilitative effects operating in the arrival and establishment phases of invasion are not completely negated by subsequent negative interactions between the same species, enabling the invader to persist. Models that quantify the relative strength and cumulative effects of these interactions are needed to improve predictions of community invasibility.

Key-words: Chinese tallow, exotic, facilitation, floating marsh, invasive species, Mississippi River Delta, *Morella cerifera*, *Myrica cerifera*, *Sapium sebiferum*, *Triadica sebifera*, wax myrtle, wetland

Introduction

Resident species, including natives and exotics already established, affect invasibility of communities through facilitative and inhibitory interactions with invaders (Von Holle 2005). Studies of interspecific interactions have focused mainly on inhibition by residents, for example, competition and predation, and the biotic resistance these interactions may produce (Levine & D'Antonio 1999; D'Antonio & Thomsen 2004; Levine *et al.* 2004). Although positive interactions between native species are common (Bertness & Callaway 1994: Bruno & Bertness 2001; Bruno *et al.* 2003; Pennings *et al.* 2003; Brooker *et al.* 2008), more work is needed that addresses the role of facilitation of exotic invasions by native species (Vitousek & Walker 1989; Bruno *et al.* 2005; Hughes & Denslow 2005). A community might be less invasible if it contained strong competitors (MacDougall & Turkington 2005). Similarly, an assemblage might be more vulnerable if it contained species acting as facilitators. The balance of negative and positive interactions between residents and the invading species (Bulleri *et al.* 2008), in conjunction with propagule pressure of exotics, should influence the level of biotic resistance, thereby preventing or enabling successful establishment by an exotic, as well as controlling the rate and extent of its invasion.

Communities with high inputs of exotic propagules (Brown & Peet 2003; Von Holle & Simberloff 2005) and resource availability (Stohlgren *et al.* 2003) are especially prone to invasion by exotic species. Resident species may indirectly

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control invasion success of exotics through their effects on these two factors. One of the most common ways reported in which native species may facilitate exotic species is through dispersal (Bruno *et al.* 2005). Structural and compositional variation of the resident vegetation can affect the behaviour of animal dispersal agents and thus the seed rain of exotic species with zoochoric fruits (Renne *et al.* 2002). Likewise, a resident species having a symbiosis with a nitrogen fixer may promote establishment of an exotic that requires high nitrogen availability (Vitousek & Walker 1989; Maron & Connors 1996; Hughes & Denslow 2005). Resident species that facilitate the establishment of other species by ameliorating abiotic stress (Bertness 1991; Bertness & Callaway 1994; Badano *et al.* 2007) may also create an avenue for invasion of exotic species in systems with strong abiotic stresses (Von Holle 2005) or low resource availability (D'Antonio & Hobbie 2005). Once established, it is possible for the invader to compete with that same resident for resources. Thus, species interactions can change with life-history stage of the invader (Ruesink 2007).

Floating freshwater marshes in the Mississippi River Delta are characterized by strong abiotic stresses and therefore exotic species may require native facilitators to invade it. These oligotrophic ecosystems are typically dominated by herbaceous species rooted in a mat of living roots and peat of variable thickness that floats upon a column of water overlaying layers of organic sludge and clay (Swarzenski *et al.* 1991); few woody species are capable of establishing and completing their life cycle in the floating marsh (*flotant*) (Williamson *et al.* 1984; Battaglia *et al.* 2007). The most abundant woody native species by far is *Morella cerifera* (L.) Small (wax myrtle, formerly *Myrica cerifera* L.) (Battaglia *et al.* 2007), an actinorhizal, evergreen shrub (Wijnholds & Young 2000). Its congener *M. faya* (Ait.) Wilbur, itself an exotic species in Hawaii, has been shown to alter nitrogen cycling (Vitousek *et al.* 1987) and may favour establishment of additional exotic species that thrive where nitrogen availability is enhanced (Vitousek & Walker 1989).

The only exotic tree species that has established in the *flotant* in Louisiana is *Triadica sebifera* (L.) Small (Chinese tallow, formerly *Sapium sebiferum* (L.) Roxb.); with the exception of one study (Battaglia *et al.* 2007), there has been no other work done on this species in floating marshes. This native of Asia was introduced to the U.S. in the late-1700s (Bruce *et al.* 1997) and is projected to spread northward with global warming (Pattison & Mack 2008). Since its introduction, it has spread widely and is considered to be invasive (*sensu* Pyšek *et al.* 2004) in a wide array of communities in the southeastern and south-central U.S. (Barilleaux & Grace 2000; Matlack 2002). In coastal prairies, it is considered a transformer species (*sensu* Pyšek *et al.* 2004) in that it can alter nutrient cycling (Cameron & Spencer 1989), increase rates of primary productivity (Harcombe *et al.* 1993) and convert the grassland community to woodland (Bruce *et al.* 1995). *Triadica* becomes reproductive at a young age and produces many bird-dispersed seeds (Renne *et al.* 2000, 2001) that can be secondarily dispersed by water. Passage through the gut of some bird species (Renne *et al.* 2001; but see Conway *et al.* 2002) and fluctuating soil temperatures (Donahue *et al.* 2004) are known to enhance its germination. *Triadica* is considered to be moderately tolerant of salinity (Conner 1994), flooding (Jones & Sharitz 1990) and shade (Jones & McLeod 1989).

A survey of *Triadica* distribution, a seed rain study, glasshouse experiments and *in situ* growth rates were collectively used (i) to determine *Triadica* distribution patterns with respect to resident vegetation structure; (ii) to assess effects of resident *flotant* vegetation on *Triadica* seed rain, establishment patterns and growth; and (iii) to explore the relative importance of facilitation and inhibition by resident vegetation in the invasion of *Triadica*. Because *Triadica* is endozoochorous and dispersed by animals that use woody plants as perches, we hypothesized that *Triadica* disperses more readily into floating marsh dominated by woody species compared to herbaceous marsh. We also hypothesized that germination of *Triadica* would be invariant with respect to type of resident vegetation and that its growth rates would be higher in association with *Morella* because of greater nitrogen availability. Thus, we predicted net facilitative effects of shrub vegetation dominated by *Morella* but no effects of herbaceous marsh vegetation on *Triadica* invasion.

Methods

SITE DESCRIPTION

The study area was located 4.3 km south of New Orleans, Louisiana, USA in the Barataria Preserve Unit of the Jean Lafitte National Historical Park and Preserve. The Barataria Preserve is at the seaward limit of the bottomland hardwood forest ecosystem on the Mississippi Deltaic Plain (29.799°N, 90.123°W), and *Triadica* is locally common in forest canopy gaps and backswamp understoreys (Denslow & Battaglia 2002), roadsides, dredge fills and landscaping. At its western edge, the bottomland forest grades into a bald cypress (*Taxodium distichum* (L.) L.C. Rich.) swamp–marsh ecotone that is non-floating and then into a floating freshwater marsh. Floating marshes are common in the Mississippi River Deltaic Plain (Russell 1942) and comprise approximately 70% of the 383 000 ha of freshwater marshes in Louisiana (Mitsch & Gosselink 2000). The herbaceous floating marsh at Barataria Preserve consists of a diverse assemblage of grasses and forbs, dominated by *Sagittaria lancifolia* L. and *Panicum hemitomon* (J.A. Schultes). *Morella* has invaded the *flotant* in some areas, creating shrub thickets with shaded understoreys dominated by ferns, vines and bryophytes (Battaglia *et al.* 2007). A narrow band of oligohaline marsh borders the eastern edge of Lake Salvador (Nolfo-Clements 2006). Interlacing the marsh are canals that were dug through the marsh for oil exploration and navigation purposes (Turner 1997) and are lined by spoilbanks dominated by *Triadica*. These are all common vegetation types in the Mississippi Deltaic Plain (Visser *et al.* 1998), especially in *flotant* marshes (Sasser *et al.* 1996).

TRIADICA SURVEY

In May 2001, we conducted a survey of *Triadica* on a 500 × 250-m grid in the floating marsh to determine its distribution patterns with respect to native vegetation structure; each grid intersection had been marked by a 2-m wooden stake. Previous research on native

Table 1. Presence and absence of *Triadica sebifera* in plots of four sampled vegetation types in the floating marsh ecosystem

Vegetation type	Present	Absent	Total
Oligohaline Herbaceous	3*	3	6
Freshwater Herbaceous	10†	48	58
Sparse *Morella*	48‡	53	101
Dense *Morella*	30	2	32
Total plots	91	106	197

*All *Triadica* individuals were found on narrow, partially sunken spoilbanks lining canals and not in the oligohaline marsh proper.
†In three of these plots, only one *Triadica* sapling was present; in each case it was directly under the plot stake marker.
‡Seven of these plots were under power lines.

community structure and composition indicated four major floating vegetation types in this system (Battaglia *et al*. 2007): (i) oligohaline marsh; (ii) freshwater herbaceous marsh; (iii) sparse shrub marsh (*Morella* present and cover < 25%); and (iv) dense shrub marsh (*Morella* cover ≥ 25%). At each grid intersection (n = 197), we established a 25-m radius circular plot (1963.5 m^2) in which resident vegetation type, plant species presence and absence, and *Triadica* abundance were recorded. All *Triadica* individuals were counted, including small seedlings. The oligohaline marsh was not included in experiments outlined below because it is an uncommon assemblage type at this site and *Triadica* rarely establishes in this vegetation (see Table 1).

The relationship between *Triadica* and resident assemblages was examined using two analyses. A χ^2-contingency table analysis was used to test whether presence and absence of *Triadica* were independent of resident vegetation type. Compositional trends in resident vegetation were explored using non-metric multidimensional scaling (Minchin 1987), and abundance of *Triadica* was then examined in relation to resident species composition. The ordination, based on resident species presence/absence data from the plots and dissimilarities calculated using the Bray-Curtis index (Bray & Curtis 1957), was performed in one to six dimensions, in each case using 100 random initial configurations. Starting from an initial ordination, the positions of plots are gradually adjusted to minimize 'stress,' a measure of the badness-of-fit of a rank-order regression of ordination distances on dissimilarities (Minchin 1987). A Scree plot with stress vs. dimensionality (1–6) was used as an aid for selecting the ordination with the appropriate dimensionality. The correlation between *Triadica* abundance and resident species composition was computed and tested using vector fitting (Dargie 1984; Kantvilas & Minchin 1989). Statistical significance of the correlation is tested by randomly permuting the values of the variable (*Triadica* abundance in this case) among plots, simulating the null hypothesis of no trend. The ordination and vector fitting were performed using the DECODA software package (Minchin 1989).

SEED RAIN

Floating seed traps were used to measure effects of vegetation structure on dispersal of *Triadica* seeds. In August 2000, we removed all *Triadica* seedlings, saplings, and trees from a 10 × 50-m strip inside four dense *Morella* shrub thickets so that dispersal into the strips could be measured. We installed a floating seed trap at 10 m intervals (0, 10, 20, 30 and 40 m) along the central axis of each removal strip within the dense shrub thickets and paired it with an identical line of traps distributed within the adjacent freshwater herbaceous marsh and parallel to each dense shrub transect. *Triadica* was not present in the herbaceous marsh strips, so it was never removed. Traps were set out in late December 2000 and seeds were collected monthly during the peak dispersal period (February–May) of the following year. Each seed trap (0.18 m radius) was covered with 3.5 cm wire mesh to deter animals from robbing the trap. Traps were tethered to PVC posts driven into the floating mat.

The cumulative number of *Triadica* seeds collected per trap was square-root transformed to meet assumptions of normality and homoscedasticity (Manly 1992). Seed counts were tallied for each thicket by summing over the five traps in each thicket or adjacent herbaceous marsh site. A paired t-test was used to compare seed rain in shrub thickets to adjacent marsh.

GERMINATION EXPERIMENT

In August 2004, we collected a sample of the top 5 cm of soil at three haphazardly located points within each of the major floating vegetation types (dense shrub, sparse shrub and herbaceous marsh). The area over which each sample collected was approximately 1 m^2. In a glasshouse, each soil sample was spread into a 25 × 50-cm flat (n = 3 per community, total n = 9) at a depth of 5 cm and kept saturated with water. In October 2004, we collected a large stock of seeds from 10 haphazardly selected *Triadica* trees along spoilbanks at the study site. Seeds were cold-stratified for two months and in December 2004, nine sets of 144 *Triadica* seeds were randomly selected from this stock and sown into each of the nine flats (total seeds = 1296). Seedling emergence was monitored daily from 1 January to 30 September 2005 and the final tally of *Triadica* seedlings that germinated in each flat was recorded.

Final germination percentage for each flat was arcsin transformed and we used a one-way ANOVA to compare germination in soils from dense shrub, sparse shrub and herbaceous marshes. Significant ANOVA results ($P \leq 0.05$) were subjected to Tukey's multiple means tests.

GLASSHOUSE SEEDLING GROWTH EXPERIMENT

In October 2004, we collected *flotant* mat cores (10 cm diameter × 48.5 cm in depth) from three sites at Barataria Preserve using a Hargis corer. Sites were haphazardly selected and were required to have a dense shrub thicket, sparse shrub edge and freshwater herbaceous marsh present. At each site, we removed two cores from the three assemblage types (total cores = 18). Adjacent to each core, we also collected a substrate sample (10–12 g) from the top 5 cm of the floating mat for nutrient analyses. Each intact core was transported in a plastic bag and stored at 4 °C until February 2005 when the contents were transferred into a perforated plastic cylinder of the same dimensions, wired upright in a plastic bucket (18.93 L) and kept saturated to one cm below the soil surface in a glasshouse. To mimic canopy cover inside and outside of the thickets, nine of the buckets (one from each assemblage type × 3 replicates) were left in open sunlight, while the other nine buckets were placed under neutral shade fabric. We used Gap Light Analyzer (Frazer *et al*. 1999) to analyse 10 fisheye colour canopy photos taken at haphazardly chosen locations under the *Morella* understorey. Mesh size of the shade fabric for the experiment was chosen to allow transmission of 45% full sun, which was similar to mean percent canopy openness calculated from the canopy photos (mean percent ± SE: 41.27 ± 3.79).

At the onset of the glasshouse experiment, we determined inorganic nitrogen (N) availability in the substrates derived from each assemblage. Inorganic N concentrations were determined by extracting 10–12 g of substrate with 50 mL of 2 M KCl, agitating solutions at 200 rpm

for 1 h and filtering through 0.4-μm polycarbonate membranes. Extracts were analysed for NH_4-N and NO_3-N using segmented flow analysis on an OI Analytical Flow IV autoanalyzer (College Station, TX). The phenol blue method was used for colorimetric determination of NH_4-N and diazotization with sulphanilamide after reduction of nitrate to nitrite through a cadmium coil was used to determine NO_3-N concentrations (Keeney & Nelson 1982). Two 10–12 g samples were removed from each replicate bucket, then averaged by replicate, treatment and site before statistical analyses ($n = 3$ per location or community source).

We used the remaining cold-stratified *Triadica* seeds to produce a seedling stock for the seedling growth experiment. Seedlings (with cotyledons and one true leaf) were selected randomly and one seedling was transplanted into each core in February 2005. Initial seedling height was recorded when planted, and each seedling was measured every 2 weeks until the end of the growing season in November 2005.

Differences in inorganic N availability among the three community substrates used in the glasshouse experiment were analysed according to a randomized complete block design using the mixed model procedure in SAS (SAS Inc. 2002), with block assigned as a random effect. Relative growth rates of *Triadica* seedlings over time were determined using linear regression models. All regression slopes were then compared across the factorial combination of substrate source (marsh vs. thicket edge vs. thicket centre) and light (sun vs. shade) combinations using the mixed procedure in SAS, with block assigned as a random effect. Differences in growth rates were determined using the least squares means comparison procedure ($P \leq 0.05$).

STEM CROSS SECTIONS

We measured *Triadica* growth rates on stem cross sections from trees growing in dense shrub, sparse shrub and freshwater herbaceous marsh communities. In October 2002, *Triadica* tree cross sections were taken from these assemblages using a stratified random selection of plots from the sampling grid established in 2001. We collected five sections from each of five replicate sites in dense shrub marsh, sparse shrub marsh, and three replicate sites in freshwater herbaceous marsh (total sites = 13; total tree sections = 78). In each plot, we selected healthy trees representing the range of size classes present. Each stem was cut close to the base using a chainsaw, and a cross section was taken from the stem near the base. In the laboratory, one side of each disk was sanded first with 80-grit sandpaper, followed by 100-grit and 150-grit sandpaper.

We identified annual growth rings on each cross section to determine age and annual growth increments in *Triadica* stems. Each sample was observed by the unaided eye and then under an Olympus microscope at ×10 magnification. Annual rings were triple-checked for consensus by two of the authors (JRI & LLB). We measured annual growth increments using a stereoscope and a linear encoder device to the nearest 0.01 mm. We used the following equation to calculate relative growth rates: $RGR = (\ln BA_2 - \ln BA_1)/(t_2 - t_1)$, where BA_1 and BA_2 are tree basal areas at times t_1 and t_2. Relative growth rates of *T. sebifera* trees were log-transformed to meet assumptions of normality and homoscedasticity and compared among the three community assemblages using a one-way ANOVA. Significant ANOVA results ($P \leq 0.05$) were subjected to Tukey's multiple means tests.

Results

Triadica was present in all of the vegetation types in the floating marsh that we surveyed (Table 1). Its presence and absence were not, however, independent of vegetation type ($\chi^2 = 48.78$, d.f. = 3, $P < 0.0001$). Plots with dense *Morella* cover were the most frequently invaded. In the sparse shrub plots, *Triadica* was present almost as often as it was absent. In freshwater herbaceous marsh, it was absent more often than it was present.

Based on the scree plot, we found that stress levelled off with a three-dimensional solution for the non-metric multidimensional scaling ordination. The predominant trend in the three-dimensional ordination was a gradation from herbaceous assemblages, namely the freshwater herbaceous marshes (H), to assemblages increasingly dominated by *Morella* (D) (Fig. 1). Abundance of *Triadica* ranged from 0 to 2.05 m^{-2} (0–4204 per plot) and had a significant, positive relationship with the major trend in the ordination ($r = 0.4214$, $P < 0.0001$).

In general, seed capture rates and germination of *Triadica* were low; many traps captured no seeds during the study. Although we trapped more seeds in shrub thickets than in herbaceous marshes, the differences were not significant at the $P \leq 0.05$ level ($t = 2.65$, $P = 0.08$). Percentage of germination of *Triadica* seeds was highest in dense shrub thicket substrates (6.0%), intermediate in sparse shrub cover (2.7%) and lowest in herbaceous marsh substrates (0.7%); germination did not differ significantly among substrate types at the $P \leq 0.05$ level ($F = 4.45$, d.f. = 2, $P = 0.07$).

Inorganic N availability varied among the community source substrates used in the glasshouse experiment. Total inorganic N was higher in soil derived from the shrub thickets dominated by the N-fixing species relative to the thicket edge and herbaceous marsh ($F = 9.04$; d.f. = 2, 5; $P = 0.02$; Fig. 2). All available inorganic N was in the form of NH_4-N in the centre and edge locations. The herbaceous marsh had 0.17 ± 0.12 μg g^{-1} NO_3-N, constituting < 3% of total inorganic N.

The linear regressions of seedling relative growth rates were all significant ($P < 0.001$, data not presented). Analysis of regression slopes across shade/substrate combinations indicated a main effect of light ($F = 11.23$; d.f. = 1, 10; $P = 0.007$) and a main effect of substrate ($F = 4.98$; d.f. = 2, 10; $P = 0.03$) but no interaction between light and substrate source ($F = 1.57$; d.f. = 2, 10; $P = 0.26$). Growth rates of *Triadica* seedlings were greater in open sun than in the simulated shade of dense shrub cover ($P = 0.01$) and greater in thicket centre substrates compared to those from thicket edge ($P = 0.01$) and herbaceous marsh ($P = 0.05$) types.

Average relative growth rate (cm^2 cm^{-2} $year^{-1}$) differed across vegetation types ($F = 9.31$; d.f. = 2, 10; $P = 0.01$) and was significantly higher in freshwater herbaceous marsh than in sparse and dense shrub marshes, which did not differ (Fig. 3).

Discussion

FACILITATION AND INHIBITION — EFFECTS OF RESIDENT VEGETATION ON INVASION SUCCESS

Triadica is a widespread invader that has established in all vegetation types in the floating marsh ecosystem at Barataria

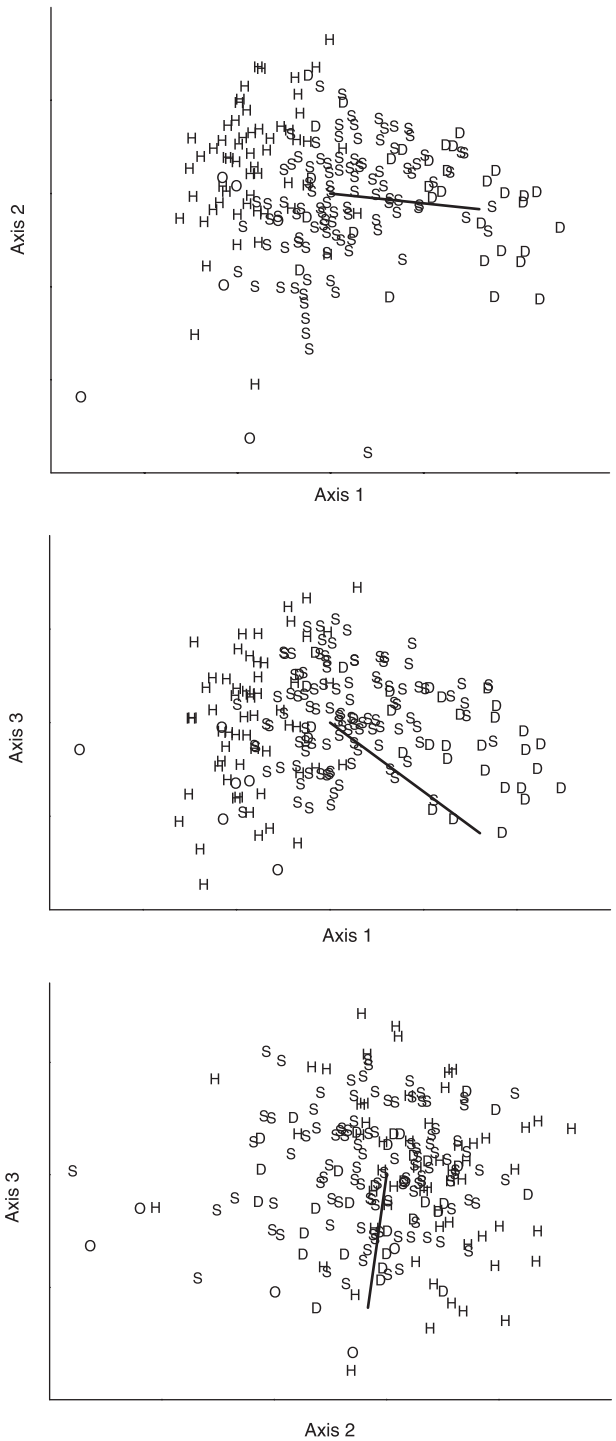

Fig. 1. Three-dimensional non-metric multidimensional scaling ordination (stress = 0.179) based on presence/absence of marsh species with a fitted vector for *Triadica sebifera* abundance ($r = 0.4214$, $P < 0.0001$). The length of the vector corresponds to the strength of the correlation. Letters in the ordination represent the different vegetation types (O, oligohaline marsh; H, freshwater herbaceous marsh; S, sparse shrub marsh; and D, dense shrub marsh).

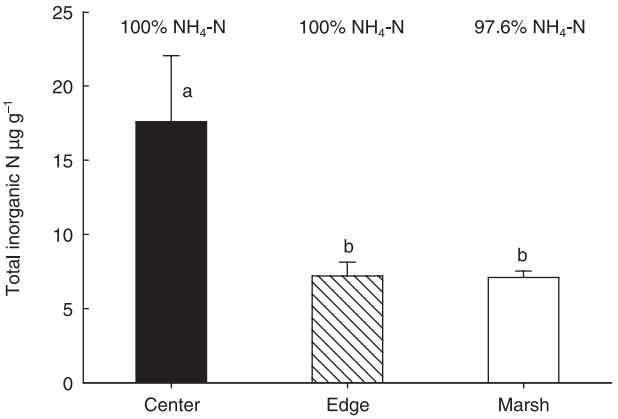

Fig. 2. Average (± 1 SE) total inorganic N availability in substrates derived from three locations relative to three *Morella* thickets. Means accompanied by the same letter were not significantly different ($\alpha = 0.05$).

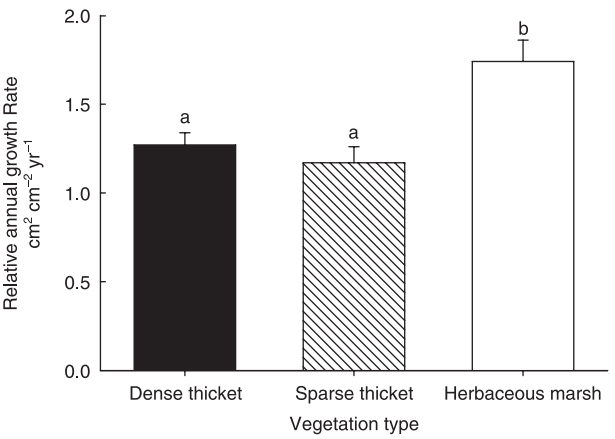

Fig. 3. Average (±1 SE) annual relative growth rate of trees from three marsh vegetation types. Means accompanied by the same letter were not significantly different ($\alpha = 0.05$).

Preserve. Its distribution and high abundance in some areas indicate an advanced state of invasion (Battaglia *et al.* 2007) but are also suggestive of facilitation by some types of resident vegetation. In the vegetation types we examined, *Triadica* was highly abundant and more likely to be present in the dense *Morella* shrub thickets. In the thickets, *Triadica* density is high and ranges from an estimated 5813 to 27 625 stems per hectare (Battaglia *et al.* 2007). In contrast, *Triadica* is much less common and abundant in the herbaceous marsh. Taken alone, these patterns suggest that *Morella* has an overall facilitative effect on the invasion of *Triadica* in this system.

When we evaluated the effects of *Morella* on individual life-history phases and stages of the invasion process, we instead found a mixture of weak and strong interactions (Table 2). In the early life-history stages, dispersal and germination, *Morella* effects on *Triadica* were not statistically significant at the conventional α-level of 0.05; the effects were, however, significant at an α-level of 0.10. Although statistically weak, we suggest that these relationships are noteworthy because they may be ecologically significant in the invasion process of *Triadica*. In this study, we experimentally segregated dispersal and germination (i.e. seeds trapped were not used for field germination trials), as well as other phases. Under

Table 2. *Morella cerifera* effects on different life-history stages and environment of *Triadica sebifera*

Triadica Life-History Stage/ Environment	Relationship with *Morella*
Seed rain	Weakly positive*
Seed germination	Weakly positive*
Seedling growth – nitrogen	Positive
Seedling growth – shade	Negative
Tree growth – nitrogen	Neutral
Tree growth – shade	Negative

*Statistical comparisons were significant at the $P \leq 0.10$ but not at the $P \leq 0.05$ level.

field conditions, however, they would be sequential. A weakly positive effect of *Morella* on *Triadica* dispersal could be magnified by a weakly positive and congruent effect on germination, possibly contributing to the pronounced and disproportionately high densities of *Triadica* we find in association with *Morella*. Studies that omit critical life-history stages or consider effects in isolation such as this study may fail to detect critical sequential and cumulative effects (Gundale *et al*. 2008) that influence invasion outcomes.

Features such as perches that enhance the inputs of exotic propagules make communities more susceptible to invasion (Vitousek & Walker 1989; Brown & Peet 2003). In this floating marsh ecosystem, the woody canopy provides perches for birds and may facilitate dispersal of *Triadica* seeds and other bird-dispersed species including *Morella* (Kwit *et al*. 2004). Fruits of both species have white, waxy coatings that are attractive to birds (Renne *et al.* 2001) and have high caloric content (Renne *et al.* 2002). When an exotic plant species becomes incorporated into the diet of native birds, as in this case, the exotic's ability to spread can be greatly enhanced (Bartuszevige & Gorchov 2006), thereby reducing the filter of dispersal limitation. Non-native birds have also been found to contribute to seed rain of exotic and native plant species (Williams & Karl 1996). For example, the exotic European starling was the most important avian dispersal agent of *Triadica* in spoilbank habitat in South Carolina USA (Renne *et al*. 2002). The extent to which exotic birds contribute to spreading *Triadica* and *Morella* in the *flotant* ecosystem is unknown.

Morella canopies may not be the only structural features that influence *Triadica* dispersal. In several of the open herbaceous marsh plots, the only *Triadica* individual present was adjacent to the wooden stake that marked the centre of the plot. It is likely that the stakes function as solitary perches for birds, thereby facilitating its dispersal. Several of the sparse *Morella* plots where *Triadica* occurred coincided with an electrical power line that traverses the marsh. In these plots, *Triadica* individuals were typically underneath the power line in a row, indicating that it also functioned as a perch for birds dispersing *Triadica* seeds. These findings indicate that a variety of perch types can facilitate invasion of this exotic and function as foci for recruitment (Holl *et al*. 2000), whether there are food rewards (*e.g*. *Morella* fruits) or not.

In addition to physical structure, phenology can also play an important role in determining spatial patterns of species. Co-occurrence may be driven in part by overlapping periods of fruit ripening (Clark *et al*. 2004). In this case, *Triadica* and *Morella* fruits ripen in autumn and both may persist on the plants for several months (Renne *et al*. 2002; Kwit *et al*. 2004). Thus, frugivorous birds foraging during this time are likely to encounter fruits of both species and disperse their seeds jointly.

Although seed germination was low in this study, germination percentages from all marsh types, particularly of seeds sown in *Morella* substrates, were considerably higher than those found in coastal prairie (Siemann *et al*. 2007) within this region. The floating peat mat may be more vulnerable to *Triadica* invasion, at least during the seedling regeneration stage, than coastal prairie. If *Morella* further enhances germination of *Triadica*, the mechanisms are unknown but warrant further study.

While *Morella* may facilitate *Triadica* during the arrival and establishment stages, shade cast by the woody residents inhibits the growth of *Triadica* seedlings and trees. In the absence of shade, *Triadica* seedlings in the glasshouse experiment grew better. Similarly, the few *Triadica* individuals that established in herbaceous marsh had greater tree growth without *Morella* canopy than those in shrub thickets. We hypothesized that inhibition by shade may be offset in the shrub thickets because *Morella* enhances nitrogen levels in the soil (Tolliver *et al.* 1995). In the case of seedlings, *Triadica* did experience higher growth in substrates taken from dense *Morella* thickets compared to those from sparse *Morella* and open herbaceous marshes. However, there was no indication of facilitation *vis a vis* nitrogen enhancement for *Triadica* trees and light was clearly the primary limiting factor on tree growth. Elevated inorganic N levels in *Morella* thickets appear to be beneficial to *Triadica* during the seedling stage, but no effects were detectable at the tree stage. Foliar N data collected from *Triadica* trees support this conclusion (data not presented).

MODEL OF *MORELLA*–*TRIADICA* DYNAMICS IN THE FLOTANT ECOSYSTEM

Whether *Triadica* densities increase, decrease or remain stable over the long term may depend on the fate of *Morella*, rate of organic accretion within the mat as well as the flotation capacity of the mats. Williamson *et al.* (1984) speculated that *Morella* shrub dieback occurs when the floating mat can no longer support the weight of larger individuals and the stems are killed by inundation. *Morella* populations may be limited in part by flooding, with dying shrubs producing small gaps in the thicket canopy, as they do in barrier island communities (Crawford & Young 1998). At Barataria Preserve, we have observed submergence of the mat, death of larger *Morella* stems and small gap formation. In some cases, these gaps are colonized by herbaceous marsh vegetation. We have not observed a broad-scale wave of decline in *Morella* cover. It is unlikely that small and local declines in *Morella* populations are sufficient to slow the invasion of *Triadica*. Once established,

Triadica does not require *Morella* to persist and perhaps even proliferate.

Persistence of scrub–shrub cover in the floating marsh ecosystem may have dire ecological consequences on a longer time scale. Maintenance of the floating peat mat is critical for all species that are rooted in and float with it. Graminoids that have high above- and below-ground productivity such as *Panicum hemitomon* are the major mat builders (Sasser *et al*. 1996); broad-leaved macrophytes such as *Sagittaria lancifolia* build mats that are much thinner. In the scrub–shrub areas that are often highly infested with *Triadica*, the understoreys are shaded with lower herbaceous productivity (Battaglia unpublished) and the mats are often degraded and in varying stages of breakup (Battaglia *et al*. 2007). Reduced productivity of the major mat-building species may lead to reduced organic material inputs into the mat and reduced organic accretion. Whether the contribution of woody species to organic inputs and mat building is sufficient for the peat mat to keep pace with decomposition is unknown. Other studies have shown that encroachment by N-fixing shrubs into areas formerly dominated by grasses can drive shifts in C and N cycling (Brantley & Young 2008; Kurten *et al*. 2008) and lead to permanent changes in species composition (Day *et al*. 2004). Furthermore, the elevated inorganic N could influence decomposition rates of the mat if N is normally limiting to microbes. Changes that jeopardize the sustainability of the *flotant* marsh will also have negative impacts on *Triadica* populations. Therefore, the long-term persistence of *Triadica* in this ecosystem is uncertain.

The frequent co-occurrence of *Triadica* and *Morella* suggests that they are moving together in the landscape, and the apparent preference of *Triadica* for communities in which *Morella* is present may be useful in predicting its pattern of spread into previously uninvaded plant communities. *Morella* shrub populations have been steadily increasing in this floating marsh ecosystem and others like it over the last 50 years (Shirley & Battaglia 2006, 2008), providing an expanding invasion front for *Triadica* establishment. Although it is conceivable that *Triadica* and/or *Morella* may experience a period of dieback (Williamson *et al*. 1984), its invasion of coastal prairies demonstrates that *Triadica* is capable of transforming (*sensu* Pyšek *et al.* 2004) herbaceous communities to persistent woody assemblages in which it is a dominant member (Bruce *et al.* 1995; Grace 1998). It is likely that *Triadica* invasion will continue to advance into areas where *Morella* spreads. Furthermore, it is possible that established *Triadica* patches may become foci of future invasions of conspecifics (Reinhart *et al*. 2006) as well as other small-stature exotic shrubs and trees that are bird-dispersed such as *Ligustrum sinense* Lour. (Chinese privet).

Conclusions

Collectively, these results support the idea that resident species can have mixed effects on invaders that vary depending on the demographic variable examined. Some interactions between resident and invading species may take primacy in their influence on success of an invader. In this case, the weak, facilitative effects operating in the arrival and establishment phases of invasion are not negated by subsequent negative interactions between the same species. Communities with resident facilitators may be prone to chronic invasion risk through direct and indirect interactions with invaders.

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