Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavourable but variable environments and can be exploited to streamline restoration

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Summary

1. Reinvasion pressure is the rate of new exotic recruitment following mature exotic removal and it can vary broadly among similarly invaded habitats. Reinvasion pressure drives restoration outcomes and costs but is difficult to predict and poorly understood. Chinese tallow tree *Triadica sebifera* is a major invader demonstrating broad variation in average reinvasion pressure. We hypothesize this variation arises from differences in moisture regimes among habitats, which drive differences in *Triadica* recruitment but are masked because *Triadica* exhibits ontogenetic niche expansions (increases in niche breadth during development) that enable dominance in habitats where average recruitment success is low.

2. We began testing this hypothesis by quantifying *Triadica*'s capacity for ontogenetic moisture niche expansions. We performed greenhouse experiments examining how soil moisture affects germination likelihood and timing and how soil moisture and seedling age influenced seedling survival and performance, plus a field experiment quantifying survival and performance of differently aged seedlings within a restoration site that has exhibited low average reinvasion pressure.

3. Moisture requirements for germination were the most constrained of any life stage. No germination occurred in saturated or flooded soils despite high seedling survival in comparable conditions. Germination timing varied among suitable moisture treatments.

4. Seedling survival increased rapidly with age across moisture treatments and in the field. Above-ground biomass increased with age; tissue-specific performance metrics also increased but reflected seed provisioning, age-specific carbon allocation preferences, or tissue shedding for survival. Crucial moisture*age interactions that signify ontogenetic niche expansions were significant for all survival metrics and all but one performance metric.

5. Survival and performance were generally highest in intermediate moistures, modestly reduced in saturated conditions and lowest in water-limited conditions.

6. Synthesis and applications. Our results show Triadica exhibits rapid ontogenetic moisture niche expansions, which could decouple mature Triadica density and average reinvasion pressure. Therefore, density is an unreliable predictor of reinvasion but is commonly used to guide Triadica management, and cryptic opportunities exist for inexpensive and straightforward restorations. Reliable moisture niche-based estimates of Triadica's average reinvasion pressure are feasible and may improve restoration efficacy and efficiency by informing site selection and optimal management strategies.

Key-words: germination cuing, invasive plant control, ontogenetic niche shift, recruitment limitation, reinvasion pressure, *Sapium sebiferum*, stress tolerance, *Triadica sebifera*, weed management

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Introduction

Invasive species degrade ecosystems and impede restoration world-wide, particularly in the habitats they dominate (Kettenring & Adams 2011). When restoring ecosystems dominated by an exotic plant, reinvasion pressure is the rate of new exotic recruitment following mature exotic removal and it can vary broadly between similarly invaded habitats (Buckley, Bolker & Rees 2007). Reinvasion pressure is crucial to restoration outcomes and costs because plant density moderates invader effects on communities and ecosystem functions (Grime 1998) and influences required management methods, which have manifold non-target impacts (Rinella et al. 2009) and vary widely in cost (Epanchin-Niell & Hastings 2010). Reinvasion pressure is difficult to predict, but accurate estimates are feasible and may improve restoration efficacy and efficiency by informing site selection and optimal management strategies (Gabler & Siemann 2012). Despite broad implications for applied ecology, reinvasion pressure and the mechanisms of its variation are poorly understood (Kettenring & Adams 2011).

Triadica sebifera Chinese tallow tree is a major invader in the south-eastern United States with broad variation in average reinvasion pressure during restorations of habitats it dominated (Donahue, Rogers & Siemann 2006; C. Gabler & E. Siemann, unpublished data). We hypothesize this variation arises because Triadica exhibits ontogenetic niche expansions (increases in niche breadth during development) that enable individuals to persist in habitats where moisture regimes range from being frequently, highly suitable for Triadica recruitment to being rarely, marginally suitable. If so, we theorize abiotic variation among invaded habitats drives differences in recruitment success that underlie observed variation in average (longterm mean) reinvasion pressure (Gabler & Siemann 2012). Whether recruitment is regular or episodic, ontogenetic niche expansions would permit high densities of Triadica to develop over time that mask underlying abiotic variation and thus average reinvasion pressure. We refer to the phenomenon where average reinvasion pressure is relatively low despite high mature exotic density as 'densityreinvasion decoupling'. This work begins testing this hypothesis by quantifying Triadica's capacity for ontogenetic moisture niche expansions.

Ontogenetic niche expansions are increases in niche breadth during an individual's life (Parrish & Bazzaz 1985; Gabler & Siemann 2012); niche contractions (Quero *et al.* 2008) and directional shifts also occur (Eriksson 2002). Ontogenetic changes in plant abiotic requirements may permit coexistence (Grubb 1977) and can influence species distributions and population dynamics (Parrish & Bazzaz 1985; Eriksson 2002; Donohue *et al.* 2010), plant– plant interactions (Miriti 2006; Quero *et al.* 2008) and succession (Young, Petersen & Clary 2005). However, ontogenetic niche changes in plants are understudied, rarely used to explain reinvasion and seldom considered in practice, despite their relevance to population and community ecology and a review by Young, Petersen & Clary (2005) emphasizing their importance to restoration and scarcity of applicable research.

Ontogenetic niche expansions can explain density -reinvasion decoupling, but we posit that short-term reinvasion pressure is determined by exotic propagule abundance and spatiotemporal availability of realized recruitment windows (Gabler & Siemann 2012). Realized recruitment windows are based on 'safe sites' (Harper 1977) and coexistence (Chesson 2000) and invasion hypotheses that stress spatiotemporal variation (Davis, Grime & Thompson 2000; Shea & Chesson 2002) but emphasize ontogenetic niche expansions. Realized windows are periods of variable duration that permit recruitment of exotics with expanding niches and are fundamentally defined by abiotic conditions. Thus, spatiotemporal (e.g. interannual) variation in abiotic conditions within habitats is crucial to reinvasion pressure.

We emphasize *Triadica*'s moisture niche and moisture variation among habitats because we expect water to be particularly important to *Triadica* recruitment and persistence. Temperature defines *Triadica*'s northern limits, but water regime is crucial to its local distribution and can vary considerably on small spatial scales in its introduced range (Bruce *et al.* 1997). Preliminary results from experimental restorations of *Triadica*-dominated sites suggest reinvasion pressure correlates with soil moisture but not pre-removal *Triadica* density (C. Gabler & E. Siemann, unpublished data). In other systems, interannual variation in precipitation can influence seed production (Perez-Ramos *et al.* 2010) and establishment success (Bartha *et al.* 2003) and cause episodic recruitment (Crawley 1990), which are all important to reinvasion.

If ontogenetic niche expansions in *Triadica*'s moisture tolerance underlie observed variation in its reinvasion pressure, we may be able to predict short-term and average (long-term mean) *Triadica* recruitment within particular habitats by emphasizing climate forecasts or average abiotic conditions, respectively. Such predictions would be extremely valuable decision-making tools in planning and executing restoration and/or exotic removal in habitats invaded by *Triadica*, and this approach should be applicable for other species and systems. Great potential to avoid unnecessary management lies in our capacity to identify density-reinvasion decouplings. Generally, accurate estimates of reinvasion pressure could improve restoration efficacy, efficiency and predictability in any ecosystem dominated by exotic plants.

We investigated whether *Triadica* undergoes ontogenetic niche expansions by performing three experiments quantifying breadths of moisture tolerance at different stages early in *Triadica* development. If *Triadica*'s moisture niche expands ontogenetically, its germination niche will be most constrained and older seedlings will survive across a broader range of moisture conditions and exhibit higher performance than younger seedlings. To better

understand how ontogenetic patterns of moisture tolerance in an important invasive plant and moisture patterns in recipient habitats may influence reinvasion pressure, we ask: (i) What are *Triadica*'s moisture requirements for germination and seedling survival and growth? (ii) Does *Triadica* undergo ontogenetic niche expansions? If so, how and when do its moisture tolerances change during development? (iii) Can niche expansions explain observed *Triadica* recruitment patterns? That is, can seedling age influence survival of *Triadica* in habitats exhibiting very low average reinvasion pressure?

Materials and methods

FOCAL SPECIES AND STUDY SITE

Chinese tallow tree [Triadica sebifera (L.) Small, Euphorbiaceae; synonym Sapium sebiferum; 'Triadica' throughout] is an invasive exotic species in the south-eastern United States naturalized from Texas to Florida and northward from Arkansas to North Carolina and in California (Bruce et al. 1997; Aslan 2011). Triadica aggressively displaces native species in grasslands (including imperiled coastal prairies), wetlands and forests to form monocultures in as little as two decades (Bruce et al. 1997). Triadica demonstrates competitive superiority arising from high growth rates (Lin et al. 2004), prolific seed production (Renne, Gauthreaux & Gresham 2000), broad abiotic tolerances (Jones & McLeod 1989; Butterfield, Rogers & Siemann 2004) and low herbivore loads (Siemann & Rogers 2003a). Triadica's high capacity for vegetative regrowth from stumps or rootstocks complicates control efforts (Bruce et al. 1997). Seeds require oscillating temperatures characteristic of exposed soil to break dormancy, which promotes Triadica germination in disturbed conditions (Nijjer et al. 2002; Donahue, Rogers & Siemann 2004, 2006). Established Triadica seedlings have broad moisture tolerances (e.g. Hall & Harcombe 1998; Butterfield, Rogers & Siemann 2004), but moisture requirements for Triadica germination and early development have not been quantified and are crucial to our framework.

We performed our field experiment within a 1.2-ha experimental restoration site in Justin Hurst Wildlife Management Area (JHWMA) near Jones Creek, Texas, USA (28·959502 N, -95.461348 W). JHWMA is ~100 km south of Houston and spans 4835 ha of grasslands and wetlands characteristic of the United States Western Gulf Coastal Plain ecoregion. Land is nearly level and poorly drained with elevation generally <2 m above mean sea level. Average annual temperature is 20·8 °C, and average annual rainfall is 1320 mm with 60% between April and September. Study area soils are expansive Pledger (85%) and Brazoria Clay (10%) vertisols (very-fine, smectitic, hyperthermic Typic Hapluderts) with 60–80% clay content (classification follows USDA/NRCS Soil Taxonomy).

The restoration site encompasses a seasonally flooded freshwater depressional wetland that was dominated by closed-canopy *Triadica* woodland with minimal native understorey before restoration began in 2006. In 2010, the study area had an understorey dominated by *Carex oxylepis* Torr. and Hook. (Cyperaceae; 55% cover) with various other forbs (13%) and grasses (5%) and an open, low-statured overstorey of woody *Sesbania drummondii* (Rydb.) Cory (Fabaceae; 31% canopy cover). *Triadica* saplings contributed only 1.8% canopy cover and no seedlings were observed. Since restoration began, *Triadica* has remained exceedingly rare site-wide including within unmanaged areas and *Triadica* seed addition plots (C. Gabler & E. Siemann, unpublished data). *Triadica* reinvasion pressure has been substantially lower here than in any other documented restoration of *Triadica*-dominated habitat.

GERMINATION EXPERIMENT

The germination experiment quantified impacts of soil moisture and source tree on germination likelihood and timing. The full factorial design used 46.6-ml polystyrene vials (25 mm wide \times 95 mm tall) filled with ~34 ml field soil from JHWMA with six moisture treatments, ten source trees and eight replicates per combination (n = 480 vials). In June 2010, we planted two washed Triadica seeds (see Appendix S1 in Supporting Information) collected in 2009 in each vial and immediately imposed moisture treatments: (i) 'drought' - 15 ml water added (watered) every 28 days, vials bottom draining; (ii) 'dry' - watered weekly, bottom draining; (iii) 'field capacity' - watered daily, bottom draining; (iv) 'subsurface saturation' - watered daily, side draining so the top 35 mm of soil drained and bottom 35 mm remained saturated; (v) 'saturated' - watered daily, side draining so all soil remained saturated without standing water and (vi) 'flooded' - 'topped off' daily and undrained so 20-25 mm (depending on evaporation) standing water remained. Moisture treatments here and below mimic the range of typical moisture conditions in sites where juvenile and mature Triadica are commonly observed.

We housed vials in a climate-controlled greenhouse under natural light with day temperatures of 34-36 °C and night temperatures of 23-25 °C, which approximates summer in south-east Texas. Triadica germination peaks in spring but can occur throughout the growing season in dry to temporarily flooded soils. We watered, maintained drainage and surveyed vials daily. We removed germinated seeds and smoothed soil surfaces immediately to maximize microclimate consistency within vials. After 60 days, we observed zero germination (in vials and independent trials under optimal conditions), presumed Triadica seeds utilized were unviable and planted two or three additional seeds collected in 2008 from one of eight novel source trees in each vial. We continued as before for 91 days and concluded experimentation in November 2010 after 14 consecutive days with no germination. We report germination timing based on the second planting but germination likelihoods (germinant abundance/total seeds) based on both plantings. We used repeated measures ANOVA (aov in R 2.13; R Foundation for Statistical Computing, Vienna, Austria) to test effects of soil moisture, source tree, time and their interactions on Triadica germination likelihood. Error was partitioned across subjects (vials) for factors excluding time and within subjects for factors including time. We used Holm-Bonferroni adjusted pairwise t-tests to identify differences between treatments means.

GREENHOUSE EXPERIMENT

The greenhouse experiment quantified survival and performance of differently aged *Triadica* seedlings along a moisture gradient. The unbalanced full factorial design used 2-8-L pots with six moisture treatments, six seedling age treatments and 5–10 replicates per treatment combination (n = 287 pots). In June 2008, we

added washed (see Appendix S1) *Triadica* seeds from each of 21 source trees to separate trays of Metro-Mix[®] (Sun Gro Horticulture, Washington, USA) for germination. We watered trays daily and housed them in a climate-controlled greenhouse under natural light with day temperatures of 29–31 °C and night temperatures of 19–21 °C, which approximates spring in south-east Texas. We transplanted newly germinated seedlings into 2.8-L tapered square plastic Treepots (36 cm tall, 6–10 cm diameter; Stuewe & Sons, Oregon, USA) filled with ~2 L field soil collected from JHWMA, assigned each an age and moisture treatment and recorded its source tree.

We established six age treatments by exposing seedlings to identical well-drained and well-watered conditions for 1, 7, 14, 28, 42 or 56 day(s) before imposing moisture treatments. We established six soil moisture treatments by manipulating pot drainage and thrice weekly watering as follows: (i) 'drought' (DRT) - well-drained, watered as needed to maintain soil moisture at 25% field capacity by mass (see Appendix S2); (ii) 'dry' (DRY) - well-drained, watered as needed to maintain 50% field capacity; (iii) 'field capacity' (CAP) - well-drained, well-watered; (iv) 'subsurface saturation' (WET) - well-watered, pots inside non-draining containers so the top 10 cm of soil drained and bottom 16 cm remained saturated; (v) 'saturated' (SAT) - pots sealed with drainage holes 1 cm above the soil surface and topped off so all soil remained saturated with minimal standing water and (vi) 'flooded' (FLD) - pots sealed and topped off so 8 -10 cm of standing water (depending on evaporation) remained. We synchronized when seedlings were exposed to moisture treatments as much as possible by assigning germinants to age treatments sequentially from oldest to youngest. The three youngest age treatments have fewer replicates than older age treatments because seed viability was low.

We surveyed seedling height, leaf count and basal stem diameter at onset of moisture treatments and 56 days later and surveyed survival at least thrice weekly. After final surveys, we harvested above-ground biomass of all survivors and root biomass from survivors in the 56 days age treatment. Biomass samples were oven-dried at 70 °C for 48 h and weighed. We used survival analyses to examine dependence of seedling survival time on experimental treatments. We fit right-censored survival data with parametric accelerated failure time models (survreg in R) utilizing Weibull distributions. We included moisture treatment (categorical) and seedling age (continuous) as covariates and used likelihood ratio tests to determine whether survival time depended on moisture, age and/or their interaction. We also performed these analyses with source tree as a covariate. This marginally improved our models but did not affect significance of other factors and source tree was insignificant $[\chi^2]$ (21) d.f.) = 26.09, P = 0.20], so we excluded source tree from further analyses. As an alternative to survival analysis because 77% of seedlings survived and survival time is more informative than binary survival, we fit number of days survived using a generalized linear model (GLM; glm in R) with a Poisson distribution and used analysis of deviance (ANODEV, a form of likelihood ratio testing; anova in R) with chi-square tests to evaluate whether experimental treatments and their interactions influenced survival time.

To examine effects of experimental treatments on seedling performance, we fit performance data with GLMs because mortality variation among treatments and/or experimental design artefacts produced unbalanced sample sizes. We used ANOVAS (anova in R) to test whether soil moisture, seedling age (categorical), source tree and/or their interactions influenced absolute changes in seedling height, leaf abundance and stem diameter (square root transformed), final above- and below-ground biomass (both \log_e transformed), and root/shoot (\log_e transformed). We also fit GLMs and used ANOVAS to test dependence of relative [(ln final – ln initial)/($t_1 - t_0$)] performance variables and age-scaled aboveground biomass on experimental treatments and their interactions. These results were qualitatively equivalent to their counterparts based on absolute or unscaled data and are not shown.

FIELD EXPERIMENT

The field experiment quantified survival and performance of differently aged Triadica seedlings under field conditions. We used a simple one-way design by transplanting Triadica seedlings from six age treatments with 10 replicates into the JHWMA restoration site (n = 60 seedlings). In June 2010, we germinated *Triadica* seeds as above in the same greenhouse conditions as the germination experiment. We established six age treatments by transferring new germinants to pots of JHWMA soil and exposing them to identical well-drained, daily-watered conditions for 1, 13, 20, 34, 48 or 62 day(s) prior to transplantation. To avoid restricting below-ground growth, we used 6.2-L tapered square Treepots (Stuewe & Sons) for 62 and 48 days treatments, 2.8-L Treepots for 34 and 20 days treatments, 1.75-L round pots for the 13 day treatment and 115-ml Cone-tainers™ (Stuewe & Sons) for the 1-day treatment. We moved all seedlings except the 1-day treatment outside into partial shade to 'harden off' for 7 days prior to transplantation.

On 17 September 2010, we measured seedling height and leaf abundance and transplanted seedlings with their soil monoliths into the JHWMA restoration site along a randomized 6×10 grid with 1 m spacing. To minimize environmental heterogeneity, we removed vegetation within 10 cm of seedlings and clipped vegetation within 4 m to ~5 cm in height. Flooding occurred in late September only (~15% of experiment duration). Given average rainfall, the site is intermittently flooded (~75% of the time) yearround (personal observation). We surveyed seedling survival 13 days post-transplantation and approximately weekly thereafter. Turbid standing water prevented a survival survey 6 days posttransplantation, so we measured depth at grid nodes, confirmed depth was independent of age treatments (ANOVA, $F_{5.54} = 1.32$, P = 0.27) and excluded depth from further analyses. After 56 days, we measured seedling height and leaf abundance and harvested, dried and weighed above-ground biomass of all survivors. Our timing was unusual but realistic (Triadica can germinate February-November in Texas). This experiment was a test of mechanism requiring exposure of age classes that would not typically co-occur to identical, realistic conditions. Our methods achieved this end, thus timing was inconsequential. Analyses followed the same approach as in the greenhouse experiment.

Results

GERMINATION LIKELIHOOD AND TIMING

Germination likelihood depended on moisture treatment, source tree, time and all interactions (Table 1). Final germination percentages in subsurface saturation, field capacity and dry treatments were not significantly different but

Table 1. Results of repeated measures ANOVA testing effects of soil moisture, source tree, time and their interactions on *Triadica* germination in the germination experiment

Factor	d.f.	F ₄₇₈	Р
Moist	5	28.76	<0.0001
Tree	9	4.18	<0.0001
Moist*Tree	45	1.70	0.0044
Factor	d.f.	F ₃₈₃₂	Р
Time	8	103.28	<0.0001
Moist*Time	40	19.38	<0.0001
Tree*Time	72	3.04	<0.0001
Moist*Tree*Time	360	1.42	<0.0001
Model	539	4.46	<0.0001

were higher than in drought, saturated and flooded treatments (Fig. 1). Mean time to germination was 31.4 days but timing varied by moisture, with percentage germination in drought and dry treatments plateauing earlier (~30 days) than in intermediate moisture treatments (~70 days; Fig. 1). Germination timing also depended on source tree but followed no apparent pattern.

GREENHOUSE SURVIVAL AND PERFORMANCE

Survival time in survival analysis depended on soil moisture $[\chi^2 (5 \text{ d.f.}) = 116.65, P < 0.001]$, seedling age $[\chi^2 (1 \text{ d.f.}) = 28.80, P < 0.001]$ and moisture*age interaction $[\chi^2 (5 \text{ d.f.}) = 31.51, P < 0.001]$, which signifies an ontogenetic niche shift. This was supported by ANODEV of days survived, which showed that moisture, age, source tree and all interactions thereof influenced survival time (Table 2). Uncensored survival time averaged 51.6 days overall and was highest in intermediate and saturated moisture treatments, slightly reduced in the flooded treatment and lowest in water-limited treatments



Fig. 1. Cumulative germination over time by moisture treatment in the germination experiment. Vertical bars at 91 days are 95% confidence intervals for final percentage germination.

(Fig. 2). Survival time increased rapidly with age, although there was a non-significant decrease among the oldest seedlings in the driest treatment (Fig. 2). Survival likelihoods followed similar patterns (Table S1).

All metrics of seedling performance depended on soil moisture and seedling age, and source tree affected changes in height and stem diameter but not leaf count nor final above-ground biomass (Table 2). The moisture*age interaction influenced above-ground biomass and changes in height and leaf count but not stem diameter (Table 2). Every performance metric was significantly higher in intermediate moisture treatments than in water-limited treatments; performance in saturated treatments was generally in between (Fig. 3; Tables S1 & S2). Above-ground biomass increased with age, but increases in height and leaf abundance were highest among seedlings aged 1 and 42 days and increases in stem diameter were highest among seedlings aged 14 and 28 days (Table S1).

Root biomass among seedlings aged 56 days was influenced by soil moisture ($F_{5,41} = 7.63$, P < 0.001) but neither source tree ($F_{8,41} = 0.74$, P = 0.65) nor moisture*tree ($F_{12,41} = 1.93$, P = 0.11). Root/shoot depended on source tree ($F_{8,41} = 4.41$, P = 0.006) but was independent of moisture ($F_{5,41} = 2.43$, P = 0.08) and moisture*tree ($F_{12,41} = 1.59$, P = 0.19). Root biomass followed prior moisture patterns: lowest in DRT (182 mg) and DRY (237 mg), highest in CAP (789 mg), WET (609 mg) and SAT (591 mg), and reduced in FLD (401 mg). Root/shoot ranged from 0.39 to 0.61 among source trees, and there was an insignificant trend for it to decrease as moisture increased (from 0.87 in DRT to 0.43 in FLD).

FIELD SURVIVAL AND PERFORMANCE

Average survival time was 30.9 days and 23 of 60 Triadica seedlings (38.3%) survived until final surveys 56 days posttransplant. Seedling age influenced survival time in survival analysis $[\chi^2 (1 \text{ d.f.}) = 66.69, P < 0.001]$ and ANODEV of days survived $[\chi^2 (5 \text{ d.f.}) = 502.48, P < 0.001, McFadden's$ pseudo $R^2 = 0.489$]. Survival increased with age less rapidly than in the greenhouse (Fig. 4; Table S3). All seedlings aged 1 or 13 day(s) died within 26 days. Only 25% of seedlings aged 20 or 34 days survived, but 80% survived among seedlings aged 48 days. All seedlings aged 62 days survived. Seedling age influenced above-ground biomass ($F_{3,22}$ = 3.89, P = 0.025, pseudo $R^2 = 0.219$) and change in leaf count ($F_{3,22} = 5.21$, P = 0.009, pseudo $R^2 = 0.081$) but not change in height $(F_{3,22} = 1.29, P = 0.31, pseudo$ $R^2 = 0.015$). Biomass increased with age as in the greenhouse, but most seedlings lost leaves under field conditions and older seedlings lost more (Table S3).

Discussion

Reinvasion pressure is crucial to restoration outcomes and costs, but it can vary broadly among habitats invaded by the same species and is difficult to predict (Buckley,

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Table 2. Influence of soil moisture, seedling age, source tree and their interactions on *Triadica* seedling survival time (ANODEV χ^2 test), absolute changes (final – initial) in seedling height (ANOVA), leaf count (ANOVA) and stem diameter (square root transformed, ANOVA) and final above-ground biomass (log_e transformed, ANOVA) in the greenhouse experiment

Factor				Absolute change (final – initial)											
	Days survived			Height		Leaf count		Stem diameter		Final AG biomass					
	d.f.	χ^2	Р	d.f.	F ₂₂₁	Р	d.f.	F ₂₂₁	Р	d.f.	F ₂₁₀	Р	d.f.	F ₂₁₈	Р
Moist	5	102	<0.0001	5	38.57	<0.0001	5	60.33	<0.0001	5	14.37	<0.0001	5	21.59	<0.0001
Age	5	186	<0.0001	5	13.80	<0.0001	5	10.19	<0.0001	5	8.54	<0.0001	5	70.43	<0.0001
Tree	20	37	0.0190	20	1.78	0.0405	20	1.66	0.06	20	2.27	0.0069	20	0.95	0.53
Moist*Age	25	78	<0.0001	24	2.19	0.0060	24	1.89	0.0212	24	1.23	0.25	24	2.24	0.0051
Moist*Tree	66	183	<0.0001	54	0.66	0.94	54	1.07	0.40	52	1.23	0.21	54	1.08	0.37
Age*Tree	25	52	0.0012	20	0.78	0.73	20	1.52	0.10	19	1.31	0.21	20	1.10	0.37
Moist*Age*Tree	42	65	0.0125	23	0.95	0.53	23	0.71	0.82	20	1.57	0.09	22	0.95	0.54
Model	192	703	<0.0001	151	2.80	<0.0001	151	3.55	<0.0001	145	2.14	0.0004	150	4.23	<0.0001



Fig. 2. Survival time ± 1 SE (maximum 56 days) by seedling age (inset legend) and moisture treatment (*x*-axis) in the greenhouse experiment. Ontogenetic niche expansions appear as rapid increases in survival time across the moisture gradient as age increases. Moisture treatments: DRT – well-drained, 25% field capacity; DRY – well-drained, 50% field capacity; CAP – well-drained, well-watered (field capacity); WET – well-watered, subsurface saturation; SAT – well-watered, surface saturation; FLD – constantly flooded.

Bolker & Rees 2007; Kettenring & Adams 2011). Ontogenetic niche expansions can promote density-reinvasion decoupling that masks average reinvasion pressure and has important implications for restoring invaded ecosystems (Gabler & Siemann 2012). Our results clearly show that invasive *Triadica sebifera* Chinese tallow tree exhibits rapid ontogenetic moisture niche expansions. This may enable *Triadica* seedling persistence within habitats with conditions typically unsuitable for recruitment, thereby permitting mature exotic density and average reinvasion pressure to become decoupled over time.

Triadica survival increased rapidly with seedling age in the greenhouse and field. Biomass also increased with age, but tissue-specific performance metrics had more complex relationships with age that probably reflected seed provisioning, preferential carbon allocation in different



Fig. 3. Final above-ground biomass ± 1 SE by seedling age (inset legend) and moisture treatment (*x*-axis) in the greenhouse experiment. Ontogenetic niche expansions appear as variable increases in mass across the moisture gradient as age increases. Moisture treatments: DRT – well-drained, 25% field capacity; DRY – well-drained, 50% field capacity; CAP – well-drained, well-watered (field capacity); WET – well-watered, subsurface saturation; SAT – well-watered, surface saturation; FLD – constantly flooded.

developmental stages, or tissue shedding for survival. Considerable seed provisioning in Triadica could explain large increases in some treatments among the youngest seedlings but offered little benefit in flood treatments, where seedlings aged 1 day generally performed worst (Table S1). Whether seedlings had any emergent leaves appears crucial to success. In FLD pots, depth reached ~80 mm between watering, and 38% of seedlings initially ≤ 80 mm tall survived, but 100% of seedlings initially >80 mm tall survived. In the field experiment, none of the seedlings aged 1 or 13 days survived. We doubt that transplant shock contributed to this mortality because our well-established transplantation protocols yield >95% survival. Generally, greenhouse survival and performance were highest in intermediate soil moisture treatments, modestly reduced in saturated treatments and lowest in drier treatments.



Fig. 4. Survival time +1 SE of differently aged *Triadica* seedlings in the field experiment. Shared letters above bars indicate means that were not significantly different. Numbers within bars are abundances of live seedlings (maximum ten) after 56 days.

Our findings support the hypothesis of Parrish & Bazzaz (1985) that germination niches are most specific for species with seed dormancy. Donohue *et al.* (2010) suggest narrower germination niches (i.e. ontogenetic niche expansions) restrict spatial distribution but reduce seedling mortality by promoting germination under optimal conditions. Abrupt attenuation of *Triadica* germination in moisture conditions suboptimal for seedlings suggests selective cuing. This may enable *Triadica* to select favourable conditions within temporally variable land-scapes across a broad geographic range (Donohue *et al.* 2010) and could contribute to invasion success.

Crucial moisture*age interactions mean moisture effects depended on seedling age and indicates ontogenetic change in moisture tolerance. Extreme moisture conditions reduced survival and performance among older seedlings less than among younger seedlings, ergo tolerances increased (moisture niches expanded) as seedlings aged. Moisture*age was significant for all greenhouse survival metrics and all but one greenhouse performance metrics (Table 2). Triadica seedling survival increased with age across our greenhouse moisture gradient and under field conditions (Figs. 2and 4; Tables S1 and S2). In driest conditions (DRT) only, seedlings aged 42 and 56 days were less likely to survive and survived for less time (not significantly less) than seedlings aged 28 days. This was probably an experimental artefact from using pots that constrained root depth and architecture of larger seedlings. Larger plants have greater absolute maintenance requirements and are likely more susceptible to transpirational loss, but typically exhibit greater root depth and area that buffer against low soil moisture (Parrish & Bazzaz 1985). Thus, large seedlings in the greenhouse experiment experienced all costs of their size but not all benefits pertinent to moisture tolerances.

In the field experiment, the oldest seedlings showed the highest net losses in height and leaf count (Table S3) but

grew most after initial losses (personal observation). This is likely to be due to flooded and perhaps windy conditions and older seedlings having more biomass to lose as plants lost tissue or died back but survived. Given *Triadica*'s high capacity for compensatory regrowth (Bruce *et al.* 1997), shedding tissue when upkeep requirements exceed available resources may be an effective drought tolerance strategy akin to the herbivore tolerance strategy demonstrated by introduced *Triadica* genotypes (Zou *et al.* 2008; Huang *et al.* 2011).

Alternative mechanisms could decouple mature Triadica density from average reinvasion pressure. Differences in Triadica seed availability among habitats could promote density-reinvasion decoupling. However, we expect 'supersaturated' seed banks subject to self-thinning are commonplace given Triadica's high fecundity (Renne, Gauthreaux & Gresham 2000) and density where dominant. If so, differences in seed abundance should impact reinvasion relatively little because germination and spatial carrying capacity would depend more on abiotic conditions. This saturation effect would be temporary and diminish as seed banks decrease. Differences in nutrient availability are unlikely to impact germination (Parrish & Bazzaz 1985) but, by influencing seedling performance, could impact recruitment in marginal habitats and lead to density-reinvasion decoupling. Ontogenetic changes in nutrient requirements are possible (Parrish & Bazzaz 1985; Quero et al. 2008) and merit study in Triadica. Other ontogenetic changes in Triadica's niche could promote density-reinvasion decoupling if there are inter- and intra-site variation in the factor(s) associated with these changes. For example, herbivore and disease prevalence vary spatiotemporally, thus ontogenetic increases in herbivore (Barton & Koricheva 2010) or disease resistance or tolerance (Develey-Riviere & Galiana 2007) could lead to density-reinvasion decouplings. However, natural enemies are unlikely to produce such patterns where exotics are subject to enemy release, as with Triadica (Siemann & Rogers 2003b; Siemann, Rogers & Dewalt 2006).

Differences among source trees may reflect genetic variation among individuals or environmental effects on parent trees (maternal effects), which often appear as differences in seed provisioning. We cannot differentiate between genetic and maternal effects, but our foci are effects of seedling age, soil moisture and their interaction. Knowledge of how source trees affect recruitment success holds limited value as it provides little actionable insight into reinvasion.

IMPLICATIONS FOR RESTORATION AND MANAGEMENT

Major challenges to restorations of invaded habitats include impacts of exotic management on non-target species and availability of management resources (Rinella *et al.* 2009; Firn, House & Buckley 2010; Kettenring & Adams 2011). Thus, exotic management efficiency is vital to restoration efficacy (by minimizing non-target negative impacts) and resource optimization. Management is most efficient when performed only when necessary and to the degree required, and when selecting sites with the lowest management requirements or highest management benefits (sensu Epanchin-Niell & Hastings 2010). We established that *Triadica* undergoes ontogenetic moisture niche expansions, and moisture conditions clearly vary within and among *Triadica*-dominated habitats, thus density-reinvasion decoupling is possible. This has two major implications for restoration and management.

First, mature Triadica density is an unreliable predictor of average reinvasion pressure. Unfortunately, publically available management recommendations for Triadica and other invasive plants are often based on adult density. Where density-reinvasion decoupling occurs, density-based guidelines can lead to highly inefficient management and/or unnecessary negative nontarget impacts (sensu Rinella et al. 2009; Epanchin-Niell & Hastings 2010). Therefore, our foremost recommendation is to centre management strategies on niche-based estimates of average reinvasion pressure (detailed in Gabler & Siemann 2012), rather than density-based estimates. Reliable estimates based on Triadica's niche and habitats' environmental conditions are less likely to overestimate average reinvasion pressure and typically feasible in its introduced range - particularly now that we better understand Triadica's recruitment niche. Other environmental factors influence reinvasion pressure (Gabler & Siemann 2012), but our results otherwise suggest Triadica reinvasion pressure should be highest where rainfall is regular (>weekly) but flooding is rare, lowest where rainfall is episodic (<monthly) or periods between floods are <30 days, and otherwise scale with availability of favourable conditions. Niche-based approaches also enable forecasts of future reinvasion pressure based on short-term weather forecasts, mid-term climate cycles (e.g. ENSO) or long-term climate change projections (sensu Young, Petersen & Clary 2005). Given Triadica's seed longevity (5+ years; Bruce et al. 1997), the latter only applies where external seed input is expected. Reliable niche-based estimates of average reinvasion pressure and forecasts of short-term reinvasion success would greatly benefit restoration planning and cost estimates. This approach should be useful in other systems, especially where invaders exhibit ontogenetic niche expansions. Detailed approaches to estimating reinvasion pressure and specific strategies for various reinvasion scenarios are described by Gabler & Siemann (2012).

Second, habitats with low average reinvasion pressure masked by *Triadica* dominance provide cryptic opportunities for relatively inexpensive and straightforward restorations. Identifying and prioritizing cryptically opportune habitats would enhance restoration efficiency and, given limited resources, could increase extent of successful restoration of *Triadica*-invaded habitats on a landscape scale. This requires estimates of average reinvasion pressure as above, and broader strategies should consider metapopulation dynamics (Buckley, Bolker & Rees 2007; Epanchin-Niell & Hastings 2010). Triadica's selective germination requirements and rapid ontogenetic moisture niche expansion paired with its hydrochorus dispersal and capacity to bank seeds for 5+ years may make it well equipped to recruit during rare moisture windows. Beyond normal ranges of interannual variation (i.e. 10-year events), extreme weather such as droughts, floods or tropical cyclones (100-year events) could trigger exceptionally rare but widespread recruitment. Given Triadica's northern Gulf of Mexico distribution, hurricanes in particular could facilitate dispersal and establishment in typically unsuitable habitats. If so, density-reinvasion decouplings and thus cryptically opportune habitats may be quite common.

Managers can exploit Triadica's specific moisture requirements for germination and seedling survival during restoration. Where water control is possible, e.g. in former rice fields, it is likely to be impractical to maintain flooding to prevent germination due to seed longevity, but one could use flood pulses to kill young seedlings. Efficacy of increasing drainage to reduce moisture to kill seedlings would depend on rainfall and soil. Both approaches would have non-target effects and could substantially influence community development given durations of flooding or drought required to kill seedlings. These trade-offs should be weighed against management alternatives. Where controlling moisture is not feasible, managers should use knowledge of Triadica recruitment requirements and local historical environmental patterns to estimate average reinvasion pressure when developing optimal management strategies. When possible, managers should use local climate forecasts to anticipate short-term recruitment and prepare commensurate management measures if different from base strategy. Actionable changes in Triadica reinvasion success need only be predicted in time to perform management while it would have the desired effect. This would be most beneficial in habitats where recruitment is highly pulsed, especially because many Triadica management methods are most or only effective when seedlings are young, for example burning or grazing. Generally, accurate estimates of average and short-term reinvasion pressure could improve restoration efficacy, efficiency and predictability in ecosystems dominated by Triadica or other exotic plants, especially plants exhibiting ontogenetic niche expansions and subject to density-reinvasion decoupling.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Seed preparation.

Appendix S2. Watering protocols.

Table S1. Greenhouse survival and performance.

Table S2. Greenhouse performance by moisture.

Table S3. Field survival and performance.