



Size-dependent analyses provide insights into the reproductive allocation and plasticity of invasive and native *Typha*

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Abstract Invasive species increasingly threaten ecosystems worldwide making it important to better understand the traits, including sexual reproductive allocation and its plasticity, that make certain species more successful invaders than others. Size differences between native and non-native invasive congeners are common, yet, when comparing allocation within and

among species many studies fail to consider the size-dependency (allometry) of allocation patterns. Using a mesocosm experiment conducted at two locations and incorporating a nutrient gradient, we compared sexual reproductive allocation and its plasticity (correcting for size) between three closely related taxa of cattails with varying degrees of invasiveness: *Typha latifolia* (native, non-invasive), *Typha angustifolia* (non-native, invasive), *Typha* × *glauca* (their hybrid, invasive). We found that the non-native and hybrid taxa (both invasive) allocated more to sexual reproduction than the native, non-invasive taxon even after correcting for aboveground plant size. However, the non-native and hybrid taxa did not differ from each other when accounting for plant size, even though a size-independent analysis indicated they did. This reveals these two taxa differed in plant size, not allocation patterns. Surprisingly, the most invasive taxon (the hybrid) was the least plastic in sexual reproductive allocation in response to nutrients at one site. Our study adds to the growing body of literature suggesting trait values rather than trait plasticity contribute to invasiveness, but ours is unique in its size-dependent analysis of sexual reproductive allocation, its plasticity, and differential taxon invasiveness.

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Introduction

Sexual reproductive allocation, generally viewed as the plant's distribution of resources to reproductive structures at a given size (Weiner 2004), may contribute to the competitive success of invasive plants (Weiner et al. 2009). All else equal, greater sexual reproductive allocation and output could result in greater dispersal and establishment ability for non-native invasive plants, contributing to their ability to rapidly reproduce and colonize new habitats (Mason et al. 2008; Lembrechts et al. 2018). Indeed, several studies have shown that measures of sexual reproductive output such as fecundity (Mason et al. 2008; Jelbert et al. 2015; Lembrechts et al. 2018), propagule pressure (Colautti et al. 2006), and sexual reproductive allocation (McDowell and Turner 2002; Brown and Eckert 2005) are higher in invasive species than in native species. However, these results may depend on the nature of the comparison. One meta-analysis indicated that invasive species allocate more to sexual reproduction than conspecifics in the invasive species' native range but allocate less than native congeners from the invasive species' introduced range (Hawkes 2007).

In addition to trait values themselves, a complementary hypothesis suggests that phenotypic plasticity, the change in phenotypic expression of a genotype in response to environmental factors (Bradshaw 1965; Davidson et al. 2011), contributes to invasiveness. Plasticity can increase establishment success, decrease extinction risk, and promote invasiveness by allowing plants to better respond to variable environments (Baker 1965; Richards et al. 2006; Godoy et al. 2011; Forsman 2015). However, strong plasticity may be disadvantageous if the plasticity is maladaptive (Alpert and Simms 2002) and/or if environmental variability is high but environmental predictability is low (Reed et al. 2010). For example, Ghalambor et al. (2007) found that phenotypic plasticity was inversely related to shade tolerance in four temperate forest tree species, indicating that under shaded conditions plasticity may be disadvantageous for these species. Additionally, if the rate of environmental change exceeds that of the plastic response the plant's phenotype may lag behind what would be advantageous for the new environmental condition (Alpert and Simms 2002). A meta-analysis by Davidson et al. (2011) examined the correlation between plasticity and invasiveness

and found that invasive plant species were more plastic than native species in a range of morphological, physiological, and fitness traits. More recent studies, however, did not find that invasive species differed in their plasticity of several biological, growth, and functional traits, including seed number (Godoy et al. 2011; Matzek 2012; Ruprecht et al. 2014).

Surprisingly, most studies comparing reproductive allocation and/or plasticity in allocation patterns do not consider the plant size dependency of allocation (but see: Weiner et al. 2009; Nicholls 2011; Jelbert et al. 2015). The ratio of sexual to aboveground, vegetative mass (sexual reproductive allocation ratio) varies among species but, importantly, can also change within a single plant as it grows. Thus, comparing sexual reproductive allocation ratios alone may suggest differences in allocation that are due to changes in size rather than changes in intrinsic allocation patterns (Kozłowski and Wiegert 1987; Weiner 2004; Nicholls 2011; Liu and Pennings 2019). For example, Sugiyama and Bazzaz (1998) found accounting for size revealed sexual reproductive allocation patterns were consistent across a nutrient and competition gradient (also see Batzer et al. 2017).

No previous study of which we are aware has considered the size dependence of reproductive allocation when assessing the relationships between invasiveness and sexual reproductive allocation and its plasticity in response to an environmental variable. Here, we compared the allometry of sexual reproductive allocation in three closely related taxa of *Typha* (commonly referred to as cattails) that differ in invasiveness: *Typha angustifolia* (non-native to the Great Lakes region of the northern Midwest, USA; Galatowitsch et al. 1999), *Typha latifolia* (native to the region), and *Typha x. glauca* (their hybrid). We define invasiveness as the ability to spread aggressively in new environments and have negative ecological or economic impacts on the existing community (Lockwood et al. 2013). While the native taxon can dominate wetlands in the region (Houlihan and Findlay 2004), it does not have the same negative ecological impacts as the non-native and hybrid taxa (Bansal et al. 2019). Non-native *T. angustifolia* and hybrid *T. x. glauca*, however, are both considered invasive because they spread rapidly and have negative impacts on coastal wetland ecosystems throughout the continental US (Larkin et al. 2012; Bansal et al. 2019). They form dense, monotypic stands

(Lawrence et al. 2016; Bansal et al. 2019) that alter the physical structure of vegetation (Lishawa et al. 2017) and increase plant and litter biomass, alter nutrient cycling, and limit light availability, leading to decreased plant diversity (Farrer and Goldberg 2009; Tuchman et al. 2009; Bansal et al. 2019). This results in negative impacts on higher trophic levels such as macroinvertebrates, waterfowl, fish, amphibians, and reptiles (Lawrence et al. 2016; Bansal et al. 2019). The hybrid is considered to have greater impacts and spread more rapidly than the non-native taxon (Galatowitsch et al. 1999; Larkin et al. 2012; Bansal et al. 2019); therefore, we consider the hybrid to be more invasive than the non-native. While the dense, monotypic stands characteristic of invasive cattails at high nutrients are probably due largely to clonal growth, establishment of new stands is mostly a consequence of sexual reproduction and seed dispersal.

By comparing three closely related taxa in the present study, we reduce the risk of confounding the trait differences of interest with disparities attributable to phylogeny (Richards et al. 2006). Because both the non-native and hybrid are particularly invasive at higher nutrient levels (Woo and Zedler 2002; Farrer and Goldberg 2009; Bansal et al. 2019), we assessed plasticity in response to different nutrient conditions. Nutrient concentrations in Great Lakes wetlands range from 109 to 4234 $\mu\text{g L}^{-1}$ and 6 to 227 $\mu\text{g L}^{-1}$ for total nitrogen and total phosphorus, respectively (Trebitz et al. 2007), and nitrogen influxes in the Midwest region can be as high as 48 $\text{gN m}^{-2} \text{yr}^{-1}$ (Green and Galatowitsch 2002). Using a mesocosm experiment in which we created a wide range of nutrient availability to induce a plastic response, we tested the hypotheses that invasiveness is related to sexual reproduction and/or its plasticity even after incorporating the size-dependence of allocation.

Specifically, we predicted: (1) sexual reproductive allocation depends on plant size (Weiner 2004; Jelbert et al. 2015) and that, for a given size, more invasive *Typha* (2) allocate more to sexual reproduction and (3) are more plastic in sexual reproductive allocation (van Kleunen et al. 2010; Davidson et al. 2011). Based on previous work, we further predicted (4) that size-dependent sexual reproductive allocation decreases as nutrient availability increases (Bai et al. 2009; Yang and Kim 2016). Under our predictions, the most invasive taxon (hybrid, *T. × glauca*) would allocate the most to sexual reproduction and be

the most plastic in sexual reproductive allocation, followed by the non-native (*T. angustifolia*) and then the native (*T. latifolia*).

Methods

Experiment design

Individual *Typha* ramets were sampled from experimental wetland mesocosms from two sites in Michigan: a southern site, the Edwin S. George Reserve (ESGR) (42.4580506, -84.0117986) located near Pinckney and a northern site, the University of Michigan Biological Station (UMBS) (45.558653, -84.6797864) near Pellston (Ruiz 2018). The two sites were selected to assess effects of climate, but confounding factors arose which limited this assessment for this paper (see below and Discussion for additional details). The mean annual temperature at the southern site is 8.56 °C and the mean growing season length is 173 days (NOAA 2010), while the northern site has a mean annual temperature of 5.5 °C and a mean growing season length of 122 days (NOAA 2010).

Mesocosms were constructed in fall 2011 as part of a larger study examining invasion dynamics in Great Lakes' wetlands. Mesocosms were composed of 1135-L galvanized steel livestock tanks, approximately 1.8 m across and 61 cm deep, lined with plastic to prevent leaching of heavy metals and filled almost entirely with sand sourced from a local quarry near each site. A thin (1.5 cm) layer of reed-sedge peat was added to the surface to mirror soil conditions within Great Lakes coastal wetlands. Tanks were sunk flush with the ground to prevent overheating, and a buried irrigation system was installed to provide constant water flow into and out of the tanks to mimic groundwater flows through a wetland. Water was delivered to the bottom of the tank at an average rate of 2.5 L min^{-1} . Water filtered up through the soil profile and any water in excess of evapotranspiration exited an outflow pipe at the soil surface to maintain constant saturated but unflooded conditions; for additional details see (Ruiz 2018). The well water used to irrigate the mesocosms at each site differed significantly in base levels of several nutrients: the southern site was higher in nitrate and calcium, while the northern site was higher in phosphorus, sodium,

and magnesium. All mesocosms (48 at each site) were initially fertilized to create a nutrient gradient in 2012 and half of the mesocosms (24 at each site) were planted with native wetland plants at this time while the other half were left bare. In spring 2013 all mesocosms were planted with *Typha* to simulate invasion into existing communities (previously planted mesocosms) or in absence of native communities (unplanted mesocosms).

For this study, we used the subset of 24 mesocosms from each site (48 total) in which *Typha* rhizomes were planted in absence of other plants, because sample sizes of *Typha* were too low in mesocosms with pre-existing native communities (unpublished data). Rhizomes were collected in and around Ann Arbor, Michigan and one rhizome of each *Typha* taxon (*T. angustifolia*, *T. latifolia*, and *T. × glauca*) was planted within each mesocosm. Two months after the initial planting, new rhizomes from the same wild populations as the originals were planted to replace those that had died. After both rounds of planting, the native taxon suffered the highest mortality, leaving over half of the mesocosms (26) with no native individuals (*T. latifolia*). Notably, mortality did not differ between sites, across all taxa, or among nutrient levels within each taxon (unpublished data). The native taxon also exhibited the least clonal spread over the course of the experiment, resulting in fewer individuals to sample even in mesocosms in which it was present.

Each mesocosm was randomly assigned to one of 12 nutrient addition rates (0, 1.5, 3, 6, 9, 12, 15, 21, 27, 33, 39, or 45 g N m⁻² yr⁻¹) with two replicate mesocosms per rate at each site. Initially, fertilizer was applied by hand-broadcasting twice in 2012. Beginning in 2013, fertilizer was applied through a slow-release “fertigation” system that was replenished six times during the growing season, creating a relatively even release of nutrients over time (data not shown). Two slow-release fertilizers were mixed to create an N:P ratio of 30, which is the median N:P ratio of an extensive survey of surface water nutrient concentrations throughout Michigan (Luszcz et al. 2015). These 12 nutrient addition rates were chosen to represent the full range of nutrient inputs reported in the literature for Midwestern wetlands (Davis et al. 1981; Green and Galatowitsch 2002), where the maximum addition rate (45 g N m⁻² yr⁻¹) represents an above average nutrient influx to accommodate the

potential for extreme nutrient loading events in highly agricultural regions. Overall, we had a total of 48 experimental mesocosms, from two sites, each site having two replicate mesocosms for each of 12 nutrient addition rates.

Sampling

The mesocosms were harvested in summer 2016, three years after planting *Typha*. To ensure all individuals had reached sexual maturity, we started the harvest in mid-July at the southern site then moved to the northern site, where *Typha* phenology is delayed to the end of July (Selbo and Snow 2004; Ball and Freeland 2013). Stems were sampled for individual measurements by cutting at ground level. The majority (61%) of the individually-sampled stems were collected from 3 of the 12 nutrient addition rates distributed across the whole range: 0, 21, and 45 g N m⁻² yr⁻¹. In these nutrient addition rates, we sampled all *Typha* stems in each mesocosm, finding up to a maximum of 130 stems per taxon and 177 stems total per mesocosm. Due to logistical constraints, for the remaining nutrient addition rates we sampled *Typha* stems for individual measurements in only four subplots, of 20 cm diameter each, within each mesocosm. If no or very few (typically <5) stems were found in the subplots, we sampled additional *Typha* stems from near the subplots in the same mesocosm.

For each stem collected, we measured basal diameter, leaf width, and height, as well as inflorescence length, width, and gap length for flowering stems. Each stem was given a field identification based on the morphological measurements, following Snow et al. (2010), and then bagged separately, and dried at 60 °C for 48 h. We weighed each stem for total dry mass and inflorescence mass (if present); vegetative dry mass for flowering individuals was calculated by subtracting inflorescence dry mass from total dry mass.

Genetic confirmation

A subset of our samples appeared to have unusual sexual reproductive allocation values that fell beyond the sample cloud for a given taxon (Figure S1). We re-weighed all such outlier samples. To check field identifications of all questionable

observations and a haphazard sample of stems that fell within the sample cloud in Figure S1, we performed genetic analyses following methods in Snow et al. (2010), as modified by Ruiz (2018). Samples with inconclusive genetic results, due for example to poor DNA isolation or amplification, were either re-analyzed or dropped from the analysis; this resulted in a loss of 49 stems out of the 338 that were genetically analyzed.

Field identifications of flowering, non-outlier samples consistently matched genetic identifications (Table S1), although, not surprisingly, the flowering hybrid was somewhat more difficult to identify in the field than the two parent taxa. In contrast, the field identifications of the outlier samples as identified in Figure S1 rarely matched the genetic identifications, especially those originally identified as hybrids, which genetic analyses revealed were mostly natives (Table S1). Overall, we were less successful at identifying non-flowering than flowering samples (Table S1). Our main interest, however, is comparing sexual reproductive allocation between native and invasive *Typha*, so the majority of our analyses are based on flowering samples, and we were especially good at identifying the native taxon when flowering. Therefore, we feel confident in the identifications used for the statistical analyses and the conclusions we draw from them.

Analysis

As described above, samples were concentrated at, but not restricted to, 3 of the nutrient addition rates (0, 21, and 45 g N m⁻² yr⁻¹) so models with nutrients as either a continuous or a discrete variable could be appropriate. To determine which was more appropriate, we fit the final size-dependent allocation model described below using nutrients as both a continuous variable and a discrete factor where all nutrient addition rates were pooled into one of three levels: low 0–6 g N m⁻² yr⁻¹, medium 9–21 g N m⁻² yr⁻¹, and high 27–45 g N m⁻² yr⁻¹. Difference in AIC values indicated that the discrete model provided a better fit (Table S2) and, therefore, we reported results using the three discrete nutrient levels of the pooled nutrient addition rates for all analyses. All statistical analyses were performed in R version 4.1.3 (R Core Team 2022).

Size-independent analysis

We performed the traditional size-independent allocation analysis using sexual reproductive allocation ratios (AR), calculated as follows:

$$AR = \frac{\text{inflorescence mass}}{\text{vegetative mass}} \quad (1)$$

where vegetative mass includes above-ground mass excluding inflorescence mass. We then modeled the AR as a linear combination of site, nutrient level, taxon, and all possible two-way interactions as fixed effects and with mesocosm as a random block effect on the intercept using the lmer function in R from the lme4 package (Bates et al. 2015). We were unable to include a three-way interaction due to lack of native *Typha* samples in low nutrient levels at the southern site (eq. S1 in Supplement: Detailed Model Description).

To assess the overall impact of each variable and their interactions on sexual reproductive allocation ratios, we performed an ANOVA on the completed model (Pinheiro and Bates 2000), using the Anova function (car package; Fox and Weisberg 2019) combined with the lmerTest package (Kuznetsova et al. 2017). To evaluate the overall plasticity within each taxon at each site, we determined the nutrient levels with the minimum and maximum allocation values and then calculated the difference by subtracting the lower nutrient level from the higher. Thus, a positive difference indicates an increase in allocation and a negative difference indicates a decrease in allocation as nutrients increase. We then divided the difference by the allocation value at lower nutrient level and multiplied by 100% to calculate percent change. A greater absolute value for percent change indicates a more plastic response to nutrient addition.

Size-dependent analyses

To examine the shape of the relationship between sexual reproductive mass and vegetative biomass we fit four equations using the nls function (stats package; R Core Team 2022), where V represents aboveground vegetative mass (excluding inflorescence mass), R represents inflorescence (reproductive) mass, c is a scaling factor, β (x-intercept) represents a minimum

size for reproduction, and α estimates sexual reproductive allocation adjusted for size (Klinkhamer et al. 1992).

$$R = cV \quad (2a)$$

$$R = c(V - \beta) \quad (2b)$$

$$R = cV^\alpha \quad (2c)$$

$$R = c(V - \beta)^\alpha \quad (2d)$$

An isometric relationship between allocation and size would result in a linear equation with an intercept equal to zero (Eq. 2a); note that in this equation c is equal to AR in our size-independent analysis (Eq. 1). An allometric relationship between allocation and size would result a linear equation with non-zero intercept (Eq. 2b) or in a non-linear equation (Eqs. 2c and 2d) (Klinkhamer et al. 1992). Finally, a minimum size for reproduction would lead to an equation with a positive x-intercept (Eqs. 2b and 2d) (Klinkhamer et al. 1992; Weiner et al. 2009). We compared the fit of these four equations for each taxon in each nutrient level at each site using AIC tests to determine which equation resulted in the model with the best fit for each combination of taxon and nutrient level. We then calculated the change in AIC value between the model of best fit and the other three models within each subgroup (model AIC—best fit AIC). However, there were four taxon by nutrient level by site sub-groups which had three or fewer samples and therefore could not be fit with individual models. As described in the Results, we determined that the non-linear, zero-intercept function (Eq. 2c) was the most appropriate for subsequent analyses of size-dependent sexual reproductive allocation.

In this nonlinear model, vegetative mass is part of the underlying equation while the allocation coefficient (α in Eq. 2c) varies in response to the variables of interest: taxon, nutrient level, and site (eq. S2 in Supplement: Detailed Model Description). We modeled all possible two-way interactions among these variables with mesocosm as a random effect using `nlmer` function in R (`nlme` package; Pinheiro et al. 2022). Again, we performed an ANOVA to find the significance of variables within the model (Pinheiro and Bates 2000) using the `anova.lme` function in R (`nlme` package; Pinheiro et al. 2022).

We calculated overall plasticity in the same manner as described previously, but instead of mean AR we used the population mean reproductive allocation coefficient estimate (α from Eq. 2c) within the different taxon by nutrient by site subgroups. Again, a positive change indicates a decrease in allocation while a negative change indicates an increase in allocation as nutrients increase, and the greater the absolute value of percent change the more plastic the response.

Minimum size for reproduction

An x-intercept equal to zero does not necessarily indicate the lack of a minimum size for reproduction (Klinkhamer et al. 1992; Weiner et al. 2009), so we investigated this more directly by conducting logistic regressions for the probability of flowering while correcting for vegetative mass. The inflection point of the prediction line and its slope can suggest whether there is a threshold for minimum size of flowering and its value. Unfortunately, data were insufficient to examine probability of flowering in the native *Typha*, so we could only compare the non-native and hybrid. Our allocation model indicated that including mesocosm as a random effect accounted for little (< 1%) of the variation within the observed data (calculations derived from Table S3b). Therefore, we used a standard fixed effects logistic regression model to examine odds of flowering as a function of aboveground, non-inflorescence vegetative mass, taxon (without the native), site, and nutrient level as variables, including all possible interactions (eq. S3 in Supplement: Detailed Model Description). Using an AIC analysis, we compared this full model with nested models lacking one or more of the above variables or interactions. The model lacking site but with all other variables and possible interactions had the lowest AIC value ($\Delta\text{AIC} \geq 2$; Table S4) indicating good support for this model over the others (Burnham and Anderson 2004).

We then used this model to conduct an ANOVA similar to our previous analyses (with the `Anova` function in R) to assess overall impacts of the variables (Venables and Ripley 1997). The non-native and hybrid differed considerably in maximum size, meaning size and taxon were not completely independent, therefore, some of the results attributed to taxon described below may instead be due to size.

Results

Size-independent model

Taxon, nutrients, site, and the interactions between site and nutrients and site and taxon (but not between nutrients and taxon) significantly influenced AR, the simple ratio of sexual to vegetative biomass (Table 1a). As predicted, in both sites the native allocated less to sexual reproduction than the non-native and the hybrid in the size-independent model, although the degree of difference between the non-native and the hybrid differed between sites (Fig. 1). Interestingly, while nutrients affected sexual reproductive allocation overall (significant main effect of nutrients—Table 1a), the taxa did not differ in their response to nutrient levels (non-significant nutrient \times taxon interaction—Table 1a). Thus, all three *Typha* exhibited plasticity, but this plasticity was similar among the three taxa. The effect of nutrient availability and the differences among taxa (independent of nutrients) differed between sites (significant nutrient \times site and taxon \times site interaction—Table 1a). Results from the northern site were consistent with our prediction that allocation ratios would decrease as nutrients increased (negative difference), however, there was an increase in allocation (positive difference) at the southern site for the native and to a lesser extent the hybrid (Table 2a). Additionally, contrary to our prediction, at both sites the hybrid taxon was the

least plastic (smallest absolute percent change in AR) in sexual reproductive allocation ratios in response to nutrient availability (Table 2a).

Size-dependent model

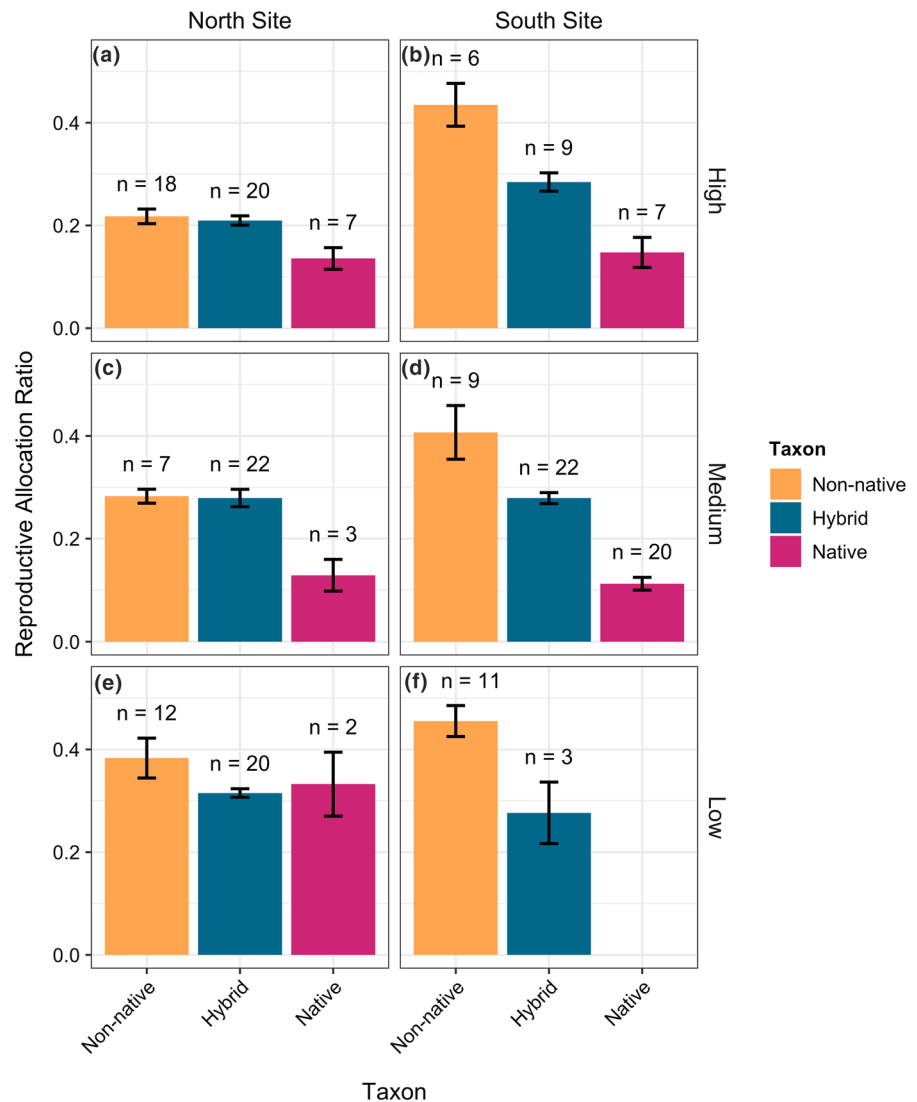
Contrary to our prediction (1), the AIC analyses did not provide consistent evidence for an allometric relationship between aboveground, non-inflorance, vegetative size (hereafter simply referred to as size), and sexual reproductive allocation in our size-dependent modeling analysis (Table 3). Of the 14 taxon-nutrient-site combinations with sufficient data to test, 9 supported the isometric Eq. 2a, and 5 supported allometric equations (3 for Eq. 2c, 1 for Eq. 2b, and 1 for Eq. 2d). Only two combinations supported a minimum size for flowering, so we did not include an intercept parameter in our final model. Even though the isometric model (Eq. 2a) had the lowest AIC value for more sub-groups, in each of these cases the delta AIC value between Eq. 2a and 2c (nonlinear, zero-intercept; the runner up) was less than two (Table 3). This indicates that there is little evidence to support one model over the other and both can be assumed to fit the data equally well (Burnham and Anderson 2004). Therefore, we used the allometric Eq. 2c so that our final model would have the flexibility to accommodate both linear and nonlinear relationships.

Table 1 ANOVA results for the (a) size-independent sexual reproductive allocation ratio model and (b) size-dependent sexual reproductive allocation model

	Df	(a) Size-independent model		(b) Size-dependent model	
		F-value	p-value	F-value	p-value
Intercept	1			17,389.61	<0.001***
Taxon	2	66.48	<0.001***	108.84	<0.001***
Nutrient level	2	14.90	0.001**	9.97	<0.001***
Site	1	19.83	<0.001***	2.52	0.114
T \times N	4	1.77	0.138	11.52	<0.001***
N \times S	2	5.85	0.011*	2.51	0.085
T \times S	2	13.35	<0.001***	3.54	0.031*
Shape parameter (c)	1			15.12	<0.001***
Error	146				

Variables are abbreviated as follows: nutrient levels (N), taxon (T), and site (S). The shape parameter is “c” in Eqs. 2a–2d and allows the model to adjust the height of the curve, but we do not use it for ecological interpretations. The F-test was used in all cases to facilitate comparison. Significant variables are indicated with an asterisk * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Fig. 1 Mean allocation ratios (top of colored bars) and error bars (\pm SE) from size-independent model for each taxon (color) within each nutrient level (rows) at each site (columns). The number of individual stems within each subgroup are indicated above their respective bars. The native is not invasive while both the non-native and hybrid are considered invasive in the Great Lakes region. Coefficients from the mixed effects linear model are in Table S5 and an ANOVA of the model is in Table 1a



For the resulting size-dependent model (eq. S2 in Supplement: Detailed Model Description) taxon, nutrients, their interaction, and the interaction between site and taxon, but not site alone or its interaction with nutrients significantly influenced sexual reproductive allocation (Table 1b). These results indicate that the three taxa differed significantly in their sexual reproductive allocation (significant main effect of taxon—Table 1b). Consistent with our prediction (2), the non-native and the hybrid (both invasive) appear to have greater sexual reproductive allocation than the native at medium and high nutrient levels (Fig. 2). Interestingly, the non-native and hybrid have similar allocation trajectories to each other, but

the hybrid appears to flower at a greater size (Fig. 2). While site was highly significant in the size-independent model, its impact on sexual reproductive allocation became insignificant once size was accounted for. Additionally, unlike the size-independent model the effect of nutrients did not differ between sites (insignificant $N \times$ site interaction—Table 1b), although, as in the size-independent model, the relationship between taxa differed somewhat between sites (significant effect of taxon \times site—Table 1b).

The taxa were plastic in sexual reproductive allocation in response to nutrient availability (significant main effect of N) and, unlike in the size-independent model, differed in their plasticity (significant $N \times$

Table 2 Degree of plasticity in allocation as measured by the difference in mean sexual reproductive allocation ratios (size-independent) or sexual reproductive allocation coefficients (size-dependent) between the maximum and minimum allocation measure for each taxon, non-native (*T. angustifolia*), hybrid (*T. × glauca*), and native (*T. latifolia*)

Site	Taxon	Comparison	(a) Size-independent plasticity		(b) Size-dependent plasticity	
			Difference	% Change	Difference	% Change
North	Non-native	High–low	– 0.17	– 43.20	– 0.14	– 13.96
	Hybrid	High–low	– 0.11	– 33.49	– 0.11	– 11.54
	Native	Med–low	– 0.20	– 61.19	– 0.25	– 25.01
South	Non-native	Med–low	– 0.05	– 10.63	– 0.05	– 4.69
	Hybrid	High–low	0.01	2.87	0.01	1.22
	Native	High–med	0.03	30.57	0.13	17.69

Extreme values were found and then the value at the lower nutrient level was subtracted from the higher resulting in different nutrient comparisons among the subgroups. The comparison column indicates the nutrient groups being compared: low, medium (med), and high. Negative sign indicates decrease in allocation from low to high. The measures of allocation plasticity are not directly comparable between the size-independent and size-dependent analyses

Table 3 Comparison of equation forms within taxon × nutrient level × site combination using AIC

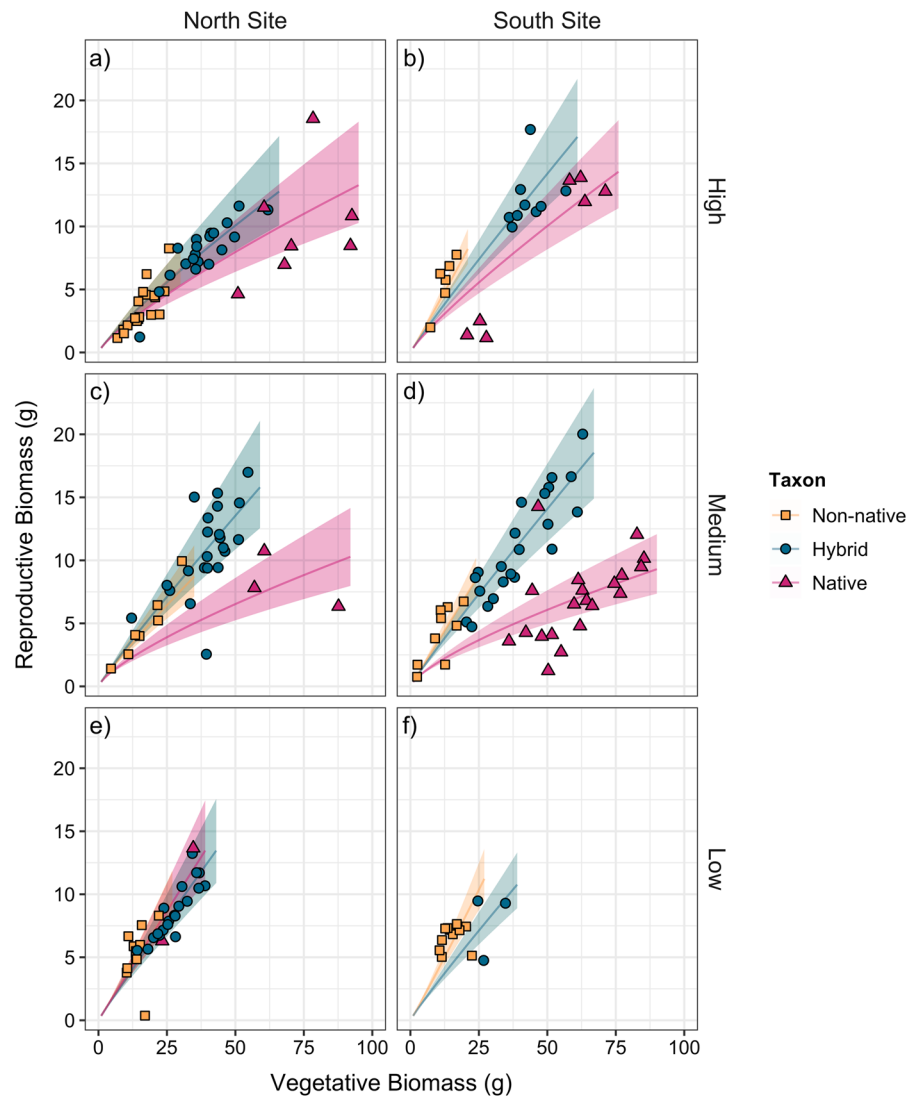
N-level	Equation	North Site			South site		
		Non-native	Hybrid	Native	Non-native	Hybrid	Native
Low	(a) $R = cV$	0	0	NA	12.01	NA	NA
	(b) $R = c(V - \beta)$	2.00	2.00	NA	14.01	NA	NA
	(c) $R = cV^\alpha$	0.84	1.48	NA	0	NA	NA
	(d) $R = c(V - \beta)^\alpha$	2.84	3.48	NA	^a 8.05	NA	NA
Medium	(a) $R = cV$	0.80	0	NA	0	0	0
	(b) $R = c(V - \beta)$	1.71	2.00	NA	2.00	1.99	2.00
	(c) $R = cV^\alpha$	0	1.72	NA	0.88	1.99	1.99
	(d) $R = c(V - \beta)^\alpha$	2.00	3.72	NA	2.50	3.99	3.99
High	(a) $R = cV$	0	5.46	0	0	0.20	4.39
	(b) $R = c(V - \beta)$	1.39	7.46	2.00	1.02	2.20	0
	(c) $R = cV^\alpha$	1.40	5.90	1.85	1.39	0	2.00
	(d) $R = c(V - \beta)^\alpha$	3.39	0	^a 1.76	1.40	^a 0.47	1.67

Equation a represents an isometric (size-independent) relationship, while b-d represent allometric (size-dependent) relationships. Within each combination the minimum AIC value was found and subtracted from the values of the other models to calculate the differences displayed in the table. A difference of zero indicates that the given model is the model of best fit for that taxon × nutrient level × site combination. Four combinations were not analyzed due to insufficient data (NA). (a) Three combinations would not converge with model 4 as specified in table. To achieve convergence we altered the equation to $R = (V - \beta)$. In this instance $c = 1$. As this was not the model of best fit in any combination this change in model formula does not affect the overall conclusions of the AIC analysis

taxon interaction—Table 1b). The percent changes in allocation coefficients were smaller than those in the size-independent mean allocation ratios, but the among taxa pattern remained the same where, contrary to prediction (3), the native was the most plastic and the hybrid the least (greatest and smallest absolute percent change respectively—Table 2b). Similar to the size-independent analysis, the strength and,

occasionally, directionality of changes within taxa varied between the two study sites (Table 2b, Figure S2). Consistent with our prediction (4), at the northern site all taxa allocated less to sexual reproduction as nutrients increased, but at the southern site the native and to a much lesser extent the hybrid allocated more to sexual reproduction at higher nutrient levels (Table 2b, Figure S2). Note, however, that the

Fig. 2 Size-dependent model mean sexual reproductive allocation predictions (dark lines) for each taxon (color and shape) within each nutrient level (rows) at each site (columns). The native is not invasive while both the non-native and hybrid are considered invasive in the Great Lakes region. Symbols indicate observed data with color and shape indicating taxon. Shading indicates the range of estimates among mesocosms due to their random effect. Coefficients from the mixed effects nonlinear model are in Table S3a and an ANOVA of the model is in Table 1b. Sample sizes for each taxon \times nutrient \times site combination are in Fig. 1



native taxon lacked observations at the low nutrient level at the southern site, so the comparison was made between medium and high nutrient levels at which the native exhibited similar patterns within both sites (Fig. 2 and S2).

Minimum size for reproduction

The logistic model suggests that the odds of flowering depend on aboveground, non-inflorescence size for both invasive taxa (Table 4) and that both have a minimum size of flowering (Fig. 3). The non-native and the hybrid differ in odds of flowering at a given size, are both plastic in their size-dependent odds of

flowering in response to nutrient additions, and this plasticity differs between the taxa (significant main effects of all three factors, taxon \times size interaction, and three-way interaction—Table 4). For a given size the non-native consistently had a greater probability of flowering, lower minimum size of reproduction (lower inflection point), and more distinct threshold for minimum size (steeper slope at inflection point) than the hybrid. Generally, as nutrients increased, the odds of flowering decreased and the minimum plant size for flowering increased, though the non-native taxon had similar predicted values at medium and high nutrient levels. While the hybrid had similar slopes across all nutrient levels, the non-native had a

Table 4 ANOVA results for the final size-dependent probability of flowering logistic regression model

Variable	Df	F-value	p-value
Taxon	1	85.47	< 0.001***
Nutrient level	2	19.78	< 0.001***
Vegetative mass	1	285.49	< 0.001***
T × N	2	2.35	0.096
T × V	1	8.04	0.005**
N × V	2	3.13	0.044*
T × N × V	2	4.02	0.018*
Error	784		

Variables are abbreviated as follows: nutrient level (N), taxon (T), and vegetative mass (V). The F-test was used to facilitate comparison between the other models' results. Significant variables are indicated with an asterisk * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

more distinct threshold for minimum size of reproduction at low than at medium or high nutrient levels (Fig. 3). Though we were unable to fit a regression for the native taxon, its flowering and non-flowering observations were similar to, or larger than, that of the hybrid taxon (Fig. 3).

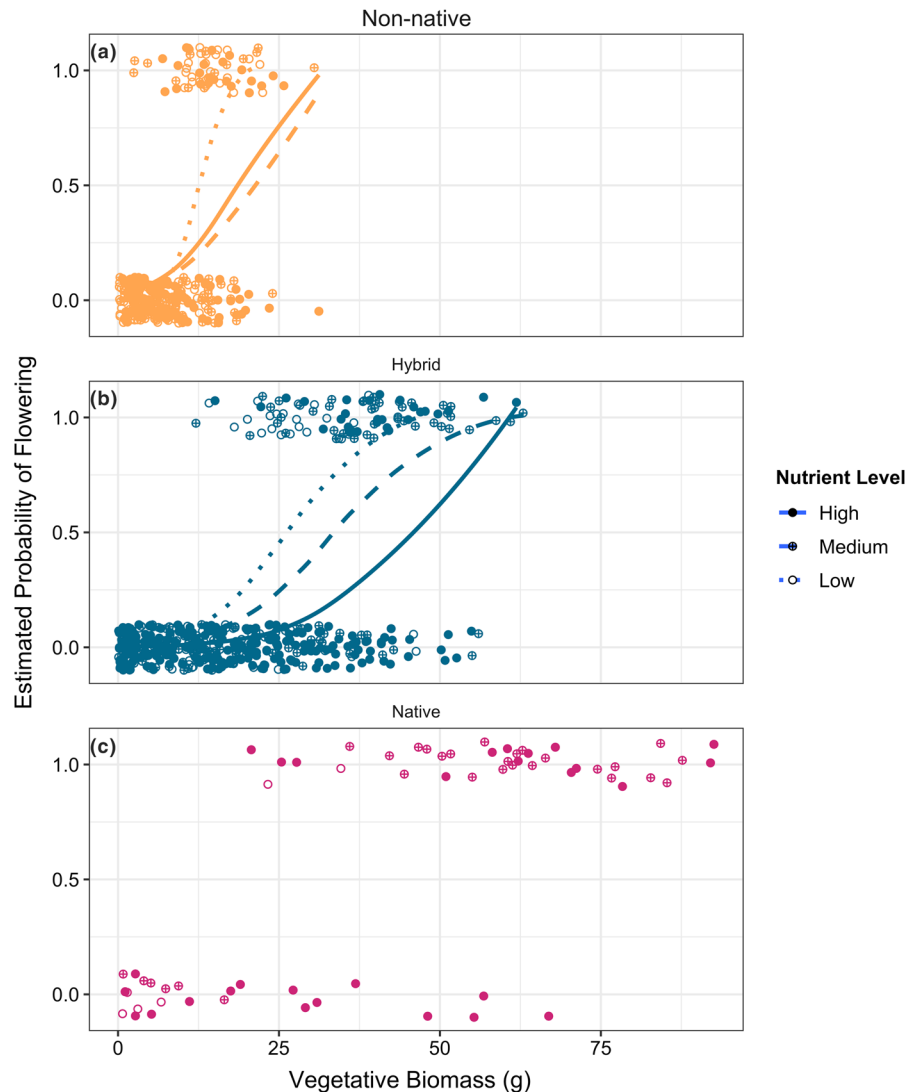
Discussion

We examined sexual reproductive allocation and plasticity of three closely related taxa of cattails with varying degrees of invasiveness in response to nutrient availability using a size-independent model and a size-dependent (allometric) model. Contrary to our first prediction (1) there was not consistent support for an allometric relationship within all three taxa. Consistent with our second prediction (2), the invasive non-native (*T. angustifolia*) and hybrid (*T. × glauca*) had higher sexual reproductive allocation than the non-invasive native (*T. latifolia*). Additionally, our results indicate that sexual reproductive allocation within each taxon is plastic. However, contrary to our third prediction (3), the most invasive taxon (the hybrid) was the least plastic in sexual reproductive allocation while the native appeared to be the most plastic. Finally, the results at the northern site supported our last prediction (4) that sexual reproductive allocation generally decreases as nutrients increase, but this relationship was inconsistent at the southern site.

Our initial size-dependent equation selection indicated that the relationship between size and sexual reproductive allocation ranged from isometric to allometric for all three taxa depending on site and nutrient level. Despite the lack of consistent evidence for significant allometric relationships, modeling sexual reproductive allocation as a function of vegetative mass provided insights that were not apparent when comparing size-independent allocation ratios. The size-independent analysis did not provide evidence that the taxa differ in their plasticity in sexual reproductive allocation, but once size was considered the taxa differed significantly in their plasticity (Table 1). Site affected the size-independent allocation ratios but not the size-dependent allocation coefficients, possibly indicating these site differences were due simply to size differences rather than allocation per se. Additionally, when correcting for size, the three taxa differed less in sexual reproductive allocation but maintained the same general pattern in which the two invasive taxa allocated more to sexual reproduction than the native (see Figs. 1 & 2). Furthermore, the size-dependent analysis revealed that the non-native and hybrid follow similar allocation trajectories but that the hybrid flowers at a greater vegetative biomass. Therefore, we argue that even if there is an isometric relationship between vegetative mass and allocation it is still important to incorporate size into allocation analyses.

Even after correcting for size, our results are consistent with previous studies indicating that invasive species allocate more to sexual reproduction than native species (McDowell and Turner 2002; Brown and Eckert 2005). Increased sexual reproductive allocation in the two invasive taxa (the non-native and hybrid) could help explain their increased success in colonizing new environments (Mason et al. 2008; Lembrechts et al. 2018), as their wind dispersed seeds have the potential to travel long distances to new locations (Bansal et al. 2019). Furthermore, our findings align with life history theory, which predicts that species on the leading edge of range expansions allocate more resources to dispersal and reproduction and that these life history traits are retained in populations even after the edge of the range has moved on (Phillips et al. 2010). Previous work has similarly indicated that life history traits for dispersal and reproduction are greater in invasive species than native species (Radford and Cousens 2000). Additionally, a

Fig. 3 Logistic regression predictions for probability of flowering at a given size for each taxon (row and color) at each nutrient level (low = dotted line, medium = dashed line, high = solid line). Symbols represent observed data at low (open), medium (shaded), high (solid fill) nutrient levels, with color indicating taxon, and were spread around 0 and 1 for visibility. The native is not invasive while both the non-native and hybrid are considered invasive in the Great Lakes region. Too few data points were available to fit a model for the native taxon. Coefficients from the logistic regression model are in Table S6 and ANOVA results for the model are in Table S5



previous study by Elgersma et al. (2015) found that the two invasive taxa (the non-native and hybrid) translocated more resources to clonal daughter ramets and that these daughter ramets had a greater response to increased maternal resources than the non-invasive native taxon. Combined with our results, this suggests the invasive non-native and hybrid invest more resources in both sexual and asexual reproduction than the non-invasive native.

The three taxa were plastic in sexual reproductive allocation but differed in the magnitude of their plasticity. At both sites, contrary to our prediction, the most invasive taxon (the hybrid) was the least plastic while the non-invasive native was the most plastic.

This suggests that plasticity in sexual reproductive allocation does not contribute to the invasiveness of the non-native and hybrid taxa. Ruprecht et al. (2014) found that plasticity in relative sexual reproductive allocation was significantly greater in invasive species than in non-invasive alien species, however, they could only compare two congeneric species pairs (*Amaranthus* and *Galinsoga*). Additionally, they compared sexual reproductive allocation as a ratio of sexual reproductive biomass to total biomass, which can lead to falsely significant findings (Sugiyama and Bazzaz 1998; Weiner 2004; Jelbert et al. 2015; Batzer et al. 2017). Additionally, asexual reproduction contributes to the invasiveness of the non-native

and hybrid cattails (Elgersma et al. 2015; Bansal et al. 2019), but plasticity in this trait needs further examination. Perhaps their plasticity in asexual reproduction outweighs plasticity in sexual reproduction. Our results contribute to a growing body of work suggesting that plasticity in some traits is not as important to invasiveness as previously thought (Godoy et al. 2011; Matzek 2012; Ruprecht et al. 2014).

The directional change in response to nutrients differed between the two study sites. While our results at the northern site supported our prediction that sexual reproductive allocation would increase as nutrient availability decreased, the results from the southern site showed no pattern and limited plasticity for both invasive taxa. This inconsistency emphasizes the importance of site characteristics in sexual reproductive allocation, but because we had only two sites that differed in both climate and base nutrient levels (due to water sources used for irrigation), it is difficult to attribute the allocation differences to any particular environmental characteristics with confidence. Our own results and those of previous studies (e.g. Bai et al. 2009; Nicholls 2011; Yang and Kim 2016) show a potential role for nutrients and Zhang et al (2018) have shown that mean annual temperature, latitude, and their interaction can influence reproductive allocation. Alternatively, although clonal allocation was beyond the scope of this study, a trade-off between sexual reproductive allocation and asexual reproductive allocation (Yang and Kim 2016) could have contributed to the discrepancies between sites. Future research could examine other variables that impact *Typha's* sexual reproductive allocation, asexual reproductive allocation, and how the relationship between the two traits changes under different environmental conditions.

The invasive non-native and hybrid did not differ in their sexual reproductive allocation, but they did differ in their minimum size for reproduction. The hybrid consistently grew larger and flowered at a larger size than the non-native. As nutrient level increased, the minimum size for reproduction generally increased for both taxa, except in the non-native between medium and high nutrient levels. Thus, our results suggest that it is likely both taxa have a minimum size for sexual reproduction which is plastic. This is consistent with previous research indicating that as conditions become less stressful, the minimum size for reproduction increases (Liu and

Pennings 2019). Our results are also consistent with the observation that larger plants have a larger minimum size of reproduction (Liu and Pennings 2019). The hybrid taxon follows this pattern as it has both a larger maximum size and a larger minimum size of reproduction than the non-native. Sexual reproduction consumes resources that would otherwise be used for growth, so the hybrid's larger minimum size for reproduction may give it an advantage over the non-native by facilitating increased growth and consequently greater inflorescence mass (Metcalf et al. 2003; Bonser and Aarssen 2009).

If generalizable, our findings would suggest that invasive plants allocate more to sexual reproductive allocation at a given plant size than native species, moving beyond previous results that did not account for size. While plasticity in sexual reproductive allocation may not contribute to invasiveness, perhaps the combination of increased sexual and asexual reproduction (Elgersma et al. 2015) contributes to the success of invasive species. Alternatively, the maintenance of greater sexual reproductive allocation over varying environments could provide a greater fitness advantage than does flexibility in this trait (Baker 1965; Richards et al. 2006). Additional research using size-dependent (allometric) analyses is needed to test whether these patterns persist in other clonal and non-clonal invasive plant species.

Our results have several potential caveats. Most importantly, each mesocosm initially contained all three taxa and therefore our observations of sexual reproductive allocation could be influenced by competitive interactions among the taxa, along with effects of nutrients and site. If the lower allocation in the native compared to the hybrid and non-native was due to a plastic response to competition rather than an intrinsic difference in allocation patterns, we would expect the native to be smaller in size than the invasive taxa (Sugiyama and Bazzaz 1998) but have greater sexual reproductive allocation for a given size because competition creates a more stressful environment (Liu and Pennings 2019). However, we consistently observe the opposite trend in allocation across taxa and individuals of the native taxon are consistently larger on average than the other two taxa (Figs. 2, 3). Thus, it seems unlikely that competition rather than intrinsic differences among taxa would be the main driver behind

the lower sexual reproductive allocation in the native, although we cannot exclude the possibility.

It seems more plausible that competition could have influenced the native's higher allocation to sexual reproduction at higher nutrient levels, because this trend coincided with an increase in the relative proportion of the native taxon's biomass (Tables S7, S8). On the other hand, the native's proportion of total biomass was relatively low across all nutrient levels (1–10%) and it likely experienced high inter-specific competition at all nutrient levels. Thus, even though the native's proportion of biomass increased with nutrients, it may not have experienced significant changes in inter-specific competition. While altering nutrient addition rates was a means to induce plasticity, the plasticity we observed cannot be directly attributed to changes in nutrient availability independent of competition.

Second, we cannot directly assess the causes of plasticity among nutrient levels and the slight differences in plasticity between sites. Climate, base levels of several nutrients, and degree of herbivory all differed between the two sites. Although the degree of herbivory was relatively low overall (unpublished data), it was significantly higher at high nutrient levels for all three taxa at both sites (unpublished data), potentially impacting allocation patterns (Peschiutta et al. 2018). However, these interactions among possible drivers of plasticity in allocation are impossible to disentangle with our data. Instead, we emphasize that multiple environmental and biotic factors can influence allocation in a plastic way, so that detecting general patterns in allocation among taxa should always involve multiple environments.

Third, there were substantially fewer native taxon samples relative to the non-native and hybrid taxa, which could also be a consequence of competitive dynamics reducing survival of the native. We do note however that native ramets were sparse even at the beginning of the experiment when density within the mesocosms was low and competitive dynamics were unlikely to play a role (unpublished data). With so few observations in some of the site by nutrient level combinations for the native, it is possible that our results were unrepresentative of the larger native population. The small sample size for the native also meant we were unable to include it in the logistic regression analysis to examine minimum size of reproduction. Having a larger sample size for the

native would have increased our ability to make pairwise comparisons and strengthened our model.

Finally, the genetic results revealed that while field identifications for flowering, non-outlier samples consistently matched genetic identifications, the non-flowering samples were more difficult to identify correctly. Our main findings, however, are derived from flowering samples and therefore we feel confident that most of our samples were correctly identified.

Our study adds to the existing body of literature examining trait values and plasticity in invasive species, but is unique in its consideration of allometry, sexual reproductive allocation, and invasiveness. We demonstrated that even when accounting for allometry, sexual reproductive allocation in *Typha* is plastic, but this plasticity is not correlated with invasiveness. Rather, invasive *Typha* consistently allocated more to sexual reproduction than their native congener.

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Author contributions DG, WC, KE, and JM contributed to the original mesocosm experiment conception and design, construction, and planting. Field sampling was performed by DG, KE, and JM. All authors contributed to the specific concept and design of the manuscript. Post-sampling data collection and analysis were performed by EJ and KE. The manuscript was written by EJ and all authors commented on previous versions of the manuscript. All authors read and approved the final version of the manuscript.

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Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files. Additionally, the data and code used to run all analyses and generate all figures can be downloaded from GitHub (https://github.com/ejameson/Jameson_et_al_Typha_Analyses.git).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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