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A Meta-analysis Reveals Knowledge Gaps in Our Understanding of the *Spartina-Geukensia* Mutualism

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Abstract

The relationship between Atlantic ribbed mussels (*Geukensia demissa*) and smooth cordgrass (*Spartina alterniflora*) represents a textbook example of a facultative mutualism. It is also foundational to wetland ecosystems along the Atlantic coast of North America. *Spartina* plantings play an essential role in marsh reconstruction projects, and *Geukensia* is rapidly gaining popularity as a tool in coastal restoration to help marshes resist erosion and to remove nutrient pollution. However, it remains unclear whether positive effects documented primarily in natural settings will translate to urban and constructed estuaries where they are most needed. Using systematic review and meta-analysis, we compared the influence of the *Spartina-Geukensia* mutualism on growth of the species and on nitrogen-cycling processes. Our review suggests the potential for context dependence in this mutualism, with substantial implications for coastal marsh resilience and restoration. Notably, the positive effect of the species on the growth of their mutualist found in natural marshes was absent in constructed marshes and negative in urban marshes. Encouragingly, the effect of each species on nitrogen cycling was similar regardless of context. We found that this mutualism remains severely understudied in urban and constructed marshes, and we suggest future directions to address the knowledge gaps identified in our analysis.

Keywords Salt marsh · Coastal resilience · Restoration · Urban estuaries · Ribbed mussel · Positive species interactions · Facilitation

Introduction

Species interactions mediate how organisms respond to and modify their environments, as well as the distribution and abundance of organisms within the environment. Positive interactions, which have been historically overlooked by ecologists (Bruno et al. 2003), may have particularly strong impacts on community diversity and ecosystem processes. Because they often confer greater resilience to abiotic stress, positive species interactions also have the potential to enhance the success of ecological restoration (Valdez et al. 2020). However, positive species interactions are also highly variable, and benefits received from mutualisms may differ as a result of changes in environmental context (Chamberlain et al. 2014). Rather than having a single linear relationship across all environments in which they are found, many mutualisms operate along gradients of abiotic and biotic stressors (He and Bertness 2014). A mutualism may be obligate in one site but facultative in another, and a relationship that is normally positive could become neutral or negative for one or more participants depending on environmental conditions (van der Heide et al. 2021). Moreover, asymmetries in positive species interactions (i.e., one species benefits more from the interaction than the other) are quite common and may even be critical in maintaining biodiversity (Bascompte et al. 2006). Context dependence in mutualisms, particularly facultative mutualisms, presents a substantial challenge for management of ecosystems facing an unprecedented rate of human-induced change (Gamfeldt et al. 2015; van der Heide et al. 2021).

Spartina alterniflora, smooth cordgrass, and *Geukensia demissa*, the Atlantic ribbed mussel, participate in a textbook example of a facultative mutualism. This relationship is foundational to the structure and function of coastal wetlands throughout the Atlantic coast of North America, and

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studies of this mutualism have significantly contributed to the ecological theory of positive species interactions (Bertness 1984; He et al. 2013). *Spartina* facilitates successful growth of *Geukensia* by providing structure that promotes recruitment of planktonic larvae and by forming a canopy that provides shelter from abiotic stressors (Bertness and Grosholz 1985). During the summer, *Spartina* protects *Geukensia* from heat stress that could lead to desiccation (Altieri et al. 2007). In the winter, *Spartina* protects *Geukensia* from ice shearing caused by wave action, which is often a major source of mortality (Franz 2001). *Geukensia* helps to stabilize *Spartina*'s root structure by attaching to its substrate with byssal threads (Bertness 1984). As a suspension-feeding bivalve, *Geukensia* provides additional inputs of nitrogen to the sediment surface in the form of feces and pseudofeces, which fertilize *Spartina* growth (Jordan and Valiela 1982).

Within their native range, *Spartina* and *Geukensia* contribute to the long-term resilience of marsh ecosystems and a host of ecosystem services that coastal marshes provide including the removal of nutrient pollution (Barbier et al. 2011; Bilkovic et al. 2017). *Spartina* assists in sediment construction by depositing slow-decaying biomass to the marsh benthos, promoting settlement of sediments from the water column, and stabilizing sediments through its root structure (Bertness 1984; Morris et al. 2016). *Spartina* also influences the rate of sediment microbial reactions by aerating the rhizosphere and releasing labile organic carbon from its roots (McClung et al. 1983). *Spartina* supports biodiversity within the marsh community by driving coastal primary production, providing structure for benthic species to attach and settle, and serving as refugia from predators (Gan et al. 2009; Chen et al. 2018). *Geukensia* increases the availability of nutrient-rich organic biodeposits in marsh sediments, providing greater energy for heterotrophic microbial reactions (Jordan and Valiela 1982). On the Pacific coast of North America, and in areas throughout Southeast Asia, the invasion of *Spartina* has led to rapid, irreversible changes to ecosystem structure, local biodiversity, and biogeochemical cycles (Li et al. 2009; Strong and Ayres 2013; Gao et al. 2019).

Foundational plant species like *Spartina alterniflora* are known to be an essential component of successful restorations. *Geukensia* is also rapidly gaining popularity as a tool in coastal restoration, particularly where the primary goal of restoration is nutrient remediation (Galimany et al. 2017; Bilkovic et al. 2021). *Geukensia* filter a wide diversity of particles from the water column, including bacteria < 1 µm in size, and are more tolerant of variation in salinity, temperature, and tidal inundation than other bivalves commonly used in nutrient-remediation projects like *Crassotrea virginica* (Kreeger et al. 2018). Recent work has also shown that the mutualism between these species can achieve even greater recovery of ecosystem function and greater resistance to abiotic stress (Derksen-Hooijberg et al. 2017).

On the Atlantic coast of North America, increasing rates of sea-level rise and eutrophication resulting from nutrient pollution near urban centers present two stressors that could drive context dependence in the *Spartina-Geukensia* mutualism (Kennish 2001; Gedan et al. 2009). Urban salt marshes are often lost at higher rates than their non-urban counterparts due to their proximity to multiple human disturbances including nutrient enrichment and altered hydrology due to coastal development (Zedler and Kercher 2005; Wigand et al. 2014). While urban managers can respond to marsh loss with restoration and reconstruction, constructed marshes may also face higher risk than their natural counterparts because they lack components and processes that contribute to long-term resilience, which only develop over decades of ecological succession (Gore and Shields 1995; Craft et al. 2003; Gutrich and Hitzhusen 2004; Herrick et al. 2006). Despite the obvious utility in identifying components and processes that contribute to resilience in highly stressed marsh ecosystems, urban and constructed marshes remain understudied relative to their natural counterparts (Grimm et al. 2008).

The mutualism between *Spartina* and *Geukensia* may confer greater resilience for marshes experiencing increasing rates of sea-level rise (Bertness 1984; Morris et al. 2016). *Geukensia* biodeposits fertilize both aboveground and belowground production of *Spartina* (Bertness 1984), both of which contribute to vertical marsh growth (Fig. 1A). Aboveground plant production increases sediment capture, and belowground production stabilizes sediments and contributes to the accumulation of organic material, both of which help the marsh to keep pace with sea-level rise and resist growing rates of tidal inundation (Cahoon et al. 2019). Enhanced belowground plant growth also aerates sediments, allowing for the oxidation of potentially harmful reduced substances like hydrogen sulfide and ammonium that often accumulate in flooded soils (Teal and Kanwisher 1966; Linthurst and Seneca 1981; Alldred et al. 2020). This plant-mediated aeration also promotes oxidation of ammonium to nitrate by nitrifying bacteria (Hamersley and Howes 2005), and subsequent removal of nitrate by denitrifying bacteria, thus promoting the ecosystem service of nitrogen removal (Fig. 1A). *Spartina* and *Geukensia* both produce labile organic matter, which provides an energy source for denitrifying bacteria (Sherr and Payne 1978; Bilkovic et al. 2017), further enhancing rates of microbial nitrogen removal. However, the outcome of this interaction may depend on the initial elevation of the marsh relative to local mean sea level, i.e., the marsh's "elevation capital," and delivery of sediment from the coastal watershed (Cole Ekberg et al. 2017; Gittman et al. 2018; Cahoon et al. 2019) (Fig. 1).

Coastal urban marshes are subject to multiple stressors including eutrophication, rising sea levels, and land-use alterations that reduce inputs of sediment while increasing rates of erosion (Mudd 2011; Kirwan and Megonigal 2013; Wigand

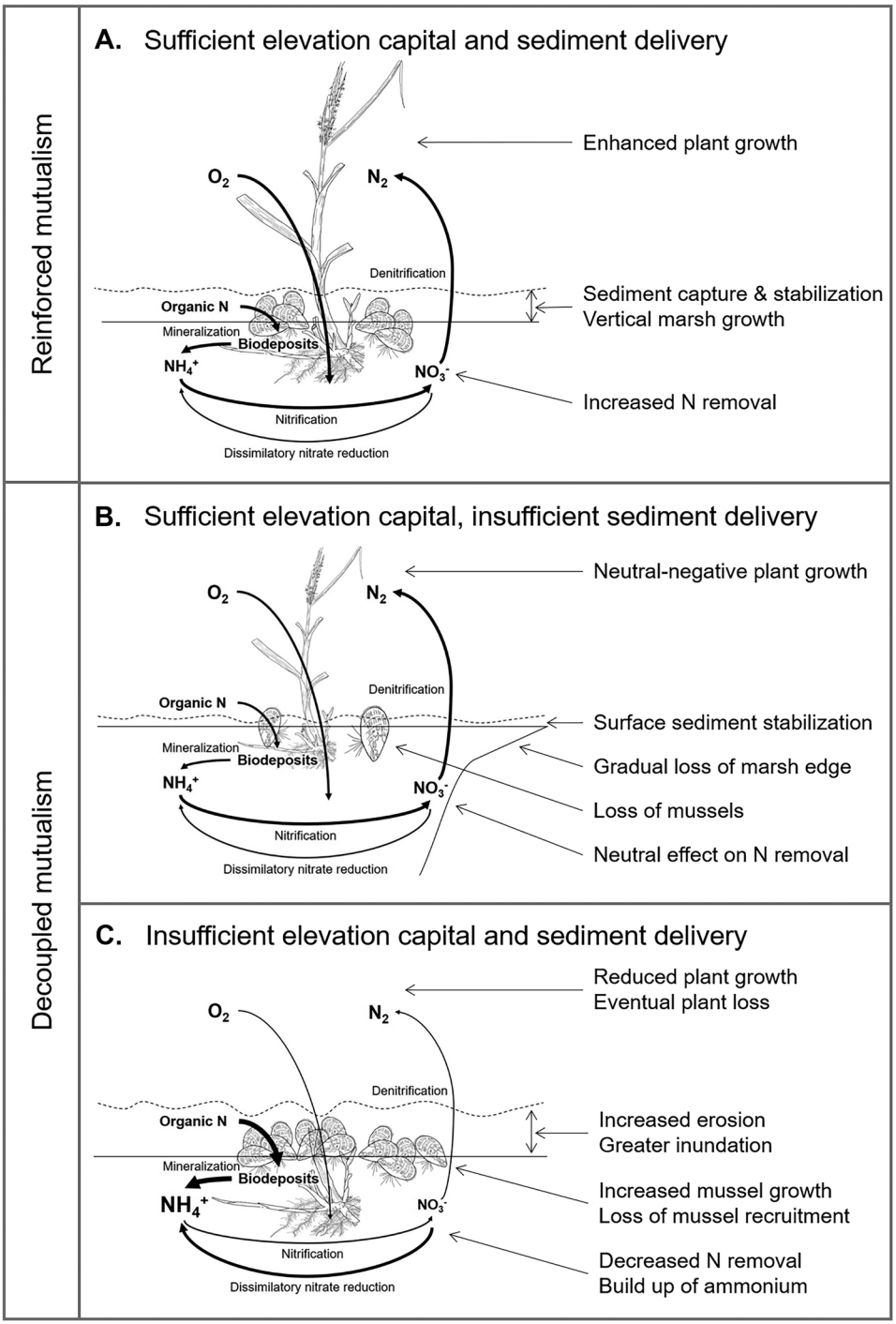


Fig. 1 Hypothesized outcomes of the *Geukensia-Spartina* mutualism in marshes with **A** sufficient elevation capital and rates of sediment delivery, **B** sufficient elevation capital but insufficient sediment delivery, and **C** insufficient elevation capital and insufficient sediment delivery. The dashed line represents mean local sea level, and the solid line indicates the position of the sediment-water interface

et al. 2014). Under these conditions, we hypothesize that the mutualism between *Spartina* and *Geukensia* could become decoupled (Fig. 1B, C). In a eutrophic system, regular inputs of nutrients from the watershed and from incoming tides may be sufficient, such that *Spartina* growth would not be limited by nutrient availability. Increased nutrient levels in the surrounding environment can also lead *Spartina* to develop less fine root structure (Darby and Turner 2008; Deegan et al. 2012; Alldred et al. 2017), leaving the marsh susceptible to erosion while simultaneously lowering rates of vertical accretion from the accumulation of belowground biomass (Turner 2011; Deegan et al. 2012). Under this scenario, additional nutrients provided by *Geukensia*'s biodeposits would no longer provide a positive subsidy for the plant and could potentially inhibit belowground plant growth.

If a marsh begins with sufficient elevation capital, and thus experiences shorter periods of daily tidal inundation, the plants may be less susceptible to increasing rates of

inundation for some time (Cole Ekberg et al. 2017), continuing to accumulate sufficient belowground biomass and aerating surface sediments to promote nitrogen removal. However, marsh sediments below the zone of active plant growth and aeration could experience symptoms of eutrophication including increased rates of peat decomposition and prolonged anoxia that suppresses the formation of deep plant roots (Davey et al. 2011; Wigand et al. 2014). These conditions may result in a stable marsh platform but gradual loss of the marsh edge (Fig. 1B). In this scenario, we would expect to observe a decrease in the *Geukensia* population as its preferred edge habitat is lost (Franz 1996). In contrast, when a marsh with insufficient elevation capital and sediment delivery is exposed to sea-level rise and eutrophication, we expect that *Geukensia* would respond well in the short term, benefitting from longer periods of inundation and thus a greater amount of time to feed on organic material from the water column (Gittman et al. 2018). However, longer inundation periods would adversely affect plant growth by inhibiting root respiration and facilitating the buildup of harmful reduced substances (Alldred et al. 2020), and the loss of plant structure may eventually inhibit recruitment of juvenile *Geukensia* to the marsh (Fig. 1C). As sediments become inundated for longer periods of time, permanent anoxia would decrease the availability of nitrate, thereby decreasing rates of microbial nitrogen removal via denitrification and promoting accumulation of ammonium from dissimilatory nitrate reduction (Koop-Jakobsen and Giblin 2010; Giblin et al. 2013).

Here, we conducted a systematic review and meta-analysis to address the following questions and to identify any knowledge gaps in our understanding of the *Spartina-Geukensia* mutualism:

1. How does the presence of *Spartina alterniflora* affect the growth of *Geukensia demissa* and vice versa, and are there asymmetries in benefits received from the mutualism?
2. How does the presence of *Spartina alterniflora* and *Geukensia demissa* affect the components of the salt marsh nitrogen cycle?
3. How do these trends change depending on environmental context, specifically in the cases of urban vs. non-urban wetlands and constructed vs. natural wetlands?

If the outcome of the *Spartina-Geukensia* mutualism does indeed differ in urban and/or constructed marshes, then much more information is needed to understand the long-term trajectory of marsh development in highly impacted coastal ecosystems. If the standard reinforced mutualism pathway occurs (Fig. 1A), then the mutualism could serve as a useful tool for conserving and restoring salt marsh ecosystems by regulating nitrogen and helping the marsh to keep pace with sea-level rise. However, if either decoupled mutualism pathway occurs (Fig. 1B or C), then the relationship between *Spartina* and *Geukensia* may not enhance long-term resilience, and may even accelerate rates of salt marsh loss. Investigating the outcome of the mutualism under differing salt marsh conditions is crucial to maintaining these highly valuable but highly threatened ecosystems.

Methods

Systematic Review Methods

To study the influence of the mutualism on species responses, we performed a search for records on 6/2/2020 using the database "Web of Science," using eight search phrases (Table 1). We performed a similar search on 3/12/2020 to investigate the effect of each species on components of the marsh nitrogen cycle, using 14 search phrases (Table 1). Searches were limited to records published between 1970 and 2020 and sorted for relevance, using the first 40 records for each search phrase. Due to the low number of records returned for effects on species responses ($n = 31$), we performed a second search on 7/20/2020 with the search engine "Google Scholar," using the same search phrases and search limitations. For all searches, if a record was returned that did not appear to correspond to any existing academic or scientific material (e.g., conference paper/abstract, advertisement, book review), we did not count it as part of the 40 records for that search phrase.

After compiling a list of records from our searches, we eliminated duplicates, including where the same data were presented in different sources (e.g., a graduate thesis and the papers published from that thesis) (Fig. 2). We then scanned abstracts for relevance and eliminated any record that featured neither of the two target species. Records were then read in full. For effects on species responses, we eliminated records in which both species were featured but the study focus was not on their interaction (Fig. 2A). For effects of species on the nitrogen cycle, we discarded studies that failed to include either of our species of interest and an estimate of its effect on a component of the nitrogen cycle (Fig. 2B). We also discarded measurements of the nitrogen cycle that were irrelevant to our study (e.g., identifying fraction of biologically incorporated nitrogen coming from specific sources). Records in which the published data were insufficient to perform meta-analysis (e.g., missing sample sizes, missing standard deviations or other estimates of error) were also eliminated. We identified 18 suitable publications for estimates of the species on the growth of their mutualist, from which we extracted 45 independent measurements. We identified 24 suitable publications for estimates of the effect of either species on the marsh nitrogen cycle, from which we extracted 49 independent measurements.

Table 1 List of search phrases included in systematic review

Species response	Nitrogen cycling
Geukensia demissa AND Spartina alterniflora AND biomass	Geukensia addition
Ribbed mussels AND Spartina alterniflora AND biomass	Ribbed mussel addition
Geukensia demissa AND smooth cordgrass AND biomass	Ribbed mussels AND nitrification
Ribbed mussels AND smooth cordgrass AND biomass	Ribbed mussels AND denitrification
Geukensia demissa AND Spartina alterniflora AND growth	Geukensia AND nitrification
Ribbed mussels AND Spartina alterniflora AND growth	Geukensia AND denitrification
Geukensia demissa AND smooth cordgrass AND growth	Ribbed mussels AND nitrogen
Ribbed mussels AND smooth cordgrass AND growth	Geukensia AND nitrogen
	Smooth cordgrass addition
	Spartina alterniflora addition
	Smooth cordgrass AND nitrification
	Smooth cordgrass AND denitrification
	Spartina alterniflora AND nitrification
	Spartina alterniflora AND denitrification

Meta-analysis Methods

Once a final list of records was identified, we extracted independent measurements from these records. For studies measuring species responses to the mutualism, the treatment group included the co-occurrence of both species, and the control group included the species in the absence of its mutualist. For studies of nitrogen cycling, we compared

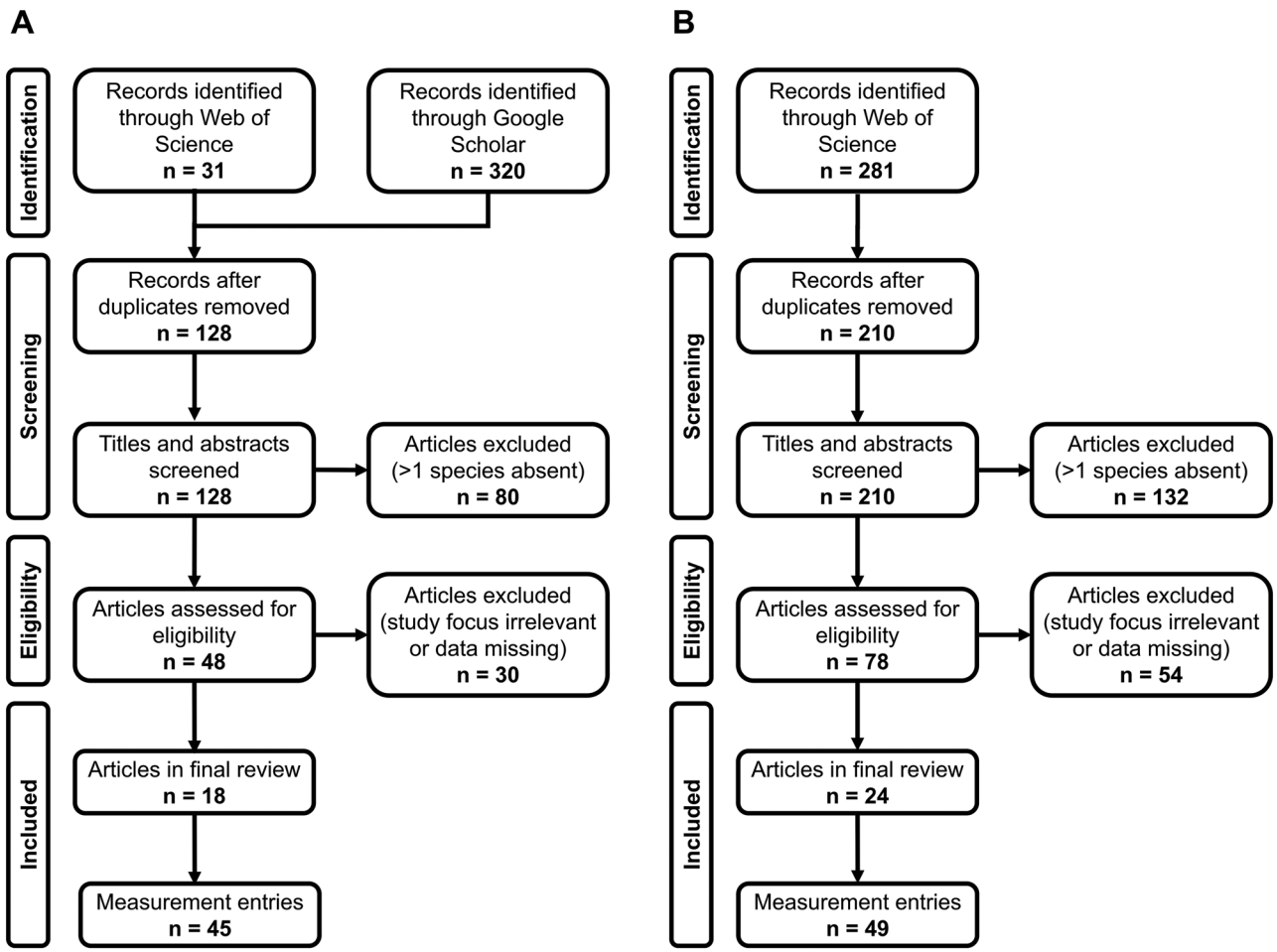


Fig. 2 PRISMA diagram for systematic review of **A** responses of *Spartina* and *Geukensia* to the presence of their mutualist and **B** influence of either species on nitrogen cycling

nitrogen processes or pools in the presence of either *Spartina* or *Geukensia* to the same process or pool in "control" measurements where the species was absent. For studies involving *Spartina* presence, it was not possible to have a standard definition for "control" sites across all studies. Whenever possible, bare sediments were used as controls, but in some studies *Spartina* presence could only be compared to the presence of other marsh plant communities. In all cases, the presence of *Geukensia* was compared to a control group in which marsh plants were present but *Geukensia* was not, and the treatment group included both *Geukensia* and *Spartina*. Studies of *Geukensia* in isolation were rare, and we found only one study that conducted a full factorial study that included both species, in combination and alone, relative to bare sediment controls (Bilkovic et al. 2017). We were therefore unable to include all of these combinations in our analysis. Responses of components of the nitrogen cycle to *Geukensia* are thus best understood as the added value of *Geukensia* to the marsh, relative to a vegetated marsh where *Geukensia* is absent. We extracted means, standard deviations, and sample sizes directly from the text of the records for treatment and control groups. In many cases, these data were not available in the text, and we used the image analysis program ImageJ (Schneider et al. 2012) to extract measurements from figures.

Information about the environmental category of each study site (i.e., urban vs non-urban and constructed vs natural) was obtained directly from the record. Sites were categorized as "urban" if they were identified as urban, highly impacted, or highly eutrophic in the site description. When this information was not available in the record, we looked at publicly available maps of the study site (using coordinates from the record if available) as well as photographs and geographic descriptions from official sources to characterize each site. In these cases, sites were considered "urban" if they were located within a densely populated or highly developed local watershed. Both artificial laboratory mesocosms and reconstructed or restored full-scale marshes were placed under the "constructed" category.

After all the data were extracted and compiled, we analyzed and visualized them using R version 4.1.1 (R Core Team 2021) and the packages meta, metafor, and dmetar (Viechtbauer 2010; Harrer et al. 2019; Balduzzi et al. 2019). We estimated mean effect sizes using the Hedges' *g* estimator for species responses and nitrogen process/pool using a random-effects model. A random-effects model was used because we anticipated random variance in effect sizes among studies, both in terms biotic and abiotic characteristics of the study locations and the measurement techniques used to estimate effect sizes (Gurevitch and Hedges 2001). Hedges' *g* was used as the measure of effect size due to the prevalence of small sample sizes in the analyzed studies (Hedges 1981). We performed subgroup analyses to compare the relative change in species growth variables when the species is in the presence of its mutualist. These responses included aboveground and belowground biomass and clonal outgrowth for *Spartina alterniflora*, and growth constant, population density, and shell length for *Geukensia demissa*. We then performed separate subgroup analyses to test whether the overall effect of the mutualism on species growth differed between urban and non-urban systems and between constructed and natural systems.

We performed subgroup analyses to compare the relative change in components of the nitrogen cycle in the presence of either of the species; these components included nitrogen fixation, nitrification, denitrification, nitrous oxide emissions, and *Spartina* tissue N concentrations. We subdivided studies of nitrogen cycling into urban vs. non-urban and constructed vs. natural systems and repeated the subgroup analysis to determine whether the effects of species on components of the nitrogen cycle differed depending on environmental context. For all subgroup analyses, effects were considered significant if the 95% confidence interval did not overlap zero. Subgroups are considered significantly different from each other in cases where the 95% confidence intervals of the subgroups did not overlap with each other. To investigate the possibility of publication bias within our literature sample, we generated a funnel plot and a *p*-curve for both the species-response and nitrogen-cycling data.

Data and metadata from our systematic review are publicly available (Alldred and Whaley 2022), and complete documentation of our analyses, including annotated R code, is available in the supplementary material (Online Resource 1). The published dataset includes categorizations that were applied to each measurement (e.g., urban vs. non-urban) and additional information including measurement techniques used in each study.

Results

Influence of Mutualism on Species Growth

While measurements were well distributed throughout the native range of the species (Fig. S1, Online Resource 1), many of the species-response data (33/45 measurement entries) come from two areas in the USA: New England and Georgia. All the Georgia studies (19/45 measurement entries) were performed on Sapelo Island. Natural and non-urban systems dominate the data, with a minority of data from urban systems (9/45 measurement entries) and an even smaller minority from constructed systems (4/45 measurement entries). Notably, all of the urban sites were located in the northern half of the species' native range, including New York, NY, USA; Town Point, Nova Scotia, CA; Branford, CT, USA; and Arlington, NJ, USA (Fell et al. 1982; McClary 2004; Watt et al. 2011; Zhu et al. 2019). Likewise, the four studies in constructed

systems were performed in Connecticut and New York, USA (Peck et al. 1994; Swamy et al. 2002; Zhu et al. 2019). Two of the studies in constructed marshes were performed at sites that had been wholly reconstructed using dredge material, and two involved impounded marshes that had natural tidal hydrology restored. Of the two species, *Spartina* was more commonly the focus of measurements (26/45 measurement entries) than *Geukensia*. In 6/19 measurement entries in which *Geukensia* growth was measured, the control for *Spartina* presence was a different plant species rather than bare sediment; these were either invasive *Phragmites australis* or other high marsh natives such as *Spartina patens*, *Distichlis spicata*, or *Juncus gerardii* (Fell et al. 1982; Peck et al. 1994; Swamy et al. 2002; McClary 2004). The funnel plot and *p*-curve for these data did not show any substantial evidence for publication bias (Online Resource 1).

Increases in aboveground *Spartina* biomass and belowground *Spartina* biomass from *Geukensia* presence were both significant, but aboveground biomass was more strongly affected (Fig. 3A). Clonal outgrowth showed a nonsignificant increase (Fig. 3A). *Geukensia* populations showed a significant increase in growth constant in the presence of *Spartina*, although the low number of observations makes it hard to draw meaningful conclusions for this response measure (Fig. 3B). *Geukensia* showed a nonsignificant increase in population density and a non-significant decrease in shell length due to *Spartina* presence (Fig. 3B). Removing the studies with non-sediment controls did not change results (Fig. S2, Online Resource 1).

Influence of Mutualism on Nitrogen Cycling

Most of the data for this analysis either come from the Atlantic coast of the USA (19/48 measurement entries) or the east coast of China (23/48 measurement entries) (Fig. S1, Online Resource 1). A small number of measurement entries (4/48) come from Brazil and Argentina. Many US studies were performed on Sapelo Island Reserve in Georgia (8/48 measurement entries), with the other 11 US measurement entries from Virginia, New York, and Rhode Island. These measurements represent fairly comprehensive coverage of *Spartina*'s native range. Many Chinese studies are from Dongtan Reserve in Shanghai (8/48 measurement entries). The majority of data come from natural (37/48 measurement entries) and non-urban systems (35/41 measurement entries), while constructed and urban systems are underrepresented in the literature. Urban sites were equally distributed between the native and invasive range of *Spartina alterniflora*, with three measurements in New York and Rhode Island, USA (Bertness 1984; Zhu et al. 2019), and four measurements in the Shandong and Zhejiang provinces in China (Zhang et al. 2019b, c). Most of the constructed studies come from laboratory mesocosms (7/11 constructed measurement entries) rather than field sites. All of the constructed field sites were located in urban watersheds in either New York, USA (Zhu et al. 2019) or Zhejiang Province, China (Zhang et al. 2019a). As in the species-response dataset, no urban or constructed sites were sampled within the southern half of the species' native range. Of the two species, *Spartina* was the more-studied species (38/48 measurement entries) with regard to nitrogen processes. In 25/38 measurement entries focusing on *Spartina* addition, the grass is acting as an invasive. Eleven of 38 *Spartina* measurement entries, all of them when *Spartina* was an invasive, had other plant species as the controls rather than bare sediment; the control was commonly *Phragmites australis*, but *Kandelia obovata* and *Cyperus malaccensis* were also used as controls (Cheng et al. 2007; Zhang et al. 2013, 2016, 2019a; Jia et al. 2016; Huang et al. 2016;

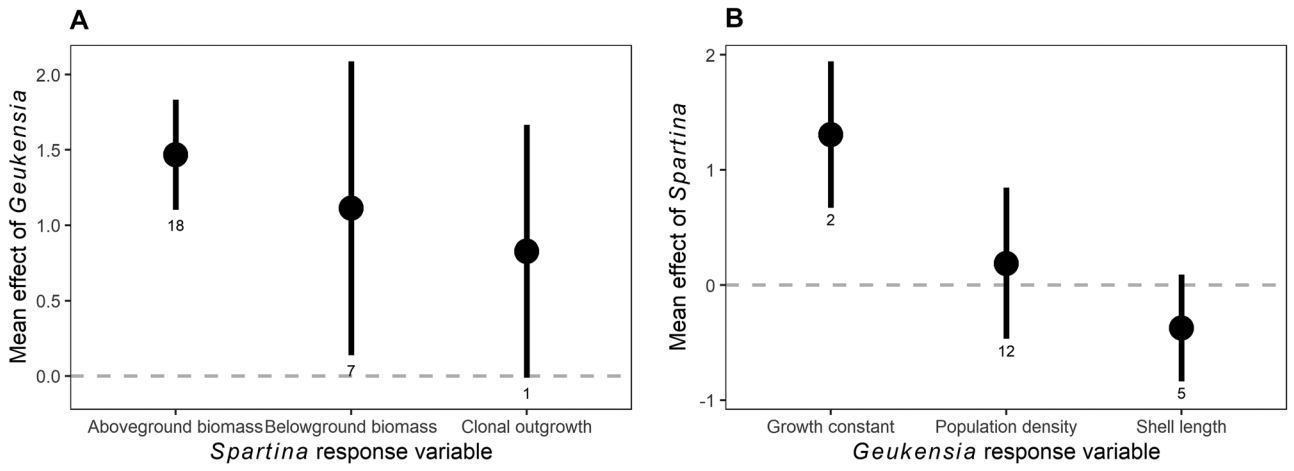


Fig. 3 **A** Influence of *Geukensia* on *Spartina* characteristics. **B** Influence of *Spartina* on *Geukensia* characteristics. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies

Yang and Silver 2016; Gao et al. 2017). The funnel plot and *p*-curve for these data did not show any substantial evidence for publication bias (Online Resource 1).

Denitrification and N_2O emission increased significantly in the presence of *Spartina* (Fig. 4A). *Spartina* had no consistent effect on dissolved organic nitrogen, nitrogen fixation, or nitrification (Fig. 4A). Removing the non-sediment control studies led to similar results, with the exception of N_2O emission, which became non-significant (Fig. S4, Online Resource 1). *Geukensia* presence showed little consistent effect on denitrification relative to vegetated marshes in which *Geukensia* was absent (Fig. 4B). *Geukensia* presence did correspond to a nonsignificant increase in nitrification and a significant increase in *Spartina* tissue nitrogen content (Fig. 4B).

Evidence of Context Dependence

The effect of the mutualism differed between natural and constructed marshes and between non-urban and urban marshes (Fig. 5). The mutualism had a significant positive effect on species growth in natural systems, while having no effect in constructed systems (Fig. 5A). In non-urban systems, the mutualism has significant positive effects for its component species, while having significant negative effects in urban systems (Fig. 5B). Bare-sediment-control-only results showed no significant differences from results with all control types included (Fig. S3, Online Resource 1).

We detected no significant differences in the effects of *Spartina* on components of the marsh nitrogen cycle when comparing natural and constructed marsh ecosystems (Fig. 6A). Results remain similar when non-sediment control studies are removed, with the exception that no studies have reported the influence of *Spartina* relative to bare sediment on nitrogen fixation or nitrification in constructed marshes (Fig. S5, Online Resource 1). The influences of *Geukensia* on nitrification and denitrification were not significantly different (Fig. 6B). However, in each case, only one study has estimated the effect of *Geukensia* in a constructed system, and no studies have estimated the effect of *Geukensia* on *Spartina* tissue N in a constructed marsh system (Fig. 6B).

We detected no significant differences in the effect of *Spartina* on components of the marsh nitrogen cycle between non-urban and urban marsh ecosystems, with the exception of one study that found a very large effect of *Spartina* on

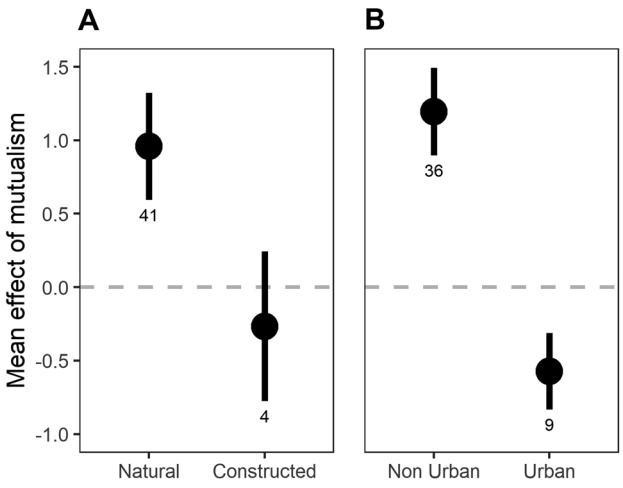


Fig. 5 **A** Overall effects of the mutualism on species growth in natural vs constructed marshes and **B** non-urban vs. urban systems. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies

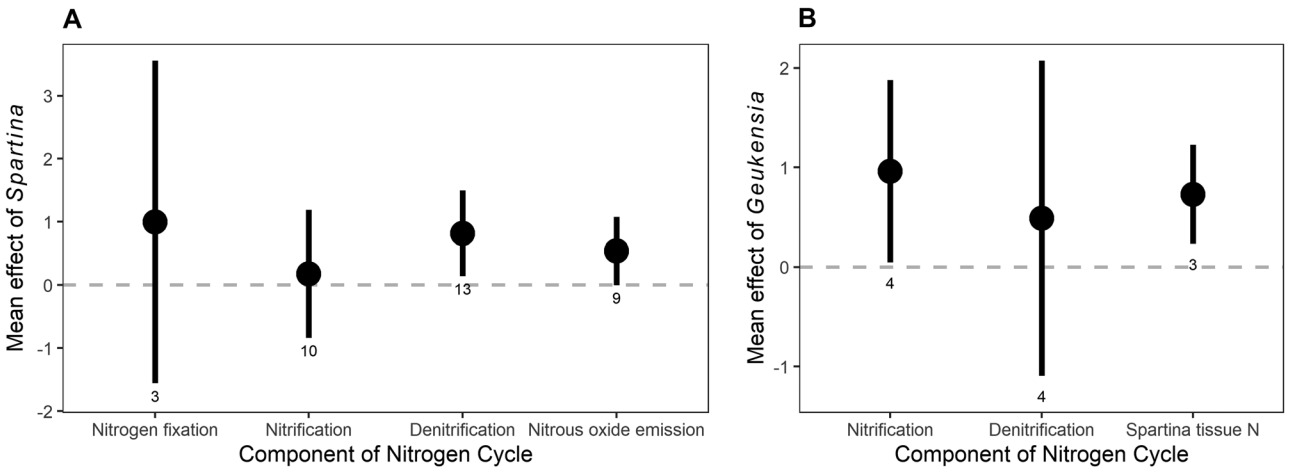


Fig. 4 **A** Influence of *Spartina* on pools and rates of the marsh nitrogen cycle. **B** Influence of *Geukensia* on rates and pools of the marsh nitrogen cycle. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies. Mean effect of *Spartina* on pools of dissolved organic nitrogen SMD = −10.46, 95% CI = [−34.10, 13.19], $n = 3$

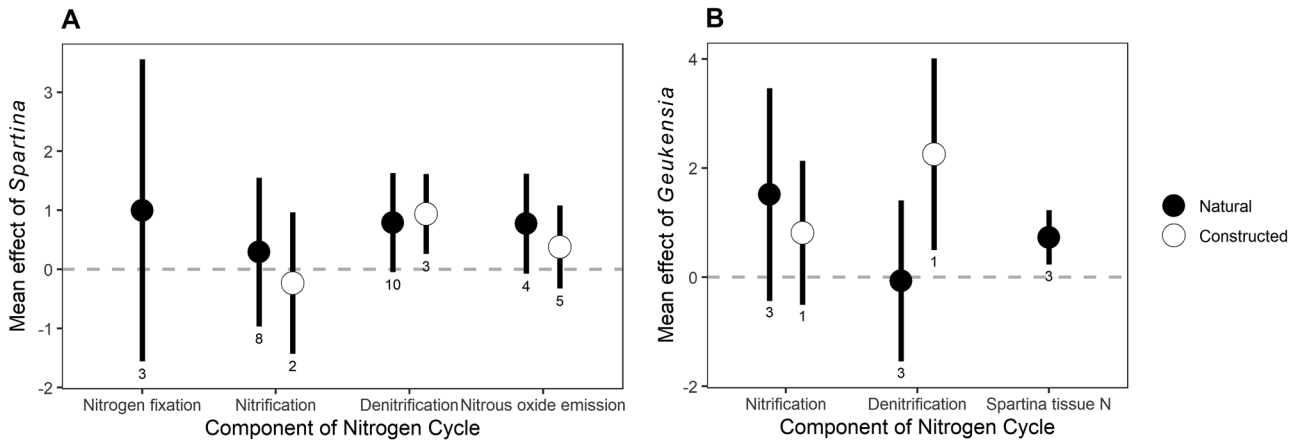


Fig. 6 **A** Overall effect of *Spartina* and **B** *Geukensia* on components of the marsh nitrogen cycle in natural vs. constructed marsh ecosystems. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies. All estimates of the effect of *Spartina* on dissolved organic nitrogen were conducted in natural marshes, SMD = −10.46, 95% CI = [−34.10, 13.19], $n = 3$

denitrification at an urban site (Fig. 7A). However, our sample sizes for urban systems were extremely limited, with only one study estimating the effects of *Spartina* on nitrification, denitrification, and nitrous oxide emissions in urban systems, and no studies estimating the effect of *Spartina* on nitrogen fixation in urban systems (Fig. 7A). When non-sediment control studies were removed, no studies remained that allowed us to estimate the influence of *Spartina* in urban systems (Fig. S6, Online Resource 1). The influence of *Geukensia* on components of the marsh nitrogen cycle also did not differ between non-urban and urban marshes (Fig. 7B). However, our sample sizes for urban marshes were again limited, with only one estimate for each component of the nitrogen cycle.

The influence of *Spartina* on components of the marsh nitrogen cycle did not differ between its native and invasive range (Fig. 8). The one study that estimated the effect of *Spartina* on nitrogen fixation in its invasive range did find a significant positive effect, which differs from the non-significant effect observed between the two studies conducted in its native range. Notably, no studies estimated the influence of *Spartina* on nitrous oxide emissions in its native range (Fig. 8). Results were similar when studies that did not use bare-sediment controls were removed, with the caveat that the one study that estimated the influence of *Spartina* on nitrogen fixation was eliminated from the analysis (Fig. S7, Online Resource 1).

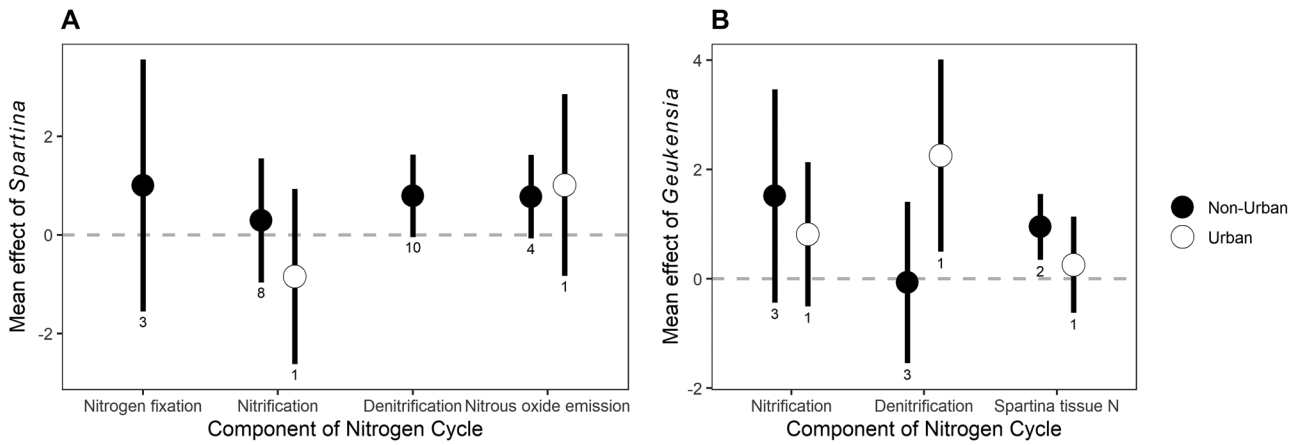


Fig. 7 **A** Effect of *Spartina* and **B** *Geukensia* on components of the marsh nitrogen cycle in non-urban vs. urban marsh ecosystems. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies. One study investigated the effect of *Spartina* on denitrification in an urban marsh and found a very large effect size, SMD = 22.40, 95% CI = [0.71, 44.09], $n = 1$

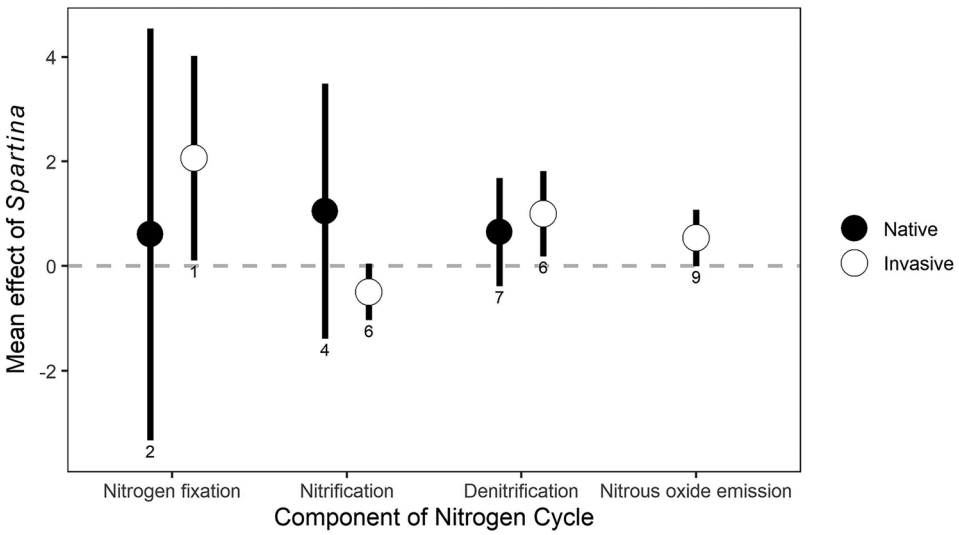


Fig. 8 Effect of *Spartina* on components of the marsh nitrogen cycle in its native and invasive range. Mean effects are standardized mean differences; error bars represent 95% confidence intervals; and numeric labels indicate number of studies. All estimates of the effect of *Spartina* on dissolved organic nitrogen were conducted in its invasive range, SMD = −10.46, 95% CI = [−34.10, 13.19], $n = 3$

Discussion

Though studies in urban and constructed marshes were extremely limited, our analysis provides compelling evidence that the mutualism between *Spartina alterniflora* and *Geukensia demissa* may function differently in highly impacted sites than in natural salt marshes. As expected (Fig. 1A), both species responded positively to the presence of their mutualist in studies conducted in natural and non-urban salt marshes. However, responses of the species to the presence of their mutualist were inconsistent in constructed marshes and significantly negative in urban marshes. Documentation of these benefits was stronger for *Spartina*, with significant increases in both aboveground and belowground growth in the presence of *Geukensia*. Responses of *Geukensia* to the presence of *Spartina* were more modest, with a positive effect on growth but no clear pattern in population density and a negative but nonsignificant trend in shell size. The difference in documented benefits for *Spartina* and *Geukensia* hints at a potential asymmetry in benefits derived from this mutualistic interaction, a common feature among mutualisms (Bascompte et al. 2006). However, the lack of clear trends in *Geukensia* could also result from complex interactions among recruitment of young mussels and growth and survivorship of adults (Franz and Tanacredi 1993; Franz 1996). Because *Spartina* is expected to facilitate recruitment of mussels, we may expect to observe a larger abundance of small juvenile mussels where *Spartina* is present compared to areas where it is absent. Size and age are directly related in mussels, but growth constant and age are inversely related (Borrero and Hilbish 1988). A greater abundance of juvenile mussels would therefore correspond to a smaller body size but faster growth, which is consistent with the results of our analysis.

Future studies that focus on juvenile recruitment and survival of *Geukensia* in the presence and absence of *Spartina* would allow us to clarify how, and in which contexts, *Geukensia* benefits from participating in this mutualism. Varying densities of *Spartina* among studies, which we were not able to document consistently enough to include in this analysis, may also have contributed to variance in the response of *Geukensia* to its mutualist. Because effects of *Spartina* may vary depending on plant density, future studies should also take care to document density of *Spartina* in field surveys or experiments. Notably, none of the studies included in our analysis measured adult survivorship for *Geukensia* in the presence and absence of their *Spartina* mutualist. Because enhanced adult survivorship is one of the primary benefits *Spartina* is thought to provide to its partner (Bertness 1984), it is possible that the absence of these measurements may have resulted in our underestimating the benefit of the mutualism to *Geukensia*.

We hypothesized that the positive effect of *Geukensia* in fertilizing *Spartina* may be absent or even negative in urban systems (Jin et al. 2005; Fig. 1B, C). Available data support this hypothesis. In urban systems, the presence of a mutualist had a significant negative effect on species growth (Fig. 5). However, a number of variables including the presence of predators (Hughes et al. 2014; Hensel et al. 2021), rates of sediment delivery and erosion, and extreme weather events (Derksen-Hooijberg et al. 2019) may differ between urban and non-urban systems. The lack of published studies in urban systems as of 2020 hampered our ability to investigate these variables in greater detail.

Studies of urban marshes in the southern half of the species native range were notably lacking, which is troubling given that these variables likely differ across the species' native range. Likewise, we were unable to distinguish whether this

potential decoupling in the mutualism we observed in urban systems was consistent with a scenario of sufficient or insufficient elevation capital (Fig. 1B or C). In a scenario of sufficient elevation capital, we would expect to observe negative effects on mussels consistent with the loss of edge habitat (Fig. 1B); whereas, in a scenario of insufficient elevation capital, we would expect to see negative effects on plant growth and a temporary increase in mussel growth consistent with increased rates of inundation (Fig. 1C). Our analysis revealed a modest but significant negative response of both species to the presence of their mutualist in urban systems, which may be consistent with either scenario (Fig. 5B). Given the stark difference in the outcome of the *Spartina-Geukensia* mutualism between urban and non-urban marshes, the precise mechanisms that may result in context dependence in urban marshes are worthy of investigation in future studies, with particular emphasis on urban areas in the southeastern Atlantic coast and the Gulf coast. Studies in constructed marshes were even more limited, and the variation in restoration techniques (e.g., reconstruction on dredged sediment vs. restoration of tidal regime to an impounded marsh) (Peck et al. 1994; Swamy et al. 2002; Zhu et al. 2019) likely resulted in the lack of a clear signal in species responses to the presence of their mutualist (Fig. 5A). The rapid increase in wetland construction and "living shoreline" projects (Zhu et al. 2019; Bilkovic et al. 2021) will provide exciting opportunities to study potential mechanisms of context dependence in this mutualism over the next decade.

While our analysis strongly suggests context dependence in the effect of the mutualism on responses of the species, we observed no such evidence of context dependence in the effect of the species on components of the marsh nitrogen cycle. Contrary to our predictions for an urban eutrophic marsh (Fig. 1C), the influence of the species on nitrogen cycling appears to be relatively consistent, even in cases where the species no longer have a positive influence on each other. While this result is encouraging for managers hoping to restore function to urban marshes, it should also be viewed with caution given the extremely limited number of studies that have been performed in constructed and urban systems. Moreover, the effects of either species on many processes of the nitrogen cycle, including nitrogen fixation and dissimilatory nitrate reduction to ammonia (DNRA), remain poorly quantified (Fig. 4). Our understanding of the effect of both species on the marsh nitrogen cycle would be greatly enhanced by a larger number of experimental field studies in a variety of newly constructed, stable, and degraded marsh sites throughout the species' native range.

The overall effect of both species on the marsh nitrogen cycle among studies was largely consistent with our expectations for stable marshes with sufficient elevation capital (Fig. 1A or B). The increase in denitrification rates in the presence of *Spartina* is consistent with the commonly held consensus on *Spartina's* effects on marsh sediments (Sherr and Payne 1978; Hamersley and Howes 2005; Alldred and Baines 2016). Nitrogen removal is often a management goal of marsh ecosystems, so these results are promising for management purposes (Cheng et al. 2020). As a byproduct of denitrification, it is likewise unsurprising that nitrous oxide emissions also increase in the presence of *Spartina*. However, because nitrous oxide is a potent greenhouse gas, increases in the local service of nitrogen removal may also contribute to global climate challenges.

Contrary to our expectations, we did not observe significant increases in sediment nitrification rates in the presence of *Spartina* (Sherr and Payne 1978; Hamersley and Howes 2005) relative to when *Spartina* was absent (Fig. 1C). As many of the *Spartina*-focused nitrogen cycling studies took place in *Spartina*'s invasive range, where it is often compared to *Phragmites australis*, another species that aerates the rhizosphere, differences in study design may have confounded results. However, removing the measurements where *Phragmites* and other plants were used as controls did not change the results of our analysis (Online Resource 1), nor did we observe any differences in the effect of *Spartina* on nitrogen cycling between its native and invasive range (Fig. 8).

The strongest effect of *Geukensia* on nitrogen cycling was an increase in *Spartina* tissue nitrogen content. This result was not surprising given that fertilization of *Spartina* should increase opportunistic uptake of nitrogen. Among all studies, *Geukensia* had a positive effect on nitrification, relative to vegetated marshes in which *Geukensia* was absent, likely as a result of increasing ammonium availability in sediments (Fig. 1A). However, contrary to our expectations, we observed considerable variation and no clear effect on denitrification rates, suggesting that *Geukensia*'s effects on marsh nitrogen cycling may be more variable than is commonly assumed (Kreeger et al. 2018). Studies of the influence of *Geukensia* on components of the marsh nitrogen cycle remain very limited. An additional challenge is that very few studies have quantified the effect of *Geukensia* on nitrogen-cycling processes in the absence of its *Spartina* mutualist (Fig. 1C), despite observations that *Geukensia* assemblages may persist in isolation (Watt et al. 2011). A greater number of full-factorial studies that address the effects of the species, alone and in combination, is needed to fully clarify the role of *Geukensia* in marsh nitrogen cycling, particularly within constructed and urban systems.

That the *Spartina-Geukensia* mutualism may vary in its effects depending on environmental context is a highly valuable piece of knowledge for land management and restoration projects. Although the mutualism could prove useful in restoring and maintaining naturally occurring salt marshes that receive little human influence, the mutualism may have less value and may become detrimental to long-term marsh stability in urban systems. More work is needed to identify variables

within the urban environment that could decrease the value of the mutualism to the growth of *Spartina* and the overall stability of the marsh ecosystem. Urban and constructed systems require greater attention in the future, especially given the vulnerability of these systems to threats from human activities and their immense value to coastal communities.

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