Research

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# Quantifying ecological filters: the relative impact of herbivory, neighbours, and sediment on an oligohaline marsh

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The objective of this experiment was to quantify the relative importance of herbivory, interactions with neighbours and sediment addition as filters in controlling the species present in an oligohaline marsh in southeastern Louisiana, USA. We planted 16 species of wetland plants in 3 × 3 m plots either inside or outside herbivore exclosures, with or without presence of established vegetation, and with or without added sediment. These species, representing 12 families and diverse morphologies, included herbaceous and woody plants. At the end of the growing season above- and below ground biomass were measured. In cleared plots (no neighbours) inside herbivore exclosures, 12 of the 16 species grew well, indicating that they could tolerate the physical conditions in the habitat. Competition significantly reduced the biomass of four of these species (*A. calamus, C. occidentalis, P. hemitomon, P. cordata*), suggesting that it is the strongest species-specific filter operating in the marsh. These results confirm the general consensus that competition from existing plants is the strongest filter operating in high biomass habitats, and further imply that competition has the potential to remove 33% of the species from the community. Facilitation occurred for one species, *R. corniculata.* Herbivory had the largest general effect of reducing biomass, as determined in the full ANOVA model, but on a species-specific basis, significantly reduced the biomass of only two species (*T. distichum, T. domingensis*). These results support the emerging view that herbivory is an important filter in coastal wetlands. Although several other studies have argued for the importance of sedimentation in controlling plant species composition in wetlands, we found no effect of sediment addition. Competition and herbivory appear to be two critical biological filters that control plant composition of coastal wetlands, and they must be considered in future studies and restoration efforts along the Gulf of Mexico.

A central challenge of ecology is the explanation and prediction of species diversity and composition of ecological communities (May 1981, Huston 1994). The framework of pools and filters provides one unifying approach to the assembly of ecological communities (Keddy 1992). It directs attention to the raw material of communities (the pool of species available), and to fundamental organizing forces (the ecological factors that sort this raw material into local communities). The growing literature on pools and filters suggests the potential of this framework for directing community ecology toward prediction of community outcomes (Pärtel et al. 1996, Weiher et al. 1996, Gough and Grace 1998, Weiher and Keddy 1999, Grace 2001, Butaye et al. 2002).

We might estimate the intensity and number of filters operating to create a community by comparing the total species pool with the number of species in the community. For example, consider a total species pool of 1000, and a target community with observed species richness of 20 to 70. The target community could be obtained if ten filters operate cumulatively, each strong enough to remove 30% of the species. Conversely, two filters each strong enough to remove 80% of the species could also produce the same community. Such an analysis might seem naïve, but consider the following example. The wetland flora of the Gulf Coastal Plain of the southeastern USA has a total species pool of around 1000 species (Godfrey and Wooten 1979, 1981). Two strong filters exist along the coast: high flooding frequency and salinity (Grace and Ford 1996, Gosselink et al. 1998, Howard and Mendelssohn 1999). They are likely to be strong because such a small proportion of the global flora has adapted to each of them (Sculthorpe 1967, Tomlinson 1986). Provisionally assigning a quantitative estimate of 0.8 to the strength of each of just two filters, we obtain a flora of around 40 species, which is the right order of magnitude for saline coastal marshes (Penfound and Hathaway 1938). If we remove the filter of salinity, leaving only high flooding frequency, then we can expect a flora closer to 200, which also is not unreasonable for freshwater coastal wetlands (Penfound and Hathaway 1938). Brackish marshes fall somewhere in between. The addition of other filters such as competition or herbivory would reduce expected community richness further.

Although we should not presume that we can yet assign quantitative values to filters – except, perhaps, in the rather special cases of species tolerant of salinity, flooding, or fire – this preliminary exploration illustrates the value of being able to measure (1) the number of filters and (2) their relative strength as tools for predicting the number of species in a local community, given knowledge of the total species pool.

Our experiment was conducted in an oligohaline marsh in southeastern Louisiana. It has a large total species pool, which we define as the wetland flora of the Gulf Coastal Plain (ca 1000 species; Godfrey and Wooten, 1979, 1981, USDA, NRCS 2004). We evaluate the importance of three potential filters (competition, herbivory, sedimentation) in producing a community with relatively low richness (ca 40 species). Using 16 wetland plant species that belong to the total species pool (i.e. occur in wetlands along the Gulf Coastal Plain), we asked:

1. Which, if any of these species, could tolerate the current physical conditions of this habitat? These conditions include flood duration, salinity, and other soil conditions, all of which are important environmental factors in wetlands (Keddy 2000, Mitsch and Gosselink 2000).
2. Are some of these species filtered out by one of three factors:
   a. competition from established plants? Competition has been shown to be an important factor in wetland plant communities, both specifically in Louisiana (Myers et al. 1995, Taylor et al. 1997) as well in many other wetland types (Twolan-Strutt and Keddy 1996, Keddy 2000, 2001).
   b. mammalian herbivores, primarily nutria? Nutria (*Myocastor coypus*), large semi-aquatic rodents native to South America, established wild populations in USA in the early 1940s (Lowery 1981). Herbivory by nutria has a significant effect on other wetland plant communities (Shaffer et al. 1992, Llewellyn and Shaffer 1993, Taylor and Grace 1995, Grace and Ford 1996, Taylor et al. 1997).
   c. lack of sedimentation from the Mississippi River? Due to the construction of levees, thousands of hectares of wetlands associated with the river no longer receive sediment from flood events that is necessary to maintain their elevation. The resulting subsidence of the wetlands (Boesch et al. 1994, Gosselink et al. 1998) has led to greater flood depths and duration (Thomson 2000). Sediment addition might promote growth by increasing elevation and adding nutrients (Gough et al. 1994, Keddy 2000, Mendelsshon and Kuhn 2003). Conversely, it has been shown that sedimentation can have a negative effect on wetland plant communities by decreasing species diversity through burial (Werner and Zedler 2002, Kercher and Zedler 2004).
3. What is the relative strength of these three filters in determining the wetland community composition?

## Material and methods

### Study area

The experiment was conducted at southeastern Louisiana University's Turtle Cove Experimental Marsh (30°17′N, 90°20′W, 0.3 m elevation) located within the 3369 ha Manchac Wildlife Management Area, about 50 km northwest of New Orleans, in southeastern Louisiana. This region was a bald cypress (*Taxodium distichum*) dominated swamp during the 1800s (Saucier 1963), but in the early 1900s the area was clear-cut (Heleniak and Dranguet 1987, Louisiana Department of Wildlife and Fisheries 2004a). Following logging, bald cypress regeneration was limited due to alterations in hydrology from logging practices and relative sea level rise (Platt 1988, Thomson 2000). Today the area is an oligohaline marsh (mean salinity: 1.2 ppt, LUMCON 2004). Vegetation cover of the community in the experimental area averages 86%, with 5.7 species per 3 × 3 m plot (T. McFalls, unpubl.). It is dominated by *Schoenoplectus americanus* (28%), *S. robustus* (10%) and *Sagittaria lancifolia* (8%) (means for n = 6 control plots in unfenced portion of study area, Geho 2004). Taxonomy follows ITIS (2006).

## Study species

Adult plants of 16 species, representing a diversity of morphologies and plant families associated with oligohaline marshes (Appendix 1), were transplanted into the study area. The 12 herbaceous species were perennial graminoids and forbs and included species with minimal rhizomes (*Juncus effusus*, *Peltandra virginica*, *Rhynchospora corniculata*), short rhizomes (*Acorus calamus*, *Cladium mariscoides*, *Pontederia cordata*) and extensive rhizomes (*Panicum hemitomon*, *Rhynchospora inundata*, *Saururus cernuus*, *Schoenoplectus americanus, Typha domingensis*). An *Eleocharis* species was also used, but did not survive long enough to be identified. The four woody plants included a shrub (*Cephalanthus occidentalis*) and three tree species (*Acer rubrum*, *Nyssa aquatica, Taxodium distichum*). All are marsh or swamp species found in the Gulf Coastal Plain and are therefore part of the total species pool.

Only *S. americanus* was observed in the study area prior to the experiment. There are no historical data for the community in our study area, but 15 years earlier a species list was compiled for the entire Manchac Wildlife Management Area based on a field survey (Platt 1988). Platt found nine of our study species – *P. hemitomon* (in only two widely scattered areas) and *P. cordata* (one site) were extremely rare, while *N. aquatica* and *T. distichum* were confined to elevated sites along spoil banks. *Acer rubrum*, *C. occidentalis*, *J. effusus, Eleocharis* spp. and *P. virginica* were also present. Another five species, *A. calamus*, *R. corniculata*, *R. inundata*, *S. cernuus* and *T. domingensis*, are found in the coastal zone of Louisiana and adjacent Mississippi (Penfound and Hathaway 1938, Chabreck 1972, Godfrey and Wooten 1979, 1981). Given the strong dispersal vectors in the coastal zone, including storms (Hackney and Bishop 1981) and inputs from nearby rivers (e.g. Tangipahoa River), the species above likely disperse to the site on occasion. *C. mariscoides* is not found in coastal Louisiana but is found elsewhere in the Gulf Coastal Plain in Florida and Texas.

Plants were obtained from a local grower, 50 km north of the study area. All herbaceous plants were grown in 1-liter containers and had good root and rhizome systems when they were acquired. Woody plants were obtained as 1-year old bare root seedlings.

## Experimental design

The experiment used a 2 × (2 × 2) × 16 split-split plot design (Steel and Torrie 1980), with three sizes of nested experimental plots. Herbivory treatments, the main plots (produced by 40 × 60 m herbivore exclosures) contained factorial combinations of competition removal and sediment addition (in 3 × 3 m sub-plots) while individual species were then transplanted into 50 × 50 cm sub-sub-plots (Fig. 1).

The main herbivory treatment, three 40 × 60 m fenced exclosures, was paired with three open areas to form blocks. We built the exclosures in January 2002 using a wood frame and vinyl coated wire fencing with a mesh size of 4 × 10 cm. The fence was 1.8 m tall with approximately 45 cm of fencing below ground. The primary herbivore excluded was nutria (*Myocaster*

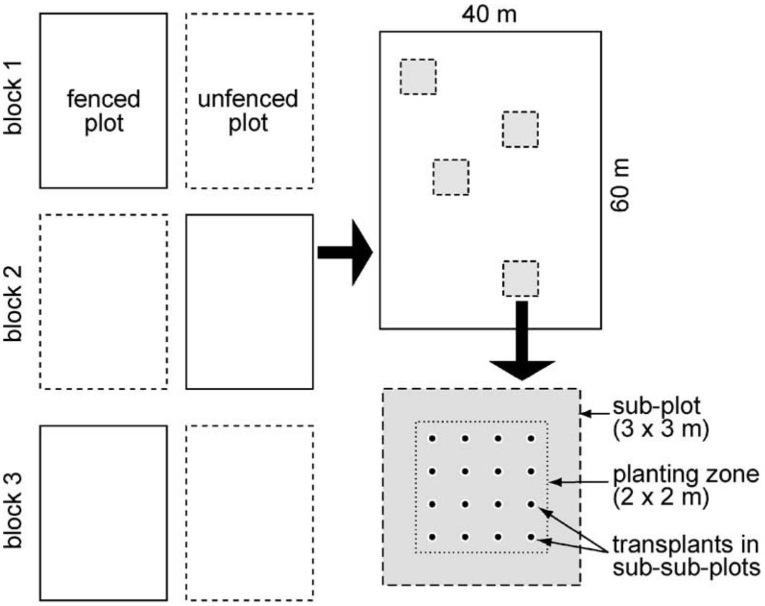

Fig. 1. Layout of experimental plots.

*coypus*) although additional excluded mammalian herbivores were muskrat (*Ondatra zibethicus*), wild boar (*Sus scrofa*) and swamp rabbit (*Sylvilagus aquaticus*).

The 3 × 3 m sub-plots received factorial combinations of neighbour removal and sediment addition. As such, sub-plots consisted of (1) natural vegetation controls, (2) clearings made by removing neighbours, (3) natural vegetation with a layer of added sediment, and (4) clearings made by removing neighbours with a layer of added sediment.

To remove neighbours, the aquatic-approved glyphosate herbicide (Rodeo) was applied to each entire 3 × 3 m sub-plot in mid-February and again at the beginning of March 2003 using a backpack sprayer, before the planting of test species. Entire sub-plots were carefully re-herbicided or weeded by hand throughout the experiment, taking care that no herbicide was applied to the test species.

Sediment was manually spread approximately 1 cm thick across each entire 3 × 3 m sub-plot one week after planting of test species. The sediment was obtained from excavations in an alluvial hardwood forest in southeastern Louisiana. It was analyzed by Louisiana State University's AgCenter Soil and Plant Test Laboratory for total soluble salts (242 ppm), calcium (874 ppm), magnesium (110 ppm), phosphorus (41.5 ppm), potassium (58.3 ppm), sodium (57.3 ppm), pH (4.84), and organic matter (2.3%) (McFalls 2004).

The 16 study species were transplanted on 15–16 March, 2003, after the herbicide application but before the sediment addition. They were randomly assigned to locations in a 4 × 4 grid within a 2 × 2 m planting zone in each sub-plot. Plants were therefore 50 cm from each another, with a 75 cm buffer between the outer plants and the edge of the subplot. Gloves were worn during planting to avoid unwanted herbivore effects (Hik et al. 2003). Herbaceous plants were removed from their containers and the root mass gently massaged to remove any excess soil. They were planted in holes dug to match their root volume and minimize disturbance to the existing vegetation. For woody plants, the roots were carefully inserted in a slit in the soil (made by a spade) to accommodate their normal branching pattern and to avoid bending them horizontally.

Plants that died within the first month of planting were replaced unless death could be directly linked to a treatment (e.g. herbivore activity). Plants not breaking dormancy within two months after transplanting were replaced with spare plants, with the exception of *R. corniculata* (no additional plants were available). In plots within exclosures and without neighbours, only 4% of the transplants without sediment and 2% with sediment died within the first month. Other than *Eleocharis* sp., which did not grow well in any treatment, only one individual (of *A. calamus*) from the remaining 15 species did not break dormancy within two months. Further, all plants of *S. americanus*, a prominent species in these wetlands, survived in all treatments.

## Data collection

Plants were harvested between September and November 2003, divided into below- and above ground biomass, and cleaned with water. Fine roots lost during cleaning were collected by hand, however some fine root loss was unavoidable. Biomass was dried in an oven at 70°C until a sub-sample (approximately 10% of bags in oven) remained at a constant weight, and then weighed. Plants that died after the first month were treated as having zero biomass, not as missing values. This decision was made for several reasons; the most important was that if all plants were killed by a treatment (e.g. herbivores, competition), this indicated a treatment effect, not a lack of information on the species response to the treatment. Voucher specimens are deposited in the Southeastern Louisiana University Herbarium for all species except *Eleocharis* sp.

## Statistical analyses

Total biomass was log-transformed and first analyzed as a single, full model ANOVA with a split-split plot design, having three error terms corresponding to each plot size (Steel and Torrie 1980). Block and exclosure effects were analyzed at the level of main plots in this ANOVA using the first error term. Factorial combinations of sediment and competition effects and their interactions were tested at the level of the sub-plots using the second error term. Plant species and their interactions were analyzed at the level of the sub-plots using the third error term. *Eleocharis* sp. was excluded from the analysis since none survived.

Individual ANOVAs were then completed for selected plant species. To select species, we plotted total biomass of individual species for treatment effects which were significant in the full model (exclosure, neighbour or sediment effects). Species with non-overlapping error bars between these treatments or their interactions were selected for individual analysis. Biomass data were log-transformed when necessary and outliers removed when necessary (0 to 2 outliers per species), as determined by graphical analysis of residuals. Distance from running water was used as a co-variable when applicable (determined by whether or not it reduced the error term). We used a Bonferroni protected alpha (0.05 divided by number of individual models run).

## Results

In the full model ANOVA (not shown, Geho 2004), herbivory was highly significant ($p < 0.0001$) indicating that herbivores consistently reduced overall biomass of species. The presence of neighbours also reduced overall biomass, although this effect was less significant ($p = 0.017$). The addition of sediment had no overall effect on biomass ($p = 0.765$), and was not considered further in the analysis of individual species below. The herbivory × neighbours interaction was highly significant ($p < 0.0001$), with a stronger effect in plots exposed to herbivores but without neighbours (Fig. 2). The lack of surrounding plants may have made our transplanted species more apparent to herbivores present outside the exclosures. Biomass differed strongly among the 15 plant species ($p < 0.0001$). Two other interactions were highly significant, herbivory × plant species ($p = 0.0001$), and neighbours × plant species ($p < 0.0001$), indicating that the effects of herbivory and neighbours differed among the 15 species (Fig. 3).

Ten species were analyzed individually with ANOVA. We did not individually analyze *A. rubrum, N. aquatica, P. virginica, S. cernuus* and *S. americanus* because of minimal or no response to both herbivory and neighbours. Three other species were analyzed individually, *C. mariscoides*, *J. effusus* and *R. inundata* but did not show any response to both herbivory or neighbours after Bonferroni correction. The exclusion of herbivores produced significant effects for two species: *T. domingensis* and *T. distichum* (Table 1, Fig. 3). For *T. domingensis* mean total biomass increased over an order of magnitude inside the exclosure relative to outside, while it doubled for *T. distichum*. Removal of neighbors had a significant effect on five species: *A. calamus, C. occidentalis, P. hemitomon, P. cordata,* and *R. corniculata* (Table 1). With the exception of *R. corniculata*, these species grew twice to over twenty times greater in plots without neighbours, indicating that competition with surrounding vegetation reduced growth. *R. corniculata* actually grew more poorly in plots without neighbours, indicating that surrounding vegetation may have facilitated its growth.

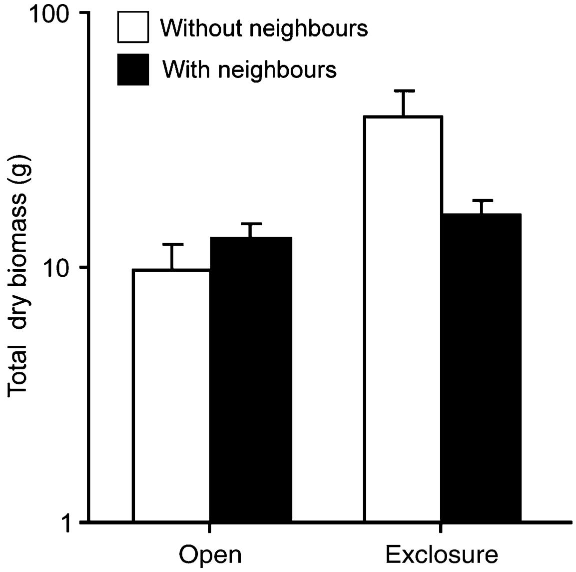

Fig. 2. Effects of exclosure and neighbour removal treatments on the total dry biomass across all species (mean + SE).

The interaction of neighbours and herbivory was significant for only two species, *C. occidentalis* and *T. distichum*, but was close to being significant for *J. effusus*, *R. corniculata, R. inundata* and *T. domingensis* (Table 1). For *C. occidentalis, T. distichum* and *T. domingensis* the interaction was due to a large increase in mean total biomass when plants in plots without neighbors were simultaneously protected from herbivores – that is there appeared to be a stronger effect of neighboring plants in plots without herbivores. It appears that *C. occidentalis*, *T. distichum* and probably *T. domingensis* can attain high standing crop in the study area only when both herbivores and competitors are excluded, or at least limited. Although *J. effusus*, *R. corniculata* and *R. inundata* did not grow much larger in exclosures, their biomass was reduced outside exclosures when no neighbours were present. The lack of surrounding plants may have made these latter three species more apparent to herbivores.

## Discussion

### Species pools

Kelt et al. (1995), studying the assembly of mammal communities, introduced a conceptual model with four types of species pools that can be related to the local community at any site, and which might be used to interpret our results (Fig. 4). At the largest scale, the "total species pool" contains all species within a large region that includes the site of interest. This region could be defined as having a similar climate and physiography as the site, such as a floristic region (Takhtajan 1986). We can further define this pool to include those species associated with the same general habitat type (e.g. grassland, wetland, forest) as the local community (Zobel 1997). Kelt et al. (1995) identified two subsets of the total species pool. The "geographical species pool" includes only those species whose geographic ranges encompass the study site. These species are present or capable of dispersing to the site, although they may not be able to survive there. The proximity of nearby populations, adaptations for propagule dispersal and the availability of dispersal vectors constrain the membership of the geographical species pool. The

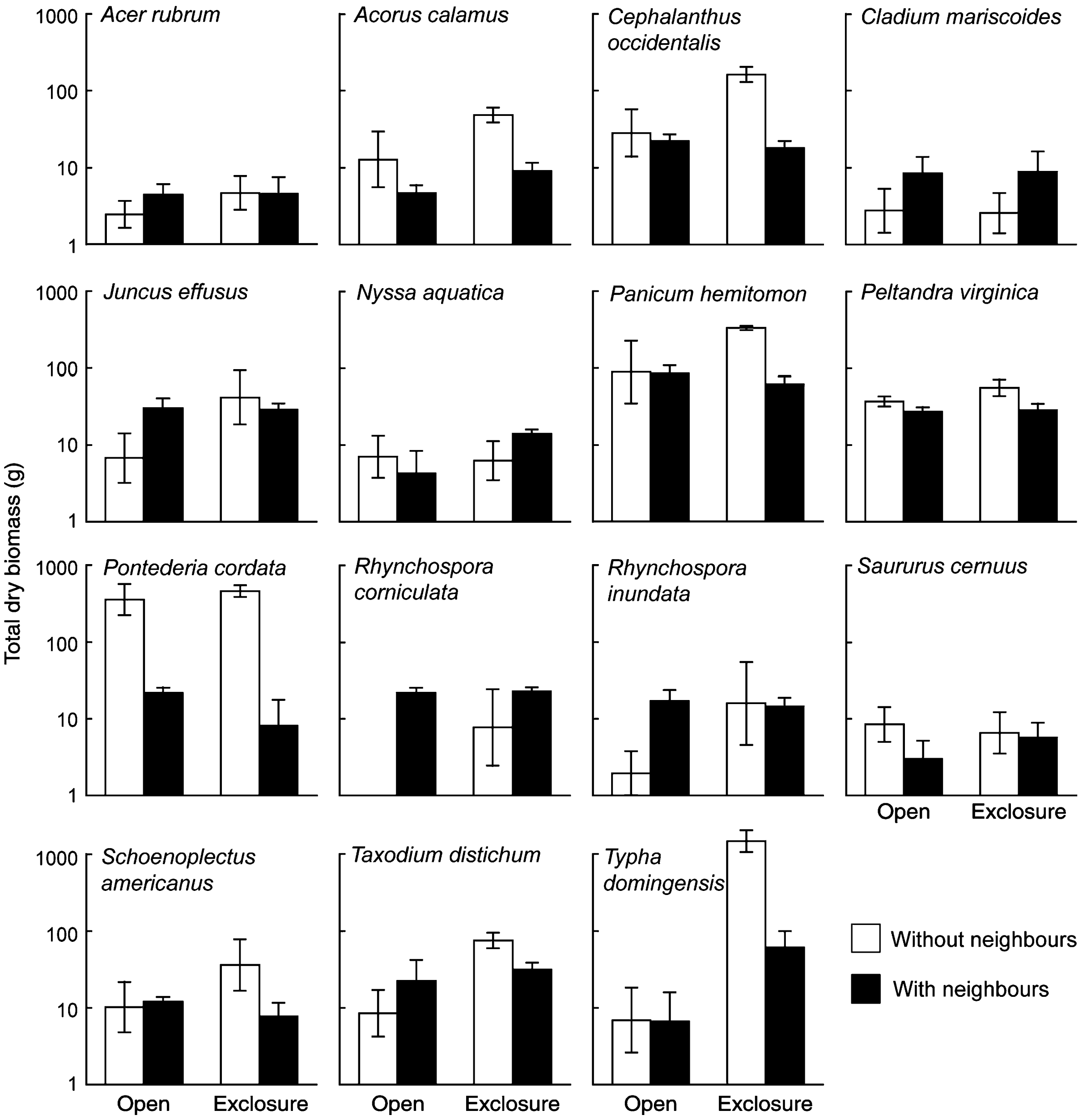

Fig. 3. Effects of exclosure and neighbour removal treatments on the total dry biomass of 15 wetland plant species (mean ± SE).

"habitat species pool" includes only those species whose habitat requirements include those in the site of interest. Abiotic filters at the site remove other species. The intersection of the geographical and habitat species pools is the "ecological species pool." These species can simultaneously reach the site and also grow there. For completeness, one can add a fifth level, the "community species pool," which consists of the actual species that occur in the community at the site (Pärtel et al. 1996, Pärtel and Zobel 1999, Butaye et al. 2002). Biotic interactions between species in the ecological species pool and stochastic processes limit the size of the community species pool.

*Eleocharis* sp., while part of the total species pool, did not survive in any treatment (Fig. 4). It is removed from the community by filters not examined here. It is not therefore part of the ecological species pool, but is part of the geographical species pool since several *Eleocharis* species occur nearby and could be expected to disperse here.

Table 1. Evaluation of the ANOVAs run for individual species for the main effects of herbivory, competition and their interaction. Significant p-values ($p < 0.005$, Bonferroni adjustment of $\alpha = 0.05$ to adjust for multiple comparisons) are bold. Empty cells indicate the interaction term was pooled into the error term ($F < 1.7$).

| Species | Herbivores (exclosure) | Nieghbours (herbicide) | Herbivores × neighbours |
|---|---|---|---|
| Acorus calamus | 0.1589 | **0.0003** | – |
| Cephalanthus occidentalis | 0.0283 | **0.0000** | **0.0044** |
| Cladium mariscoides | 0.9805 | 0.0293 | – |
| Juncus effusus | 0.055 | 0.2007 | 0.039 |
| Panicum hemitomon | 0.8656 | **0.0000** | 0.1041 |
| Pontederia cordata | 0.2044 | **0.0000** | – |
| Rhynchospora corniculata | 0.2848 | **0.0002** | 0.0086 |
| Rhynchospora inundata | 0.274 | 0.0362 | 0.0076 |
| Taxodium distichum | **0.0024** | 0.0931 | **0.0022** |
| Typha domingensis | **0.0000** | 0.0111 | 0.0126 |

Similarly, *A. rubrum*, *C. mariscoides,* and *N. aquatica* also do not appear to be able to tolerate the abiotic conditions of the habitat and are not part of the habitat species pool (Fig. 4). We draw this conclusion from the poor growth and relatively low survival (50–67%) of these species in the treatments without neighbours and without herbivores. (Ideally, of course, one would run such an experiment long enough to observe 100 percent mortality of all these species, but given both the number of species and number of treatments used, it was necessary to compromise by comparing relative performance). *Cladium mariscoides* does not occur in Louisiana but does occur in the coastal plain, and is therefore also excluded from the geographic species pools.

This left 12 species that were candidates for survival in the community and part of the ecological species pool, although they might be excluded from it if further study showed conditions were unsuitable for germination or seedling establishment. Even if germination were not possible, however, dispersal by fragments during storms might be sufficient to ensure colonization. Of these, four (*A. calamus, C. occidentalis, P. hemitomon, P. cordata*) are potentially excluded from the community species pool by competition with neighbours, and two (*T. domingensis, T. distichum*) are excluded by herbivory. *Schoenoplectus americanus* was a common species already in the study area (28% cover), and was included to confirm that our experimental treatments would allow a known member of the community to survive. No conclusions could be drawn for *J. effusus, P. virginica*, *R. inundata*, *R. corniculata* or *S. cernuus*. The causes could include untested filters, untested filter interactions, tested filters acting on other life cycle stages, and low seed dispersal.

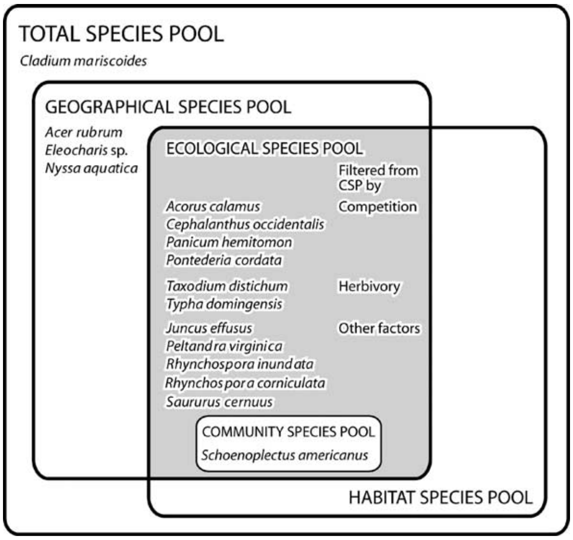

Fig. 4. Pool allocations and controlling filters for 16 plant species in relation to the plant community at Turtle Cove Experimental Marsh.

## Filters

Herbivory had the largest general effect of reducing biomass, as determined in the full ANOVA model, but on a species-specific basis, had only a modest impact (0.17, 2/12 species). As such, herbivores appear to be efficient at reducing biomass, but are somewhat general in their choice of food plant. This result supports an emerging view that herbivory can be an important filter and it has probably been dismissed too readily in the past. Although herbivory is known to have a significant impact on wetland vegetation, often reducing biomass by 30 to 60% (Lodge 1991, Keddy 2000), properly designed field exclosure experiments that 1) involve large, non-domestic herbivores at abundance levels found in nature and 2) examine the effects on individual plant species are rare. Two other nutria exclosure experiments conducted in different Louisiana marshes also support the importance of herbivory as a filter. Shaffer et al. (1992), using 50 × 40 m exclosures, found that herbivory by nutria reduced the cover of some plant species and species richness, and likely influenced the distribution of plant species. More recent work by Taylor and Grace (1995), using smaller exclosures, showed that herbivory by nutria reduced the biomass of dominant plant species such as *Panicum virgatum*, *Spartina patens* and *S. alterniflora*, but they were unable to detect any change in the number of plant species.

Interactions with neighbours had a lower general effect of reducing biomass than did herbivory, as determined in the general ANOVA model, but affected more species on a species-specific basis. Competition has a potential strength of 0.33 (4/12 species) as a filter acting on the ecological species pool to produce the community. Competition has been recognized as a fundamental force in structuring plant communities. Characterization of plant species traits to assess competitive ability and make predictions about how plant communities are assembled has received considerable attention (Grime 1973, 1979, Gaudet and Keddy 1988, Weiher and Keddy 1995, Keddy 2001). The growth of one species (*R. corniculata*) apparently was facilitated by surrounding vegetation, providing another example of the positive interactions that are possible in marshes (Bertness and Hacker 1994, Callaway and King 1996), as well as in other communities (Callaway and Walker 1997).

The interaction of neighbour removal and herbivory was also significant, illustrating that, in nature, filters may not simply be additive in their effects. A previous experiment at the same study site looking at the effects of salinity, flooding, and herbivory on *Sagittaria lancifolia* also found an interaction among all three filters (Grace and Ford 1996). The importance of biotic interactions in coastal wetlands may therefore be underestimated (Silliman and Bertness 2002, Keddy et al. in press).

The addition of sediment had no effect on any species in our experiment. In the long term, of course, lack of sedimentation combined with rising sea levels might lead to the loss of the entire marsh while increased sedimentation might allow invasion of woody species and reversion to swamp (Barras et al. 1994, Boesch et al. 1994, Reyes et al. 2000). In wetlands where natural sedimentation rates have been increased by land-use change, sediment as a filter may be significant. Field observation of patterns in species richness and sediment deposition (Werner and Zedler 2002) and experimental studies have shown that sediment can filter plants from communities, but sediment depths in these studies are much greater (van der Valk et al. 1983 (5–15 cm), Rybicki and Carter 1986 (10–30 cm), Allison 1995 (10 cm)) than ours (1 cm). This depth is typical of coastal deltas (Boesch et al. 1994). In experimental mesocosms containing 25 herbaceous plant species, Kercher and Zedler (2004) found that even a sediment depth of 5 cm was insufficient to have an effect on species richness. Walls et al. (2005) using one of our study species (*A. rubrum*) and a similar sediment depth (2 cm) found that sediment reduced biomass only when it was applied in conjunction with prolonged flooding (2 weeks). Such flooding durations do not occur in our study area.

## Experimental limitations

Our experiment examined 16 of roughly 1000 species in the total species pool as potential members of the community. In an effort to address this limitation, we deliberately used a diverse set of species, as judged by taxonomy (12 families), or morphology (graminoid, forb, tussock, rhizomatous herbs as well as trees and shrubs). We also biased the experiment toward transplant success by including species that a priori were thought to be candidate members of the community (potential members of community's ecological species pool, Appendix 1). That is, we did not introduce wetland species from wet pine savannas, or bottomland hardwoods. The genera and species we used are widespread and typical of coastal wetlands, enhancing the breadth of the application of the results.

The duration of the experiment was limited to one year; however, it took place in a region with a long growing season (260 days), and there was sufficient time for half the species (6 of the 12) that were judged able to tolerate the abiotic conditions to be significantly influenced by either neighbour removal or herbivory. Had the experiment continued a second season, more species would likely have been significantly affected by these two filters and the response of those already affected would likely have been greater, resulting in increased filter strengths. Filter strengths might also have been higher had we used plants in earlier stages of development, when their environmental tolerances are typically more restricted than those of adult plants (Steenbergh and Lowe 1969, van der Valk 1981, King and Grace 2000, Seliskar et al. 2004). We considered that species significantly affected by competition or herbivory were excluded from the community, and the ecological species pool. In fact, we observed only reduced biomass, not complete exclusion. Had the experiment run longer, we expect that these species would have become excluded eventually; however, low populations of affected species might still survive in the community, possibly as fugitive species colonizing empty habitat patches or in stands with poor herbivore access. Again, a longer term experiment would be required to address this possibility. The effects of occasional perturbations from hurricanes (e.g. salinity pulses, flooding, added sediment) would also have to be considered in such studies.

While we used just three filters, they were selected based upon knowledge of community composition (Penfound and Hathaway 1938, Gough and Grace 1998), the general factors most likely to influence wetland plant species (Keddy 2000, Mitsch and Gosselink 2000), and previous studies using similar species (Grace and Ford 1996, Howard and Mendelssohn 1999). Further, the experimental design allowed examination of interactions among them, resulting in seven filter combinations with three replicates of each. Greater sediment depths (see filter discussion), or placement earlier (prior to planting) or later (in middle of growing season) might have yielded different results (Rybicki and Carter 1986, Wang et al. 1994). Other filters that may be operating which we did not manipulate include insect herbivory (Menzel et al. 2006), salinity pulses (Gough and Grace 1998), and flood duration (Grace and Ford 1996). We were also unable to manipulate alligator density or hurricane intensity, although both of these may be important in this habitat.

### Implications for coastal restoration

Our study demonstrates that both competition and herbivory filter out species from the total species pool. This has important implications for the restoration of wetlands along the coast of the Gulf of Mexico. For establishing reasonable restoration objectives and enhancing the likelihood of success, it is important to have an understanding of the filters operating and the pool of species that could occupy the site. Success with species establishment could be increased with the use of filter-tolerant species. For example, it may not be cost-effective to plant species that are preferred foods for nutria (*T. distichum* and *T. domingensis*), or species that are intolerant of competition (e.g., *A. calamus, P. cordata*). Alternatively, restoration could be hastened by decreasing the strength of the filters. The intense herbivore filter, for example, might be weakened through economic incentives for nutria harvest (Louisiana Department of Wildlife and Fisheries 2004b), putting herbivore protection devices on plants (Myers et al. 1995), or increasing alligator populations (Keddy et al. in press). The value of our results for restoration will be enhanced by similar studies in different vegetation types, allowing quantitative comparisons among ecological communities.

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## Appendix 1

Species used in the experiment. Nomenclature follows ITIS (2006). Growth habit and wetland indicator status are from Godfrey and Wooten (1979, 1981) and USDA, NRCS (2004). OBL: obligate wetland species, almost always found in wetlands. FACW: facultative wetland species, usually found in wetlands. FAC: facultative species, equally likely in wetlands or non-wetlands.

| Species | Family | Growth habit | Wetland indicator status |
|---|---|---|---|
| Herbaceous plants | | | |
| *Acorus calamus* | Acoraceae | short-rhizomatous perennial forb | OBL |
| *Cladium mariscoides* | Cyperaceae | short-rhizomatous perennial graminoid | OBL |
| *Eleocharis sp.* | Cyperaceae | perennial graminoid | FACW |
| *Juncus effusus* | Juncaceae | bunch-forming perennial graminoid | FACW |
| *Panicum hemitomon* | Poaceae | rhizomatous perennial graminoid | FACW |
| Peltandra virginica | Araceae | bunch-forming perennial forb | OBL |
| *Pontederia cordata* | Pontederiaceae | short-rhizomatous perennial forb | OBL |
| *Rhynchospora corniculata* | Cyperaceae | bunch-forming perennial graminoid | OBL |
| *Rhynchospora inundata* | Cyperaceae | rhizomatous perennial graminoid | OBL |
| *Saururus cernuus* | Saururaceae | rhizomatous perenial forb | OBL |
| *Schoenoplectus americanus* | Cyperaceae | rhizomatous perennial graminoid | OBL |
| *Typha domingensis* | Typhaceae | rhizomatous perennial forb | OBL |
| Woody plants | | | |
| *Acer rubrum* | Aceraceae | deciduous tree | FAC |
| *Cephalanthus occidentalis* | Rubiaceae | deciduous shrub | OBL |
| *Nyssa aquatica* | Nyssaceae | deciduous tree | OBL |
| *Taxodium distichum* | Taxodiaceae | deciduous tree | OBL |