Effects of Dominant Species Removal on the Salt Marsh Wetland Ecosystem of Chongming Dongtan (Postprint)

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Abstract

Salt marsh ecosystems exhibit pronounced environmental gradients and relatively simple species composition, making them ideal model systems for investigating the relationship between biodiversity and ecosystem functioning. This study, conducted in the Chongming Dongtan salt marsh wetland, examined the effects of dominant species removal on plant community structure and benthic animal communities. The results demonstrated that: (1) The removal treatment exerted a highly significant effect exclusively on plant community ramet density ($P<0.01$). The divergence in species composition between removal and control plots diminished over time, indicating a gradual attenuation of treatment effects. (2) Benthic animal density in removal plots was consistently lower than in control plots, though these differences lacked statistical significance. (3) Salt marsh plant community characteristics exhibited strong associations with benthic animal communities, with plant density and canopy height showing highly significant correlations with benthic animal density. Following dominant species removal, plant community ramet density increased, the proportional representation of remaining species within the community rose, and sub-dominant species contributed substantially to community compensatory responses. Conversely, benthic animal community density declined, while trends in biomass and diversity indices diverged from density patterns. These findings indicate that biodiversity alterations influence the structure of both plant and benthic animal communities in salt marsh wetlands, potentially cascading to affect material cycling and energy flow processes.

Full Text

Preamble

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Effects of Dominant Species Removal on Salt Marsh Ecosystem in Chongming Dongtan

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Abstract

Salt marsh ecosystems exhibit steep environmental gradients and relatively simple species composition, making them ideal for studying biodiversity-ecosystem functioning (BEF) relationships. These ecosystems are among those most affected by anthropogenic activities, drawing attention to the urgent need for intensive protection and restoration. Current BEF research has focused primarily on grassland ecosystems rather than salt marshes, and understanding of how removal of specific species or functional groups influences salt marsh structure and function remains limited. This study examined the effects of dominant species removal on plant community structure and macrobenthic invertebrate communities in the Chongming Dongtan salt marsh of the Yangtze estuary, and analyzed relationships between plant community attributes and macrobenthic invertebrates using linear regression to provide a scientific basis for wetland restoration.

The major findings are as follows: (1) Community type, season, and their interaction had significant effects on ramet density and canopy height of manipulated plant communities ($p < 0.01$), whereas removal treatment had significant effects only on ramet density ($p < 0.01$). Ramet density in species removal treatments was higher than in controls, but the difference was not significant. Differences in species composition among different plant communities decreased over time, indicating that the effects of species removal treatment weakened gradually, likely because the system recovered from initial disturbance and became more similar to intact communities. (2) Community type and season significantly affected the density and Shannon-Weiner diversity index of macrobenthic invertebrate communities ($p < 0.01$), while community type and the interaction between season and community type significantly affected biomass ($p < 0.01$). The density of macrobenthic invertebrates in removal treatments was lower than in controls, but effects were not significant. The highest density, biomass, and Shannon-Weiner diversity index were observed in the *Spartina alterniflora-Scirpus mariqueter* community, mainly due to differences in environmental factors and plant species attributes among communities. (3) There was a close relationship between salt marsh vegetation and benthic communities.

Macroinvertebrate density was positively correlated with shoot density and negatively correlated with canopy height of the plant communities (all $p < 0.01$). After removal of dominant species, plant community ramet density and the proportion of remaining species increased, while subdominant species contributed greatly to the compensatory effect. Macroinvertebrate density decreased, but patterns of biomass and diversity index change differed from density patterns, probably due to influence of other environmental factors. These results indicate that biodiversity change could affect the structure of plant and macrobenthic invertebrate communities to different degrees, which may then alter biogeochemical cycling and energy flow processes. During our study, removal effects were relatively weak in the intertidal zone of Chongming Dongtan and diminished with time. Therefore, simple removal of dominant species may be insufficient to restore salt marsh ecosystem functions, and further management measures should be implemented to maintain long-term effects of habitat modification.

Keywords: Chongming Dongtan; macrobenthic invertebrate community; salt marsh community; species removal; wetland restoration

1. Study Area Description

Chongming Island is China' s third largest island and the world' s largest alluvial estuarine island, located at 31°26 -31°37 N, 121°46 -122°02 E. Chongming Dongtan, at the island' s easternmost tip, extends eastward to the East China Sea and is formed by sediment deposition from the Yangtze River, representing a typical estuarine coastal wetland. The area has a subtropical monsoon climate with mild temperatures throughout the year. The tidal regime is irregular semidiurnal, with two daily tidal cycles.

Before the introduction of the exotic species *Spartina alterniflora*, the intertidal zone had no higher plant distribution in the bare mudflat areas. *Scirpus mariqueter* and *Scirpus triqueter* primarily occurred in mid- and high-tide zones at elevations of 2.0–2.9 m. *Phragmites australis* was mainly distributed in the upper high-tide zone above 2.66 m elevation, where scattered patches of *Typha angustifolia*, *Imperata cylindrica*, *Carex scabrifolia*, *Suaeda glauca*, and *Juncus setchuensis* also occurred. After *S. alterniflora* introduction to Chongming Dongtan, it rapidly colonized and spread due to strong reproductive capacity, creating intense competition with native species, especially *S. mariqueter*. Two typical expansion patterns have formed: *S. alterniflora*-bare mudflat and *S. alterniflora*-*S. mariqueter*-bare mudflat. Currently, the high-tide zone is dominated by monocultures and mixed communities of *P. australis* and *S. alterniflora*, while the mid-tide zone features mixed communities of these two species with *S. mariqueter*. In northern Chongming Dongtan, *S. mariqueter* has been largely replaced by *S. alterniflora*, while Tuanjiesha in the south remains the main distribution area for *S. mariqueter* communities.

2. Research Methods

We selected four typical community types at Chongming Dongtan: *Phragmites australis-Spartina alterniflora* (Pa-Sa), *Phragmites australis-Spartina alterniflora-Scirpus mariqueter* (Pa-Sa-Sm), *Typha angustifolia-Phragmites australis-Carex scabrifolia* (Ta-Pa-Cs), and *Spartina alterniflora-Scirpus mariqueter* (Sa-Sm). For each community type, we randomly selected six 50 cm × 50 cm quadrats, with three designated as removal treatments and three as controls. In May and September 2015, we performed clipping treatments to remove above-ground parts of dominant species: *S. alterniflora* was removed from Pa-Sa, Pa-Sa-Sm, and Sa-Sm communities; *T. angustifolia* was removed from the Ta-Pa-Cs community. Bamboo poles were used to mark the four corners of each quadrat.

Plant community surveys were conducted in May and September 2015, recording total ramet density and canopy height within each quadrat. Below-ground biomass was obtained by coring sediment at quadrat boundaries with a 10 cm diameter corer to minimize community disturbance. Above-ground parts were only surveyed for background data in May. Plant material was oven-dried at 80°C to constant weight to determine above- and below-ground biomass.

Macrobenthic invertebrate samples were collected simultaneously with plant surveys following national standards (GB/T 12763-2007). Quantitative sampling was performed at quadrat boundaries using a 25 cm × 25 cm × 30 cm frame to reduce disturbance. Sediment samples were washed through a 1 mm mesh sieve, and macrobenthic animals were fixed in 75% ethanol solution for laboratory identification and weighing.

3. Data Analysis and Processing

We used repeated-measures ANOVA to test effects of plant community type and removal treatment on plant ramet density, canopy height, and below-ground biomass, as well as on macrobenthic invertebrate density, biomass, and diversity index. Tukey' s test was used for multiple comparisons. Linear regression analyzed relationships between plant community attributes and macrobenthic invertebrate density and diversity index. The Shannon-Weiner diversity index was calculated as $H = -\Sigma(Pi \times \ln Pi)$, where Pi is the proportion of the ith species. All statistical analyses used STATISTICA 10.0 with significance level at $p = 0.05$, and figures were produced using SigmaPlot 10.0.

1. Effects of Dominant Species Removal on Plant Communities

Removal treatment had highly significant effects on plant community ramet density ($p < 0.01$) but not on canopy height or below-ground biomass. In all communities, ramet density in removal groups was higher than in controls, though differences were not significant. Except for the Pa-Sa-Sm community

in spring 2015, where canopy height in removal groups was significantly lower than controls, no significant differences existed between treatments in other communities. Removal of dominant species caused some decrease in below-ground biomass, but not significantly.

Species composition changed over time. After *S. alterniflora* removal in Pa-Sa and Pa-Sa-Sm communities, the proportion of *P. australis* increased while *S. mariqueter* decreased, with greater magnitude in control groups. By autumn 2015, *S. mariqueter* had completely disappeared from the Pa-Sa community, while proportions of *P. australis* and *S. alterniflora* increased. In the Sa-Sm community, only *S. mariqueter* remained initially, but by spring 2015, proportions of *S. alterniflora* and *P. australis* increased while *S. mariqueter* decreased. In the Ta-Pa-Cs community, after *T. angustifolia* removal, the proportion of *C. scabrifolia* increased while *P. australis* decreased, whereas in controls, *P. australis* and *T. angustifolia* proportions increased while *C. scabrifolia* decreased. By autumn, differences between control and removal groups were smaller than in spring, with community composition closer to initial states, indicating that treatment effects weakened over time.

2. Effects of Dominant Species Removal on Macroinvertebrate Communities

Community type and season had highly significant effects on macrobenthic invertebrate density and Shannon-Weiner diversity index ($p < 0.01$), while community type and the interaction between season and community type significantly affected biomass ($p < 0.01$). Removal treatment effects were weak, with no significant differences in density, biomass, or diversity index between control and removal groups across all surveys. However, density in removal groups was consistently lower than in controls.

The Sa-Sm community supported significantly higher macroinvertebrate density than other communities in both seasons. In spring 2015, Sa-Sm community biomass was significantly higher than Pa-Sa and Pa-Sa-Sm communities, and by autumn, Sa-Sm biomass increased while Ta-Pa-Cs community biomass decreased. Shannon-Weiner diversity index declined from spring to autumn across all communities. These patterns were primarily caused by environmental differences, as the Sa-Sm community in lower intertidal zones experienced higher flooding frequency and greater tidal influence, providing abundant food and nutrients for benthic animals.

3. Correlations Between Macroinvertebrate Community Changes and Plant Community Characteristics

Before removal treatment in autumn 2015, macroinvertebrate density was positively correlated with plant ramet density ($r = 0.633$, $p < 0.01$) and negatively correlated with canopy height ($r = -0.325$, $p < 0.05$). After removal treatment, these relationships strengthened: density showed a highly significant positive

correlation with ramet density ($r = 0.718$, $p < 0.01$) and a highly significant negative correlation with canopy height ($r = -0.451$, $p < 0.01$). Biomass was positively correlated with plant community diversity index ($r = 0.261$, $p < 0.05$). These results demonstrate close linkages between salt marsh vegetation and benthic communities.

3. Discussion

3.1 Effects of Species Removal on Plant Communities

The reduction or loss of a species, particularly a dominant one, typically produces strong effects on remaining community members. Dominant species contribute substantially to community canopy height, coverage, and biomass, so their removal can significantly impact ecosystem function. Our results show that removal treatment significantly affected ramet density and altered species composition. After removing *S. alterniflora*, the proportion of *P. australis* increased in Pa-Sa and Pa-Sa-Sm communities, while *S. mariqueter* proportion increased in the Sa-Sm community. Similar to findings by Wardle and Tilman, removal of one or more functional groups promoted growth of remaining species in the short term. In relatively unstressed mid- and high-tide zones, species competitive ability is particularly important. Cyperaceae species like *S. mariqueter* and *C. scabrifolia* are often competitively inferior to larger species such as *T. angustifolia* and *S. alterniflora*. After dominant species removal, remaining species gain more space and resources, enhancing community stability.

The compensatory effect, where reduced abundance of one species or functional group allows others to increase and maintain ecosystem function, is crucial for stability. Subdominant species contributed substantially to this compensation: in Sa-Sm and Ta-Pa-Cs communities, subdominants *P. australis* and *C. scabrifolia* increased in proportion after removal. However, because only above-ground parts were removed, recovery ability of dominant species must be considered. *S. alterniflora* possesses well-developed aerenchyma in its root system and maintains vigorous activity after clipping, with different recovery capacities across seasons. Clipping can even promote increased ramet density by reducing shading and increasing available space, though this effect diminishes by the end of the growing season.

Biodiversity effects on ecosystem function are dynamic. In our study, removal treatment effects weakened over time as differences between control and removal groups decreased, likely because initial disturbances—including resource alteration and physical habitat modification—diminished as communities recovered. Lepš similarly noted that disturbance effects vary with temporal scale, and the physical perturbation from removal activities cannot be ignored.

3.2 Effects of Dominant Species Removal on Macroinvertebrate Communities

Macrobenthic invertebrates are secondary producers in estuarine ecosystems that play vital roles in metabolizing pollutants, food web structure, and material cycling. Salt marsh plants provide habitat and food resources, so plant community structure strongly influences benthic community composition and distribution. Species removal altered habitat conditions, affecting benthic density, biomass, and diversity, though removal treatment effects were weak. Density decreased in removal groups, while biomass and diversity patterns differed from density patterns, probably due to other environmental factors.

Studies by Larned and Kilroy found that river hydrological properties caused greater variation in benthic communities than removal treatments. Plant root architecture also matters: *P. australis* and *S. alterniflora* have coarse, complex root systems that inhibit benthic animals, while *S. mariqueter*' s fine roots and nutrient-rich rhizomes provide better feeding conditions, supporting higher benthic densities. In our study, benthic density, biomass, and diversity increased from high- to mid- and low-tide zones, with Sa-Sm community supporting the highest values due to lower elevation, higher flooding frequency, and greater tidal influence that supplied abundant food and nutrients.

3.3 Implications for Wetland Restoration

Wetland restoration typically prioritizes plant protection and recovery. While removing dominant plants can increase community density and canopy height in the short term, with remaining species proportions rising, single mowing measures have weak overall ecosystem effects that diminish over time. Effective restoration requires comprehensive consideration of different taxa responses and long-term community trajectories. Because wetland restoration is also strongly influenced by salinity, flooding duration, and other environmental factors, targeted management measures and appropriate habitat modifications are needed to improve restoration efficiency. Simple removal of dominant species may be insufficient to restore salt marsh ecosystem functions, and further management should be implemented to maintain long-term habitat modification effects.

Note: Figure translations are in progress. See original paper for figures.