



Biotic communities of freshwater marshes and mangroves in relation to saltwater incursions: implications for wetland regulation

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Abstract. An ecosystem-level study was conducted in the Guandu wetlands in subtropical coastal Taiwan to examine how salinity influences the abundance, diversity, and structure of biotic communities. We surveyed eight permanent study sites, spanning freshwater marshes, to the gate on the dyke, and mesohaline mangroves representing a gradient of the extent of saltwater incursions. Analyses of abiotic variables showed that salinity was the primary determining factor for discriminating habitat types in the wetlands, but communities differed in their sensitivity to salinity. The composition of plant and insect communities was most affected by the salinity gradient, suggesting the utility of these communities for ecological monitoring of saltwater incursions. However, spatial changes in communities at higher trophic levels, including macrobenthos, mollusks, fish, and birds, could not be explained simply by the salinity gradient. Instead, changes in these communities were more relevant to the composition of other biotic communities. Our results show that species richness and diversity of plant communities were higher in the marshes than in the mangroves. Nevertheless, insect communities censused in the mangroves had higher diversity, despite lower abundance and species richness. Macrobenthos surveyed in the mangroves showed higher biomass and number of taxa. Mollusks and fish were also more abundant at sites near the gate compared to the marsh sites. This suggests that maintaining a tidal flux by means of gate regulation is necessary for conserving the spatial heterogeneity and biodiversity of coastal wetlands.

Introduction

Coastal wetlands are widely distributed in estuaries throughout the world. Because of the tremendous volumes and varieties of inhabiting plants, they are regarded as being among the most productive ecosystems (Teal 1962; Day et al. 1989). They are known to provide food sources and diverse habitats for large numbers of resident and migratory organisms. Wetlands have also been shown to be very efficient in the removal of nutrients from agricultural runoff (Comín et al. 2001). Nevertheless, large-scale destruction and alteration of coastal wetlands have been reported worldwide (World Conservation Monitoring Centre 1992). Adverse effects of habitat alteration on biodiversity are a major cause for concern. An important

obstacle to effective management and conservation of biodiversity in coastal wetlands is a lack of knowledge of how environmental factors control communities within a given wetland.

The Guandu wetlands (25°7' N, 121°27' E) lie in the western part of the Guandu floodplain, which is located in an estuary at the confluence of the Tanshui and Keelung Rivers in subtropical northern Taiwan. In 1955, a dyke 3.5 m high was built across the northern part of this floodplain to create rice fields. This dyke interrupted the tidal flow of salt water and decreased soil salinity in the northern part, whose development has diverged from that of the southern part. While the southern part has continued to have a hydrological connection with salt water from the estuary of the Tanshui River, the northern part has been hydrologically separated from the salt water and is fed primarily by runoff from the surrounding catchment and by regional precipitation. As a result, the northern part has become freshwater marshes, but the southern part continues to be mangroves.

Later, ditches were constructed in the freshwater marshes to increase drainage rates. The marsh areas were subsequently connected to the adjacent mangroves again by a ditch with a semi-closed gate on the dyke. Since then, saltwater incursions into the marshes occur at daily high tide, creating a gradient of increasing salinity from the freshwater marshes to the gate on the dyke and to the mesohaline mangroves. These different habitat types provide the chance to study how salinity affects biotic communities in coastal wetlands.

Salinity has often been investigated as a constraint on the growth of oligohaline macrophytes (Howard and Mendelssohn 1999) and has been suggested to be an important factor affecting the vegetation of coastal wetlands (Colonnello and Medina 1998; Holm and Sasser 2001). Vegetation diversity in and around ponds is important in determining their usage by waterbirds (Froneman et al. 2001). Changes in vegetation may thus be assumed to affect their usage by insects, birds, and other animals in the wetlands. Effects of grazing by animals may inversely affect the community structure of plants and associated insects (Rambo and Faeth 1999). Nevertheless, the inland movement of salt water may enhance the immigration of estuarine fish (Lin and Shao 1999) and invertebrates into freshwater wetlands, and then may increase the biodiversity.

Other studies have determined the effect of periodic salinity incursions on plant compositions (Holm and Sasser 2001); however, few studies have elucidated changes in other communities in response to saltwater incursions in coastal wetlands. Management decisions regarding the regulation of gates on dykes and ditch maintenance can be mediated more clearly with an understanding of how salinity affects biotic communities in coastal wetlands. For example, adjustment of tidal flux and freshwater drainage can create proper salinities at a site. The success of restoration of coastal wetlands depends largely on maintaining proper salinities at a site.

This work is an integrated study on the biodiversity of the Guandu wetlands. The main purposes of this study were to undertake an ecosystem-level study to (1) understand whether saltwater incursions influence the abundance, diversity, and structure of biotic communities in the wetlands; (2) determine to what extent

saltwater incursions affect these communities; (3) assess the sensitivity of different communities in response to saltwater incursions; and (4) examine the correlation between community structures and abiotic variables.

Materials and methods

Study site

The Guandu wetlands (Figure 1) are composed of freshwater marshes (ca. 57 ha) and mangroves (ca. 55 ha), which have both been designated as wildlife reserve sites. According to an annual report of water quality at Guandu (Environmental Protection Administration 1998), values of water conductivity were low in the marshes (25–66 $\mu\text{mho}/\text{cm}$) and high in the mangroves (1210–1670 $\mu\text{mho}/\text{cm}$). The concentrations of dissolved inorganic nitrogen and phosphorus of the water column in the wetlands ranged between 2.1–12.1 and 0.05–1.48 mg/l, respectively. No clear spatial patterns in nutrient concentrations were observed.

The side of the wetlands near the Keelung River is subjected to a semi-diurnal tidal regime with a tidal amplitude of about 1–2 m. Water temperature of the river at Guandu ranged from 18 °C in February to 28 °C in July (Environmental Protection Administration 1998). Salinities of the overlying waters ranged from 7 to 12 practical salinity units (PSU) at low tide and might reach 25 PSU at high tide. Considerable changes in turbidity (5 to 26 nephelometric turbidity units, NTU) in the water column were observed, but there were no clear seasonal patterns.

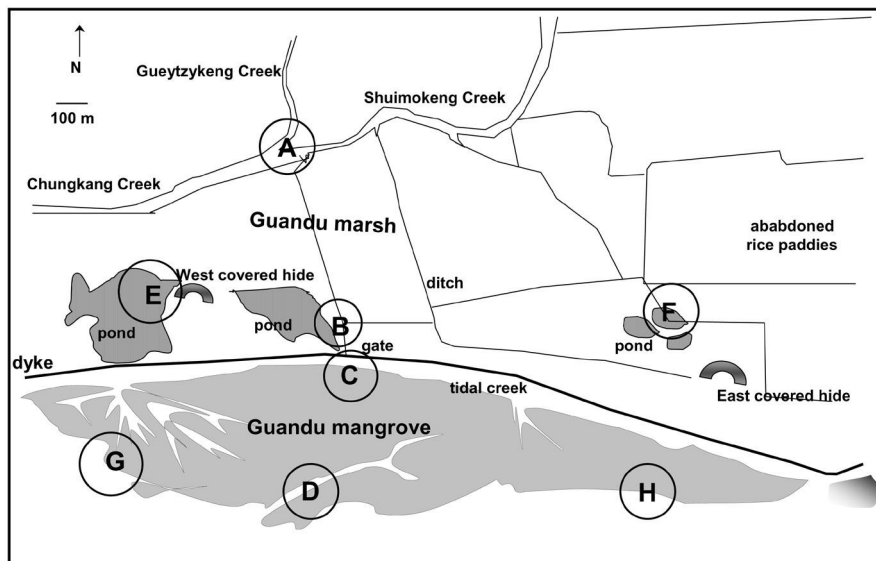


Figure 1. Study sites in the Guandu wetlands.

Biotic communities and abiotic variables of the Guandu wetlands were monitored at eight study sites (Figure 1). Site A was located at a freshwater fringe wetland at the confluence of Gueytykeng and Shuimokeng Creeks, northern Guandu wetlands. Sites E and F were located at freshwater fringe wetlands of shallow ponds (about 20 cm deep), which are outside the West Covered Hide and the East Covered Hide used for bird observation, respectively. Sites A, E, and F were in the freshwater marshes.

Site B was located at a ditch beside the gate in the marshes. Site C was located at a tidal creek beside the gate in the adjacent mangroves. These two sites were interconnected and separated by a semi-closed gate on the dyke. Outflowing water consisted of runoff from the surrounding catchment at low tide, and inflowing water was salt water from the estuary of Tanshui River at high tide.

Site D was located at a tidal creek opening onto the Keelung River in the southern part of the mangroves. Sites G and H were located in mangroves of fringe wetlands of the Keelung River. These sites were subject to daily tidal inundation by salt water from the estuary of the Tanshui River.

Abiotic variables

Abiotic variables of sediment, including pH, grain size, silt/clay content, soil salinity, sorting coefficient of sediment, total organic content (TOC), and total nitrogen (TN), were determined at the eight monitoring sites (Figure 1) for 1 year in October 1998, November 1998, January 1999, March 1999, May 1999, July 1999, and September 1999. For the collection of sediment, PVC corers with an inner diameter of 2.6 cm were pushed 2 cm deep into the sediment. One of the two sediment samples collected was used for analysis of granulometry, while the other was refrigerated and used for analysis of organic content. Granulometry of the sediment was determined following Buchanan and Kain (1971) and Hsieh (1995). The TOC content of the sediment, expressed as percent dry weight, was measured by adding 1 N HCl to remove inorganic carbon. The TOC and TN contents were then measured using an elemental analyzer (Perkin-Elmer EA 2400 Series II).

Biotic surveying and sampling

A variety of major communities of the Guandu wetlands, including plants, insects, mollusks, macrobenthos, fish, and birds were studied bimonthly at the eight monitoring sites (Figure 1) for 2 years from September 1998 to July 2000. The study periods of biotic communities and abiotic variables overlapped in the first year. During this period, they were studied as close in time as possible in the middle portion of January, March, May, July, September, and November. An exception is bird communities. Because bird fauna frequently varies with weather and time of day, surveys in this study were conducted in three 2-day series spread out in the early, middle, and late portion of each month in order to cover as much of the variation as possible.

A line-intercept method was used to survey the coverage area of plants in a community. Ten lines, each measuring 30 m long were surveyed at each site. These

lines were parallel to each other and separated from each other by 10 m. The fraction of the line covered by the canopy of a particular species was recorded as its estimated coverage.

Light traps and sticky paper were used for insect collection. A light trap was composed of an 8-W ultraviolet light-tube, a 12-V storage battery, and a water container measuring $18 \times 28 \times 10 \text{ cm}^3$ (width \times length \times depth). Within the container, 500 ml of a 1% sodium dodecyl sulfate solution was added for trapping insects. Sticky paper surrounded the light trap to catch those insects which landed around the light trap instead of dropping into the solution. Each light trap was supported on a wooded stand. These stands were 2.5 m high in the marshes and 4 m high in the mangroves, so that the light traps would be higher than the mangroves and marsh vegetation and above sea level at high tide. These light traps were set for a period of 12 h from dusk of the previous day to dawn of the following day. Collected insects were preserved in 75% alcohol for enumeration and identification in the laboratory.

PVC corers with an inner diameter of 10 cm were pushed about 20 cm deep into the sediment for macrobenthos collection. The contained sediment was sieved through a 0.5-mm screen. Specimens retained on the screen were relaxed in menthol and then fixed in 10% formalin. In the laboratory, macrobenthos were sorted, counted, and identified. Because the macrobenthos were so diverse, the species data were assembled into major taxonomic groups.

Mollusks were collected and quantified by a square sampling tool ($30 \times 30 \text{ cm}^2$), and samples were brought back to the laboratory for weighing and identification.

Fish were collected using cast nets. Each net measured 10 m^2 with a mesh size of 1 cm. Fish were collected at low and high tides (at about 12-h intervals), respectively, on consecutive days for 3 days on each sampling occasion to account for tidal changes. Five casts were thrown for each collection. Samples from the two tides were combined for later analyses. All collected fish were brought back to the laboratory where they were identified, counted, and weighed.

For bird surveys, the eight observation sites were visited in sequence on any field day, and this was repeated the next day. Field data included the survey point, the time of day, and the identity, number, and habitat used, as well as behavior of all birds seen. Altogether, these surveys provided data on the avifauna for six field days each month.

Abiotic data analyses

The eight study sites (Figure 1) were aggregated into three habitat types: freshwater marshes, the vicinity of the gate, and mangroves. Differences in abiotic variables among these three habitats were detected using Kruskal–Wallis tests. In order to reveal between-site relationships, abiotic variables for all sites were standardized, and normalized Euclidean distances were applied to produce a dissimilarity matrix. This matrix was then used to construct a two-dimensional MDS (non-metric multidimensional scaling techniques) plot using the PRIMER (v. 5.2.2) computer

package (Clarke and Gorley 2001). Stress values <0.2 indicate that a two-dimensional MDS plot gives a usable summary of site relationships of abiotic variables.

Biotic data analyses

Species abundance data were used in this study for most biotic communities except plants and macrobenthos. Area cover data were used for plants, but biomass data were used for macrobenthos. In practice, multivariate analyses of abundance and biomass data give remarkably similar results (Clarke and Warwick 1994). In order to reveal spatial changes in communities caused by saltwater incursions, the data from 2 years at each site were pooled for each community for multivariate analyses using PRIMER.

The Diverse routine in PRIMER was used to calculate Margalef's species richness and Shannon–Wiener diversity indices for each community at each site except those of macrobenthos. Prior to multivariate analyses, data of insects and mollusks were $\log_{10}(n+1)$ -transformed, and data of birds, macrobenthos, and fish were 4th root-transformed. The Bray–Curtis coefficient was applied to produce a similarity matrix for each community between any two sites according to the relative abundance of each species or taxonomic group. The data matrix was then used to construct a plot of MDS ordination. When values of abundance, species richness, and diversity, represented by circles of differing sizes, are superimposed on the MDS ordination, it gives a graphic demonstration of the correlation between spatial changes in a community and these community attributes.

The ANOSIM (analysis of similarities) routine was used to determine whether the effect of saltwater incursions on the composition of each community was significant by comparing the observed statistics to its permutation distribution for the absence of differences (Clarke and Warwick 1994). ANOSIM is a non-parametric analog to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. If the results of the global test indicated significance at the 0.05 probability level, the pairwise R values were used to determine their separation due to the limited number of possible permutations. Communities were well separated when $R > 0.75$, overlapped but clearly different when $R > 0.5$, and barely separable at all when $R < 0.25$ (Clarke and Gorley 2001). Similarity of percentages (SIMPER) was employed to reveal the most representative species or taxonomic group for the communities within a habitat type. The RELATE routine was used to measure how closely related these communities and abiotic variables were, for a matching set of two similarity matrices, by calculating a rank correlation coefficient (ρ statistic) between all elements of their respective similarity matrices. This routine used a Monte Carlo permutation procedure to recompute the distribution of statistics derived from sample relationships under permutations for the absence of a relation. The significance level was then determined by referring the observed statistic to the permutation distribution (Clarke and Warwick 1994). The ρ statistic itself can be regarded as a similarity measure, so the triangular matrix of ρ statistics between all pairs of ordinations can be re-entered in the MDS routine by using the second-stage

Table 1. Abiotic variables in sediments (mean \pm SD, $n = 5-7$) of the Guandu wetlands recorded bimonthly from September 1998 to September 1999.

Site	Marsh			Gate			Mangrove			Test
	A	E	F	B	C	D	G	H		
Grain size (mm)	0.024 \pm 0.011	0.063 \pm 0.065	0.040 \pm 0.029	0.030 \pm 0.017	0.029 \pm 0.020	0.031 \pm 0.014	0.025 \pm 0.007	0.028 \pm 0.015	NS	
Silt/clay content (%)	71 \pm 17	59 \pm 20	67 \pm 19	72 \pm 13	64 \pm 27	75 \pm 17	71 \pm 13	80 \pm 16	NS	
Soil salinity (PSU)	2.8 \pm 2.0	5.2 \pm 3.9	7.3 \pm 3.7	12.8 \pm 8.8	10.4 \pm 5.8	13.5 \pm 8.5	14.5 \pm 7.3	12.4 \pm 10.1	**	
Sorting coefficient	2.1 \pm 0.4	2.6 \pm 0.8	2.0 \pm 0.4	2.0 \pm 0.2	1.7 \pm 0.6	2.1 \pm 0.9	1.9 \pm 0.5	1.7 \pm 0.6	*	
TOC (%)	3.4 \pm 0.1	2.5 \pm 0.3	3.7 \pm 0.3	3.1 \pm 0.6	2.2 \pm 0.6	2.1 \pm 0.1	1.9 \pm 0.3	2.9 \pm 1.2	**	
TN (%)	0.27 \pm 0.01	0.21 \pm 0.03	0.26 \pm 0.01	0.31 \pm 0.10	0.17 \pm 0.04	0.16 \pm 0.01	0.14 \pm 0.02	0.26 \pm 0.12	*	

Kruskal-Wallis tests were used to detect differences among the three habitats; NS – not significant; * $P < 0.05$; ** $P < 0.01$. TOC – total organic carbon; TN – total nitrogen.

MDS analysis in PRIMER. This gives a succinct summary of the relationships among various biotic and abiotic ordinations in a two-dimensional picture.

Results

Abiotic variables

Three habitat types were differentiated by different extents of saltwater incursion according to measurements of soil salinity (Table 1). MDS plots of abiotic variables of all study sites showed that there was a clear underlying gradient, corresponding to an increasing level of salinity from the marsh sites, to the gate, to the mangrove sites (Figure 2). These results suggest that salinity is the primary determinant of different habitat types in the Guandu wetlands. A Kruskal–Wallis test confirmed these differences in salinity. Values of soil salinity significantly differed among the three habitats.

In addition to salinity, there were significant differences in other abiotic measurements among these habitats (Table 1). Sorting coefficients of sediment were significantly lower at the mangrove sites and the sites near the gate than at the marsh sites ($P < 0.05$). TOC and TN contents of sediment at the mangrove sites were significantly lower than at other sites ($P < 0.05$).

Community changes

In total, 154 plant species belonging to 43 families were recorded in the Guandu wetlands during the study period. The composition of plant communities closely matched the salinity gradient in the wetlands, suggesting profound influences of salinity on the vegetation (Figure 3a). One-way ANOSIM indicated that plant

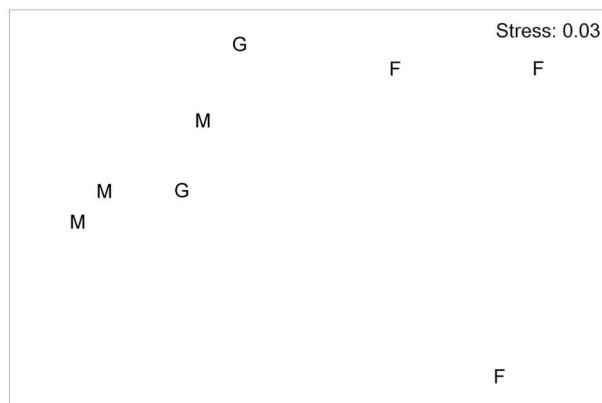


Figure 2. MDS ordination of normalized Euclidean distances from standardized abiotic sediment data for the study sites in the Guandu wetlands (F = freshwater marshes, G = gate, M = mangroves).

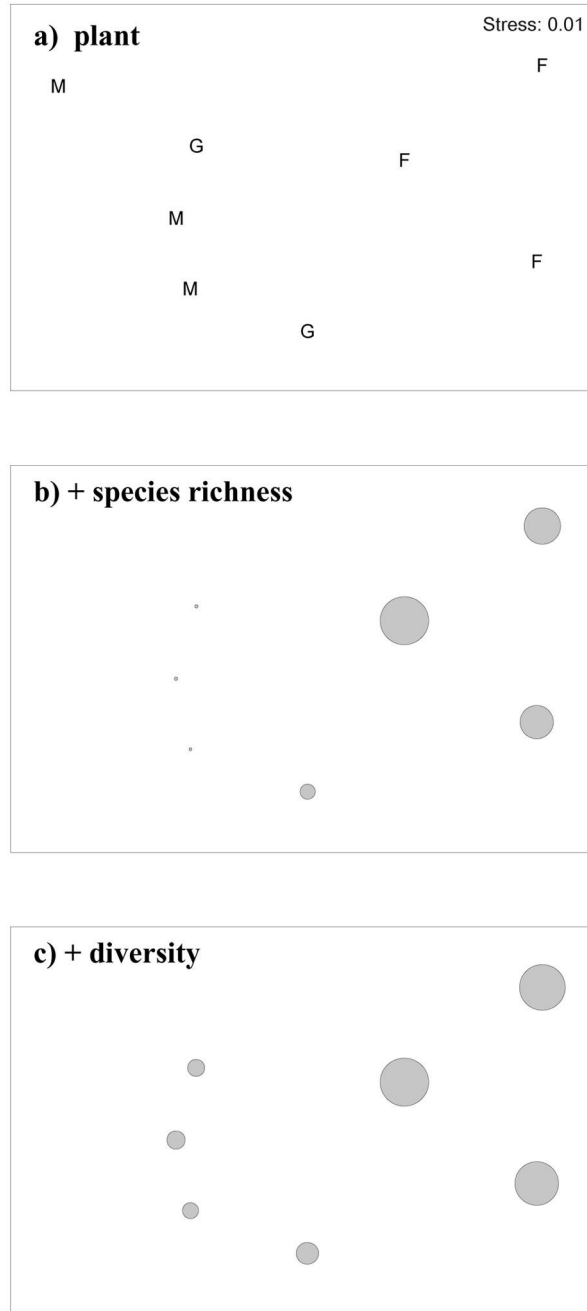


Figure 3. MDS ordination of Bray–Curtis similarities from (a) plant cover data for the study sites in the Guandu wetlands (F = freshwater marshes, G = gate, M = mangroves); (b) the same MDS but with superimposed circles of increasing size with increasing species richness, and (c) increasing diversity.

Table 2. Summary of the results from one-way ANOSIM statistic (R) for global tests for differences between study sites and a summary of the pairwise tests.

Biotic community	Site	R	P	Result
Plant	Global	0.80	0.007	*
	Marsh vs. gate	0.78	0.250	*
	Marsh vs. mangrove	0.94	0.029	*
	Gate vs. mangrove	0.42	0.400	NS
Insect	Global	0.61	0.021	*
	Marsh vs. gate	-0.33	0.750	NS
	Marsh vs. mangrove	0.76	0.029	*
	Gate vs. mangrove	0.75	0.200	*
Macrobenthos	Global	0.52	0.036	*
	Marsh vs. gate	-0.33	1.000	NS
	Marsh vs. mangrove	0.75	0.029	*
	Gate vs. mangrove	0.75	0.200	*
Mollusk	Global	1.00	0.010	*
	Marsh vs. gate	1.00	0.100	*
	Marsh vs. mangrove	1.00	0.100	*
	Gate vs. mangrove	1.00	0.330	*
Fish	Global	0.73	0.004	*
	Marsh vs. gate	0.82	0.100	*
	Marsh vs. mangrove	0.75	0.100	*
	Gate vs. mangrove	0.67	0.100	NS
Bird	Global	0.59	0.007	*
	Marsh vs. gate	0.67	0.100	NS
	Marsh vs. mangrove	0.30	0.100	NS
	Gate vs. mangrove	1.00	0.100	*

If the results of the global test indicated significance (*) at $P = 0.05$, then pairwise R values were used for their separation due to the limited possible permutations. * Indicates that two assemblages were well separated when the pairwise $R > 0.75$; NS – not significant.

communities at the marsh sites were well separated from those in mangroves and near the gate (Table 2). SIMPER revealed that the marshes were consistently dominated by *Commelina diffusa*, *Panicum repens*, and *Alternanthera philoxeroides*. However, *Phragmites communis* and *Kandelia candel* were dominant at sites near the gate and in the mangroves, respectively. Superimposition of values of species richness and diversity on the MDS ordination of plant communities indicates that species richness and diversity of plant communities in the mangroves were relatively low (Figure 3b and c).

In total, 556 insect species belonging to 120 families were collected in the Guandu wetlands during the study period. Effects of salinity on insect communities were also evident. The MDS ordination revealed that insect communities in the marshes were far from those in the mangroves (Figure 4a). One-way ANOSIM confirmed this difference, but communities at the marsh sites were barely separable from those near the gate (Table 2). SIMPER identified *Chironomus* sp., *Culicoidini* sp., and *Cricotopus (Isocladius) sylvestris* to be the most representative insect species in the mangroves, but *Staphylinus* sp., *Chironomus* sp., Pyralids, *Psychoda* sp., and *Forcipomyia* sp. to be consistently dominant in the communities near the

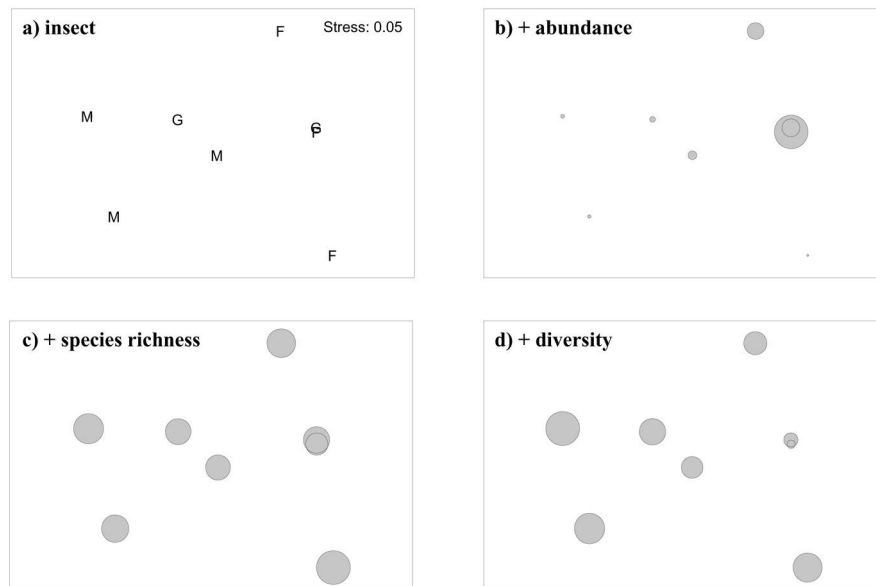


Figure 4. MDS ordination of Bray-Curtis similarities from (a) $\log_{10}(n + 1)$ -transformed insect abundance data for the study sites in the Guandu wetlands (F = freshwater marsh, G = gate, M = mangrove); (b) with superimposed circles of increasing size with increasing abundance, (c) increasing species richness, and (d) increasing diversity.

gate and in the marshes. Superimposition of community attributes on the MDS ordination suggests that abundance and species richness of insect communities in the mangroves were relatively low (Figure 4b and c), but the diversity was high (Figure 4d).

In total, 22 macrobenthic species were identified in the Guandu wetlands during the study period. Nine taxonomic groups were aggregated for multivariate analyses, including oligochaetes, polychaetes, snails, amphipods, shrimps, crabs, insects, sea anemones, and leeches. Macrobenthic communities were also separable between the mangrove sites and the marsh sites on the horizontal axis (Figure 5a). This separation was significant and confirmed by one-way ANOSIM (Table 2). But the two sites near the gate were also separable on the horizontal axis (Figure 5a). SIMPER indicated that the most representative taxa at the marsh sites were snails, insects, and oligochaetes, but the consistently dominant taxa at the mangrove sites were polychaetes and snails. Superimposition of community attributes on the MDS ordination revealed that the macrobenthic communities at sites in the mangroves and near the gate generally had large biomass (Figure 5b) and a high number of taxa (Figure 5c).

In total, 43 mollusk species belonging to 19 families were collected in the wetlands during the study period. There were three distinct groups on the MDS ordination of mollusk communities, but they did not correspond to the salinity gradient in the wetlands (Figure 6a). One-way ANOSIM confirmed that these

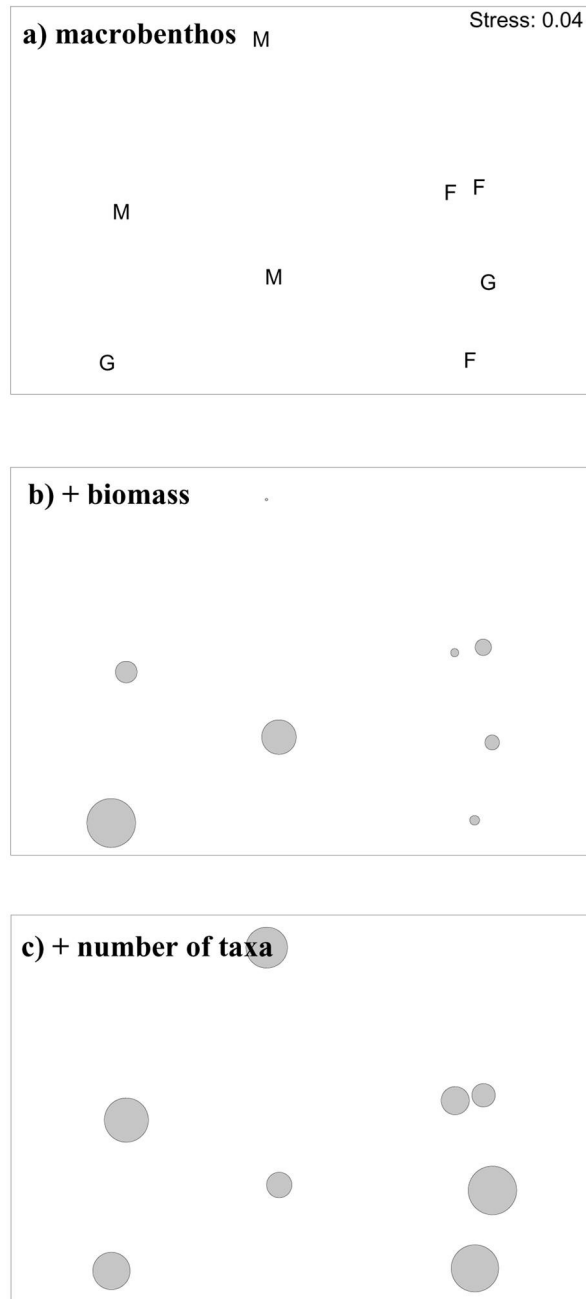


Figure 5. MDS ordination of Bray–Curtis similarities from (a) 4th root-transformed macrobenthic biomass data for the study sites in the Guandu wetlands (F = freshwater marshes, G = gate, M = mangroves); (b) with superimposed circles of increasing size with increasing biomass, and (c) increasing number of taxa.

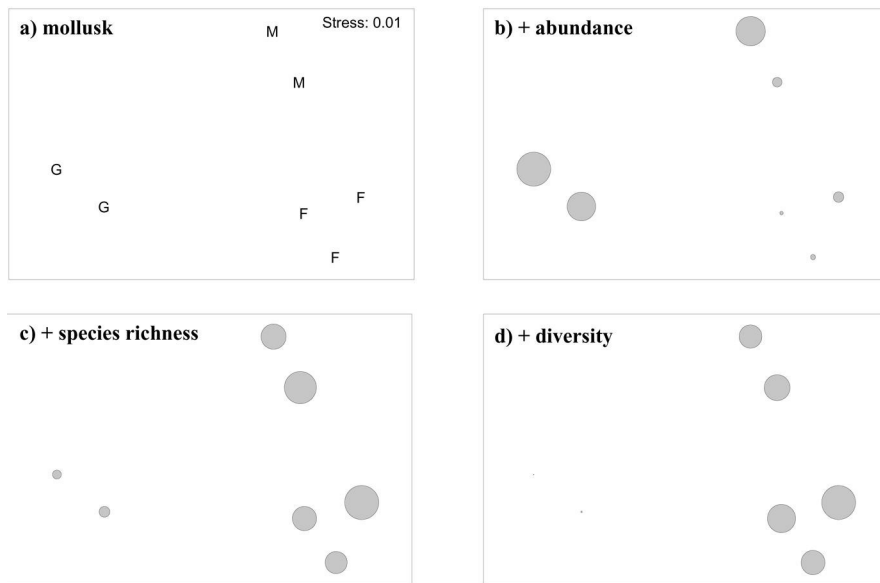


Figure 6. MDS ordination of Bray–Curtis similarities from (a) $\log_{10}(n + 1)$ -transformed mollusk abundance data for study sites in the Guandu wetlands (F = freshwater marsh, G = gate, M = mangrove); (b) with superimposed circles of increasing size with increasing abundance, (c) increasing species richness, and (d) increasing diversity.

mollusk communities differed significantly (Table 2). SIMPER identified the most representative species at marsh sites to be *Thiara tuberculata* and *Pomacea canaliculata*, that at the sites near the gate to be *Mytilopsis sallei*, but those at the mangrove sites to be *T. riqueti*, *T. tuberculata*, and *Assiminea* sp. Superimposition of community attributes on MDS ordination revealed that mollusk communities at the sites near the gate were relatively more abundant (Figure 6b), but less diverse (Figure 6c and d). No distinct differences in species richness or diversity of mollusk communities between the marshes and the mangroves were observed.

In total, 38 fish species belonging to 21 families were caught in the wetlands during the study period. Like mollusk communities, MDS ordination showed that there were three distinct groups, corresponding to the three different habitat types (Figure 7a). Despite high variation within each group, differences among groups were confirmed by one-way ANOSIM (Table 2). SIMPER indicated that *Oreochromis* hybrids were the most representative species at the marsh sites, but *Liza macrolepis* and *Oreochromis* hybrids were typical at sites in the mangroves and near the gate. No clear trend of changes in abundance (Figure 7b), species richness (Figure 7c), or diversity (Figure 7d) were observed among these groups, but it appears that abundance and species richness of fish communities were relatively higher at the sites near the gate.

In total, 119 bird species were observed in the wetlands during the study period. No distinct pattern occurred with MDS ordination of bird communities, suggesting

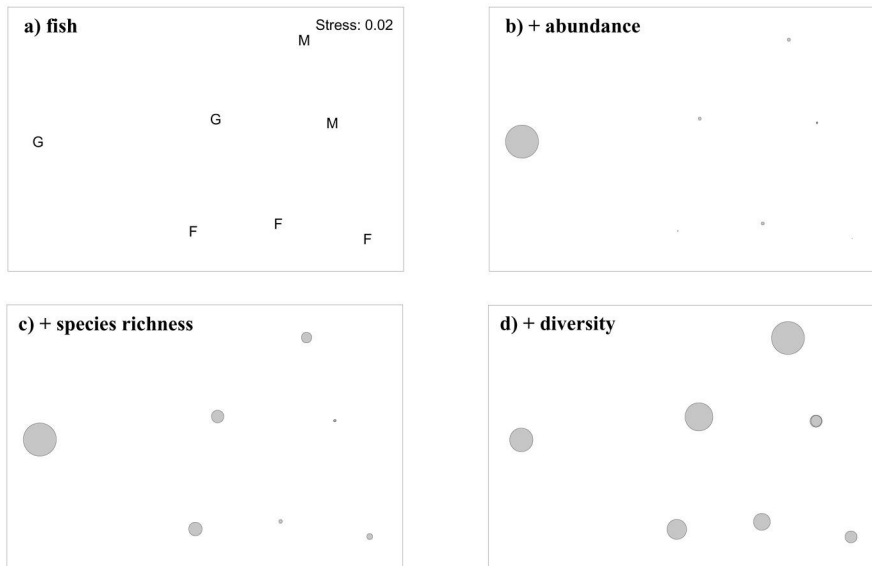


Figure 7. MDS ordination of Bray-Curtis similarities from (a) 4th root-transformed fish abundance data for study sites in the Guandu wetlands (F = freshwater marsh, G = gate, M = mangrove); (b) with superimposed circles of increasing size with increasing abundance, (c) increasing species richness, and (d) increasing diversity.

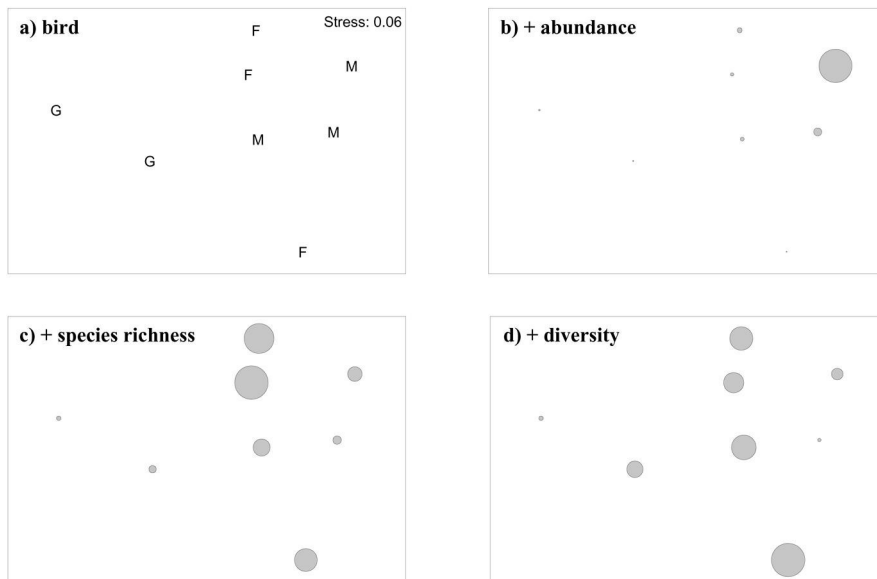


Figure 8. MDS ordination of Bray-Curtis similarities from (a) 4th root-transformed bird abundance data for study sites in the Guandu wetlands (F = freshwater marsh, G = gate, M = mangrove); (b) with superimposed circles of increasing size with increasing abundance, (c) increasing species richness, and (d) increasing diversity.

Table 3. Summary of significance tests from the RELATE statistic (R) for matching between biotic communities and abiotic variables and between abiotic and biotic communities in the Guandu wetlands.

		Sediment	Plant	Insect	Macrobenthos	Mollusk	Fish
Plant	R	0.636*					
	P	0.20%					
Insect	R	0.573*	0.559*				
	P	0.10%	0.30%				
Macrobenthos	R	0.018	0.121	0.217			
	P	25.5%	13.0%	6.70%			
Mollusk	R	-0.058	-0.083	-0.161	0.204		
	P	38.2%	49.8%	65.8%	10.8%		
Fish	R	0.138	0.151	-0.128	0.210	0.386*	
	P	19.4%	12.3%	56.1%	7.90%	1.80%	
Bird	R	-0.095	-0.012	-0.167	-0.205	0.615*	0.294
	P	46.8%	34.9%	63.9%	74.0%	0.90%	5.80%

Number of permutations = 999; * Indicates a significant correlation at $P < 5\%$.



Figure 9. MDS ordination of biotic communities (plant, insect, macrobenthos, mollusk, fish, and bird) and abiotic variables (sediment) in the Guandu wetlands by using second-stage MDS analysis.

that spatial changes in bird communities could not be explained simply by differential salinities in the wetlands (Figure 8a). One-way ANOSIM also showed that bird communities at the mangrove sites were barely separable from those at the marsh sites (Table 2). Superimposition of community attributes on the MDS ordination revealed that bird communities at mangrove sites were abundant (mainly waterbirds, Figure 8b), but species richness (Figure 8c) and diversity (Figure 8d) of bird community were relatively high at the marsh sites due to occurrence of land birds (dominated in number by *Passer montanus*, *Lonchura punctulata*, and *Pycnonotus*

sinensis) and waterbirds (dominated in number by *Anas crecca*, *Bubulcus ibis*, and *Ardea cinerea*) in the marshes.

Correlation between communities and environments

Soil salinity of the study sites appears to increase monotonically along the main axis of the MDS plot (Figure 2). This suggests that saltwater incursions are the dominant controlling processes for different habitat types in the Guandu wetlands. However, the RELATE routine demonstrated that only spatial changes in plant and insect communities were significantly correlated with the spatial patterns of study sites based on abiotic variables (Table 3). Spatial changes in fish and bird communities were significantly correlated with changes in mollusk communities, rather than with abiotic variables.

A 'second-stage' MDS ordination of interrelationships between biotic communities and abiotic variables (Figure 9) also revealed that changes in plant and insect communities were close to that of abiotic sediment variables, suggesting a high correlation. However, community changes in other communities, including macrobenthos, mollusks, fish, and birds were far distant from the abiotic variables, suggesting that spatial changes of these communities at higher trophic levels could not be explained simply by abiotic variables in the wetlands. Instead, these communities were closely intercorrelated.

Discussion

Measurement of changes in biotic communities is widely used as an ecological indicator for the detection and monitoring of changing environments induced by natural or anthropogenic disturbance. Such studies are almost always a compromise among scientific ideals, public interests, and financial and time constraints. Usually, only one component of the biota is examined, and it is assumed that the performance of this component is a general reflection of environmental conditions. For example, changes in bird communities were used for regional monitoring of forest condition (Canterbury et al. 2000); vegetation changes were documented for the influences of dam construction in an estuary (Colonnello and Medina 1998); and changes in the taxonomic grouping of sublittoral meiofauna were used for monitoring increasing levels of hydrocarbons and metals along a pollution gradient (Heip et al. 1988). There are very few cases in which more than one component of the biota has been examined in ecological monitoring studies. The choice of which component to examine in any particular study is usually made on the basis of available taxonomic expertise and research interests rather than on any objective decision about the practical and conceptual advantages and disadvantages of these components for the problem at hand (Warwick 1993). This study demonstrates that different kinds of communities might respond differently to saltwater incursions in coastal wetlands.

Although our results demonstrate that salinity is the primary determining factor for discriminating habitat types in the Guandu wetlands, not all communities

responded in the same way. Responses of communities to the salinity gradient were more complex than we expected. Our results clearly show that the sensitivities to salinity of various taxa in the wetlands differ. The positions of biotic communities relative to environmental variables of sediment in the second-stage MDS ordination (Figure 9) can be used as measures of sensitivity to salinity. Obviously, the composition of plant and insect communities was most affected by the salinity gradient. Although we cannot exclude the possibility that the correlation between insect communities and salinity was indirectly due to the close relationship between insect and plant communities, species compositions of plants and insects may be regarded as the most ecologically relevant measure in relation to saltwater incursions in the wetlands. This is possibly because plants and insects are relatively non-motile and thus useful for studying local effects of salinity. Previous studies have used vegetation changes as good ecological indicators for periodic saltwater incursions in deltaic wetlands (Holm and Sasser 2001) and the consequences of dam construction in an estuary (Colonnello and Medina 1998). This study further suggests the utility of insect community for the ecological monitoring of salinity changes in estuaries and coastal wetlands.

Although compositions of macrobenthos, mollusks, and fish at the marsh sites and mangrove sites could be well separated, it is surprising that the spatial changes in these aquatic communities failed to match the salinity gradient in the wetlands. As a matter of fact, the salinity gradient in the wetlands was small, ranging from 2.8 PSU in the freshwater marshes to 14.5 PSU in the mesohaline mangroves (Table 1). Most estuarine species occurring in coastal wetlands are euryhaline and have the ability to withstand wide variations in salinity. Although the relative abundance of each taxon in communities of macrobenthos, mollusks and fish might be influenced by differential salinities in the wetlands, most taxa occurred throughout the salinity gradient. Hence, it is difficult to distinguish differences between communities of macrobenthos, mollusks, and fish in the oligohaline and mesohaline habitats in the wetlands.

Among the communities surveyed in the wetlands, we found that the species composition of birds was least affected by saltwater incursions. Birds are often of immediate public interest, and their taxonomy is relatively easy. Therefore, studies of bird communities are more directly related to the needs of environmental managers than of other communities in coastal wetlands. However, because of their high mobility, they might be more useful for studying general effects of large areas rather than local effects (Marsden et al. 2001). That may be the reason that abiotic variables in the wetlands could not explain the spatial changes in bird communities. On the other hand, although we did not observe any significant correlation between communities of plants and birds as in the findings of Froneman et al. (2001), our analyses (Table 3, Figure 9) demonstrate that spatial changes in bird communities were more relevant to changes in mollusk communities in the wetlands.

Strikingly, our analyses show that mollusk, fish, and bird communities in the Guandu wetlands were not structured by the salinity gradient. Instead, they were mainly controlled by each other. These consumers are likely to interact trophically, since both birds (authors' personal observation) and fish (authors' unpublished data)

were observed to feed on mollusks in the wetlands. Our results, combined with the findings of Froneman et al. (2001), suggest that biological factors might be more important than physical factors in determining the spatial patterns of bird and fish communities within a coastal wetland or estuary. For environmental managers, our results also imply that in addition to preserving physical habitats, other communities should be included in conserving birds in coastal wetlands because of the tight correlation between birds and other communities.

While large-scale destruction and alteration of coastal wetlands have been reported worldwide (World Conservation Monitoring Centre 1992), the success of wetland restoration depends largely on proper salinities at a site. Regulation of gates on dykes and adjustment of saltwater incursions for proper salinity control have been debated for the management of the Guandu wetlands and other coastal wetlands. However, few studies have elucidated changes in community structures in response to saltwater incursions in coastal wetlands, except a study of plant composition conducted by Holm and Sasser (2001). In our study, the superimposition of community attributes on MDS ordinations of major communities in the Guandu wetlands might provide implications of the responses of major communities in the wetlands as a result of opening the gates on the dyke. Obviously, the most sensitive and negatively affected community would be the plant community. The species richness and diversity would decline when salt water penetrates into the freshwater wetland. Despite the close intercorrelation between plant and insect communities, the insect diversity would most likely increase in response to saltwater incursions.

The great differences in abundance and community structure of macrobenthos and fish between the freshwater marshes and the mangroves in the Guandu wetlands are consistent with findings of other studies conducted by Hsieh et al. (1998) and Shao et al. (1998) along the Keelung River. They found that macrobenthos and fish were much more abundant and diverse in the estuary than in the upper region of the Keelung River, respectively. The inland movement of salt water may thus enhance the immigration of macrobenthic and fish species, so that the abundance, species richness, and diversity would increase in the wetlands. Although no clear trend of changes in community attributes was observed in mollusk communities, the abundance was especially high at the sites near the gate. Considering the close relationship between bird and mollusk communities, our results suggest that maintenance of tidal flux through opening the gate on the dyke may be a useful way to enhance biodiversity in coastal wetlands.

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