









RESEARCH ARTICLE

Coastal wetland restoration through the lens of Odum's theory of ecosystem development

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Advancing ecological restoration assessments requires a more detailed consideration of species interactions and ecosystem processes. Most restoration projects rely on a few metrics not always directly linked with ecological theory. Here, we used Odum's theory of ecosystem development to assess and compare the ecosystem structure and services of created marshes (4–6 years old) with preexisting, reference marshes in a brackish water region of the Mississippi River Delta. We built ecosystem models for created and reference marshes that integrated large datasets of stomach contents, stable isotopes, and taxa abundances. Despite strong resemblance in community structure, created marshes were at an earlier succession stage compared to the reference marshes, having lower biomass (including exploited species), higher biomass turnover and production, less dependence on detritus, lower material cycling, and less energy flowing through specialist pathways. Although preserving preexisting marshes should be a priority, created marshes may still be an important tool for the restoration of coastal areas and their ecosystem services. In addition, our results show that comparisons of species biodiversity alone may fail to capture essential differences in ecosystem processes between habitats, which reinforces the importance of ecosystem modeling approaches to assess restoration projects.

Key words: coastal wetlands, ecosystem development, ecosystem services, Mississippi River delta, restoration, succession

Implications for Practice

- Due to the tight association between ecosystem services value and ecosystem development, ecosystem models based on Odum's theory are powerful tools in determining the success of restoration efforts in coastal marshes.
- Although created marshes provided less value for some ecosystem services (e.g. fisheries and nutrient cycling) than preexisting reference marshes, marsh creation projects can still be considered an important element for the restoration and preservation of coastal biodiversity.
- Created marshes must emulate the structure of preexisting reference marshes because differences in their physical structure (e.g. elevation, sediment coarseness, etc.) impact succession and may lead to undesired alternative ecosystem states.

Introduction

Ecological restoration is a multi-billion-dollar industry that has been growing due to recent regional and international commitments to restore natural ecosystems and cope with the unsustainable use of resources (BenDor et al. 2015). The main goal of ecological restoration is to return degraded areas to their former natural healthy state (SER 2004). However, restoration success is often assessed through only a few, sometimes arbitrary, metrics (e.g. target species densities) that are often uncoupled from ecological theory and not based on sound monitoring practices

(Lindenmayer 2020). Improving restoration assessment and monitoring programs should involve a better consideration of species interactions and ecosystem attributes (e.g. nutrient

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cycling) to ensure the provision of essential natural services (Cortina et al. 2006; Vander Zanden et al. 2016).

Ecological restoration involves the initial colonization and establishment of species at the focal site, followed by the development of the ecosystem. Odum (1969) argues that ecosystem development is an orderly and directional process of community development that progresses toward a stabilized system (i.e. the "climax"), even though this state may remain forever beyond reach due to disturbances (e.g. wildfires). Differences between early- and late-stage ecosystems are expected to involve energetics (e.g. higher rates of primary production compared to respiration in early stages that lead to biomass accumulation with time), community structure (e.g. higher biomass and species diversity at later stages), species life history (e.g. more small species with short-life cycles and broad niches at early stages), nutrient cycling (e.g. higher importance of detritus and slower exchange rates for late-stage systems), selection pressure (e.g. r-selection and K-selection at early and late stages, respectively), and overall homeostasis (e.g. higher resistance to external perturbations at later stages) (Odum 1969). Although Odum's conceptual framework has faced skepticism in the past (Hagen 1992) and its predictions have been refuted in certain ecosystems (Stoy 2010; Corman et al. 2019), it can still serve as a valuable guide for restoration projects and the establishment of evaluation measures for restoration success (e.g. Choi 2004; Lindenmayer 2020).

Coastal wetland loss rates, caused by natural (e.g. geologic subsidence, sea-level rise) and human-induced (e.g. coastal development, hydrological modifications) processes, differ worldwide (Williams et al. 2022). Some regions, such as the Mississippi River Delta, have lost up to 50% of their extent since the 1700s (Fluet-Chouinard et al. 2023). This is concerning because coastal wetlands are highly productive, support many resident and migratory species, and provide key ecosystem services for human populations (e.g. suppression and shelter against storms and tsunamis, food provision) (Chabreck 1988; Sun & Carson 2020). Tools used by managers to protect coastal wetlands include impact mitigation and new habitat construction, but their efficiency has been questioned (e.g. Lawrence et al. 2018). To date, commonly used metrics to assess coastal wetland restoration success have been based on the areal extent of land creation, flood risk reduction, and ecosystem structural diversity (e.g. vegetation density) and function (e.g. denitrification activity, secondary growth rates) (Cadier et al. 2020). Studies on ecosystem development and structure based on ecosystem modeling are still rare.

We constructed ecosystem models of created and reference coastal wetlands in the Mississippi River Delta and explored their metabolism and network structure to infer ecosystem maturity and services using an extensive diet (i.e. stomach content, stable isotopes) and biomass dataset. The region faces one of the highest coastal wetland loss rates globally, reaching up to 100 km²/year (Day Jr et al. 2007). To combat this, an ambitious and costly coastal restoration initiative is underway and requires an estimated \$50 billion investment spread over 50 years that will build and maintain approximately 2000 km² of land (CPRA 2017, 2023). A recent study found similar taxonomic diversity and composition between created and reference marshes across different assemblages that may suggest that

marsh creation is an important tool for the maintenance and restoration of coastal biodiversity (Keppeler et al. 2023). However, it is unclear whether the created marsh ecosystem properties (e.g. energetics, nutrient cycling) match those of the reference sites. Our study provides a robust and holistic analysis of the effectiveness of habitat creation in maintaining ecosystem processes and services, something that has been rarely done in the ecological restoration literature.

Methods

Study Area

Data for the ecosystem models were collected from two created marshes, known as Lake Hermitage A (LHA) and Lake Hermitage B (LHB), as well as three nearby brackish reference marshes, referred to as Lake Hermitage C (LHC), West Pointe à la Hache 1 (WPH1), and West Pointe à la Hache 2 (WPH2). The marshes are situated in Plaquemines Parish on the western side of the Mississippi River in Barataria Bay, Louisiana (Fig. 1), which has a subtropical climate (Hiatt et al. 2019). The created marshes were developed as part of the Coastal Protection and Restoration Authority's Lake Hermitage Marsh Creation Project (Base Project: BA-42; CPRA 2022). LHA was constructed from August 2012 to October 2013, and LHB was constructed from December 2013 to May 2014. Both created marshes were built with dredged, sandy material from the Mississippi River that filled open-water areas and fragmented marshes. The sediments of created marshes were coarser than reference marshes. Following the construction of the created marsh platforms, gaps were made in containment levees to allow access for aquatic animals and to re-open tidal channels. Created marshes were colonized naturally. Reference marshes had no history of restoration and existed before and during the Lake Hermitage marsh creation project. During the study period, a weak salinity gradient ranging from 12.3 to 15.6 practical salinity units (PSU) was observed, transitioning from the generally turbid waters of marshes closer to Lake Hermitage (LHA, LHB, and LHC) to those near Bay Sansbois (WPH2), respectively. The tidally influenced marsh had a mean depth of 2.3 m and diurnal tides were about 0.3 m, but the higher elevation of LHA made it experience less flooding than the other marshes. For more details about the study area and the studied marshes, see Keppeler et al. (2021, 2023).

Biomass Data

Initial biomass estimates for key components of the marsh food webs were obtained either from (1) field sampling conducted in May 2018 from a variety of marsh sub-habitats (e.g. marsh platforms, ponds, tidal creeks, and channels) and their surrounding open waters using different sampling methods or (2) from the literature.

Plants. Emergent C3 and C4 marsh plants were sampled across three 100 m long transects in each one of the five marshes studied. Within each transect, sampling stations were located at

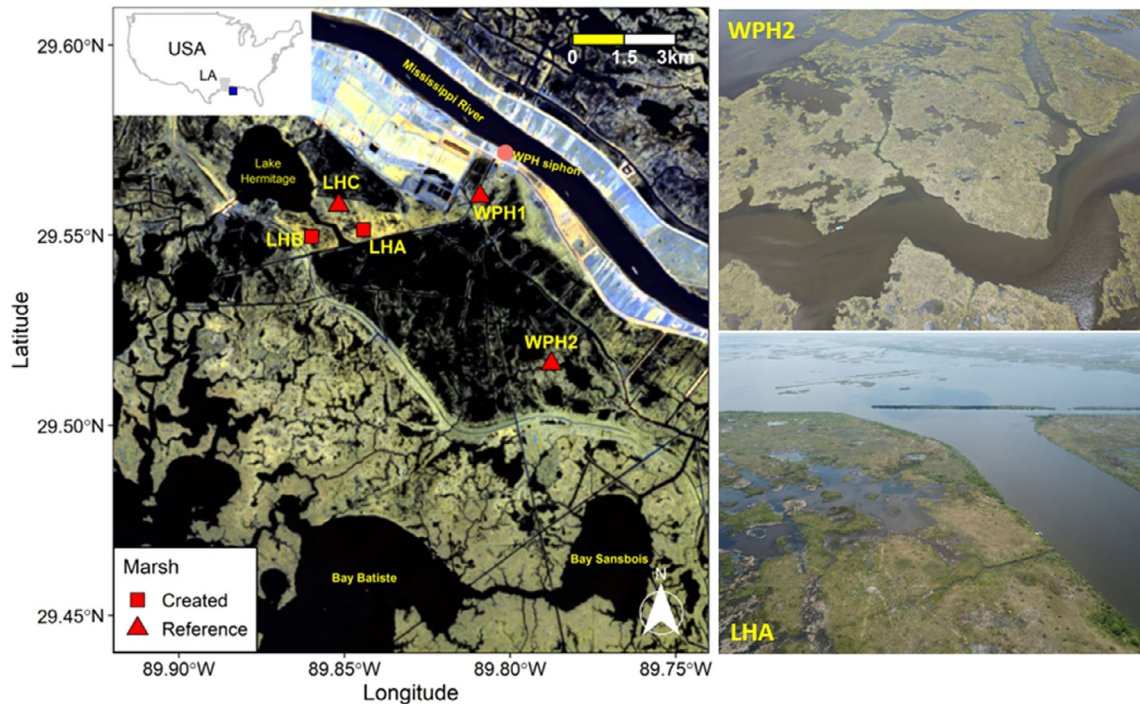


Figure 1. Location of the created and reference marshes used as references for the ecosystem models. Aerial images of WPH2 (reference) and LHA (created) marshes can be seen on the left side of the map.

1, 10, 25, 50, and 100 m. At each sampling station, we removed all aboveground biomass in a 25×25 cm quadrat placed randomly on the terrain. Plants were separated by species, rinsed free of sediment and epiphytes, dried to constant mass at 70°C , and then weighed (grams). More details can be found in Hill and Roberts (2017).

Macroinfauna. Bivalves, isopods, amphipods, tanaids, annelids, benthic microcrustaceans, nematodes, snails, and aquatic insects were sampled at 10 and 50 m distances from the marsh edge. In each sampling location, five replicates of benthic cores (approximately 46 cm^2) were taken from an area of approximately 5 m^2 . The samples were transported to the lab, where they are sieved to retain only animals larger than 0.5 mm. Animals were identified to the lowest taxonomic level possible (usually species to family) and then counted. We estimated the length of each taxon from the literature and then converted it to biomass (grams) by using length–weight relationships (see Table S1).

Terrestrial Invertebrates. Hemipterans (true bugs), dipterans (flies), formicids (ants), coleopterans (beetles), thysanopterans (thrips), orthopterans (grasshoppers), odonates (dragonflies and damselflies), and arachnids (spiders) were collected with sweep nets (37.5 cm of diameter) along a 40×2 m linear transect perpendicular to the marsh edge by swinging the net from side to side in an arc of approximately 180° . Collections were done once per day for four consecutive days from 06:30 to

10:30 hours local time. The invertebrates collected were preserved in 95% ethanol and then identified and counted in the lab. Spider identification was by morphotype and insects were generally to family or order levels. We estimated the length of each taxon from the literature and then converted it to biomass (grams) using length–weight relationships (Table S1).

On-Marsh Nekton. On-marsh fishes (cyprinids and gobiids) and aquatic macroinvertebrates (crustaceans, mainly grass shrimp and blue crabs) were sampled with wire mesh cone traps (41×22 cm, with 3 mm mesh and 3 cm-diameter opening) in three ponds in each studied marsh. Each pond was sampled for three consecutive days using three cone traps baited with dry dog food and deployed for approximately 1.3 hours ($\text{SD} = 0.24$). Animals were identified to species level and weighed (grams). For more details, see Able et al. (2015).

Off-Marsh Nekton. Off-marsh fishes (pelagic and benthopelagic species) and macroinvertebrates (shrimps and blue crabs) were collected from channels adjacent to the marsh platform with an otter trawl (4.9 m wide with a 38 mm mesh body and a 13 mm cod end mesh size). Channels were towed eight times for approximately 3 minutes at an average speed of 2.5 knots. Animals sampled were identified to species level and weighed (grams).

Other Components. We estimated the biomass of detritus, four primary producers (i.e. macroalgae, phytoplankton,

microphytobenthos, and submerged C4 aquatic vegetation), zooplankton, dolphins, and birds using literature information from Barataria Bay (Table S2). In this case, their biomasses were assumed to be the same for reference and created marshes.

Although our sampling approaches were consistent across marshes, there are caveats. First, some sampling techniques to estimate biomass and species composition are size-selective. For instance, trawling likely misses small fishes (e.g. minnows) and juveniles that pass through the net, as well as large fishes (e.g. sharks) that can overcome the trawl speed and avoid the net. Second, our sampling effort focused on a single season and year, and targeted key functional groups. As a result, we missed some resident and transitory species that occur in brackish marshes, including reptiles (e.g. alligators, snakes) and mammals (e.g. muskrats, raccoons).

Stable Isotope Data

Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$; $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$; $\delta^{15}\text{N}$) were obtained for 1600 samples of macroinfauna (isopods, amphipods, and tanaids), aquatic macroinvertebrates (shrimps, crabs, and snails), on-marsh (minnows and killifishes) and off-marsh fishes (red drum, gars, and sharks), plants (submerged C4 aquatic vegetation, emergent C3 marsh plants, and emergent C4 marsh plants), phytoplankton, macroalgae, microphytobenthos, and detritus collected in created (LHA and LHB) and reference marshes (LHC, WPH1, and WPH2) in May of 2018 (Table S3). These two tracers provide trophic information, as $\delta^{15}\text{N}$ values become higher with increasing trophic level and $\delta^{13}\text{C}$ values reflect different photosynthetic pathways and inorganic sources of assimilated carbon (Peterson & Fry 1987). To complement our field samples, we also compiled stable isotope data for birds and dolphins, which feed on prey spread across spatial scales that surpass our study area, from studies conducted in Barataria Bay (DIVER 2020; Lamb et al. 2020, 2022).

We analyzed only fresh leaves of plants, dorsal muscle of fishes, and soft tissues of invertebrates and macroalgae. Phytoplankton was obtained from water sampled from the main channel immediately adjacent to the marsh edge. Water samples were passed through 105 μm mesh screens to remove most zooplankton and large debris and then filtered through pre-combusted Whatmann GF/F glass-fiber filters. We measured chlorophyll on the screened and unscreened water to determine how much of the phytoplankton was excluded by the screening. We found that, on average, 93% of phytoplankton chlorophyll was included in our samples. Detritus, which consisted of soil organic matter, was obtained from the upper 1–2 cm of marsh soil. Microphytobenthos was extracted from the upper 1–2 cm of marsh soil. Extraction methods are based on the protocol described by Levin and Currin (2012).

Samples obtained in the studied marshes were transported to the lab in coolers with dry ice and then sealed and stored in the freezer (-20°C). Samples were cleaned with distilled water, lyophilized for 48 hours, and then grounded to a fine powder using a pestle and mortar. Lipid extraction was conducted using 2:1 chloroform:methanol following standard practices (Folch

et al. 1957). Samples were weighed into tin capsules and flash-combusted using a Costech ECS4010 elemental analyzer coupled to a Thermo-Fisher Delta Plus XP continuous-flow stable isotope ratio mass spectrometer for relative abundances of carbon and nitrogen stable isotopes at the Stable Isotope Ecology Lab at Louisiana State University. Stable isotope values were normalized using a two-point system with glutamic acid reference material (USGS-40 and USGS-41). Sample precision was based on the standard deviation of repeated reference materials (USGS-40 and USGS-41) and an internal laboratory standard (red drum muscle tissue, *Sciaenops ocellatus*). Stable isotope values were calculated with the following equation and are expressed in standard delta (δ) notation in per mil units (‰):

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The R_{standard} values were based on Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 (AIR) for $\delta^{15}\text{N}$ values. Precision based on repeated reference materials and standards was 0.1 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Trophic Interactions

Trophic interactions within the reference and created marsh ecosystems were estimated using a combination of stable isotope and literature data through EcoDiet (Hervann et al. 2022). EcoDiet is a Bayesian hierarchical model that integrates prior knowledge from the literature regarding food web topology (0—trophic link absent, 1—trophic link present) and diet proportions, and actual data of stomach contents and biotracers (e.g. stable isotopes) from sampled species. Model priors were defined using two main literature sources: (1) trophic linkages obtained from a list of trophic interaction occurrences available in the GoMexSI database (Simons et al. 2013) and previous food web studies in Barataria Bay (de Mutsert et al. 2017; McCann et al. 2017; Oken et al. 2023); and (2) diet proportions derived from Akin and Winemiller (2006), which analyzed more than 6400 stomachs from a similar coastal marsh system in Texas. The food web matrices generated with EcoDiet for created and reference marshes became the input for the ecosystem models. For more details, see Supplement S1.

Ecosystem Models

Models were created using Ecopath with Ecosim (EwE) software (version 6.6.5, available at www.ecopath.org). EwE is the ecosystem modeling framework most used in the world (Coll  ter et al. 2013) and is recognized as one of the top 10 scientific breakthroughs of the National Oceanic and Atmospheric Administration (NOAA 2007). It is composed of three major components: (1) Ecopath, which creates static mass-balanced models; (2) Ecosim, which is used to model temporal dynamics; and (3) Ecospace, which is used to model spatial-temporal dynamics. Because our biomass and stable isotope data were restricted to a single field sampling, we used Ecopath. Ecopath provides a snapshot of the ecosystem and can be applied to

explore ecosystem structure and trophic interactions, assess ecosystem services and their values to society, and can infer ecosystem development, among others. Noteworthy, Ecopath no longer assumes the original assumption of steady state proposed by Polovina (1984a, 1984b), but instead its parameterization relies on the assumption of mass balance over a given period.

Ecopath models are based on linear equations involving production and consumption that quantify the trophic flow between species and functional groups based on the premise that there is a mass balance in ecosystems (Christensen et al. 2005). Mass balance in Ecopath is governed by two master equations. The first describes the energy balance for each group, as follows:

$$\left(\frac{Q}{B}\right)_i \times B_i = \left(\frac{P}{B}\right)_i \times B_i + R_i + UN_i$$

where Q/B is consumption, B is biomass, P/B is production, R is respiration, UN is unassimilated food, and i represents a given group. So, the consumption of a given group should be equal to its production, plus respiration and excretion. The second equation divides production into five main components: predation mortality, fishing mortality, biomass accumulation, net migration, and other mortality, so that:

$$\left(\frac{P}{B}\right)_i \times B_i = \sum_{Pred,j=1}^n \left(\frac{Q}{B}\right)_j \times B_j \times DC_{ij} + E_i + Y_i + BA_i + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i)$$

where $(Q/B)_j$ is the specific consumption of prey j , DC_{ij} is the fraction of prey j in the diet of group i , BA_i is the biomass accumulation of group i , Y_i is the total fishery catches of group i , EE_i is the production of the group i used in the system, and $1 - EE_i$ is the unexplained mortality of group i . Ecopath models for reference and created marshes both had 41 compartments that included dominant groups, from primary producers (e.g. marsh plants, algae) to top predators (e.g. dolphins, carnivorous fish, and piscivorous birds) (Table 1). We estimated B for food web components mostly from our field surveys and the diet proportions were derived from EcoDiet. P/B , Q/B , and Y were estimated from previous models, empirical relationships, expert opinions, and literature data (Supplement S1). BA was considered null for all groups and UN was set to 0.2 (i.e. 20%) for vertebrates and 0.4 for invertebrates (Winberg 1980). EE for each group is unknown and, therefore, was estimated from the Ecopath model.

To construct the Ecopath models for the created and reference marshes, we followed the best practices summarized by Heymans et al. (2016). These involve diagnostics of thermodynamic rules and ecological principles that need to be checked before model balancing and the impact assessment of parameter uncertainty on the model's outcomes. We used the standard PREBAL diagnostics (Link 2010) to identify and correct issues of model structure and data quality. Then, models were tuned to achieve balance conditions (Supplement S2). The impact of uncertainty associated with input parameters (i.e. diet, B , P/B , Q/B , and removals) on Ecopath outputs was assessed through the Monte

Carlo uncertainty routine ($n = 100$), which is based on confidence intervals determined from parameter "pedigrees" (Supplement S1). Pedigrees are a categorical classification of the relative uncertainty in different parameters based on their source (Heymans et al. 2016). In this sense, we used the Monte Carlo procedure to sample the probability distribution of the input parameters to generate variation in the output parameters (Christensen et al. 2005).

Model Comparisons

We used eight ecological network and information metrics based on Odum's theory of ecosystem development (Odum 1969; Christensen & Pauly 1998) to compare created and reference marsh ecosystems, specifically: net P , B , gross P/B , gross P/R , B —throughput ratio, proportion flow from detritus, Finn cycling index, and ascendency (Table 2). Because of variance heterogeneity, nonparametric Mann–Whitney tests checked statistical significance, for which the distribution of values derived from the Monte Carlo procedure were treated as replicates in the analyses.

A heatmap of food web flows was used to explore general ecosystem patterns. In addition, we assessed the overall structure of our Ecopath models using the Lindeman spine diagram, which summarizes the flows between different trophic levels and the detritus compartment and facilitates the visualization of the energy transfer in the system (Christensen et al. 2005).

Results

Overall, the created and nearby reference marshes consisted of green food webs (i.e. having approximately 75% of its energy derived directly from primary producers) based on algal pathways, particularly phytoplankton but also microphytobenthos and macroalgae (Figs. 2 & 3). The strongest trophic flows for both marsh types were associated with phytoplankton consumption by bivalves and zooplankton. The calculated trophic level values for taxa in each marsh type were virtually identical (Table 1), although created and reference marshes had different biomass distributions across their food webs (Fig. 3). Reference marshes had higher producer and primary consumer biomasses and provided 38% more fishery catches than created marshes, but created marshes had higher secondary and tertiary consumer biomasses.

The major trophic flow differences between created and reference marsh ecosystems were associated with benthic invertebrates. Overall, primary consumers from reference marshes (i.e. mainly bivalves, snails, annelids, and grass shrimps) used approximately 11% more detritus pathways than those from created marshes. The main exception was benthic microcrustaceans in reference marshes, which tended to have lower biomass, and therefore lower consumption, of detritus, phytoplankton, and microphytobenthos. In addition, organisms from created marshes ingested approximately 5% more algae than those from reference marshes. Trophic efficiency was higher for created than reference marsh ecosystems ($\sim 3.3\%$ vs. $\sim 2.4\%$, respectively) due to the trophic flow differences and the higher

Table 1. List with all compartments of the ecosystem models for created and reference marshes. For each compartment, there is an abbreviation code (also used in Fig. 2), trophic level (TL) for reference marshes (TL for created marsh was virtually the same), biomass (B) for reference and created marshes, ecotrophic efficiency (EE) for created and reference marshes, production per biomass unit (P/B, same for created and reference marshes), consumption per biomass unit (Q/B, same for created and reference marshes), and removals (Y, same for created and reference marshes). EE and TL were estimated with Ecopath, B is based on field sampling and literature data (see Tables S1–S3), and P/B, Q/B, and Y were obtained from previous models, empirical relationships, expert opinions, and literature data (see Supplement S1).

Compartment	Code	TL	B (g/m ²)		EE		P/B	Q/B	Y
			Reference	Created	Reference	Created			
Wading birds	W.birds	3.2	0.0013	0.0013	0.000	0.000	0.13	33.85	0.0000
Pelicans	Pelicans	3.4	0.0001	0.0001	0.000	0.000	0.10	17.70	0.0000
Gulls and terns	Gulls. terns	3.5	0.0002	0.0002	0.000	0.000	0.10	50.00	0.0000
Odonata (dragonflies and damselflies)	Odon	3.2	0.0027	0.0147	0.522	0.162	6.77	13.45	0.0000
Orthoptera (grasshoppers)	Orthop	2.0	0.0300	0.0309	0.389	0.530	4.24	11.41	0.0000
Thysanoptera (thrips)	Thysan	2.0	0.0469	0.0023	0.031	0.922	23.63	78.43	0.0000
Coleoptera (beetles)	Coleo	2.0	0.0073	0.0233	0.594	0.472	11.17	36.65	0.0000
Formicidae (ants)	Ants	2.0	0.0127	0.0077	0.312	0.944	16.46	55.14	0.0000
Diptera (flies)	Flies	2.0	0.0062	0.0053	0.372	0.889	14.69	48.52	0.0000
Hemiptera (true bugs)	Hemip	2.1	0.0260	0.0185	0.203	0.695	14.65	48.12	0.0000
Dolphins	Dolph	3.6	0.0002	0.0002	0.000	0.000	0.05	25.30	0.0000
Fish, piscivorous	F.pisc	3.2	0.0144	0.0900	0.915	0.113	0.52	5.18	0.0004
Fish, marsh, carnivorous	F.M.carn	2.6	0.1944	0.7729	0.019	0.007	2.17	15.08	0.0000
Fish, carnivorous	F.carn	3.2	0.0090	0.1227	0.617	0.056	1.00	13.60	0.0002
Aquatic insect predators	Aq.ins.pred	3.1	0.1033	0.7749	0.399	0.146	4.51	8.82	0.0000
Arachnids (spiders)	Arachnids	3.2	0.0298	0.0226	0.524	0.952	1.38	3.50	0.0000
Fish, zooplanktivorous	F.zoo	2.8	0.0448	0.0495	0.137	0.121	1.45	19.40	0.0001
Fish, marsh, zooplanktivorous	F.M.zoo	2.8	0.0068	0.0308	0.808	0.203	1.50	9.40	0.0002
Gastropoda (snails)	Sna	2.0	2.5593	1.0010	0.134	0.824	2.06	10.40	0.0000
Fish, benthivorous	F.bent	2.9	0.4330	0.2194	0.051	0.095	0.74	7.11	0.0019
Fish, marsh, omnivorous	F.M.omn	2.2	0.0413	0.0146	0.048	0.149	3.44	38.57	0.0000
Fish, omnivorous	F.omn	2.2	0.2241	0.2023	0.864	0.534	1.54	8.61	0.0495
Nematoda (roundworms)	Nemat	2.3	0.0685	0.0736	0.171	0.163	28.88	77.47	0.0000
Aquatic insect omnivorous I	Aq.ins.omn	2.2	0.6061	0.6353	0.283	0.538	6.76	19.14	0.0000
Benthic microcrustaceans	Ben.micr	2.1	0.1217	1.8333	0.568	0.256	31.59	105.10	0.0000
Crabs	Crabs	2.3	0.0760	0.2437	0.875	0.444	2.40	8.50	0.0959
Fish, detritivorous	F.detr	2.0	0.0300	0.3264	0.995	0.162	0.54	12.28	0.0001
Annelida (earthworm, polychaete)	Annel	2.1	1.7245	0.7227	0.279	0.980	4.50	22.00	0.0000
Fish, marsh, detritivorous	F.M.detr	2.0	0.0910	0.0147	0.233	0.722	0.63	29.90	0.0000
Isopoda, Amphipoda, Tanaidacea	Iso.Amp.Tan	2.0	1.1428	1.0746	0.329	0.804	4.50	22.00	0.0000
Penaeidae (penaeid shrimp)	Shr.pen	2.2	0.3493	0.3634	0.119	0.155	2.40	19.20	0.0300
Palaemonidae (grass shrimp)	Shr.grass	2.0	1.5440	1.1963	0.012	0.025	4.50	18.00	0.0000
Fish, marsh, herbivorous	F.M.herb	2.0	0.0312	0.0812	0.131	0.059	1.59	20.20	0.0000
Bivalvia (bivalves)	Bivalves	2.0	25.7776	11.1623	0.027	0.070	1.66	15.42	0.0000
Zooplankton	Zoopl	2.1	4.1200	4.1200	0.187	0.262	28.80	84.90	0.0000
Submerged C4 aquatic vegetation	S.C4.vege	1.0	9.7800	9.7800	0.042	0.034	9.01	—	0.0000
Emergent C4 Marsh plants	E.C4.plant	1.0	1824.0000	1,231.1000	0.001	0.001	2.99	—	0.0000
Emergent C3 Marsh plants	E.C3.plant	1.0	223.7000	207.7000	0.007	0.004	2.99	—	0.0000
Microphytobenthos	M.phytob	1.0	29.8000	29.8000	0.102	0.009	3.91	—	0.0000
Macroalgae	Macroalg	1.0	50.0000	50.0000	0.027	0.003	4.00	—	0.0000
Phytoplankton	Phytopl	1.0	12.8000	12.8000	0.474	0.327	101.70	—	0.0000
Detritus	Det	1.0	100.0000	100.0000	0.036	0.019	—	—	0.0000

proportion of primary consumers in the latter, which were mainly composed of invertebrates with higher egestion rates.

For the ecological network and information metrics from Odum's theory of ecosystem development, we found significant differences ($p < 0.001$) in all metrics analyzed (Fig. 4). Values for B, B-throughput ratio, proportion flow from detritus, Finn cycling index, and ascendancy were higher for reference than

created marsh ecosystems. Conversely, net P, gross P/B, and gross P/R were higher for created marsh ecosystems.

Discussion

Our results indicated that Odum's attributes of ecosystem development (Odum 1969) differed between created and reference

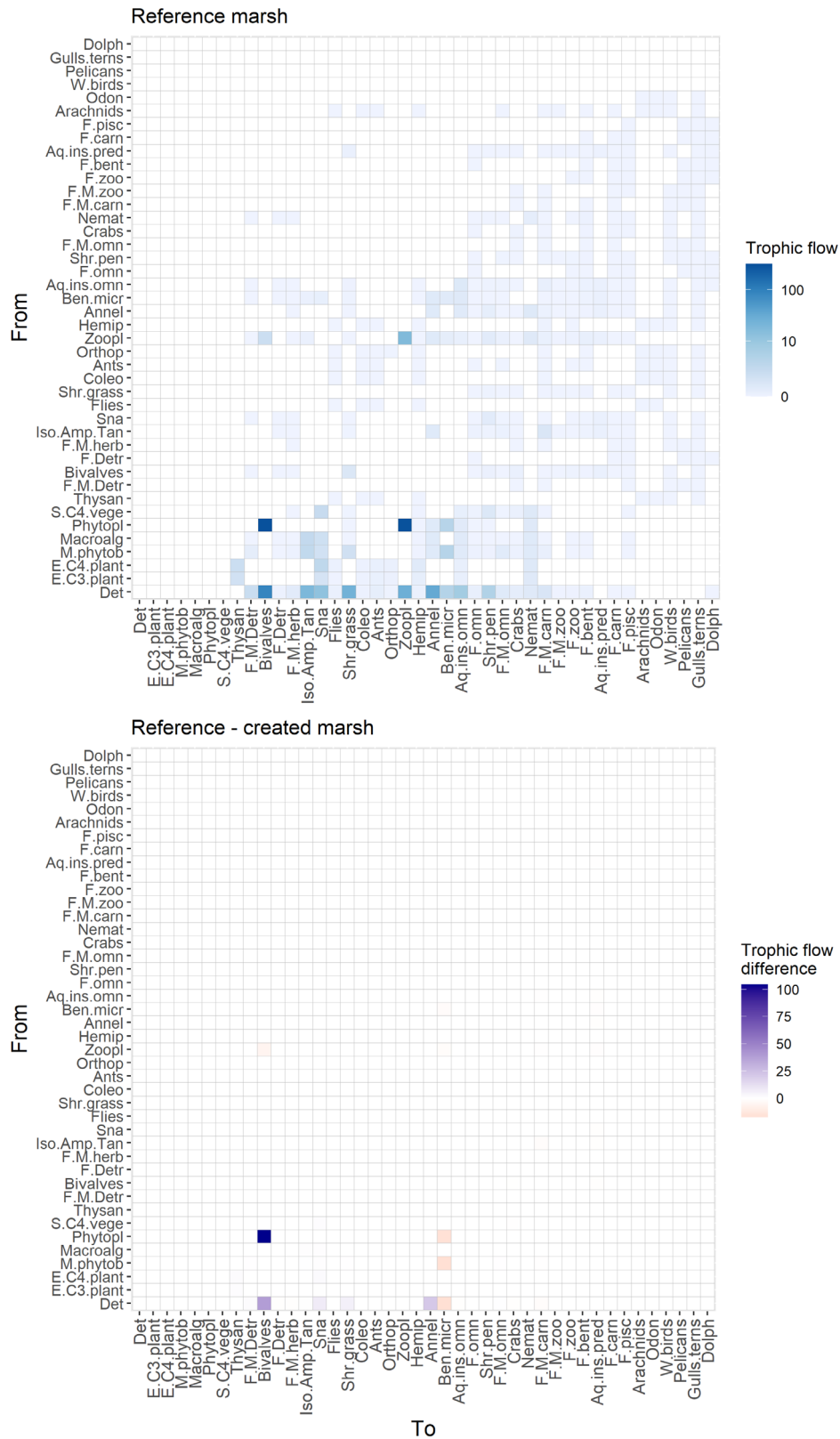


Figure 2. Heatmap of food web flows for reference marshes (upper panel) and for the difference between the flows of reference and created marshes (lower panel). Abbreviations are described in Table 1.

Table 2. Ecological network and information metrics used to compare created and reference brackish marsh ecosystems.

<i>Ecosystem attribute</i>	<i>Developing stage</i>	<i>Mature stage</i>	<i>Ecological description</i>	<i>References</i>
<i>B</i>	Low	High	Amount of biomass occupying an area at a particular time.	Odum (1969)
Net <i>P</i>	High	Low	Living organic matter accumulation	Odum (1969)
Gross <i>P/B</i>	High	Low	The turnover rate in biomass; that is, speed of biomass regeneration	Odum (1969)
Gross <i>P/R</i>	>1 or <1	~1	The ratio between the energy fixed and the cost of maintenance	Odum (1969)
<i>B</i> /throughput	Low	High	The amount of standing biomass supported by the available energy flow	Odum (1969)
Finn cycling index	Low	High	The fraction of an ecosystem's throughput that is recycled	Finn (1976)
Proportion flow from detritus	Low	High	Importance of detritus to the food web	Christensen et al. (2005)
Ascendency	Low	High	A metric that relates to the size and degree of ecosystem organization, integrating structural and functional features of network topology and energy/matter transfers between species. Ascendency relates positively with several ecosystem attributes of Odum's theory, including speciation, trophic specialization, internalization, and cycling. Overall, systems with higher ascendency have (1) more energy flows restricted to specialist pathways; and (2) more energy present in the web	Ulanowicz (2000)

marsh ecosystems in the Mississippi River Delta. Reference marsh ecosystems tended to have higher biomass, particularly for important fishery species, lower biomass turnover rates, lower net productivity rates, and faster recycling rates compared to those from created marshes. Reference marsh ecosystems also had a greater reliance on detritus, higher material cycling rate, and higher ascendency (i.e. network structure with more energy flowing through specialist pathways) than created marsh ecosystems. Collectively, as Odum's theory suggests, the youngest marshes (i.e. created) were in an earlier stage of ecological succession than the older, more mature reference marshes.

The reference marshes can still be considered at an early stage of succession because gross *P/R* (approximately 10) exceeds what should be expected for a mature ecosystem (approximately 1) (Christensen & Pauly 1998). This result is not surprising because intertidal zone ecosystems are maintained at early successional stages by frequent disturbances that provide energy and nutrients for fast nutrient cycling (Odum 1969). For example, tide-controlled and wind-driven flooding, such as from storms, facilitate species movement across the marsh landscape and likely accelerate the colonization of brackish marshes by propagules and individuals, as well as pioneer species recruits (Keppeler et al. 2021, 2023). Abrupt changes in water quality and chemical composition (e.g. salinity, turbidity) also exert a strong selection pressure on species, which may reduce local diversity and filter for species with elevated tolerance to extreme environmental conditions (Elliott & Quintino 2007). In this sense, a prevalence of r-strategist and generalist species in natural brackish marshes and other estuary systems is expected (Lechêne et al. 2018), which may accelerate the restoration process for created marshes.

A related and open question is whether the young, newly created marsh systems respond to press-pulse disturbances in the same direction and magnitude as reference marshes. This is especially relevant considering the impact of climate change on the region, as large storms and hurricanes have already

increased in frequency and intensity (Kossin et al. 2020). The effects of hurricanes on marshes are complex, as they can either (1) reduce crucial plant biomass for growth (Morton & Barras 2011), (2) stimulate marsh root growth and increase belowground biomass later (McKee & Cherry 2009), (3) erode marsh elevations and area (Barras 2006), or (4) raise marsh elevations through sediment deposition (Turner et al. 2006; Tweel & Turner 2014). Although these effects may depend on vegetation types and locations, a recent study in coastal marshes in Louisiana indicates a strong resilience of these ecosystems, with marsh areas rebuilding after 2 years of hurricane landfall (Mo et al. 2020). Because reference marshes have almost 40% more vegetation biomass than created marshes, and higher material cycling rates, it is likely that the created marshes may suffer more erosion and take more time to recover from hurricanes than the reference marsh systems. However, before-and-after study designs are needed to test this hypothesis.

Four to six years after restoration efforts were completed at the same marshes used in this study, taxonomic diversity and species compositions were found to be similar between the created and reference marshes (Keppeler et al. 2023). But, created and reference marsh macroinfauna assemblages (e.g. bivalves, benthic crustaceans, and annelids) were different. These groups are the same ones that led to ecosystem structure changes in this study. Macroinfauna and other benthic invertebrates (e.g. grass shrimps) are key to many important processes in brackish marshes, not only by serving as a source of energy to larger animals but by regulating nutrient recycling and sedimentary processes via bioturbation (Adam 1990). Ecosystem structure differences between the created and reference marshes due to changes in benthic invertebrate abundances and compositions may not only correlate to habitat age, but to marsh construction. The created marshes are at higher elevations and also consist of larger

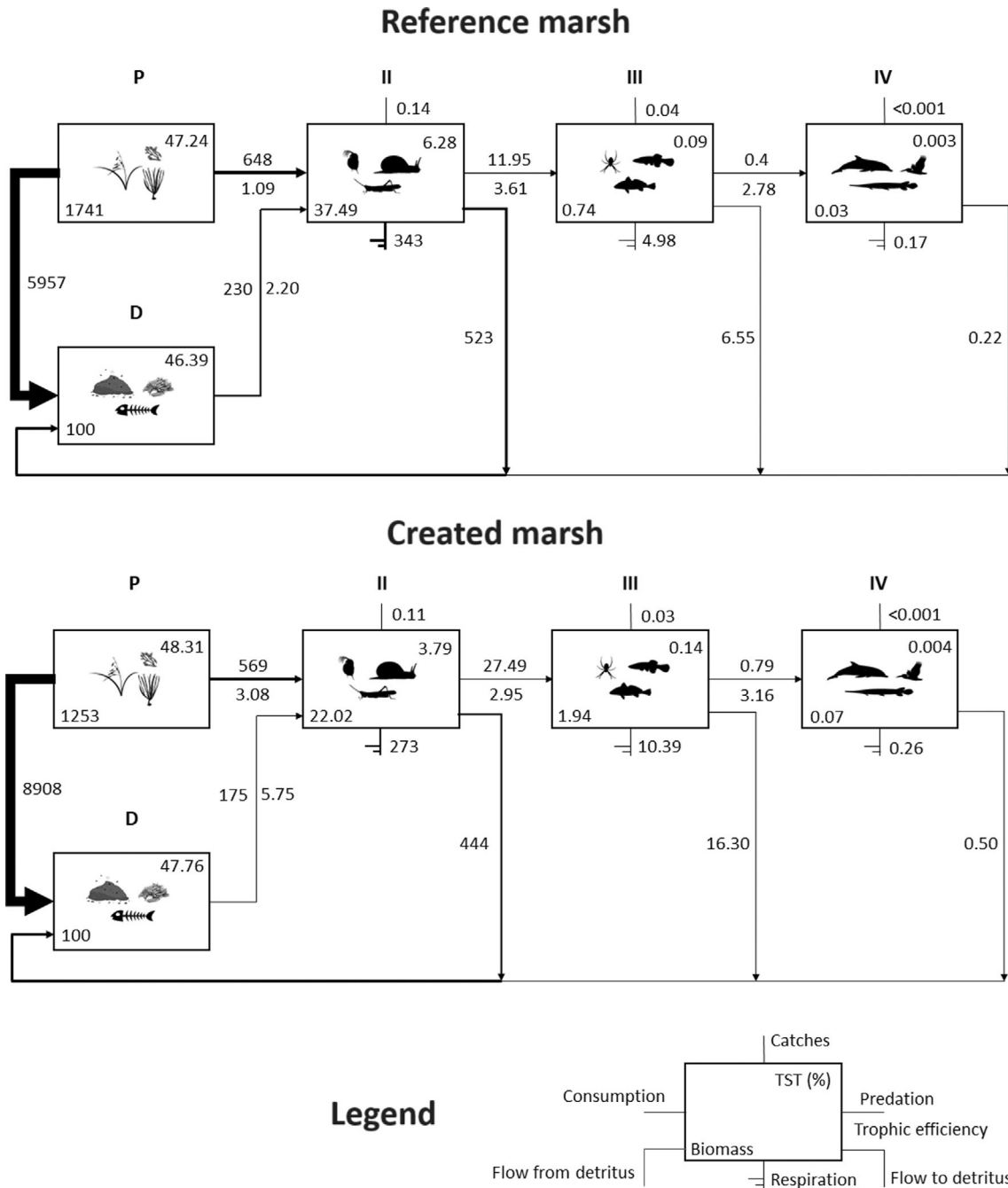


Figure 3. Lindeman spine diagram for reference and created marshes. P represents primary consumers, D represents detritus, II represents the second, III the third, and IV the fourth trophic level. TST stands for total system throughput. Line width is proportional to the magnitude of flow, which is also highlighted in numbers.

sediment grain sizes compared to the reference marshes, which affects species recruitment and colonization to marsh sub-habitats, as well as the typical behaviors of these benthic animals (i.e. burrowing) (Keppeler et al. 2023).

Differences in the physical structure between created and reference marshes may also explain differences observed in some ecosystem attributes. For example, slower material cycling rates and lower importance of detritus in created marsh ecosystems

compared to the reference marshes may be linked to their higher elevation. Marsh elevation reduces the frequency and duration of flooding events, which promotes biomass decomposition (Mueller et al. 2018) and increases the accessibility of off-marsh consumers to biomass material that accumulates in these systems (Keppeler et al. 2021). Thus, even reaching maturity states in the future, created marshes may still not function exactly as reference marshes.

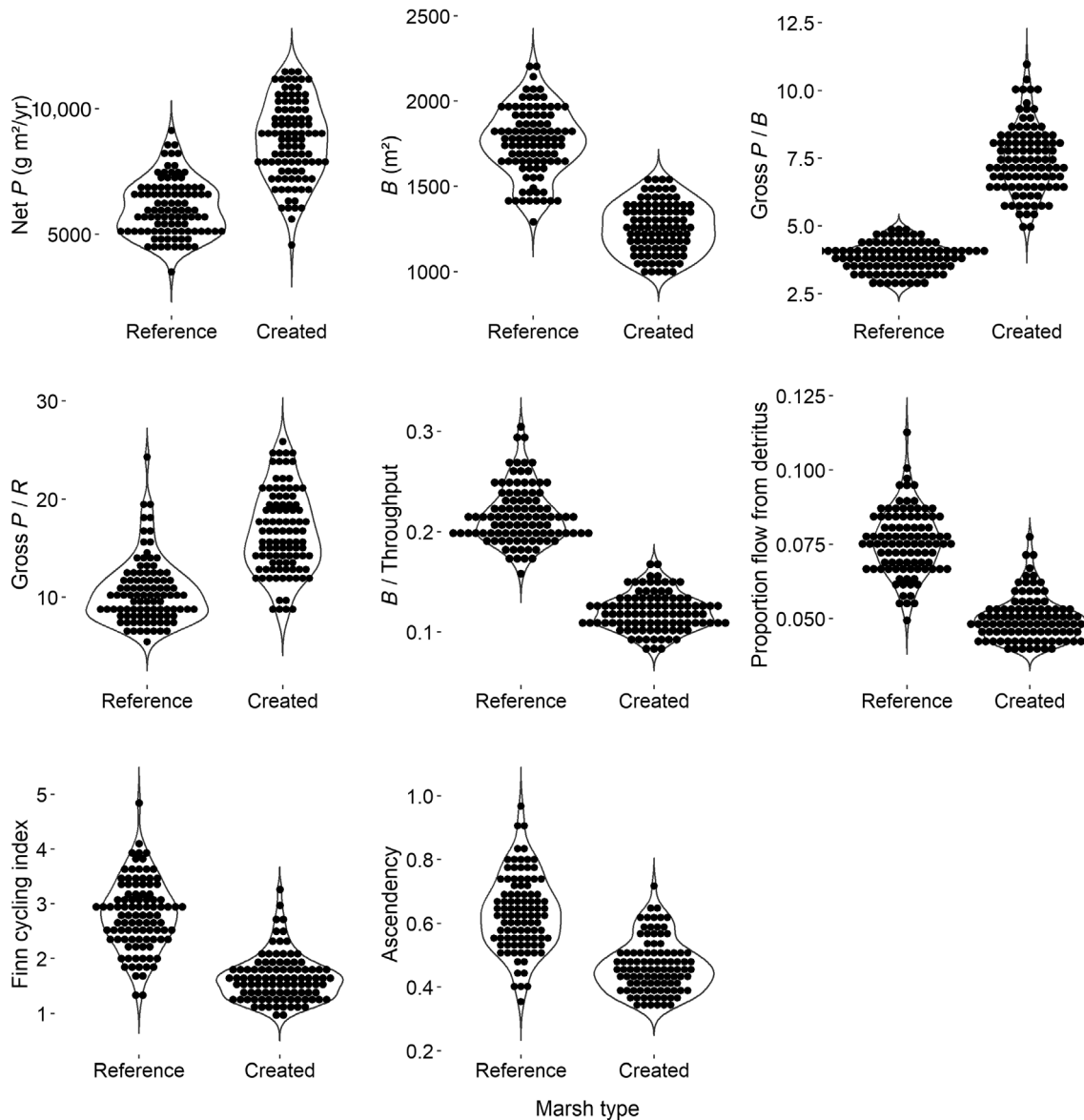


Figure 4. Comparison between reference and created marshes using eight ecological network and information metrics drawn from Odum's theory of ecosystem development (Odum 1969; Christensen & Pauly 1998). Points are output values from 100 different balanced models that were created with the Monte Carlo procedure in Ecopath. All metrics differed significantly between created and reference marshes (Mann-Whitney, p values <0.001).

The provision of ecosystem services is used as a justification to conserve biodiversity and, conceptually, has been applied to assess restoration success in recent decades (e.g. Bullock et al. 2011; Cadier et al. 2020). Here, reference marshes provided greater densities of fishery species and had faster recycling rates than created marshes, which suggests reference marshes provide more valuable ecosystem services than created marshes, at least in terms of fisheries and nutrient cycling. However, created marshes grow fast (i.e. high P/B and P/R) but also slowly accumulate organic matter that could sequester CO_2 from the atmosphere and dampen global warming (Burden et al. 2019). Moreover, the (re)construction of marsh platforms may also reduce the damaging impacts of storms and hurricanes

(Jacobsen 2019) and absorb metal and nutrient contaminants (Ezaz et al. 2020). In this sense, even at earlier development stages, created marsh ecosystems provide valuable services for society. This is important because, depending on the regional geomorphology, climate, and human population burden, coastal marsh loss rates may still exceed creation rates, and like their natural counterparts, created marshes may be lost before becoming a late-stage or climax marsh ecosystem.

Framed within Odum's theory, ecosystem modeling is a powerful approach to evaluate restoration efforts. By looking only at community or population data, as our prior work did (Keppeler et al. 2023), we concluded that created and reference marshes were virtually the same. However, we missed important

differences among emerging properties in the marsh systems. This result highlights how modeling is a key component in understanding and managing ecosystems. Building ecosystem models is also a good exercise for managers because doing so highlights knowledge gaps, guides field surveys and monitoring programs, and allows for the simulation of alternative (re)construction scenarios (Geary et al. 2020).

Should investment in marsh (re)construction continue? We believe that the answer is yes. The top priority should still be to conserve preexisting marshes. However, given the historic and predicted losses of these systems, marsh creation is crucial. Created marshes provide habitats for important coastal species, such that overall species diversity and composition reflect the diversity from the former. Considering the ongoing disturbances at a regional scale that continue to cause marsh losses, created marshes have the capacity to provide valuable services for society and critical ecosystem services, such as nutrient cycling and biomass production, despite their earlier stages of maturity. But, marsh construction has profound implications for ecosystem structure and services. More efforts are needed to better emulate the architecture of created marshes, particularly marsh elevation, substrate composition, and marsh morphology, to avoid undesirable alternative trajectories during ecological succession.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. List of taxa, which had its wet mass estimated from the literature.

Table S2. List of the food web components that had their biomass initially estimated from data available in the literature.

Table S3. Number and type of material sampled for stable isotope analysis for each food web component.

Supplement S1. Diet, P/B, Q/B, and removals.

Supplement S2. Ecopath: diagnostics, model balancing, and model sensitivity to parameter uncertainty.

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