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New perspectives on an iconic landscape from comparative international long-term ecological research

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Abstract. Iconic ecosystems like the Florida Coastal Everglades can serve as sentinels of environmental change from local to global scales. This characteristic can help inform general theory about how and why ecosystems transform, particularly if distinctive ecosystem properties are studied over long time scales and compared to those of similar ecosystems elsewhere. Here we review the ways in which long-term, comparative, international research has provided perspectives on iconic features of the Everglades that have, in turn, informed general ecosystem paradigms. Studies in other comparable wetlands from the Caribbean to Australia have shed light on distinctive and puzzling aspects such as the “upside-down estuary” and “productivity paradox” for which the Everglades is known. These studies suggest that coastal wetlands on carbonate (karstic) platforms have: (1) hydrological and biogeochemical properties that reflect “hidden” groundwater sources of water and nutrients, (2) very productive, mat-forming algal communities that present a low-quality food to aquatic consumers that encourages (3) highly diversified feeding strategies within and among populations, and (4) extensive and productive seagrass meadows and mangrove forests that promote strong cultural dependencies associated with the ecosystem services they provide. The contribution of international research to each of these general ecological topics is discussed with a particular goal of encouraging informed decision-making in threatened wetlands across the globe.

Key words: biogeochemistry; estuary; Everglades; food webs; groundwater discharge; hydrology; ILTER; karstic; LTER; mangrove; periphyton; Special Feature: International LTER; wetland.

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INTRODUCTION

Predicting ecosystem transformation across space and time is a central goal of ecology—one that is supported by long-term studies that capture variability in structural and functional properties of ecosystems and their drivers at relevant scales. As anthropogenic pressures accelerate the pace of change at local to global scales, there are concerns that ecosystems may be interacting in new ways with changing drivers, and perhaps subject to abrupt change in response to novel anthropogenic and climate stressors, or their synergistic interactions. Long-term experiments, measurements, and models that span many years to decades provide invaluable insight to this subject, especially when coordinated across ecosystems of different types that span both spatial and temporal gradients (Collins and Childers 2014). International partnerships such as those forged by the International Long Term Ecological Research (ILTER) Network have provided a mechanism for such large-scale collaborations (Gosz 1996). This paper reviews the ways in which long term research by the Florida Coastal Everglades (FCE) LTER has informed and been informed by ILTER and other collaborative research in coastal and wetland ecosystems across the globe.

The FCE has been characterized as a unique ecosystem, functioning differently from other wetlands in many ways that appear to challenge ecological theories about the drivers and patterns of ecosystem processes and structure (Davis and Ogden 1994). However, systematic comparisons of the Everglades to wetlands with similar climate (subtropical to tropical) and geological conditions support a broader interpretation of distinctiveness applicable to karstic wetlands more generally. These studies also expose limitations of ecological concepts stemming from a historical temperate ecosystem research bias (Gaiser et al. 2012). The Everglades is certainly iconic, with its great expanse of sawgrass meadows grading to thick mangrove forests in spite of oligotrophy, self-perpetuating patterns of ridges, sloughs and tree islands, and extensive estuaries lined by seagrass meadows that provide habitat for myriad distinctive, and economically important, organisms.

Because of its vastness (albeit a remnant of its former extent) and history of scientific inquiry, we

suggest that the Everglades can be used as a beacon for the processes driving transformation in karstic coastal ecosystems, and for creating effective conservation policy for other wetlands. Its large expanse encompasses multiple, interlinked ecosystems, and it has received considerable recent scientific attention in the midst of a massive restoration undertaking (Sklar et al. 2001). With climate change, eyes are on South Florida as rising seas rapidly invade the flat, porous landscape. Balancing the needs of urban development, agricultural production and Everglades restoration is a broadly recognized existential challenge. Change, driven by new and globally linked combinations of human activities and climate drivers, is the root of novelty for this system (Sklar et al. 2005).

This paper is the first to synoptically review the ways in which international research, stimulated by inquiry about the unusual properties of the Everglades, has improved our understanding of coastal subtropical wetlands and helped inform general ecological theory. Research collaborations between FCE LTER scientists and partners studying other wetlands, particularly in the subtropics and tropics from the Caribbean and Central America to Australia, have helped place the structure and function of the Everglades in a broader perspective (Fig. 1). Key areas of inquiry driven by more than a decade of FCE LTER research include: (1) Are all karstic wetlands biogeochemically “upside-down,” with marine sources supplying limiting nutrients to estuaries, rather than the other way around? (2) Are algae paradoxically productive in all karstic oligotrophic wetlands? (3) What shapes food webs in estuarine ecosystems with poor quality basal resources? (4) How can we communicate and protect the ecosystem functions and services of subtropical coastal ecosystems? Here we synthesize results of current science to help respond to these questions.

ARE ALL KARSTIC COASTAL SYSTEMS AND WETLANDS BIOGEOCHEMICALLY “UPSIDE-DOWN”?

The Everglades represents an “upside-down” estuary based upon the supply of nutrients that originate from marine sources, rather than from upland freshwater drainages, as is the case for many other coastal estuaries (Childers 2006). Long-term biogeochemical data have shown that

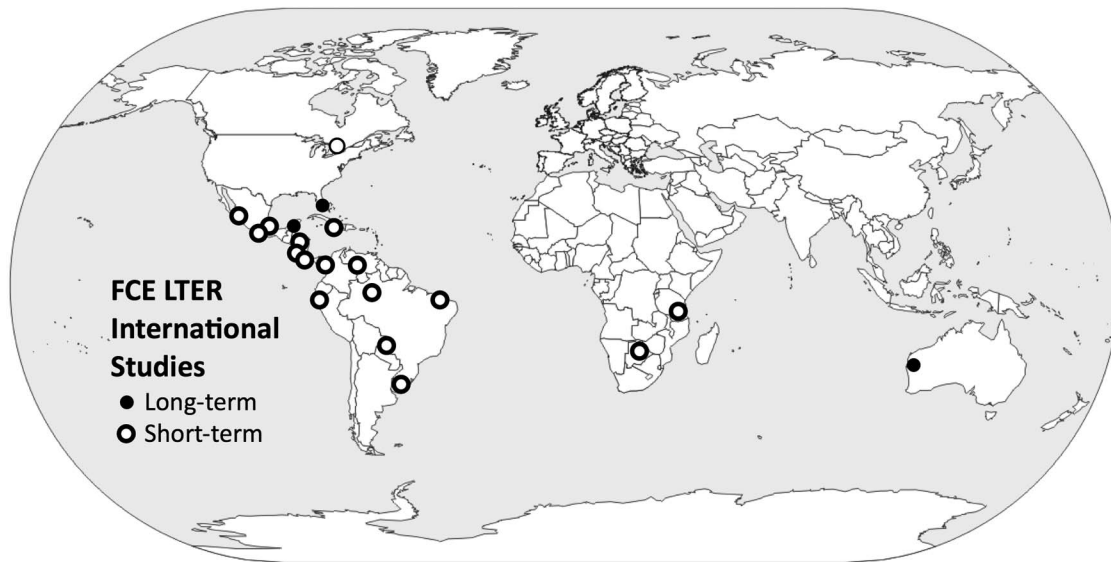


Fig. 1. Locations of long-term (closed circles) and short-term (open circles) collaborative studies coordinated by the Florida Coastal Everglades Long Term Ecological Research program.

tidal exchange with the coastal ocean (Fourqurean et al. 1992) and submarine groundwater discharge (Herbert and Fourqurean 2009) provide the primary supply of the limiting nutrient, phosphorus (P), to the seagrass meadows of Florida Bay. Geochemical tracer studies show that brackish groundwater transports P upstream as seawater intrusion into the coastal aquifer which is accessible to mangrove roots, and thereby promotes production, particularly in the dry season (Swart and Price 2002, Price et al. 2006, Stalker et al. 2009). Where mangrove forests directly meet the Gulf of Mexico, tides and storms provide a supplemental supply of marine-derived P that fuels high rates of production of fringing mangrove forests (Castañeda-Moya et al. 2011). Increases in marine exposure due to sea level rise and delayed restoration of freshwater flows into the Everglades are therefore causing rapid increases in salinity and P in the formerly oligohaline (low salinity, P-limited) ecotone that occurs between freshwater sawgrass marshes and estuarine seagrass meadows and mangrove forests (Saha et al. 2012, Zapata-Rios and Price 2012). Laboratory results suggest that P adsorbs to the limestone and marl sediment of the Everglades in the presence of freshwater, conferring oligotrophy, but desorbs from sediments in the presence of native Florida Bay water

(Price et al. 2010). This key biogeochemical feature of the Everglades suggests that increased marine exposure will further stimulate transgression of mangroves, displacing the iconic freshwater marshes of the Everglades interior (e.g., Smoak et al. 2013).

To determine whether other estuaries located on carbonate platforms are hydrologically and biogeochemically upside-down, similar studies were conducted in the karstic coastal wetlands of the Yucatán Peninsula of Mexico and in Shark Bay, Western Australia (Kendrick et al. 2012, Price et al. 2012). The upside-down nature of Shark Bay was firmly established when it was first identified as a P-limited marine ecosystem (Smith and Atkinson 1983, 1984, Smith 1984). The similar spatial pattern in C:P stoichiometry of seagrasses of Florida Bay (Fourqurean et al. 1992) and Shark Bay (Burkholder et al. 2013a) indicate a common coastal source of P, despite large differences in the water budgets of these two systems (Price et al. 2012; Fig. 2).

While water budgets have been constructed from time series of monitoring data for well-studied estuaries such as Florida Bay (Nuttle et al. 2000), sufficient data for such budgets are lacking for most karstic coastal ecosystems. FCE research has demonstrated that geochemical signatures of various water sources can be used

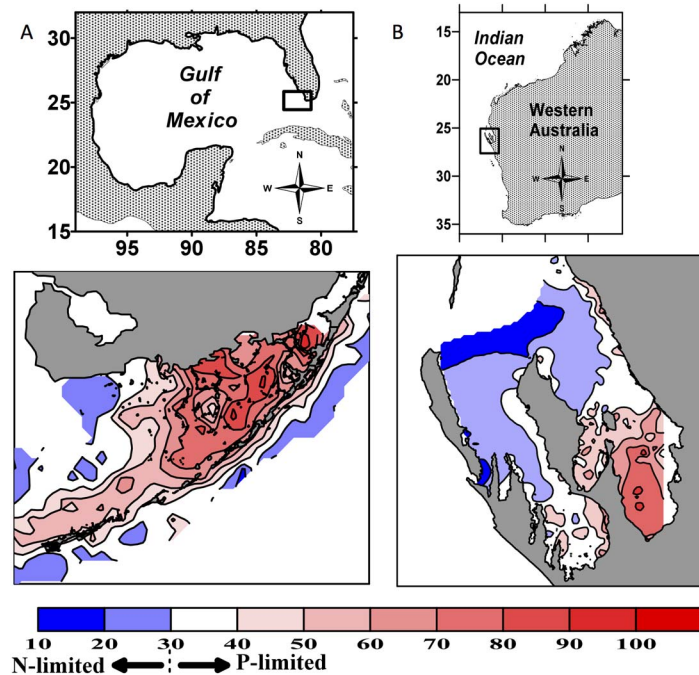


Fig. 2. Isopleths of the molar N:P of seagrasses in both Florida Bay (A) and Shark Bay (B) indicate P-limitation (i.e., N:P > 30) in regions with restricted exchange of water with the coastal ocean, suggesting that the primary source of P for these embayments in karstic terrains is the coastal ocean. Data for Florida Bay from Fourqurean et al. (2005); data for Shark Bay from Burkholder et al. (2013a).

to infer water budgets, and this approach can be applied to less well-studied karstic systems (Nuttle et al. 2000, Price et al. 2012, Stalker et al. 2014). Stable isotopes of oxygen and hydrogen and major cations and anions were used to identify the dominant sources of water (groundwater, surface water, rainfall and seawater) to the estuaries. These studies showed great variability in water budgets across karstic estuaries (Fig. 3). Estuaries in FCE receive most of their water from rainfall and surface water runoff and about 25% from marine groundwater (Saha et al. 2011, 2012, Price et al. 2012, Zapata-Rios and Price 2012). In contrast, estuaries in the Yucatán are almost devoid of surface water flow and instead supported mainly by groundwater inputs (Lagomasino et al. 2014, Stalker et al. 2014). In particular, the Yucatán's Celestún estuary receives brackish groundwater sourced from a "ring-of-cenotes," in addition to local fresh groundwater (Stalker et al. 2014), while the Yucatán's Sian Ka'an estuary receives groundwater from two separate aquifers, one containing

calcium-carbonate and another calcium-sulfate waters (Lagomasino et al. 2014). By comparison, the large, semi-arid, hypersaline estuary of Shark Bay is mainly supplied by marine surface water, receiving little to no groundwater (Price et al. 2012), and only small freshwater inputs from rainfall and surface water runoff from ephemeral rivers.

FCE LTER studies of the upside-down estuary phenomenon have extended to the Caribbean coast of Panama, where coastal and inland bay sediments are primarily comprised of carbonate muds, with peat deposits along the coastal wetland margin (Coates et al. 2005). In the province of Bocas del Toro, the Changuinola peat deposit developed coincident with early Holocene climatic changes in the Caribbean region (Phillips et al. 1997). This peatland is characterized by a P gradient that has been shown to be associated with the sequential development of an ombrotrophic bog leading to progressive P depletion over the last 10,000 years (Phillips et al. 1997, Troxler 2007). Like parts of

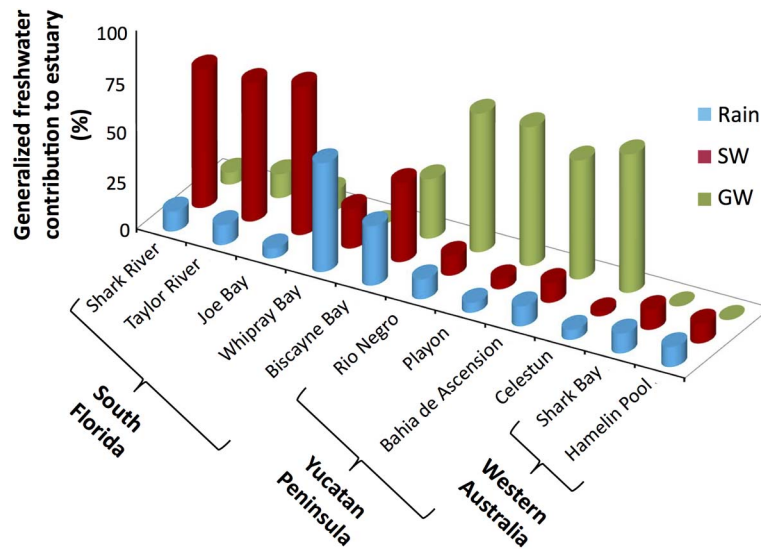


Fig. 3. Generalized relative freshwater contributions from rainfall (Rain), surface water flow (SW) and groundwater recharge (GW) to estuaries in south Florida, Yucatan Peninsula, and Western Australia.

the coastal Everglades (i.e., Ikenaga et al. 2010, Castañeda-Moya et al. 2011), natural gradients in P availability in this Caribbean coastal wetland have been shown to drive community structure and ecological function (Troxler 2007, Troxler et al. 2012). However, rather than solely a function of marine P inputs, very high precipitation has resulted in a raised bog in the interior wetland, resulting in P limitation. Interestingly, increased P limitation occurring from the coast to the interior of Panama appears to be a key driver of plant and bacterial community structure, suggesting this upside-down phenomenon is not restricted to carbonate wetlands, but perhaps a more common feature of subtropical and tropical coastal wetlands (Anderson 1983, Bridgham and Richardson 1993, Chen and Twilley 1999, Paludan and Morris 1999, McKee et al. 2002). These results suggest that the shift towards P limitation found in a coastal Panama peatland was a developmental characteristic associated with ombrotrophic conditions that developed as hydrologic inputs became dominated by precipitation (Anderson 1964, 1983). Thus, this study shows that differentiation of limiting nutrients within geologically short temporal (~1000–4000 y) and small spatial (<1 km) scales, and thus biological-physical feedbacks structuring resource availability, is a more widespread ecological phenomenon.

These hydrological and biogeochemical results have implications for ecological function in the estuaries, as groundwater tends to have higher concentrations of nutrients than surface water, either from anthropogenic inputs or from biogeochemical reactions occurring in the subsurface. The low nutrient supply upstream, high rates of nutrient cycling, and carbonate sediments create P-limited, oligotrophic conditions in the FCE, Shark Bay (Australia), Sian Ka'an (Yucatán) and Bocas del Toro (Panama) coasts. Therefore, changes in surface water and groundwater flows, land-sea interactions, and the concentration of nutrients become important when considering the source and supply of nutrients to each ecosystem. However, neither the classic terrestrial-derived nor “upside-down” nutrient models represent downstream profiles for the Taylor River in FCE and estuarine sites in Sian Ka'an and Panama. At these locations, peak nutrient concentrations occur within the brackish areas of the estuary with lower concentrations upstream and downstream (Price et al. 2006, Zapata-Rios and Price 2012, Lagomasino et al. 2014). Aqueous geochemical indicators in the groundwater and surface water provide strong evidence of brackish, coastal groundwater discharge from the mixing of fresh groundwater with intruding seawater (Price et al. 2006, Zapata-Rios and Price 2012, Lagomasino et al.

2014). High concentrations of P observed in the brackish groundwater at these locations (Price et al. 2006, Zapata-Rios and Price 2012, Lagomasino et al. 2014) have been determined to be a result of water-rock interactions resulting from seawater intruding into a coastal carbonate aquifer (Price et al. 2010). Periodic discharge of the P-laden brackish groundwater to Taylor River has resulted in observed pulses in aquatic metabolism rates (Koch et al. 2012).

Long-term hydrological and biogeochemical studies in the FCE estuaries enabled development of natural tracer methodology for determining water budgets of estuaries in carbonate terrains and in hypersaline estuaries around the world. Studies in carbonate estuaries with contrasting hydrologic regimes helped unravel the complex water exchanges mediated by porous subsurface limestone. While not all karstic estuaries are “upside-down”, these cross-system comparisons show that marine-derived groundwater can travel considerable distances, up to 30 km in the Everglades, to the interior of coastal wetlands (Price et al. 2006). The geochemical transformations driven by underground marine water sources have important implications for interpreting and modeling changes in water delivery to coastal subtropical estuaries relative to changes in management of freshwater flows, climate and sea level.

ARE ALGAE PARADOXICALLY PRODUCTIVE IN ALL KARSTIC OLIGOTROPHIC WETLANDS?

One pervasive and perplexing feature of karstic freshwater wetlands is the proliferation of calcareous mats of algae, cyanobacteria and other microbes (hereafter termed “algal mats”), which in the Everglades extend from freshwater sawgrass prairies through to the shallow marine seagrass meadows. Researchers have puzzled over the level of production observed in these communities relative to the amount of P available (usually total P in Everglades water is $<10 \mu\text{g P L}^{-1}$), calling it the “paradox of production” (Gaiser et al. 2012). FCE studies have shown that net primary production of algal mats in the freshwater marshes rivals that of native sawgrass communities (Gaiser et al. 2011), unless exposed to unnatural sources of P, which cause the mats to dissociate and disappear (Gaiser et al. 2006).

Similarly, high standing stocks of calcareous green macroalgae (particularly *Halimeda* and *Penicillus*) and associated microflora have been measured in Florida Keys and estuaries (Collado-Vides et al. 2005, 2007, Frankovich et al. 2009), where water nutrient concentrations are among the lowest in the world. Other research has documented expansive algal mat-forming assemblages in karstic regions of Belize and the Yucatán Peninsula (Rejmánková and Komárkova 2000, Novelo et al. 2007) and similarly productive macroalgal assemblages in shallow, oligotrophic embayments (Bach 1979, Hillis 1997, Van Tussenbroek and Van Dijk 2007). However, no comparative analysis has been completed to understand the origins and generality of this apparent production paradox.

FCE LTER researchers conducted explorations of freshwater coastal wetlands in the karstic landscapes of Sian Ka'an Biosphere Reserve in Mexico, New River Lagoon in Belize, and Black River Morass in Jamaica to determine the biomass, P content, and composition of algal mats and abundance of aquatic consumers in these comparable wetlands (La Hée and Gaiser 2012, Gaiser et al. 2012). Additional collections from temperate habitats were conducted using the same methodology in the dolomite limestone wetlands (“alvars”) surrounding Lakes Huron, Erie and Michigan. Calcareous mats dominated by filamentous cyanobacteria (particularly *Schizothrix* spp. and *Scytonema* spp.) were abundant throughout all of these wetlands. Phosphorus content within these mats, which often serves as an excellent indicator of P enrichment history in oligotrophic wetlands (Gaiser et al. 2006), matched that of the Everglades, with slightly higher values in the temperate systems. The subtropical and tropical diatom assemblages were compositionally similar, and all of the taxa previously denoted as endemic to the Everglades (i.e., Slate and Stevenson 2007) were encountered elsewhere. Composition of north temperate mats was compositionally similar at the genus level, but did not contain species that appear to be restricted to the subtropical and tropical mats (La Hée and Gaiser 2012).

To place benthic algal biomass and P values in perspective, an extensive literature search was completed to support a meta-analysis across a broad range of aquatic ecosystem types. A total

of 118 publications were found to report both algal biomass and P content from shallow aquatic systems including artificial flow-ways (19), wastewater effluent (7), freshwater marshes (5), lake littoral zones (12), ponds (7), rivers (11), salt marshes (5), streams (20), the Everglades (27) and other karstic wetlands in the Yucatán, Belize, Jamaica and Canada (Fig. 4). These values are reported in a variety of units in the literature, so standard approaches were used to convert all values to g m^{-2} and $\mu\text{g P g}^{-1}$ dry mass. Findings support prior conjecture that (1) biomass in karstic wetlands is at least an order of magnitude higher than reported for other systems, including those receiving external supplies of nutrients; and (2) P content in algal mats is much lower than most other aquatic systems. The causes for low values of P have been discussed elsewhere (Noe et al. 2001); in part, these ecosystems are naturally depleted in P because of scavenging of P by limestone bedrock and marl soils. Available P is quickly removed from the water column by microbes in the algal mats, and evidently rapidly cycled within these complex mat assemblages to accrue such high biomass. Notably, although the absence of a standard procedure to estimate algal productivity in shallow systems prohibited a similar meta-analysis, reviews such as Vymazal (1995) and Goldsborough and Robinson (1996) support the hypothesis that these mats are also turning over at high rates relative to nutrients available, and relative to algal communities in other types of wetlands. Importantly, turnover and metabolic rates appear to vary depending on the scale of measurement, leading to a key uncertainty in the development of carbon (C) budgets for the Everglades (Troxler et al. 2013).

Marine macroalgal and calcium carbonate (CaCO_3) production has been measured using consistent methodology by FCE LTER researchers in Florida Bay and by Mexican colleagues in Quintana Roo and the Yucatan; values range from 42–797 $\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ (annual mean 131 $\text{g C m}^{-2} \text{ yr}^{-1}$) in South Florida (Davis and Fourqurean 2001; L. Collado-Vides, *unpublished data*) compared to 580–1051 $\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ (annual mean 103 $\text{g C m}^{-2} \text{ yr}^{-1}$) in the Mexican Caribbean (Van Tussenbroek and Van Dijk 2007). The abundance of calcifying algae in South Florida and the Caribbean appears to be related to P-limitation; growth inhibition has been exhibited in

areas with elevated levels of P (Demes et al. 2009). Ongoing collaborations are attempting to resolve the potentially significant role of this community in the C cycle in shallow marine embayments. The expansive seagrass communities are known to be important sinks for “blue carbon” in the Caribbean and elsewhere, but the role of calcareous green algae in C sequestration is unclear. It is likely that their contribution is more highly regulated by the conditions affecting calcite precipitation (a net CO_2 source) versus organic C production (a net CO_2 sink), which is of particular interest as changing salinity and increased pCO_2 in marine waters is changing the conditions for, and potentially reducing, biogenic calcification (De Beer and Larkum 2001). It appears the potential for calcareous macro- and microalgae to alter the C cycle through inorganic and organic transformation is strong, especially in karstic subtropical and tropical systems where production rates remain high year-round (Troxler et al. 2013).

WHAT SHAPES FOOD WEBS IN ESTUARINE ECOSYSTEMS WITH POOR QUALITY PRIMARY RESOURCES?

Although calcareous mats of microalgae and macroalgae are abundant throughout the Everglades, studies of aquatic consumer abundances and diet suggest this is a low quality basal resource, owing to dominance by unpalatable cyanobacteria and an abundance of calcium carbonate crystals (Geddes and Trexler 2003, Chick et al. 2008). Instead, detrital organic matter (DOM) generated by palatable algae and macrophytes appears to form the base of most Everglades food webs (Williams and Trexler 2006). For this reason, the abundance, movement and fate of dissolved and particulate organic matter (POM) has been an important area of investigation in coastal Everglades research (Neto et al. 2006, Xu and Jaffé 2007, Chen et al. 2013). Data on the optical properties of DOM in the FCE are now available at unusually large spatial and temporal scales (Yamashita et al. 2010, Chen et al. 2013), which led to the development of DOM reactivity proxies to study the degradation of this important OM pool. The excitation emission matrix (EEM) fluorescence technique that was used to develop a parallel factor analysis (PARAFAC) model for the Ever-

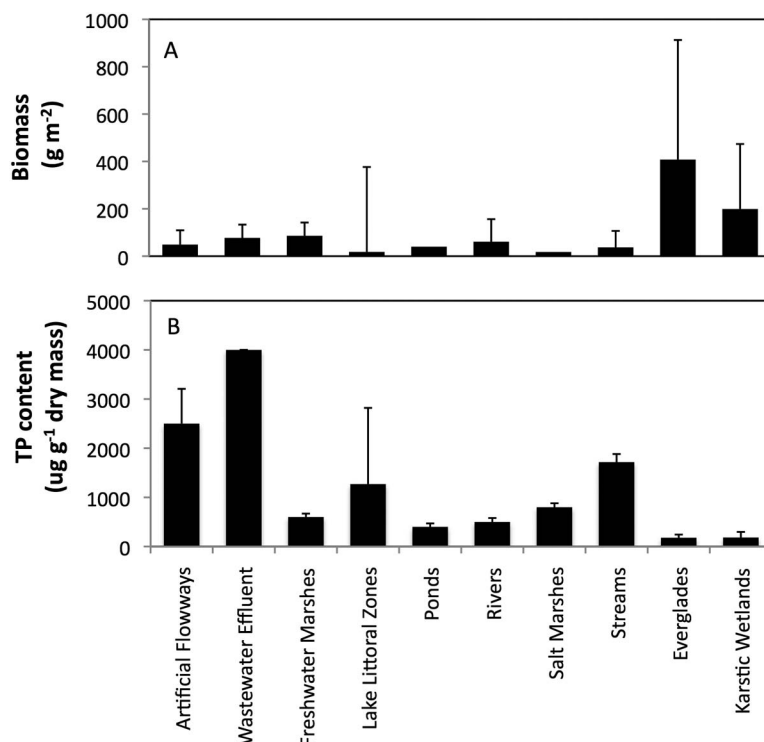


Fig. 4. Ash-free dry mass (A) and total phosphorus content (B) of attached algal assemblages across 118 aquatic ecosystems, illustrating the relatively high standing stocks relative to phosphorus content in the Everglades and other karstic freshwater wetlands.

glades (Yamashita et al. 2010) was strongly influenced by photo-degradation compared to bio-degradation, possibly as a result of P limitation. This FCE-based model was successfully applied to DOM studies in the Okavango Delta (Botswana; Cawley et al. 2012b) and the Pantanal (Brazil) and suggested similarities in the DOM composition and reactivity across subtropical wetlands. Photochemical reactivity proxies established for Everglades DOM (Chen et al., 2010) were found to be equally applicable to the Okavango Delta DOM pool (Cawley et al. 2012b). In addition, we applied the EEM-PARAFAC approach in combination with stable C isotopes to both Florida Bay (Maie et al. 2012; Ya et al. 2015) and Shark Bay (Cawley et al. 2012a) to assess the contribution of living and senescent seagrass to the DOM pool. While seagrass communities were found to be significant contributors to the DOC pool based on C release through exudation during primary productivity, these studies determined that release of DOC

through leaching from senescent seagrass also contributes to the DOC pool. The DOM dynamics in FCE estuaries (e.g., Cawley et al. 2013) also were compared to those in wetland-influenced coastal rivers in Japan and Malaysia (Watanabe et al. 2012, 2014, Maie et al. 2014). These cross-continental studies suggest that wetland-influenced coastal rivers can have highly variable DOC concentration and composition in the low salinity zone due to differences in hydrology and geomorphology, and the associated interplay between soil and primary productivity related DOC sources (Maie et al. 2014). While the effects of climate on DOM characteristics were less clear, our studies suggest that climate change might not only affect DOC fluxes but also the quality of the exported DOC (Watanabe et al. 2012).

DOM reactivity studies in the FCE led to a much larger international study of the presence of refractory OM in aquatic ecosystems. The low bioavailability of Everglades DOM led to detailed elemental and molecular characterizations

(Lu et al. 2003, Maie et al. 2005, 2006) which showed enrichment in fire-derived, pyrogenic OM such as dissolved black carbon (DBC) and dissolved black nitrogen (DBN). DBC contribution in the FCE could be as large as 20% of the DOM, which prompted studies of DBC and DBN levels in streams throughout the US LTER network (Jaffé et al. 2012, Ding et al. 2014b), other large subtropical wetlands (Ding et al. 2014a), and ultimately determining the global riverine contribution of DBC to the oceans (Jaffe et al. 2013). These studies allowed us to constrain the pyrogenic C cycle by determining the amount of charcoal that is lost from soils globally through dissolution and ultimately exported by rivers.

The refractory nature of C in coastal karstic wetlands was also shown in Shark Bay, Australia where mangrove productivity contributes little to food webs, even within mangrove creeks (Heithaus et al. 2011). Earlier research suggested that C produced by seagrasses entered estuarine food webs through detrital pathways rather than by direct grazing (Valentine and Heck 1999, Mateo et al. 2006). However, our comparative work suggests both a direct grazing pathway for C from seagrasses to higher trophic levels as well as a potentially large influence of direct seagrass grazing on seagrass community structure. We have learned that small-leaved, fast-growing seagrasses are preferentially grazed over larger, slower-growing seagrass species both in south Florida and in Western Australia (Armitage and Fourqurean 2006, Burkholder et al. 2012), and that the oligotrophic conditions of these two karstic ecosystems leads to a dominance by slow-growing, less palatable seagrass species (Fourqurean et al. 2001, Burkholder et al. 2013a). Patchiness in nutrient supply in the otherwise oligotrophic landscape can lead to patches of fast-growing, more palatable seagrasses (Dewsbury and Fourqurean 2010, Burkholder et al. 2012) and grazing on those preferred species can control the species composition of the seagrass meadow (Armitage and Fourqurean 2006, Burkholder et al. 2013b). Despite these top-down effects of grazers in seagrass beds, the ecosystem-scale relevance of direct grazing on seagrasses is still open to debate. Even in seagrass-dominated systems like Shark Bay, stable isotope tracers indicate that seagrass-derived C dominates the biomass within the food web (Burkholder et al.

2011), yet fatty acid tracers of biomass origin suggest that much of this seagrass-derived C must first pass through the microbial loop before being incorporated into higher trophic levels (Belicka et al. 2012). In addition, long-term data from both FCE and Shark Bay showed that climatic disturbances such as cold snaps and heat waves can override top-down-control of seagrass community structure (Matich and Heithaus 2012, Thomson et al. 2015), and have directly led to new hypotheses about the role that predators will play in determining post-disturbance recovery trajectories of Shark Bay seagrasses. This body of work has supported the hypothesis that seagrasses can be considered in semi-equilibrium with water quality on a regional scale (Fourqurean et al. 2003, Herbert et al. 2011), and has helped us to design experiments that will in the future help disentangle the relative strengths of top-down and bottom-up processes in determining the disturbance recovery of seagrasses. These studies will provide important insights into the role of trophic downgrading (reduction in abundance of apex predators) in disrupting ecosystem resilience in coastal systems.

Comparative research across oligotrophic estuaries is suggesting that top predators play an under-recognized role in structuring prey and primary producers in nutrient-limited settings. In Shark Bay, studies of behavioral decisions—particularly anti-predator behavior—have been conducted to examine impacts of predators on ecosystem structure (Heithaus et al. 2012). Tiger sharks are an important top predator in the bay, and induce habitat shifts in multiple prey species (e.g., dolphins, sea cows) that cascade to influence seagrass community structure (Heithaus et al. 2012, Burkholder et al. 2013b). These studies were conducted at the population level and did not consider how intraspecific variation in behavior might modify the ecological roles of particular species. Our work in the coastal Everglades took on an individual-behavior framework, identifying considerable individual variation in the behavior of large predators (bull sharks, *Carcharhinus leucas*, Matich et al. 2011; American alligators, *Alligator mississippiensis*, Rosenblatt and Heithaus 2011). These individual behaviors, measured using a combination of acoustic tracking techniques and stable isotope analyses, included differences in responsiveness to trade-

offs (food-risk and food-salinity stress, respectively). The success of these techniques and resultant discoveries led to investigations of patterns of individual behavioral variations among major predators in Shark Bay. These studies suggest that the degree of individual behavioral and dietary variability varies by species: tiger sharks (*Galeocerdo cuvier*) and loggerhead turtles (*Caretta caretta*) appear to exhibit less variability than predators in the coastal Everglades (Matich et al. 2011, Thomson et al. 2012), while others—including a diversity of rays (Vaudo and Heithaus 2011) and green sea turtles (Burkholder et al. 2011)—exhibit considerable variability among individuals. Studies on the diets of these consumers in both Florida Bay and Shark Bay using fatty acids and stable C, N and S isotopes confirmed the importance of individual variation in feeding behavior (Belicka et al. 2012), suggesting that future food web studies need to incorporate large sample sizes to account for this variability.

These results have important implications for our understanding of community dynamics in estuaries. Especially in marine ecosystems, not only are entire populations of species considered to be functionally identical, but guilds of predators often are lumped into single functional units for modeling purposes. The finding that there can be large variation within populations in behavior and ecological roles suggests that such assumptions likely are not universally valid and could lead to inaccurate predictions about how anthropogenic factors might modify community and ecosystem dynamics. By integrating studies in Shark Bay, FCE and others from around the world, we are working to develop a better understanding of the drivers of specialization within to predator populations (e.g., Bolnick et al. 2003).

PRESERVING AND COMMUNICATING THE ROLE AND SERVICES OF SUBTROPICAL COASTAL ECOSYSTEMS

By focusing on the poorly understood interface between freshwater marshes and mangrove forests, the FCE LTER program has brought new attention to the importance of resource exchange at this ecotone to the levels of production of mangrove forests. Where exposed to tidal and storm exchange with P-enriched

marine water, FCE data on atmospheric CO₂ exchange and ground-based measures of biomass turnover reveal that mangrove forests can attain productivity levels similar to those measured for tropical rainforests (~1100 g C m⁻² yr⁻¹; Barr et al. 2011, Rivera-Monroy et al. 2013). Comparisons of mangrove productivity aided by international LTER collaborations suggest these high values, promoted by biogeochemical and hydrological forces unique to subtropical karstic estuaries, typify the Caribbean region (Rivera-Monroy et al. 2008, Castañeda-Moya et al. 2010, Jardel et al. 2013, Stalker et al. 2014). Because climate disturbance is such a critical modulator of these biogeochemical and hydrological controls, collaborations between FCE and Mexican Long-Term Ecological Research Network (Red Mexicana de Investigación Ecológica a Largo Plazo) researchers are underway to identify gaps in climatological datasets and in our understanding of the frequency, duration and degree of impact of different types of disturbances structuring these forested wetlands (Calderon-Aguilera et al. 2012, Farfán et al. 2014).

Since the FCE encompasses the largest area of mangrove forests in the continental USA, it has provided fertile ground to develop hypotheses regarding the role of a wide range of drivers (e.g., deforestation, eutrophication, urban development) on the sustainability of mangrove resources (e.g., water quality, habitat, fisheries) for a wide variety of locations, such as in Central and South America. A framework was developed based on FCE studies to promote the establishment of different LTER sites in the Caribbean region to achieve a basin-scale synthesis (Rivera-Monroy et al. 2004). New collaborations of FCE researchers with scientists in Colombia, Ecuador, Honduras, Venezuela, Costa Rica and Brazil were added to those already developed in Mexico (Suarez-Abelenda et al. 2014) to determine mangrove C storage and productivity using remote sensing tools (Simard et al. 2008). These studies will also generate regional maps of short- and long-term changes in land use to determine the differentiated vulnerability of mangrove forests in the Americas to land use change and disturbance. The proof of concept in the application of such remote sensing techniques began in the FCE mangrove ecotone region (Simard et al. 2006, Zhang et al. 2008), and now has allowed

further expansion in other mangrove dominated coastal regions around the world (Fatoyinbo et al. 2008, Simard et al. 2012, Lagomasino et al. 2015). Notably, these studies integrate social science analytical frameworks with the remote sensing data to go beyond identifying the types or proximate sources of change (e.g., mangrove conversion to shrimp ponds, agriculture, urban uses) to evaluating the causal drivers of that change (e.g., population growth, local/global markets for fisheries or agricultural commodities, policies, land tenure, etc.).

Since FCE LTER studies also aim to evaluate the influence of socioeconomic and cultural drivers in mangrove resource utilization and conservation, which vary from country to country, comparative studies have been developed in less-developed countries (e.g., Tanzania, Africa) to determine the role of socioeconomic factors such as poverty traps (self-reinforcing poverty cycles) in the management of mangrove resources. This collaborative work has enabled the FCE LTER program to provide coastal management and mangrove rehabilitation protocols for economically critical coastal areas (e.g., Magdalena River delta, Colombia; Gulf of Fonseca, Honduras [Castañeda-Moya et al. 2006]; Guayas River, Ecuador) in Latin America (Rivera-Monroy et al. 2006, 2011, Simard et al. 2008), advancing our understanding of the interaction between policy decisions and socioeconomic conditions when developing resource management programs in coastal regions in tropical latitudes (Uchida et al. 2014; Fig. 5). This is particularly significant in the neotropics where mangrove restoration programs have failed due to the lack of information about the relative importance of critical environmental variables (i.e., soil fertility and hydroperiod) in regulating plant growth that should be used to select performance measures for effective restoration efforts (Twilley and Rivera-Monroy 2005, Lewis 2009). FCE research has provided the context and inspiration for comparative mangrove research across the Americas and elsewhere, including integrating spatially intensive and extensive datasets to derive multi-scale mangrove/land-use change models. Such models are critical to evaluating geographically differentiated patterns and dynamics in mangrove structure and function, and in the derivation of flexible scenarios of mangrove vulnerability that

can inform conservation policy.

FCE LTER researchers and their international partners are working together to communicate the results of this research in a variety of venues that are accessible throughout the community and across cultures. In a rapidly changing, technological world, global communications are cultivated via sound bytes, tweets, and posts. The ILTER Network fosters such remote as well as face-to-face exchanges, connecting local communities, particularly youth, to science to improve local decisions and their global impacts. A good example is the partnership between FCE LTER and the Association of American Geographers Global Connections and Exchange Program that deepens the site's ability to exchange science across Latin American cultures. This program connects US students with their counterparts in Bolivia, South Africa, and Panama through programs that use geotechnologies to study climate change and the environment. Students received academic preparation, orientation, mentoring and training in the use of geotechnical tools, and studied the impact of climate change on hurricane frequency in the FCE and on habitats in Bolivia in self-organized, cross-cultural teams. Linking scientific research to communities in an accessible format is essential to building a better understanding of the importance of sustained, integrated, long-term ecological research. Participatory science and connecting ecological research with visual and multimedia presentations provide tangible products and experiences that translate across continents, social communities, and ecosystems. The LTER/ILTER Network provides an essential platform for collaborating and integrating community based, cross-cultural programs that engage our current and future decision makers in developing sound ecological policies.

CONCLUSIONS AND FUTURE DIRECTIONS

Additional studies of estuaries in other coastal regions of the world are currently underway or in planning, drawing upon the scientific approaches employed in the FCE LTER and the lessons learned about estuary structure and function from the Everglades region and other coastal wetlands mentioned here. For example,

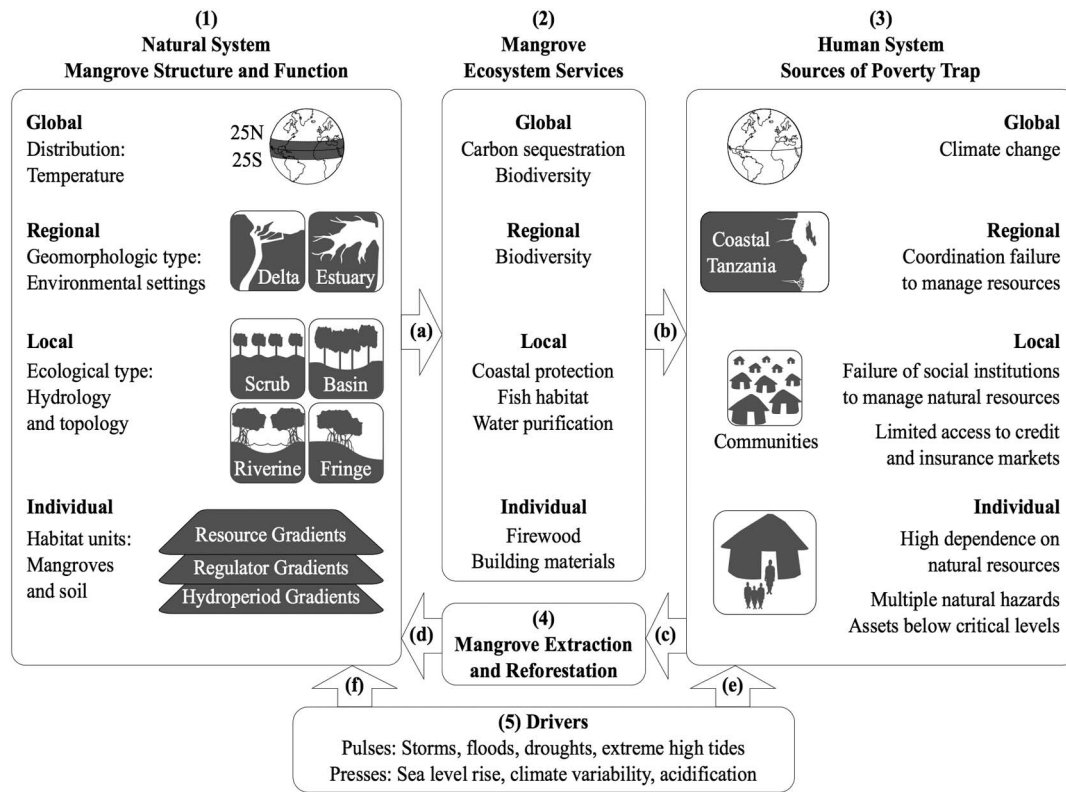


Fig. 5. Depiction of the ecosystem service and poverty trap framework applied to mangrove habitats in developing countries (Uchida et al. 2014).

estuaries along the East African coastline are likely candidates for future detailed investigation, and scientists involved with the FCE LTER have already begun a series of baseline ecological assessments in the Wami and Ruvu River estuaries in Tanzania (Anderson et al. 2007; A. Saha, *unpublished data*). Both of these rivers are highly seasonal systems, with quite distinct wet and dry season and corresponding high and low flow periods. During dry season low flows, saltwater fills the Wami River estuary, extending at least 20 km upstream from the river mouth (Anderson et al. 2007). Additionally, pressure to meet human demands for water for agriculture and industry—and in the near future for hydro-power—is resulting in an increasingly altered hydrologic regime and lowered flow to estuaries. Similar to the FCE, Saadani National Park, the newest in Tanzania's extensive system of protected areas, surrounds much of the Wami River estuary, and is home to several large predatory animals (e.g., crocodiles, lions) and terrestrial

species with strong aquatic ecosystem linkages (e.g., hippopotamus). Several questions asked in the FCE system are applicable here. Are the Wami and Ruvu upside-down estuaries, given the strong seasonality and extent of saltwater intrusion? How do large predators influence ecosystem structure and function? How do terrestrial wildlife, like hippopotamus, influence nutrient dynamics in East African estuaries, given the tendency to feed on terrestrial vegetation and reside in water bodies, excreting nutrients? What are the strengths and assets of human populations that can be put to work for protection of East African estuaries? Approaches already employed to investigate these kinds of questions in the FCE, as well as the direct involvement of FCE LTER scientists, can aid in unraveling the complexities of East African and other estuaries worldwide.

Through comparative studies in other subtropical and tropical wetlands, the iconic features of the Everglades have been placed in a larger

context to inform more general ecological theory. Long-term hydro-ecological research in coastal karstic systems suggest that textbook diagrams depicting estuaries as a conduit for energy and material transport to the sea may need to be redrawn to include the process of landward brackish groundwater intrusion as a potential mechanism for nutrient delivery to upstream oligotrophic ecosystems. This groundwater nutrient transport can provide a “hidden” fuel for production in P-starved ecosystems. Geographic expansion of LTER productivity studies throughout the subtropics suggest that these systems, albeit oligotrophic, contribute significantly to global C fluxes, including a substantial benthic algal contribution that can no longer be ignored. The apparent paradox of high rates of algal production despite low nutrient concentrations suggestive of oligotrophic conditions is ubiquitous in karstic wetlands, suggesting rapid recycling of nutrients within complex algal mats. Limited palatability of calcareous algal mats to aquatic consumers may imply an evolutionary role of grazers in shaping community structure. Dominance of recalcitrant DOC in karstic estuarine settings may also explain low secondary (consumer) biomass there, and perhaps is the source of variability in diet within populations of species. Finally, rapid climate and land use changes pose a severe threat to the persistence of coastal freshwater and estuarine resources, requiring a socio-ecological framework for transforming scientific knowledge to practices that promote resource protection and conservation. For this reason, FCE researchers have not only been advancing science locally through co-production with resource managers, but also providing a framework for building resilience in even more vulnerable regions throughout the tropics. To this end, educational initiatives have been a major component of internationally coordinated LTER efforts in the tropics with the goal of building environmental literacy in all communities and encouraging long-term sustainability of critical coastal resources.

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