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INTEGRATED CARBON BUDGET MODELS FOR THE EVERGLADES TERRESTRIAL-COASTAL-OCEANIC GRADIENT

Current Status and Needs for Inter-Site Comparisons

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#### INTRODUCTION

The future of coastal wetland ecosystems is uncertain due to a combination of climate change impacts (sea level rise, changes in storm activity, altered freshwater availability) and human activities (population growth, changes in resource and land use). Consequences of coastal ecosystem loss are not limited to the regional services they provide (e.g., storm mitigation, aquifer recharge, fisheries) but rather extend globally through impacts on biodiversity, biogeochemical cycling, and atmospheric interactions. For instance, recent studies show that vegetated coastal systems store up to 50 times more carbon (C) than tropical forests (1,000 Mg organic C ha<sup>-1</sup>) due to high productivity and low C loss through respiration (Bouillon, 2011; Mcleod et al., 2011; Fourgurean et al., 2012b). Studies examining patterns and controls on

long-term spatial and temporal patterns in C gain and loss in coastal wetlands will reduce uncertainty about their persistence and the future of related ecosystem services from local to global scales.

The Florida Everglades contains wetlands that have been profoundly transformed through a history of largescale land conversion and water diversion (Figure 1). These wetlands are now exceptionally exposed to added pressures of sea level rise, changes in storm frequency and severity, and extreme weather perturbations (i.e., drought or alterations in the timing of rain events; IPCC, 2007). The unprecedented landscape-scale restoration of the Everglades is expected to improve freshwater flow to coastal wetlands, but the degree to which restoration will mitigate the effects of sea level rise and storms, as well as how it will interact with activities of the

9 million residents in the watershed, is uncertain. Thus, the Everglades ecosystem is an exemplary model for the types of exposures threatening coastal wetlands globally. Long-term studies facilitated by the Florida Coastal Everglades Long Term Ecological Research (FCE LTER) project are providing uncommon and valuable insight into how changes in freshwater supply and climate variability interact to affect C gains, losses, and storage in the coastal wetlands. Such insights are critical to determining longterm C persistence in the face of change (DeLaune and White, 2012).

Until recently, little was known about C cycling, mechanisms controlling its variability in coastal ecosystems (Mcleod et al., 2011), or the relevance of coastal C cycling to global biogeochemical cycles (Donato et al., 2011). Initial C balance approaches applied in South Florida coastal ecosystems have shown that mangrove forests sequester globally relevant quantities of C at rates that are sensitive to climate change and disturbance (Twilley et al., 1992; Bouillon et al., 2008; Barr et al., 2012; Breithaupt et al., 2012; Malone et al., 2013). Because coastal wetlands are often characterized by tidal action or flowing water, their carbon budgets must also take into account exchange over the water-atmosphere interface and exchange of C due to lateral transport (i.e., aquatic C entering and exiting the ecosystem). In this paper, we present estimates of net ecosystem C balance (NECB), net ecosystem exchange (NEE), and aquatic C flux for Everglades freshwater marsh, mangrove forest, and seagrass ecosystems, where available, to make strides toward C budget estimates for these systems. We also identify areas of study that will reduce

uncertainty in these estimates and their drivers, and point out discoveries that can emerge from regional and global comparisons using consistent approaches and methodologies.

# FLORIDA COASTAL EVERGLADES STUDY AREA

The FCE LTER site is situated in Everglades National Park, which can be thought of as a series of linked habitats that include freshwater marshes, mangrove forests, and subtidal areas where seagrasses are the dominant producers. Freshwater marshes are characterized by flooding, with hydroperiods as short as 0–6 months or as long as 9–12 months of the year. They are dominated by sawgrass, spikerush, and expansive mats of periphyton (an assemblage of microorganisms including algae, bacteria, and fungi; Gaiser et al., 2012). Everglades periphyton assemblages form mats that are dominated by calcium carbonate (30-50% of dry mass), and their residual C is primarily detrital (Donar et al., 2004), with autotrophic and heterotrophic microbes comprising the small remainder of biomass. These freshwater marshes grade into mangrove forests through an "oligohaline ecotone" that expresses marked variability in salinity and nutrient availability, depending on freshwater flows and marine exposure (Rivera-Monroy et al., 2011; Troxler et al., 2013). Mangrove forests vary from short to tall, and most are influenced by semidiurnal tides (Chen and Twilley, 1999; Ewe et al., 2006). Shallow seagrass ecosystems (with associated macro- and microalgal assemblages) dominate the southwestern estuaries of Florida Bay. A mix of seagrass beds dominated by Thalassia testudinum and calcareous rhizophytic macroalgae of Halimeda and Penicillus spp. covers the Florida Bay subtidal marine



Figure 1. Florida Coastal Everglades Long Term Ecological Research (FCE LTER) site map, including locations of 14 biophysical research sites (red dots) along transects through Shark River Slough and Taylor Slough into to Florida Bay within Everglades National Park (ENP). Cross-cutting research will extend beyond these into the South Florida Urban Gradient to examine socio-hydrological underpinnings of current, past, and future conditions in the oligohaline ecotone. Map created by M. Rugge

environments. Distribution of seagrass species and macroalgae assemblages responds to salinity and nutrient gradients (Zieman et al., 1989).

The FCE LTER study design employs a transect approach (Figure 1) to track water flow and ecosystem properties along the two main Everglades drainages, Taylor Slough/Panhandle (which has a short hydroperiod) and Shark River Slough (which has a long hydroperiod). Research sites along these two freshwater flowpaths allow study of the contrasting influences of freshwater inputs and seawater exposure, peat and marl soils, herbaceous and woody plant species, and phosphorus (P) status (Myers and Ewell, 1990).

# APPROACHES FOR ESTIMATING C UPTAKE, STORAGE, AND TRANSPORT ACROSS THE LAND-WATER CONTINUUM

Two main approaches are available for determining NECB: (1) summing the change in C for all pools (i.e., net aboveand belowground production and soil storage), and (2) using eddy covariancebased NEE measurements combined with estimates of aquatic C flux (the C entering and leaving the system in dissolved and particulate form through aquatic transport). Ideally, NECB estimates would be independently estimated by each approach and compared. However, if aquatic flux is not known, it can be estimated by combining NECB determined from the sum of the changes in C pools with NEE. Important insights into the magnitude of ecosystem C accumulation and C flux (both vertical and lateral aquatic transport) can be achieved when applied along coastal ecosystem gradients from freshwater to mangrove forests (Engel et al., 2011; Rivera-Monroy et al., in press).

Net Ecosystem C Balance as the Change in Ecosystem C Pools

NECB can be approximated following Lovett et al. (2006) as the change in organic C pools per year:

 $NECB = \Delta AGB + \Delta BGB + \Delta S + \Delta CWD + \Delta Litter,$  (1)

where NECB (for both mangrove and sawgrass marsh) equals the sum of the change in C in aboveground ( $\triangle AGB$ ) and belowground biomass stock ( $\Delta$ BGB), soil ( $\Delta$ S), course woody debris stock ( $\Delta$ CWD), and litter stock ( $\Delta$ Litter). Assuming that the change in C stocks of CWD and litter are small relative to  $\triangle$ AGB,  $\triangle$ BGB, and  $\triangle$ S, NECB =  $\triangle$ AGB +  $\Delta$ BGB +  $\Delta$ S. The net change in soil C, approximated as soil C accumulation, integrates litter and root inputs, heterotrophic respiration, and leaching/export. Soil C accumulation can be constrained by estimating these parameters, but soil C accumulation estimated by other means (i.e., radiocarbon dating) provides a first-order approximation toward estimation of NECB.

## NECB and NEE

Following the Chapin et al. (2006) approach, the amount of C accumulating in the ecosystem (NECB; in mass of C area<sup>-1</sup> time<sup>-1</sup>) equals the net ecosystem exchange of  $CO_2$  (–NEE), with the negative sign accounting for uptake from the atmosphere, plus the net flux ( $F_{TOT}$ ) of all other forms of C through the system (dissolved inorganic C, dissolved organic C, particulate organic C, carbon monoxide, methane, and volatile organic C; Chapin et al., 2006):

$$NECB = -NEE + F_{TOT}$$
(2)

The aquatic C flux as organic C in particulate and dissolved form and dissolved inorganic C complicate estimation of NECB because wetlands can be both a source and a sink for these forms of laterally transported C. In the Everglades, all three forms of C are transported through freshwater marsh ridges and sloughs downslope along a gentle topographic gradient that develops a hydrologic and salinity gradient from freshwater marshes upstream to mangrove wetlands along the coast. For a particular Everglades wetland landscape (i.e., marsh or wetland forest), as in Figure 2, particulate organic, dissolved organic, and dissolved inorganic C also enter from upstream ecosystems, with C potentially derived from marshes, tree islands, and managed flows in canals, or seepage from associated levees. Carbon exiting the system serves as input to downstream ecosystems that include mixed marsh and scrub mangroves, mangrove forests, and seagrass meadows.

## CARBON BUDGETS FOR EVERGLADES ECOSYSTEMS

Methods for Estimation of NEE and NECB Parameters To develop estimates of NEE for Everglades coastal ecosystems, a combination of eddy covariance studies from FCE LTER sites were aggregated for a mangrove site in Shark River Slough (Barr et al., 2010) and marsh sites in Everglades Shark River and Taylor Sloughs (Jimenez et al., 2012; recent work of author Malone and colleagues). Ewe et al. (2006) summarize methods for

obtaining input parameters to estimate

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NECB in marshes and mangroves. Iwaniec et al. (2006) describe methods for determining periphyton accumulation rates and gross primary production and ecosystem respiration, and, by difference, net ecosystem production. Periphyton estimates were considered separately and not included in NECB estimates for sawgrass marsh. Soil C accumulation was estimated using radiometric analyses of soil (<sup>210</sup>Pb and <sup>137</sup>Cs) and accelerated mass spectrometry <sup>14</sup>C dating of fossilized plant material as described in Saunders et al. (2007) and Smoak et al., (2013).

# Estimates for NEE and NECB in Everglades Coastal Wetlands

In deriving estimates for each of the coastal Everglades ecosystems riverine mangrove forest, freshwater marsh in Shark River and Taylor Sloughs, and seagrass—we combined Equations 1 and 2 to determine  $\Delta AGB + \Delta BGB + \Delta S = -NEE + F_{\rm TOT}.$ 

Mangrove forests were sinks for  $CO_2$  (-NEE = 1,170 g C m<sup>-2</sup> yr<sup>-1</sup>; NECB = 1,038 g C  $m^{-2} yr^{-1}$ ). This range approximated and exceeded rates of NEE found for tropical and temperate systems in large part due to low respiration rates (Barr et al., 2010). Annual net aboveground primary production ( $\triangle AGB$ ) of litterfall and wood was 14.51 Mg ha<sup>-1</sup> yr<sup>-1</sup>. Overall, litterfall production had the highest contribution to annual net aboveground primary production, accounting for approximately 70% of the total. Total net aboveground ( $\Delta AGB$ ) and belowground ( $\Delta$ BGB) primary production was 19.2 Mg ha<sup>-1</sup> yr<sup>-1</sup>, with the total over two times higher at the Shark River riverine mangrove site as compared to an average value for Taylor River mangrove sites  $(8.3 \pm 0.3 \text{ Mg ha}^{-1} \text{ yr}^{-1})$ . Annual net belowground primary production ( $\Delta$ BGB) made a significant

contribution to this total (Castañeda-Moya et al., 2011, in press). Soil C accumulation, estimated from radiometric analyses (Smoak et al., 2013) was 194 g C m<sup>-2</sup> yr<sup>-1</sup>. Thus, employing the equation above, total aquatic C flux  $(F_{TOT})$  is  $-131 \pm 155$  g C m<sup>-2</sup> yr<sup>-1</sup> (Table 1). An upper-bound estimate of F<sub>TOT</sub> could also be derived by assuming that over the longer term (decades to centuries), the C accumulation in live biomass is negligible when considered on an annual basis (191 g C m<sup>-2</sup> yr<sup>-1</sup>, assuming wood burial is estimated as 60% of standing dead wood; Robertson and Daniel, 1989; Krauss et al., 2005) or an estimate of aquatic export of 784 g C m<sup>-2</sup> yr<sup>-1</sup>. This upper-bound value is nearly a third larger than the estimated aquatic C flux using approximations derived from studies and model estimates of dissolved organic, inorganic, and particulate organic C flux (~ 500 g C m<sup>-2</sup> yr<sup>-1</sup>; Twilley,



Figure 2. Balancing coastal Everglades ecosystem C budgets. Schematics showing CO<sub>2</sub> uptake, transport, and storage (S) components and land-water-atmospheric fluxes that will be used to balance the FCE LTER site C budget. Existing eddy covariance towers in the Shark River Slough (SRS) riverine mangroves (A) and SRS and Taylor Slough/Panhandle (TS/Ph) marsh (B) will be supplemented by new towers in the TS/Ph dwarf mangroves and Florida Bay. Aboveground and belowground net primary production and ecosystem R are measured at all sites, and C flux research is being expanded to quantify lateral transport of DIC, DOC, and POC in Taylor and Shark Rivers. Storage is estimated using sediment elevation tables and dated sediment cores. By quantifying these parameters across a spatio-temporally variable template of fresh and marine water delivery, we can create dynamic C budgets to determine how changes in water supply influence the balance of C uptake, storage, and transport. *Figure created by J. Barr* 

1985; Romigh et al., 2006, as summarized in Barr et al., 2010) but does not consider aquatic export, sedimentwater or groundwater-surface water exchange, or C transformations. These large uncertainties identify the need for estimating F<sub>TOT</sub> via measurements of dissolved organic, inorganic, and particulate organic C through tidal creeks and larger rivers, as long as drainage for these creeks and C flux approximations are further verified with process-based studies. On an annual basis, the NECB validation provides important insights into aquatic C export, although major sources of uncertainty remain.

For Everglades freshwater sawgrass marsh sites, NEE estimates show that Shark River Slough is a small source of CO<sub>2</sub>, and Taylor Slough is a small sink (Table 1). Along the Shark River Slough transect, sawgrass aboveground net primary production is about 400–700 g dw m<sup>-2</sup> yr<sup>-1</sup> and is higher than that in the Taylor Slough transect, which is 250–400 g dw m<sup>-2</sup> yr<sup>-1</sup>. In Taylor Slough, plants are smaller, but culm (stem) density is higher. Also, because Taylor Slough freshwater marsh sites dry more frequently and for a longer time, these sites are dominated by marl, a calcitic mineral soil, rather than peat soil. Annual belowground sawgrass productivity averaged 450 g dw m<sup>-2</sup> yr<sup>-1</sup>, with approximately two-thirds occurring in the top 10 cm of soil (Juszli, 2006). These root-production estimates are generally consistent with rates measured in other freshwater marshes (Birch and Cooley, 1982; Symbula and Day, 1988) but lower than those reported for salt marshes (Valiela et al., 1976; Schubauer and Hopkinson, 1984). Given the higher sawgrass aboveground primary production,  $\triangle AGB$  was higher in Shark River Slough than in Taylor Slough and  $\triangle BGB$ 

values were approximately equivalent (Table 1; Juszli, 2006). Soil C accumulation was estimated as 90 g C m<sup>-2</sup> yr<sup>-1</sup> (Saunders et al., 2007). The low values for NEE relative to aboveground and belowground net primary production, and equivalent rate of soil C accumulation, suggest that exported C mass and C accumulated in living biomass are equivalent (Table 1). This is in good agreement with rates of leaf turnover for sawgrass plants estimated to occur three to four times within a year (Childers et al., 2006). Furthermore, these low NEE values also suggest that water-table variation has a significant effect (Schedlbauer et al., 2010) and that periphyton may contribute to CO<sub>2</sub> uptake. Field tests, however, suggest that periphyton does not contribute significantly to NEE (Schedlbauer et al., 2012), although this result assumes that aquatic C import is negligible, and it neglects the role of flocculent material production and deposition, also reported to be important in Everglades freshwater marsh C cycling (Troxler and Richards, 2009, and references therein).

Periphyton biomass is high compared to algal biomass in other wetland ecosystems, averaging over 100 g C m<sup>-2</sup> and attaining up to 10,000 g AFDM m<sup>-2</sup> (AFDM = ash-free dry mass) at some localities (Ewe et al., 2006; Iwaniec et al., 2006; Gaiser, 2009; Gaiser et al., 2011)

vs. 10–50 g m<sup>-2</sup> yr<sup>-1</sup> from other wetland types (Vymazal and Richardson, 1995). Determining the influence of periphyton on NEE is complicated by difficult-to-capture metabolic pulses that occur during drying or wetting events (Thomas et al., 2006) and by exchanges of organic C among the mat, sediment, and water column that are not measured in standard approaches. Schedlbauer et al. (2012) attempted to evaluate the influence of periphyton on net ecosystem CO<sub>2</sub> exchange at the short-hydroperiod Taylor Slough marsh and found that periphyton did not significantly contribute to CO<sub>2</sub> fluxes. While it is clear that periphyton can regulate water-column oxygen concentrations (McCormick et al., 1997; McCormick and Laing, 2003) and aquatic production and respiration (Hagerthey et al., 2011), these whole-system studies suggest that heterotrophic processes in the mat and of mat-produced C in the floc and water column may, in fact, balance gross primary production (Schedlbauer et al., 2012). This is supported by the C balance estimates we determined for the freshwater sawgrass marsh in Taylor Slough. However, periphyton also likely plays a major role in the cycling of inorganic C between dissolved and particulate forms.

Carbon from primary production of seagrasses, estimated for Florida Bay at

#### Table 1. Values for annual net ecosystem C balance (NECB), net ecosystem exchange (NEE), and derived aquatic carbon (Aq C) export.

		g C m <sup>-2</sup> yr <sup>-1</sup>					AaC
Ecosystem	Site	NECB	-NEE	Soil	AG	BG	Export
Marsh	SRS	621 ± 59	-45 ± 16	90	291 ± 35	240 ± 48	666 ± 61
	TS	457 ± 61	50 ± 15	90	122 ± 12	245 ± 60	407 ± 63
Mangrove <sup></sup> Ψ	SRS	1,038 ± 88	1,170 ± 127	194	638 ±36	206 ± 80	-131 ± 155
Seagrass	FL Bay				75 ± 40		

<sup>v</sup> Mangrove root production estimates for size classes < 2 mm to 20 mm in diameter (to a depth of 90 cm). AG = aboveground. BG = belowground. SRS = Shark River Slough. TS = Taylor Slough. a rate of 31–182 g  $C_{\rm org}\,m^{-2}\,yr^{-1}$  (Zieman et al., 1989) with ~ 37% of net aboveground primary production, is channelled into belowground biomass (Herbert and Fourgurean, 2009) and, eventually, the sediment (Orem et al., 1999). New results suggest that C storage in seagrass sediment rivals that of tropical forests, and that Florida Bay sediment is C-rich compared to seagrass systems worldwide (Fourqurean et al., 2012a,b). This high capacity for storing C results from high primary production of seagrass meadows, their capacity to filter out particles from the water column, and their subsequent storage in soils (Fourgurean et al., 2012b). Low decomposition rates in the oxygen-poor seagrass soils allow accumulation over millennia and yield high stability of seagrass C<sub>org</sub> storage.

## Aquatic C Export

Although aquatic C flux can only be derived by combining estimates for NEE and NECB, FCE LTER research conducted in the Everglades illustrates some important patterns, linkages, and insights into important C processes and transformations, and it provides preliminary estimates of C flux. Figure 3 shows the main biogeochemical processes involved in organic matter (OM) source, transport, and fate for the freshwater marsh, the estuarine ecotone, and the marine end-member for the Everglades. Differences in OM between Shark River and Taylor Sloughs are derived from biomass and thus are related to vegetation cover and primary productivity and, consequently, to aquatic C exchange. In Everglades marshes, the source materials for particulate OM production, deposition, and accumulation are mainly derived from periphyton and freshwater macrophytes. Although oligotrophy limits the presence of free-floating plankton as a potential source for particulate organic C, this C pool is mainly represented in the form of flocculent material and is spatially controlled by

local vegetation patterns and periphyton production (Neto et al., 2006; Pisani et al., in press). In the estuarine ecotone, mangrove-derived OM likely dominates the particulate organic C source, either in the form of detritus or of resuspended sediment mobilized through tidal action (Mead, 2003; Ding He, Florida International University, pers. comm., 2013). Lastly, particulate organic C in the marine end-members is, to a large extent, a mixture of terrestrial particulate organic C export and marine-derived OM sources such as phytoplankton and seagrass detritus (Jaffé et al., 2001; Hernandez et al., 2001; Xu et al., 2006, 2007; Xu and Jaffé, 2007).

These studies also indicate that canal inputs (Lu et al., 2003; Yamashita et al., 2010), leachates of soils, and plant exudates (Lu et al., 2003; Scully et al., 2004; Davis et al., 2006; Maie et al., 2006; Yamashita et al., 2010) are quantitatively important inputs of dissolved organic C to the estuarine ecotone (Cawley



Figure 3. Conceptual model of organic matter (OM) compartments and fluxes, based on research conducted by the FCE. The lower diagram refers to drivers of ecosystem structure and exchange. Figure 2 summarizes the flows connecting environments and the drivers affecting the exchange of OM (timing, quality, quantity). Both particulate organic matter (POM, as floc) and dissolved organic matter (DOM, derived from freshwater plant production) are delivered to the estuarine ecotone from upstream. Seagrass-derived litter, POM, and DOM are delivered to the ecotone from downstream. Hydrology and biogeochemical processing control the degradation and residence times of these C pools, and are not fully understood. Thus, whether these allochthonous sources of OM help to fuel the estuarine productivity peak remains to be determined. Although we have made great strides in understanding OM dynamics in the FCE, there are still many OM pools and pathways to investigate in the context of a dynamic south Florida hydroscape. *Figure created by R. Chambers, R. Jaffe, and V. Rivera-Monroy* 

et al., in press). In addition, there are sources from the fringe mangrove forests (Jaffé et al., 2004; Cawley et al., in press) as well as potential exchange with groundwater (Chen et al., 2010, 2013). Mangroves were found to contribute up to 30% of the dissolved organic carbon that is transported by the Shark River.

## UNCERTAINTIES AND AREAS FOR FURTHER WORK

Key areas of uncertainty that will be better constrained by resolving input parameters and synthesizing processbased studies are estimates of net soil C change, aquatic C flux, and, specifically, the contribution of water table variation and periphyton to NEE. Soil C process-based studies can be used to constrain these values of net soil C change and, in some cases, to validate these estimates (e.g., Chambers, 2012). While the approaches we employed were useful in constraining aquatic flux estimates, further uncertainties remain with regard to C form and porewater exchange of dissolved inorganic C in mangroves, recently illustrated to exceed dissolved organic C flux (Alongi et al., 2012). Comparing these fluxes and stock changes, which can represent different temporal scales, is also a challenge that requires a unified approach beyond what is considered here (Chapin et al., 2006), especially for cross-system studies. Integrating process-based studies with estimates of NECB and aquatic flux estimates will further improve this work (e.g., Cawley et al., in press). Another source of uncertainty that would be common in estimates of NEE in wetlands is that imposed by water-table variation. A proportion of the ecosystem-atmosphere CO<sub>2</sub> exchange that would occur in wetlands with low or no water-table inundation would be reduced significantly in wetlands where plants were inundated and that fraction would likely be exported through lateral flux.

Synthesis of NEE data sets of longer time series will also improve integration of NEE and NECB. Although seagrass metabolism may be the easiest to infer from whole-system measurements, more work is needed to understand how C cycling within and among ecosystem components contributes to estimates of NECB in these ecosystems. In Everglades freshwater marshes, methane could have a substantial impact on ecosystem C balance. While ecosystemscale measures of CH<sub>4</sub> concentration are not yet available, data from small-scale experiments could be considered in order to reduce uncertainty around its potential contribution. Other areas of anticipated work include development of modeled scenarios of regional climate and hydrologic models (e.g., Fitz and Sklar, 1999) and continued mechanistic advances in microbial pathways and rates of change in fluxes (Chambers, 2012). Moreover, while the approaches we used for these initial estimates were informative, a resolved approach for addressing areas of uncertainty is critically needed for coastal wetland ecosystems. The intensive C budget studies summarized here and the approach of the Chapin et al. (2006) framework in Equations 1 and 2 can be combined to provide a strong basis for coastal LTER inter-site C research. Synthesis efforts such as these that draw on long-term, integrated data sets for multiple sites broaden the ecological, geographical, and social contexts necessary to understand drivers and effects of their interactions, reduce uncertainties, and predict change. These efforts can increase understanding of coastal ecosystem drivers and the patterns and processes

with which critical global policy issues, including land use change in the coastal zone, can be addressed.

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