Integrating Successional Ecology and the Delta Lobe Cycle in Wetland Research and Restoration

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Abstract Inactive deltas are more extensive than active deltas in most deltaic landscapes; thus, the subsurface generally is dominated by mineral sediments that rapidly accreted at different times, whereas the landscape at any one time generally is dominated by ephemeral emergent wetlands that are slowly accreting via vegetative growth. Subsidence is slow enough in most deltas that emergent wetlands, although ephemeral, can persist for millennia but accelerating global sea level rise probably will slow wetland creation in active deltas and accelerate the loss of existing wetlands in inactive deltas this century worldwide. A recent publication created confusion regarding the effects of river management on coastal Louisiana, where spatially variable subsidence is great enough in some areas to mimic extremely rapid sea level rise. I show how integrating Successional Ecology with the Delta Lobe Cycle, and correcting some omissions and errors in recent publications, clarifies the effects of river management in coastal Louisiana and provides a framework for predicting deltaic landscape dynamics worldwide. Successional Ecology provides a framework for understanding changes in natural and managed environments worldwide, whereas the Delta Lobe Cycle provides a framework for understanding river-dominated deltas worldwide. Sediment diversions are a form of river management that removes artificial barriers to river flow and are designed to mimic hydrologic conditions during the active delta stage of the Delta Lobe Cycle by focusing rapid mineral sedimentation in open water and thus creating new emergent wetlands. Freshwater diversions are another form of river management that also removes artificial barriers to river flow but are designed to mimic hydrologic conditions during the inactive stages of the

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School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA e-mail: jnyman@lsu.edu Delta Lobe Cycle by reducing salinity stress over large areas of emergent wetlands and thus promoting marsh vertical accretion via vegetative growth. The Delta Lobe Cycle and both types of river diversions also create salinity gradients that simultaneously increase the sensitivity of emergent wetlands to disturbance while increasing the ability of emergent wetlands to recover from disturbance. Freshwater diversions only slow the loss of existing wetlands because the natural Delta Lobe Cycle, artificial channels that increase salinity stress, artificial ridges that increase flooding stress, and repeated disturbances eventually will cause vertical accretion via vegetative growth to become inadequate. Formally integrating these concepts might advance research and restoration in deltaic landscapes worldwide especially in the majority of deltas where inactive deltas are more extensive than active deltas.

Keywords Wetland · Delta · Delta Lobe Cycle · Disturbance · Succession · Restoration · Diversion · Louisiana

Introduction

Coastal wetlands in Louisiana are unique partly because of their extent, the rates at which emergent vegetation converts to open water, and the scale of restoration efforts in response to such wetland loss. But these characteristics derive their uniqueness from quantity rather than quality. For example, wetland loss occurs outside Louisiana in many coastal areas (Coleman et al. 2008, Smith 2009, Carle 2011) as does wetland restoration (Merino et al. 2011, Brand et al. 2012, Chen et al. 2012). Coastal wetlands in Louisiana thus share some characteristics with many coastal wetlands worldwide: many exhibit a salinity gradient and the consequent gradients in plant and animal associations; many are associated with rivers whether on marine coasts are lake shorelines. The remainder of this paper focuses on river deltas; it should be most relevant to the Mississippi River Delta and other deltas where (1) wave and tidal energies are low enough to allow riverine currents to deposit significant amounts of fine-grained sediments in such as in the deltas of the Danube, Ebro, Patia, Po, and Rhine and (2) outside northern areas where deltas are dominated by lakes rather than emergent wetlands (Coleman et al. 2008). Most modern deltas are similar to the Mississippi River Delta in that the extent of inactive deltas is several times greater than the extent of active deltas (Coleman et al. 2008). Subsidence is spatially variable throughout the active and inactive deltas of the Mississippi River and is rapid enough in some areas, >10 mm year⁻¹ (Kolker et al. 2011), to mimic extremely rapid sea level rise expected worldwide later this century.

The conversion of emergent vegetation to open water has spawned decades of restoration efforts in Louisiana and elsewhere. These efforts have undoubtedly benefited from an understanding of ecology and geology, but I believe that insight can be gained from explicit efforts to view coastal wetland dynamics simultaneously in the context provided by Successional Ecology and by the Delta Lobe Cycle. Here, I attempt to describe such a view. Successional Ecology informs understanding of changes in natural and managed environments worldwide (McCook 1994, Platt and Connell 2003), whereas the Delta Lobe Cycle forms the foundation for research into river-dominated deltas worldwide (Coleman 1988, Blum and Roberts 2012). Successional Ecology is relevant to coastal wetlands beyond deltas and is relevant to a variety of disturbances. The Delta Lobe Cycle is applicable to lacustrine deltas and marine deltas where tidal energies are low enough to allow accumulation of fine-grained sediments. A complete review of either concept would be voluminous and is not my intent, but I must introduce Successional Ecology to coastal geologists and introduce the Delta Lobe Cycle to coastal ecologists as I attempt to integrate the two.

Synthesis

Disturbances, which here are defined as death of dominant emergent vegetation, are one factor that sometimes can cause emergent wetlands to convert to open water. Examples of disturbances in coastal wetlands include (1) fire, which generally removes aboveground biomass but leaves behind belowground biomass that can produce new shoots, (2) floods that submerge emergent plants for weeks at a time and thereby kill all above and belowground biomass but leave it in place, and (3) hurricanes, which can physically remove above and belowground biomass. Succession, which here is defined as a fairly predictable pattern in plant associations following removal of dominant vegetation, can revegetate disturbed emergent wetlands under some conditions. Cover burns in marshes dominated by *Spartina patens* are a classic example of this type of succession (Nyman and Chabreck 1995): emergent

vegetation following a cover burn consists of some annual plants whose seeds have persisted in the soil or whose seeds arrived after the fire, but emergent vegetation soon is dominated by perennial plants in the genus Schoenoplectus because they sprout vigorously following disturbance. Many months or several years are required before the perennial S. patens dominates again. In the weeks following disturbance, remotely sensed images of these area are easy to confuse with open water. These types of disturbance and succession patterns are not discussed further because they do not permanently convert emergent vegetation to open water. When a disturbance kills roots however, revegetation requires much more time because seeds and other propagules such as rhizomes are rare. If revegetation occurs before the soil erodes, then succession will proceed slower than following a cover burn but the pattern will be the same: initial domination by annual species followed by perennial species that eventually resembles pre-disturbance vegetation. In the months following disturbance, and in the subsequent winters, remotely sensed images of these area are easy to confuse with open water because perennial vegetation is scarce. Open water may replace emergent vegetation if erosion removes enough soil to almost permanently flood the area. Such erosion may occur over months with very little hydraulic energy in soil lacking live roots or over hours during hurricanes in soil containing vigorous live roots. Disturbances on the northern Gulf of Mexico coast can convert emergent marsh to open water even if they only remove the upper 20 cm of soil because of the narrow growth range imposed by microtidal conditions in the Gulf of Mexico (Fig. 1).

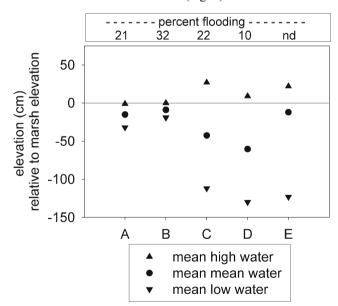


Fig. 1 Elevation of the marsh surface (0 cm) relative to mean high water, mean water, and mean low water at various coastal marshes in the USA. *A* and *B* were dominated by *S. patens* in Louisiana (Nyman et al. 2009); *C* and *D* were dominated by *S. alterniflora* and *Juncus roemerianus*, respectively in South Carolina (Morris et al. 2005; J.T. Morris, personal communication); and *E* was dominated by common reed in New York (Montalto et al. 2006). See literature cited for full citations of all data sources

One consequence of salinity gradients in coastal marshes is spatial variability in sensitivity to disturbance in coastal marshes. Soil strength depends upon live root density rather than mineral sediment density or dead organic matter (McGinnis 1997). Thus, fresher wetlands are more sensitive to disturbance because lower salinity, S. patens, soils have fewer live roots than higher salinity, Spartina alterniflora soils (Conner and Chmura 2000). My field observations suggest that soils of tidal fresh marshes have even fewer living roots and are even weaker than soil in S. patens marshes. Morton and Barras (2011) analyzed 51 years of aerial photography and satellite images and confirmed that tropical storms are more likely to erode lower salinity marshes than higher salinity marshes. Howes et al. (2010) also concluded that lower salinity wetlands were more sensitive to hurricane disturbance than higher salinity marshes. Vertebrate herbivores also can damage vegetation enough to create disturbance. Vertebrate herbivores are more likely to damage lower salinity wetlands than higher salinity wetlands because most herbivores prefer lower salinity areas over higher salinity areas (Chabreck and Nyman 2005). Thus, vertebrate herbivores, like hurricanes, are more likely to damage lower salinity wetlands than higher salinity wetlands.

Although lower salinity marshes are more sensitive than higher salinity marshes to disturbance as described above, lower salinity marshes also are more resilient than saline marshes; i.e., plant communities recover faster. Weller and Spatcher (1965) and van der Valk (1981) did the seminal work on disturbance and succession in freshwater plant communities; they noted that the conversion of low-salinity open water to emergent marsh generally begins rapidly with sexually reproducing, annual plants, in genera such as *Eleocharis*, *Cyperus*, and *Echinocloa*. Within decades however, vegetatively reproducing perennial plants convert shallow open

water to emergent marsh (Weller and C. S. Spatcher 1965, van der Valk 1981). Higher salinity marshes lack such capacity probably because sulfide is more abundant in saline areas (Koch et al. 1990). Morton and Barras (2011; Table 1) observed that 12-14 types of hurricane impacts were recovered in fresh, intermediate, and brackish marshes, but only 8 of those types of hurricane impacts were recovered in saline marsh. Three of those eight impacts were depositional impacts, which further illustrate the lower resiliency of more saline wetlands. This difference in resiliency between fresh and saline marshes also is reflected in annual plants. For example, Middleton (2009) observed that salt marsh vegetation had fewer species in the seed bank and lower seedling density following hurricane disturbance than fresher marshes. Not only does salt marsh lack the capacity to convert open water to emergent marsh via vegetative spread, it also lacks the capacity to recolonize un-eroded soil at low elevations typical in Louisiana inactive deltaic marshes (Schrift et al. 2008). Knowledge of the differences in ability to colonize shallow open water between fresh and saline vegetatively reproducing perennial plants has been used to effectively manage and restore coastal wetlands beyond river deltas (e.g., Warren et al. 2002).

Another factor that causes emergent wetlands to convert to open water is the Delta Lobe Cycle. Seminal work on the Delta Lobe Cycle was done by Russell and Fisk, who first described the cyclic nature of deltas (see Coleman 1988). Deltas are classified as being active when rivers deposit mineral sediments that vertically accrete at their mouths, reduce water depths, and eventually convert open water areas into areas capable of supporting emergent wetland plants (Fig. 2). In Louisiana, the prograding river mouth can deposit clay and silt up to 50 m deep over large areas known as prodelta and delta front deposits (Coleman 1972, p. 55). As the mouth

 Table 1
 Published objectives of both types of river diversion projects. Quotes were selected to represent the oldest and most recent descriptions of the goals and/or objectives of the diversion types

Diversion type	Source	Objectives and goals
Sediment diversions	LCWCRTF (1993)	In contrast to freshwater diversions, which carry only a dilute load of clay material (see subsequent discussion), sediment diversions are focused on capturing flows which are laden with the inorganic sediments most effective in building new land. Consequently, they also divert large quantities of river water. While this fresh water can benefit wetland by decreasing salinity in the area which receives the outflow, the primary purpose of a sediment diversion is to build new land by mimicking the natural delta-building and wetland maintenance processes.
Freshwater diversions	LCWCRTF (1993)	Project benefits for these diversions primarily focus on the change effected on a salinity regime and the response of the existing biological resources to this change. However, because the fine silt and clay portions of riverine sediment loads are uniformly distributed throughout the flow, some accretion or wetland enhancement results from as a secondary benefit of these projects.
Sediment diversion	LCWCRTF (2010)	Sediment Diversion A controlled gap (called a crevasse) is cut into a river levee, allowing river water, nutrients, and sediment to flow into nearby wetlands and mimic natural land-building processes.
Freshwater diversions	LCWCRTF (2010)	Freshwater Reintroduction Freshwater is channeled from a nearby river or water body into surrounding wetlands. This infusion of water, sediment, and nutrients helps slow saltwater intrusion, slows the loss of marsh, and creates a limited amount of new marsh.

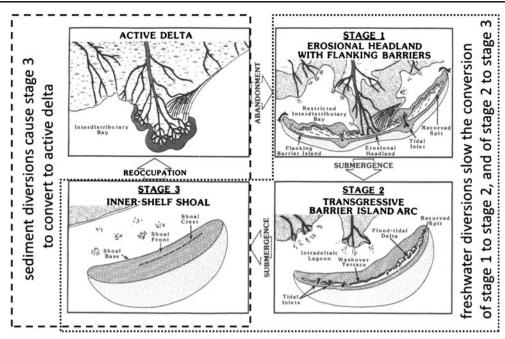


Fig. 2 Sediment diversion and freshwater diversions shown within the framework of the Delta Lobe Cycle conceptualized by Penland et al. (1988) and subsequently modified by Roberts and Coleman (1996). The term "diversion" obscures the fact that sediment diversions initiate a new cycle of the Delta Lobe Cycle, i.e., change stage 3 to active delta. The term diversion also obscures the fact that freshwater diversions restore

natural spring flooding prevented by artificial levees and thus slows conversion of stage 1 to stage 2 and conversion of stage 2 to stage 3. Note that no emergent landforms (i.e., natural levees, emergent marshes, or barrier islands) are sustainable; only the cycle that creates and destroys these landforms is sustainable

approaches an area, sand accumulates extremely rapidly on the delta front deposits and creates natural levees that confine the channel and cause the river to prograde further (Coleman 1972, p. 35). The final step in converting open water to emergent wetlands is known as crevassing (~2-m deep and $\sim 12 \text{ km}^2$) or bay filling (~ 5 -m deep and $\sim 400 \text{ km}^2$), depending on their size, and is completed within decades in lacustrine as well as in marine deltas (Coleman 1988, Tye and Coleman 1989, Wells and Coleman 1987). Freshwater inflow and mineral sedimentation then slow because the channel either progrades beyond these deposits (e.g., Tye and Coleman 1989) and/or the channel avulses, i.e., switches to a different path (e.g., Wells and Coleman 1987). Riverine inputs of freshwater and sediment into the emergent wetland then depend upon overbank flooding, which occurs only during spring floods. At this stage, organic material and mineral sediments contribute to the vertical accretion process that maintains surface elevation despite sea level rise and subsidence of the underlying sediments (Neubauer 2008, Cahoon et al. 2011). Eventually, continued progradation or larger scale evulsion deprives the wetland of riverine sediments either because river floods no longer reach the wetland or because virtually all mineral sediments are deposited on natural levees before river floods reach the wetland. Such deltas then are classified as inactive. At least in the Mississippi River Deltaic Plain, virtually all of the inactive deltas except the natural levees were flooded by spring floods that lacked sediments as indicated by

the spatial extent of the areas flooded (Lemmon et al. 2003, pp. 220–223, 271–272) and by the spatial extent of the peat deposits in inactive deltas (Roberts and Coleman 1996). Riverine sediments that reach coastal bays subsequently may be deposited indirectly on the wetland via storms (e.g., Reed 1989, Nyman et al. 1995), but the river deposits almost no mineral sediments directly onto emergent wetlands in inactive deltas. Such a delta is classified as inactive (Fig. 2). Coleman et al. (2008) estimated the ratio of inactive to active delta in 6 of the 15 deltas they analyzed; on average, inactive deltas were 4.1 times larger than active deltas. The existence of expansive, inactive deltas worldwide is evidence that wetlands in inactive deltas can offset centuries of subsidence and sea level rise by vertically accreting. During this stage, differences in mineral sedimentation can be unrelated to differences in vertical accretion which instead depends upon organic matter accumulation, i.e., vertical accretion via vegetative growth, in deltaic and non-deltaic emergent wetlands (Nyman et al. 2006 and literature cited therein). Mineral sediments are indirectly important to accretion via vegetative growth because they provide plant nutrients and Fe that may buffer sulfide stress (DeLaune and Pezeshki 1988, Nyman et al. 1994). Although vertically accreting for centuries, the resulting peats in coastal Louisiana reach only a meter or two in thickness perhaps because (a) autocompaction increases as peat deposits increase (Cahoon et al. 1995), (b) salinity stress and sulfide stress on vegetation increase as freshwater inputs decrease

(Koch et al. 1990), (c) soil organic matter decomposition increases as salinity increases (Weston et al. 2011), and/or (d) vertical accretion slows as salinity increases (Craft 2007). Eventually, organic matter accumulation is incapable of maintaining an elevation sufficient to support emergent vegetation because vertical accretion via organic matter accumulation apparently rarely exceeds 1.0 cm year^{-1} (Nyman et al. 2006). The vegetation then drowns and the emergent marsh area reverts into shallow open water (DeLaune et al. 1994). Even where vertical accretion via vegetative growth is adequate to offset subsidence and sea level rise, wetlands can revert to shallow open water via erosion because they can vertically accrete faster than adjacent ponds (Nyman et al. 1994; Erwin et al. 2006). The area can again become the site of an active delta after subsidence causes the open water area to become deep enough to accommodate a prograding river channel and if avulsion returns a river channel to the area (Fig. 2). The orderly repetition of these sedimentation events and shifting sites of sedimentation produced mineral deposits that generally are 50-m thick, but up to 200-m thick, and created southeastern Louisiana during the past 7,000 years (Coleman 1988). Subsurface southeastern Louisiana thus is dominated by mineral sediments that rapidly accreted at different times, whereas the landscape at any one time is dominated by ephemeral emergent wetlands that are slowly accreting via vegetative growth.

In addition to creating cycles of open water to emergent vegetation to open water, etc. at very large time and spatial scales, the Delta Lobe Cycle also causes spatial variability in the sensitivity and resiliency of the emergent wetlands existing at any one time by creating a salinity gradient across deltaic landscapes (Fig. 3). Active deltas consist almost entirely of fresh marshes (Visser et al. 1998) but account for little area because most deltas are dominated by inactive deltas in inactive deltas were fresh marsh when they were created,

subsequent loss of riverine inflow results in inactive deltas that contain bands of fresh, intermediate, brackish, and saline vegetation (Visser et al. 1998) that are underlain by freshwater peats (DeLaune 1986). A lack of persistent hurricane damage in active deltas (Chabreck and Palmisano 1973; Morton and Barras 2011) probably results partly from the ability of freshwater vegetatively reproducing perennials to colonize open water and partly from rapid mineral sedimentation that can fill eroded areas. Open water areas created by hurricanes in fresh marshes of inactive deltas however can persist for decades and may be relatively permanent (Morton and J.A. Barras 2011) especially where removal of floating marsh results in open water areas too deep to be colonized by vegetatively reproducing perennial vegetation. Hurricanes convert less saline marsh than fresh marsh to open but as noted saline marshes also exhibited the less recovery (Morton and Barras 2011). The likelihood that disturbed saline marshes will convert to open water also appears common in coastal marshes outside of deltas (see Kirwan et al. 2008 and literature cited therein).

Wetland restoration in southeastern Louisiana often focuses on river management because (a) artificial levees on the Mississippi River that are required for navigation also prevent spring flooding of adjacent emergent wetlands, (b) a dam at the fork of the Mississippi River and Bayou Lafourche to prevent flooding of developed areas on the natural levees of Bayou Lafourche and its distributaries (Bayous Terrebonne, Petit Caillou, Grand Caillou, Dularge, etc.) also prevents spring flooding of emergent wetlands in the inactive deltas adjacent to Bayous LaFourch and its distributaries, and (c) the Old River Control Structure prevents the Mississippi River from avulsing and accelerating a new round of delta building in Atchafalaya Bay via the Atchafalaya River. Despite a focus on restoring river flow, such projects generally are called river diversions. Diversions can be initiated by cutting a gap into a river levee so that freshwater, nutrients, and sediment flow into adjacent open water or wetlands. River diversions that are

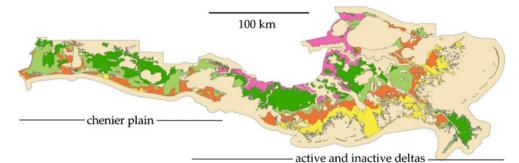


Fig. 3 This map of coastal Louisiana shows some coastal wetland forests and the most common marsh classification system in coastal Louisiana. From inland to the Gulf of Mexico: *pink areas* are bald cypress swamp (dominated by *Taxodium distichum* and *Nyssa aquatic*); *dark green areas* are fresh marsh (dominated by *Panicum hemitomon*, *Sagittaria lancifolia*, or *Typha* spp.); *light green areas* are intermediate marsh (dominated by *S. patens* and supporting many other species); *orange*

areas are brackish marsh (dominated by *S. patens* and supporting few other species); and *yellow areas* are saline marsh (dominated by *S. alterniflora*). The different plant associations also support different communities of fish and wildlife. The data were collected in 1997 and made available by LDWF (2001); the data are described in Visser et al. (1998, 2000)

intended to build new emergent wetlands are classified as sediment diversions; river diversions that that are directed at existing wetlands to slow the loss of existing wetlands are classified as freshwater diversions (Table 1). Emergent wetlands created by small sediment diversions generally are called splays. Constructing sediment diversions apparently began at the mouth of the Mississippi River in the early 1960s because Loga and Ensminger (1960) reported that

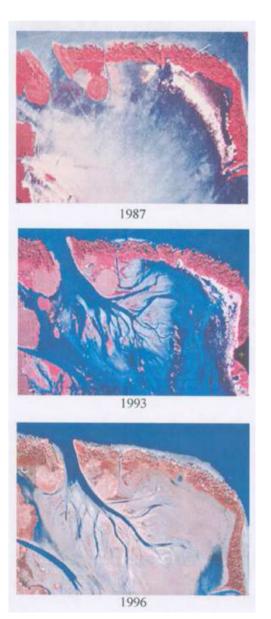
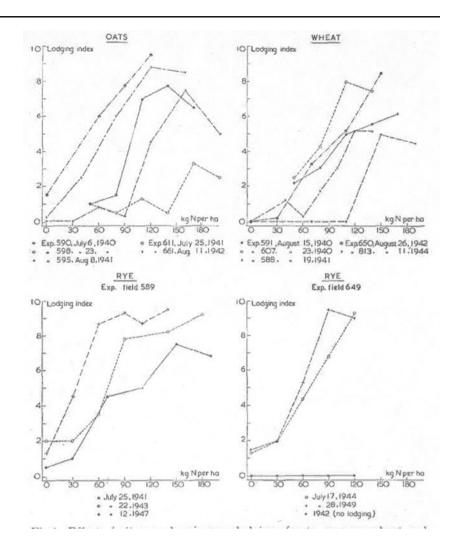


Fig. 4 One of the sediment diversions studied by Gossman (2009), i.e., #6 in his Fig. 1. I was present throughout its construction in 1986; in 1987, I concluded that this effort was a failure because I was unaware of the Delta Lobe Cycle and its temporal and spatial scales. When constructed, the channel was 108-m wide and 8-m deep. The resulting emergent wetlands, approximately 65 ha by 2012, have survived all hurricanes through 2012. This figure is from Kelly (1996). The channel is at 29°08′ 24″ (N) and 89°13′35″ (W)

The high river stages for the past two summers have been very beneficial in maintaining the marsh at Pass-a-Loutre. Several of the earthen plugs were removed to permit the silt-laden river water to enter the ponds in early spring and summer. One of the largest crops of delta duck potatoes in recent years was produced during the summer of 1961 and proved to be very attractive to wintering ducks.

Delta duck potatoes are the emergent, perennial *Sagittaria platyphyla*. Since then, scores of splays have formed naturally and been created by restoration and mitigation managers throughout the fresh and intermediate marshes at the mouth of the Mississippi River (Boyer et al. 1997; Gossman 2009). Freshwater diversions also have been constructed in Louisiana since at least the mid-1950s. Initially, they were intended only to increase oyster production by reducing salinity in bays where oysters are cultured, such as the Bayou Lamoque Diversion Structure constructed in 1956 and the Caernarvon Freshwater Diversion structure constructed in 1993 (subsequently operated also to reduce salinity stress on wetland vegetation), but recently, they were constructed primarily to reduce salinity stress on wetland vegetation, such as the West Point a la Hache Siphon constructed in 1993.

River diversions can be classified as sediment diversions or freshwater diversions as noted (Table 1), but they also can be viewed in context of the Delta Lobe Cycle (Penland et al. 1988, Coleman 1988, Kim et al. 2009). Viewed in this context, sediment diversions are analogous to creating the "active delta" stage that increases marsh coverage, whereas freshwater diversions are analogous to slowing the conversion of stage 1 to stage 2 and of stage 2 to stage 3 in the Delta Lobe Cycle (Fig. 2). Freshwater diversions are expected to slow the conversion of emergent wetlands to open water because many emergent wetlands vertically accrete via vegetative growth (see Nyman et al. 2006 and literature cited therein) and because coastal wetland plants grow more when salinity stress is low and nutrient availability is high (see DeLaune et al. 2005 and literature cited therein). Using the geologic terminology, sediment diversions are attempts to manage the foreset of a delta, whereas freshwater diversions are attempts to manage the topset of a delta. By viewing sediment diversions and freshwater diversions in the context of the Delta Lobe Cycle, it is easy to understand why restoration planners expect freshwater diversions to merely slow wetland loss to rates that would occur if management of the river for navigation and flood control did not prevent annual inputs of much freshwater, some nutrients, and a little mineral sediment. Even where freshwater diversions restore some spring flooding, wetland loss is expected to continue because of (a) subsidence associated with the Delta Lobe Cycle and with petroleum mining, (b) salt water intrusion caused by canals aligned with drainage, (c) flooding caused by spoil banks adjacent to canals perpendicular to drainage, (d) by erosion, and (e) because of **Fig. 5** Effect of nitrogen on lodging in crops reported by (Mulder 1954). Reprinted with permission of the publisher



disturbances such as hurricanes. Combining longer term patterns of change predicted by the Delta Lobe Cycle (Coleman 1988; Blum and Roberts 2012) with shorter-term patterns of change predicted by Successional Ecology (Platt and Connell 2003) and relevant knowledge of wetland vegetation (Weller and Spatcher 1965; van der Valk 1981, Koch et al. (1990) allow one to understand how freshwater diversions designed to slow some human-induced, permanent loss of emergent wetlands can increase the sensitivity of those wetlands to disturbance while also increasing the ability of those wetlands to recover from disturbance.

Application of Synthesis

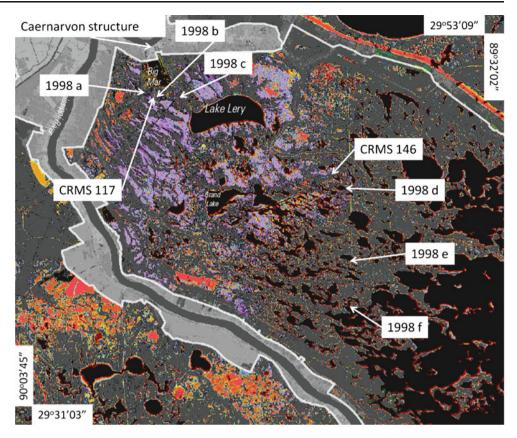
Failure to account for interactions among the Delta Lobe Cycle, disturbance, succession, and salinity gradients can create confusion when evaluating restoration efforts. For example, a recent article (Kearney et al. 2011) in *Geophysical Research Letters*, which is a journal that does not publish comments on its articles, made errors and contained omissions

that created confusion when it attributed hurricane-induced marsh loss to nutrients introduced by river diversions. This

 Table 2
 Effects of nitrogen on root growth in crops reported by Mulder (1954) as "Table VI Effect of nitrogen nutrition (lodging) on weight of roots of cereal plants"

Field and cereal	Nitrogen supply	Lodged (1) or erect (e)	Yield of roots, g (to a depth of 20 cm)
2. Summer wheat	Moderate	e	2.94
	Excessive	1	1.18
3. Summer wheat	Moderate	e	1.71
	Excessive	1	1.04
6. Oats	Moderate	e	2.46
	Excessive	1	1.57
7. Oats	Low	е	2.53
	Excessive	e	3.49
	"	1	1.97
8. Oats	Moderate	е	3.97
	Excessive	1	1.09

Fig. 6 Map showing where vegetation data were collected in 1998 (one 4-m² plot at each of six sites) and from 2007 through $2010 (10 4 \text{-m}^2 \text{ plots at each of})$ two CRMS sites). One of the 1998 sites (b) subsequently converted to open water following Hurricane Katrina in 2005. Vegetation data collected at these sites are shown in Tables 1, 2, and 3. The map is adapted from Couvillion et al. (2011). Open water areas are black. White and light gray areas are levees and developed land, respectively. Dark gray areas were emergent wetlands between 1932 and 2010. The other colors indicate areas that initially were emergent wetlands but converted to open water at different intervals between 1932 and 2010. Most losses in this area occurred between 1956 and 1973 (red) and between 2004 and 2006 (light purple)



confusion regarding how to evaluate restoration effectiveness was noted in the popular press ranging from locally through internationally distributed sources and included the headline "Louisiana marsh restoration has failed" (Nature 2011). I show how rectifying those errors and omissions allow the effects of river diversions and hurricanes on emergent wetlands to be understood in the context of Successional Ecology and the Delta Lobe Cycle.

Comment 1 Kearney et al. (2011) stated that "freshwater diversions, a major restoration strategy, have not increased vegetation and marsh coverage in three freshwater diversions operating for ~19 years." This statement from their abstract would have been more relevant in 2011 if managers planning new freshwater diversions projects were assuming that freshwater diversions increase vegetation coverage or marsh coverage. Since at least 1993 however, managers in coastal Louisiana have classified freshwater diversion projects under the heading of "Enhancement or Protection of Existing Wetlands" rather than under the heading of "Creation of Productive, Sustainable Wetlands" (LCWCRTF 1993). Descriptions of freshwater diversions from 1993 through 2010 (Table 1) also illustrate the understanding by restoration managers in Louisiana that freshwater diversions and sediment diversions simulate different parts of the Delta Lobe Cycle as described in the synthesis comment above.

Comment 2 Kearney et al. (2011) omitted relevant facts when they stated "Ultimately, the scientific basis for river diversions needs to be more convincing before embarking on a strategy that may result in marshes even less able to survive hurricanes" (paragraph 20) without acknowledging (a) the Delta Lobe Cycle noted in the main portion of the synthesis above and (b) restoration efforts designed to simulate the delta-building phase of the Delta Lobe Cycle. Boyer et al. (1997) studied 20 relatively small river diversion projects in the Bird's Foot Delta, i.e., the final 60 km of the Mississippi River, and concluded that they created new wetlands at a rate of 4.7 ha year⁻¹ on average. Gossman (2009) studied 12 relatively small river diversion projects, also located in the Bird's Foot Delta, and concluded that they created new wetlands at a rate of 1.3 ha year⁻¹ on average (e.g., Fig. 4). The Wax Lake Outlet, which was planned as a flood relief channel from the Atchafalaya River in the 1940s but accidently functions as a relatively large sediment diversion that had created $\sim 100 \text{ km}^2$ of wetlands by 2005, provides direct evidence that sediment diversions can build new marshes and also provides data used to validate models that predict river diversions from the Mississippi River could create 701 to 1,217 km² of new emergent wetlands per century (Kim et al. 2009). Even the Caernarvon Freshwater Diversion, which was the major diversion studied by Kearney et al. (2011), has been building a small delta that eventually began supporting emergent vegetation

Table 3 Vegetation that I observed in six 4-m² plots, 16 September 1998, St. Bernard Parish, LA

Species	Plot					
	1998 a	1998 b	1998 c	1998 d	1998 e	1998 f
Symphyotrichum subulatum (Michx.) G.L. Nesom				r	1	r
Borichia frutescens (L) DC				r		
Cyperus spp.		r				
Distichlis spicata (L.) Greene				4	2	1
Echinocloa spp.		r				
Ipomoea sagittata Poir.	1	1	r			
Iva frutescens L.	+				+	r
Juncus roemerianus Sheele				2	3	
Ludwigia leptocarpa (Nutt.) Hara		1	r			
Lythrum lineare L.	1	r				
Morella cerifera (L.) Small	r					
Phragmites australis (Cav.) Trin. ex Steud.					r	
Pluchea foetida (L) DC						r
Schoenoplectus robustus (Pursh) M.T. Strong				4		r
Spartina alterniflora Loisel.				1	3	2
Spartina patens (Aiton) Muhl.	5	5	5	5	5	5
Schoenoplectus americanus (Pers.) Volkart ex Schinz & R. Keller	r	3	1			
Vigna luteola (Jacq.) Benth.		1	r			
Cover	90 %	80 %	90 %	-	90 %	-
Species richness	6	8	5	7	7	7

Three of the plots (a, b, and c) are near the Caernarvon Freshwater Diversion structure; three of the plots are far from the structure (d, e, and f). Four annual species (bold) were noted in 1998. Plot locations are shown in Fig. 6

5 = 75 to 100 % cover, 4 = 50 to 74 % cover, 3 = 25 to 50 % cover, 2 = 5 to 25 % cover, 1 = 1 to 5 % cover, + = scattered, r = rare, - missing data

(Baker et al. 2011). Kearney et al. (2011) also missed an opportunity to verify and/or update the results of Boyer et al. (1997), Gossman (2009), and Kim et al. (2009) when they excluded the more numerous sediment diversions from their study and instead focused on three freshwater diversions.

Comment 3 Kearney et al. (2011) erred when they stated in their abstract that "After Hurricanes Katrina and Rita, these zones sustained dramatic and enduring losses in vegetation and overall marsh area, whereas the changes in similar marshes of the adjacent reference sites were relatively moderate and short-lived" because their own statistical tests showed otherwise: "There was no statistically significant differences in the percent of land cover for before or after diversion operations (and before Hurricanes Katrina and Rita) for the three diversions and two references sites (Figures 3b, 3d, S1b, and S1D)." Kearney et al. (2011) also failed to note that Hurricane Rita, which made landfall over 300 km west of the Mississippi River, caused more emergent wetlands to convert to open water in southwest Louisiana (293 km²), between Calcasieu Lake and the Texas border, than Hurricane Katrina did in adjacent to the Mississippi River (230 km²) (Barras 2009; Morton and Barras 2011). Kearney et al. (2011) also missed a valuable opportunity to quantify how rivers affect wetland recovery from hurricanes when they ignored hurricane-induced wetland loss in southwest Louisiana (Barras 2009 but also see Morton and Barras 2011 and Couvillion et al. 2011).

Comment 4 Information provided by Kearney et al. (2011) in their discussion of nutrients and plant roots (paragraph 19) contained factual errors and omitted relevant facts. Kearney et al. (2011) erred when they stated "The agricultural literature has established that N loading as little as 30 kg ha⁻¹ can cause severe lodging (stem collapse) and low root growth in cereals (i.e., graminoids (Mulder 1954)" because

- Mulder (1954) actually showed otherwise regarding lodging (Fig. 5)
- 2. Mulder (1954) reported that low nutrient levels resulted in fewer roots than moderate nutrient levels (Table 2)
- 3. The study of lodging has focused on stem strength rather than root strength from the 1950s through the early 2000s with stem lodging best managed via nutrient management to reduce grain production whereas root lodging best

Table 4 Cover (percent) of vegetation averaged over ten 4-m² plots during July, August, or September at CRMS Station 117, approximately 3.5 km from the Caernarvon outfall channel

Species	September 2007	August 2008	July 2009	August 2010
All species (standard deviation)	79 (17)	81 (10)	78 (8)	65 (28)
Alternanthera philoxeroides (Mart.) Griseb.			1	2
Amaranthus australis (A. Gray) Sauer			1	1
Ammannia coccinea Rottb.			1	
Bacopa monnieri (L.) Pennell		2		
Bacopa sp.			6	
Bidens laevis (L.) Britton, Sterns & Poggenb.	7	1		
Cyperus erythrorhizos Muhl.		1		
Cyperus filicinus Vahl		1		
Cyperus haspan L.			1	
Cyperus odoratus L.	1	2	6	
Echinochloa walteri (Pursh) A. Heller	1	2	6	
Eclipta prostrata (L.) L.		1	2	
<i>Eleocharis parvula</i> (Roem. & Schult.) Link ex Bluff, Nees & Schauer				1
Hydrocotyle L.		1	2	1
Ipomoea sagittata Poir.	2.3	5	1	2
Iva frutescens L.			8	
Leersia Sw.				1
Ludwigia sp.	10		1	
Ludwigia octovalvis (Jacq.) P.H. Raven		2		
Ludwigia peploides (Kunth) P.H. Raven		1	1	10
Luziola fluitans (Michx.) Terrell & H. Rob.				1
Mikania scandens (L.) Willd.	2	1	1	
Phanopyrum gymnocarpon (Elliot) Nash	1	1		
Phyla lanceolata (Michx.) Greene			1	2
Polygonum punctatum Elliot	18	1	26	29
Sacciolepis striata (L.) Nash	1	1	1	1
Sagittaria lancifolia L.	12	13	8	8
Salix nigra Marsh. Volkart ex Schinz & R. Keller	7	1	4	1
Schoenoplectus robustus (Pursh) M.T. Strong			2	
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	3			
Sesbania sp.			1	
Spartina alterniflora Loisel.		1		
Spartina patens (Aiton) Muhl.	18	6	6	1
Sphenoclea zeylanica Gaertn.	16	37	26	
Symphyotrichum tenuifolium (L.) G.L. Nesom		1		
Typha domingensis Pers.	2	6	1	
Vigna luteola (Jacq.) Benth.	11	6	1	
Zizaniopsis miliacea (Michx.) Döll & Asch.			6	2
All species richness	17	23	26	14
Annual species richness	3	7	8	3
Annual species coverage	18	46	44	3

The 12 annual species are presented in bold. Plot locations are shown in Fig. 6

managed to reduce stem density via seed density and soil rolling (Mulder 1954; Berry et al. 2004).

Comment 5 Kearney et al. (2011, paragraph 11) erred when they stated "The percent vegetation in the diversions and the

Caernaryon reference site was highest in the zone closest to the diversion inlets (Zone 1 in Figures 2a-23). Field observations and Landsat imagery collected from 27 August 1995 to 22 August 2005 indicate that this phenomenon is mostly the response of algae and floating vegetation in the open water areas, rather than to the presence of deeply-rooted marsh vegetation." Several data sets indicate that deeply rooted marsh vegetation was abundant before Hurricane Katrina in marshes nearest the Caernarvon inlet (Fig. 6). Lane et al. (2006) reported that vegetation in marshes affected by Caernarvon during the late 1990s was dominated by S. patens, and Day et al. (2009) reported that biomass exceeded 2,000 g m⁻² within 20 km of the diversion structure but was less than 2,000 g m⁻² over 40 km from the diversion structure. Likewise, the data that I collected also demonstrate that deeply rooted marsh vegetation, i.e., S. patens, was present and abundant before Hurricane Katrina, i.e., >75 % coverage, in the marshes affected by Caernarvon including some areas subsequently eroded by Hurricane Katrina (Table 3). Furthermore, publicly available data show that (a) the dominant plant, S. patens, declined to less than 20 % cover only after Hurricane Katrina (compare Table 3 to Tables 4 and 5) and that (b)

algae and floating vegetation never dominated these marshes (Tables 3, 4, and 5).

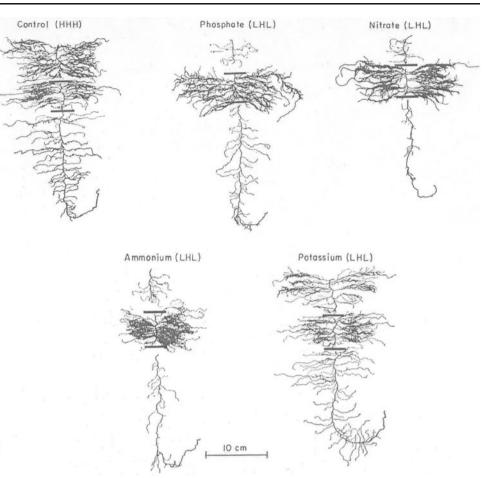
Similarly, Kearney et al. (2011) inaccurately reported findings by Valiela et al. (1976) when they stated "fertilization of brackish marshes would promote lower rhizome and root biomass (Valiela et al., 1976)" because Valiela et al. (1976; Table 1) actually reported that more belowground biomass grew into sand cores in all three fertilized treatments than in all unfertilized controls in both elevation zones studied. Subsequent work on those sites has revealed that nutrient additions increased soil elevation and/or aboveground plant biomass presumably because root production was increased more than decomposition was increased (Fox et al. 2012). Similarly, Morris et al. (2002) also documented nutrients increasing wetland elevation but presumably because increased aboveground biomass increased mineral sedimentation. Kearney et al. (2011) also omitted relevant facts when they failed to acknowledge that the vast majority of studies of the effects of nutrients on root biomass and/or root production have documented a positive effect in upland plants (reviewed by Hodge 2003 but also see Fig. 7) as well as in dune plants (Stevenson and Day 1996) and in wetland plants. In wetland plants, nutrient additions have been observed to increase root

Table 5Cover (percent) of vegetation averaged over ten 4-m² plots during July, August, or September at CRMS Station 146, approximately 20 km fromthe Caernarvon outfall channel, St. Bernard Parish, LA, USA

Species	August 2007	October 2008	August 2009	July 2010
All species	64 (21)	62 (15)	80 (9)	48 (15)
Amaranthus australis (A. Gray) Sauer			2	1
Amaranthus L.	1			
Cyperus filicinus Vahl				
Cyperus odoratus L.			2	1
Distichlis spicata (L.) Greene	1			1
Ipomoea sagittata Poir.		1		
Iva frutescens L.	1	2	4	1
Lythrum lineare L.	23	2	10	2
Pluchea odorata (L.) Cass.	1		19	4
Schoenoplectus americanus (Pers.)				
Volkart ex Schinz & R. Keller	16	5	40	13
Schoenoplectus robustus (Pursh) M.T. Strong	2		4	
Sesbania drummondii (Rydb.) Cory				
Spartina alterniflora Loisel.			6	
Spartina patens (Aiton) Muhl.	36	53	49	28
Symphyotrichum tenuifolium (L.) G.L. Nesom	1		3	1
Unknown #1		2		
Vigna luteola (Jacq.) Benth.	16	3		
Species richness	10	7	10	9
Annual species richness	1	0	3	3
Annual species cover (%)	1	0	23	6

The four annual species are presented in bold. Plot locations are shown in Fig. 6

Fig. 7 From Drew (1975; Fig. 4). Effect of a localized supply, of phosphate, nitrate, ammonium, and potassium, on root form. Control plants (*HHH*) received the complete nutrient solution to all parts of the root system. The other roots (*LHL*) received the complete nutrient solution only in the middle zone, the top, and bottom being supplied with a solution deficient in the specified nutrient. Reprinted with permission of the publisher



biomass and/or root production whether the nutrients increases are reported as pore-water nutrient concentrations (e.g., Ravit et al. 2007), soil nutrient density (e.g., Merino et al. 2010), or nutrient application rates (Table 6). Nutrients have been observed to reduce root biomass only when nutrient application rates (a) exceed several times the rates used in agriculture and (b) are added as fewer, larger doses rather than numerous, smaller doses (Table 6). For example, fertilization

Table 6 Various types and ratesof nitrogen deposition (grams persquare meter per year)

See literature cited for full cita-

^a Other nutrients were added in addition to the nutrient that affected roots and/or elevation

tions of all sources

Туре	Rate	Source			
Atmospheric inorganic N deposition in USA	0–2 N	NADP undated			
Caernarvon diversion:	0–8 N	Hyfield et al. (2008)			
Rice farming	6–14 N	Saichuck et al. (2011)			
Experiments with positive effects of nutrients on we	tland plant roots				
Coastal salt marsh, MA, USA	18.2–157.2 N	Valiela et al. (1976)			
Everglades, FL, USA	0–4.8 P ^a	Craft et al. (1995)			
Everglades, FL, USA	0-<1 P	Daoust and Childers (2004)			
Coastal salt marsh, CT, USA	2.7–7.5 N ^a	Anisfeld and Hill (2012)			
Coastal salt marsh, WA, USA	80	Tyler et al. (2007)			
Experiments with positive effects of nutrients on wetland elevation					
Coastal salt marsh, SC, USA	12.8 N ^a	Morris et al. (2002)			
Coastal salt marsh, MA, USA	18.2–157.2 N	Fox et al. (2012)			
Experiments with negative effects of nutrients on plant roots:					
Tidal freshwater marsh, GA, USA	50 N ^a	Ket et al. (2011)			
Coastal salt marsh, LA, USA	74 N ^a	Darby and Turner (2008b)			
Coastal salt marsh of the USA and Canada	224 N ^a	Darby and Turner (2008a)			

recommendations for rice in Louisiana range from 6.2 to 14.2 g N m⁻² annually (Saichuck et al. 2011), whereas the sole study cited by Kearney et al. (2011) demonstrating a negative effect of nutrients on wetland plant roots (i.e., Darby and Turner 2008a) observed negative effects when they applied 224 g N m⁻² and 425 g S m⁻². While sulfur is not a nutrient, it is crucial in wetlands because it exists as sulfide in reduced soils and is one of the most powerful plant toxins (Koch et al. 1990). It is likely that some of the sulfur added by Darby and Turner (2008a) converted to sulfide and contributed to the reduced root biomass that they observed. It is unlikely that toxic levels of nutrients were responsible for the landscape patterns observed by Kearney et al. (2011) because loadings reach only 8.0 g N m⁻² year⁻¹ and 1.06 g P m⁻² year⁻¹ even in years with highest loadings (Hyfield et al. 2008) and are reduced to background levels within 20 km (Lane et al. 1999; Day et al. 2009).

Comment 6 Kearney et al. (2011) failed to examine three factors other than nutrients as possible explanations for the spatial patterns in disturbance that they observed: spatial patterns in salinity, flooding, and herbivory. Kearney et al. (2011) failed to examine differences in sensitivity and resilience associated with differences in water salinity as described in the main portion of the synthesis above. The greater abundance of annual vegetation in marshes nearer Caernarvon than farther from Caernarvon even after Hurricane Katrina (compare Tables 4 and 5) and the increase in annual vegetation after Hurricane Katrina (compare Table 3 to Tables 4 and 5) are consistent with greater resiliency in fresh marshes than saline marshes as noted in the main portion of the synthesis above. Note that these annual plants would not yet have emerged in March when Kearney et al. (2011) made the video of vegetation that they referenced and made available in their supplemental information. As noted earlier, Hurricane Katrina caused less marsh loss in southeast Louisiana than Hurricane Rita caused in southwest Louisiana (Barras 2009) even though there are more fresh and intermediate marshes in southeast Louisiana (Sasser et al. 2008). Casual observations using Google Earth suggest that the open water near Caernaryon exhibits more revegetation than the open water between Lake Calacasieu and the Texas border as would be expected given the fresher conditions near Caernarvon. Flooding is another factor that varies across deltaic landscapes and that could contribute to disturbance patterns. Caernarvon is operated occasionally to pulse large volumes of water, which increases flooding of the marsh surface near the diversion structure (Huang et al. 2011) and thus may increase flooding stress near the diversion structure where Kearney et al. (2011) observed more marsh loss. Thus, differences in flooding stress might have contributed to differences in hurricane-induced disturbance, but Kearney et al. (2011) did not examine flooding stress nor did Howes et al.

(2010) and Kearney et al. (2011) failed to consider spatial patterns in marsh herbivores such as nutria (Myocastor covpus), muskrats (Ondanta zibethicus), and snow geese (Chen caerulescens). Vertebrate herbivores can reduce plant biomass and retard plant recovery following disturbance (e.g., Slocum and Mendelssohn 2008, McFalls et al. 2010), prefer lower salinity habitats over higher salinity habitats (Chabreck and Nyman 2005), prefer plant species with higher nitrogen content over plant species with lower nitrogen content (Stearns and Goodwin 1941, Alisauskas et al., 1988, Wilsey and Chabreck 1991), and also prefer fertilized plants within a species over unfertilized plants of the same species (Ialeggio and Nyman in review). Insect herbivores also prefer fertilized plants over unfertilized plants within the same species (Feller 1995). At least with muskrats, population dynamics are correlated with nitrogen concentrations in surface water (Visser et al. 2006) and it thus is likely that other marsh herbivores also increase in abundance where diversions increase nitrogen availability. Like hurricanes, herbivores thus are more likely to damage soil in lower salinity marsh than in higher salinity marsh with or without a nutrient gradient and even more likely to damage soil in marshes with higher nitrogen content.

(2010) in a study of the same area. Likewise, Howes et al.

Conclusions

The Delta Lobe Cycle (a) creates new emergent wetlands in active deltas, (b) promotes the persistence of older but ephemeral emergent wetlands in inactive deltas, and (c) creates salinity gradients across the deltaic landscape. Salinity gradients cause different species to dominate emergent vegetation at different places, which in turn causes differences across the deltaic landscape in (a) vegetative sensitivity to disturbance, (b) vegetative resiliency to disturbance, and (c) some disturbances such as herbivory. Salinity gradients thus complicate understanding the response of most coastal marshes to disturbance and restoration efforts but especially in deltaic landscapes where salinity gradients are especially prevalent and further complicated by the mixture of active and inactive deltas. Failure to consider interactions among the Delta Lobe Cycle and Successional Ecology increases the likelihood that researchers and managers will perceive deltaic landscape dynamics more simplistically than they are. Explicitly accounting for these interactions might advance research and restoration in deltaic landscapes worldwide especially in the majority of deltas where inactive deltas are more extensive than active deltas.

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