



Unraveling the Gordian Knot: Eight testable hypotheses on the effects of nutrient enrichment on tidal wetland sustainability

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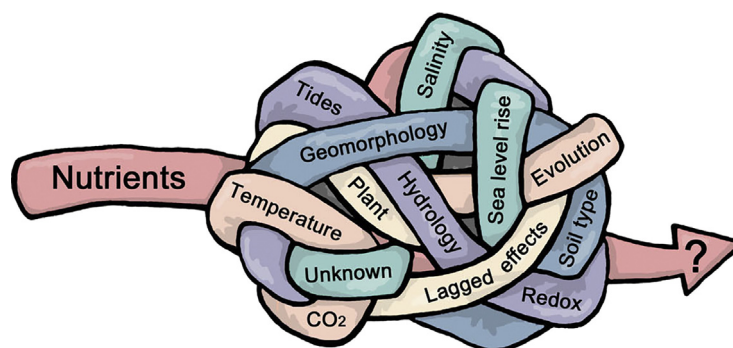
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HIGHLIGHTS

- Excess nutrients have often unclear influences on marsh sustainability.
- Clarifying these influences is important in light of climate change.
- Many factors modulate nutrient effects, forming a Gordian Knot.
- Unraveling this Gordian Knot is important for sustaining coastal ecosystems.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 31 January 2020

Received in revised form 18 June 2020

Accepted 20 June 2020

Available online 22 June 2020

Editor: Hans Brix

Keywords:

Nutrients
Nitrogen
Phosphorus
Anthropogenic
Wetlands
Salt marsh

ABSTRACT

The position of tidal wetlands at the land-sea interface makes them especially vulnerable to the effects of nutrient discharges and sea level rise (SLR). Experimental studies of coastal wetland nutrient additions report conflicting results among and within habitats, highlighting the importance of site-specific factors, and how spatial and temporal scaling modulates responses. This suite of influences as SLR accelerates creates a “Gordian Knot” that may compromise coastal habitat integrity. We present eight testable hypotheses here to loosen this knot by identifying critical modulators about nutrient form, soil type and porosity, physiochemical gradients, and eco-evolutionary responses that may control the impacts of nutrient enrichment on coastal wetland sustainability: (1) the delivery and form of the nutrient shapes the ecosystem response; (2) soil type mediates the effects of nutrient enrichment on marshes; (3) belowground responses cannot be solely explained by phenotypic responses; (4) shifting zones of redox and salinity gradients modulate nutrient enrichment impacts; (5) eco-evolutionary processes can drive responses to nutrient availability; (6) nutrient enrichment leads to multiple changed ecosystem states; (7) biogeography trumps a plant's plastic responses to nutrient enrichment; and, (8) nutrient-enhanced wetlands are more susceptible to additional (and anticipated) anthropogenic changes. They provide a framework to investigate and integrate the urgently needed research to understand how excess nutrients threaten the sustainability of coastal wetlands, and wetlands in general. While there is no single ‘right way’ to test these hypotheses, including a combination of complex and simple, highly-replicated experiments is essential.

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1. Introduction

This century is poised to bring rapid increases in relative sea level rise (SLR), atmospheric carbon dioxide concentrations, and temperature. The convergence of climate change with higher nitrogen (N) and phosphorus (P) loads coming from agricultural landscapes and urban wastewater (Bouwman et al., 2009; Greaver et al., 2012; Holtgrieve et al., 2011; Meybeck, 2003; van Puijenbroek et al., 2019) is a pressing concern for tidal wetlands given their position at the land-sea interface. These nutrient loads inevitably end at the world's coastline, with salt marshes already being the most nutrient enriched ecosystem on the planet (Pardo et al., 2011). Wetlands can adapt to some of these changes, but their long-term stability is uncertain. The aggregated ecosystem service valuation for nine habitat subdivisions of the Earth is dominated by tidal marshes (20% of the total value), despite their small area, because of their relatively high per hectare value (Costanza et al., 2014). Understanding how tidal wetlands respond to the combined global change factors therefore has global, regional and local significance.

Studies of wetlands exposed to elevated nutrients – both gradient and experimental fertilization studies – have reported what appear to be conflicting responses. Nutrient enrichment has resulted in increases in belowground biomass production when measured by ingrowth cores, but losses in biomass (Graham and Mendelsohn, 2014), and in gains, no change, or losses in vertical elevation depending on the length of nutrient exposure (Langley et al., 2009; Turner et al., 2009; Valiela, 2015), and increases or decreases in soil or root strength (Hollis and Turner, 2019; Turner et al., 2020). Because marsh elevation change, biomass production, and soil strength also play key roles in determining tidal marsh resilience to climate change, these observations have led to both confusion and conflict over how crucial controlling nutrient discharges are for sustaining coastal wetlands in future decades (Deegan et al., 2012; Krause et al., in press; Morris et al., 2013). Because high N and P loads alter nearly every facet of coastal marsh ecosystem structure and function, and interact strongly with the full range of environmental conditions in tidal marshes, and because unaffected 'reference' systems are rare, it can be difficult to impossible to conclusively determine whether nutrient pollution is negatively impacting a given tidal marsh.

We thus draw an analogy between the factors complicating the relationship between nutrient pollution and tidal marsh sustainability with the legend of the Gordian Knot. In this legend, Alexander the Great was challenged to untangle an elaborate knot as a precursor to claiming his legitimacy (Fig. 1). We seek here to untangle another elaborate knot by unraveling where, how, and through which mechanisms high nutrient loads interact with other factors to threaten tidal marsh survival. We offer eight hypotheses about nutrient form, soils, physiochemical gradients, eco-evolutionary responses, and macro-scale processes. These

hypotheses are a framework to integrate the urgently needed research about how nutrient enrichment threatens the sustainability of coastal wetlands and wetlands in general. Because there is no single 'right way' to test these hypotheses, we suggest testing them in a combination of complex and simple, highly-replicated experiments and observations.

2. Eight hypotheses on the effects of nutrient enrichment on tidal wetland sustainability

We have organized our hypotheses into two scales: (1) abiotic and biotic factors that modulate the impact of nutrients on tidal marshes, and (2) macroscale interactions. Each hypothesis then focuses on a single factor that influences the potential response to nutrient enrichment including: (1) nutrient form, (2) soil type, (3) soil structure, (4) physio-chemical gradients, (5) ecosystem state shifts, (6) biogeography, (7) eco-evolution, and (8) multiple stressors (Table 1).

2.1. Factors that modulate impacts of nutrients on tidal marsh sustainability

Nutrients entering the coastal zone are impacted by physical, chemical, and biological processes, including: uptake by wetland plants, algae, and microbes, adsorption/desorption on sediment surfaces, redox conditions, precipitation reactions, and flocculation due to salinity increases. These processes directly influence coastal marshes, as well as the forms and amounts of nutrients transported to offshore environments. Within the context of examining impacts of increasing nutrient pollution on tidal marsh sustainability we propose it is critical to first evaluate the potential roles of nutrient form, soil type, soil structure, physio-chemical gradients, and eco-evolutionary processes independently because the responses to nutrient enrichment may directly modulate the potential effect.

2.2. Macroscale interactions

In addition to abiotic or biological factors, we also posit that less mechanistic factors also modulate how tidal wetlands respond to nutrient pollution. Because nutrient enrichment typically occurs over larger spatial scales, we posit that nutrient enrichment can lead to multiple changed ecosystem states. Furthermore, because only a few foundation species dominate coastal marshes along broad geographic ranges, biogeographic evolutionary history is often ignored, but should be considered alongside the potential plastic response to nutrient enrichment. Finally, given that anthropogenic stressors such as sea level rise and warming are co-occurring with nutrient enrichment, we must also realize that such interactions may yield unanticipated outcomes.

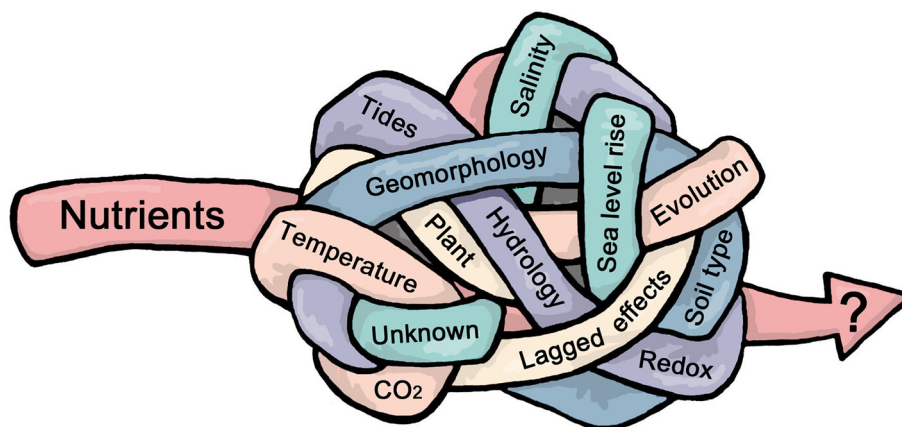


Fig. 1. We assert that environmental and macroscale variables interact to modulate the impacts of nutrient pollution on tidal marsh sustainability, making it difficult to generalize from the results of individual experiments or gradient studies to net positive or net negative effects.

Table 1

Eight hypotheses on the effects of nutrient enrichment, the scale at which each hypothesis operates, and its focus.

Hypothesis	Scale	Focus
1. The form and delivery (concentrations, duration, frequency) of nutrients shapes the ecosystem response	Abiotic and biotic factors that modulate impacts	Nutrient form
2. Soil type plays a large role in mediating the effects of nutrient enrichment on marsh sustainability		Soil type
3. Belowground responses cannot be explained solely by plant phenotypic responses		Soil structure
4. Shifting zones of redox and salinity gradients modulate nutrient enrichment impacts.		Physiochemical gradients
5. Eco-evolutionary processes can drive responses to nutrient enrichment	Macro-scale interactions	Eco-evolution
6. Nutrient enrichment leads to multiple changed ecosystem states		Ecosystem state shifts
7. Biogeographic origin, or provenance, may be more important than phenotypic plasticity in determining the response of foundation species to nutrient enrichment		Biogeography
8. Nutrient-enriched tidal wetlands are more susceptible to these anticipated additional anthropogenic changes		Multiple stressors

Below we present each hypothesis and present selected examples illustrating the conceptualization of our hypotheses.

Hypothesis 1. The form and delivery (concentrations, duration, frequency) of nutrients shapes the ecosystem response.

We assert that differences in N fertilizer species (e.g., nitrate vs. ammonium), differences in N/P/K ratios, as well as other fertilizer constituents (particularly sulfate) will elicit different responses in tidal marsh ecosystem function and sustainability. For instance, N delivered as nitrate may have a different effect than if applied as ammonium, urea, or dissolved organic nitrogen, due to differences in uptake capacities from both shoots (Mozdzer et al., 2011) and roots (Cott et al., 2018; Mozdzer et al., 2010). The aboveground biomass of *Spartina alterniflora* has been reported to increase more from ammonium fertilization than from nitrate (Mendelssohn, 1979) because of different uptake capacities (Cott et al., 2018). Further, nitrate-N may provide more pervasive negative impacts to soil integrity than ammonium-N, because it is a powerful electron acceptor demonstrated to enhance soil organic matter decomposition (Bulsecu et al., 2019), which can shift soil organic matter from fibric to sapric conditions. The soils of freshwater peat marshes of the Mississippi Delta Plain were compromised when exposed to river water with high nitrate levels, but not when isolated from river water introductions (Swarzenski et al., 2008). Freshwater wetlands may lose soil strength with added nitrate or phosphate (Turner et al., 2020). Although not as well studied, agricultural practices often involve the addition of other macronutrients, micronutrients, or soil conditioners, which might also influence wetland sustainability. One clear example is from sulfate application which is added as a fertilizer (NH_4SO_4) or as a soil conditioner to acidify basic soils and increase micronutrient availability (McCray and Rice, 2013). Sulfate can have negative downstream effects to marshes because sulfate is reduced to sulfide under the anoxic conditions found in wetland soils, which inhibits nutrient absorption by roots (Chambers et al., 1998; Koch and Mendelssohn, 1989), and has other toxicant effects.

The timing of nutrient delivery (e.g., chronic vs. pulses) is likely to strongly shape effects on wetlands. The chronic delivery of low concentrations over many years might have more far-reaching consequences than rare pulses of relatively high concentrations. In salt marshes, for example, the addition of relatively low concentrations of nitrate into

tidal creek waters resulted in the loss of low marsh through soil slumping (Deegan et al., 2012). On the other hand, the pulsing of high nutrient inputs associated with storm events is an important component of how wetlands experience elevated nutrient inputs (such as wetlands downstream of combined sewer outflow discharges in New York City, NY or Philadelphia, PA). These infrequent events may lead to the creation of biogeochemical “hot moments” of denitrification that have disproportionate impacts on nutrient processing (Groffman et al., 2009).

Marsh fertilization experiments have mostly applied N as ammonium or urea N on the surface or through slow release capsules buried in the subsurface. However, this approach may not properly represent the long-term exposure to nutrient enriched waters of the real world, thus limiting our understanding of how ecosystems respond. More studies are needed at the landscape level using realistic delivery at environmentally relevant concentrations and forms of pollutants (nitrate-N vs. ammonium-N), and better cross comparisons between the forms and types of nutrients and application modality.

Hypothesis 2. Soil type plays a large role in mediating the effects of nutrient enrichment on marsh sustainability.

Tidal wetland soils vary in organic content and sediment texture, which has important implications for nutrient availability for plant growth, as well as associated variables such as organic matter mineralization, P sorption, and microbial communities. Wetland soils vary greatly in organic matter from about 5 to 95% (Gosselink et al., 1984), and the mineral component of soils can also vary from coarse sand and even gravel, to soils that are predominately clay or peat. Soils vary functionally in redox status, soil nutrient levels, hydraulic conductivity, bulk density and porosity based on their composition, meaning that marshes growing in different soils are likely to respond differently to elevated nutrient inputs (Fig. 2).

Organic wetland soils - soils that exceed 12 to 20% organic C (or 20 to 34% organic matter), depending on flooding frequency and particle size distribution, as well as mineral soils composed of silt and clay - have higher natural sources of nutrients for wetland plants. The cation exchange capacity is high in organic and fine soils, and supports plant nutrition (Curtin and Rostad, 1997; Kirk, 2004). Alternatively, coarse mineral soils (e.g., sands) have low cation exchange capacity, often low amounts of soil organic matter, and tend to have low soil nutrient levels. Because coarse mineral soils provide less nutrition to support plant growth (Kachi and Hirose, 1983), nutrient additions may disproportionately provide positive benefits in coarse mineral soils (Wigand et al., 2015).

Another factor that differs among soil types is redox status. In wetlands, flooded organic or fine soils tend to be consistently hypoxic or anoxic, with narrow oxygenated zones limited to either the top few cm or the oxygenated zones surrounding plant rhizomes because of low soil hydraulic conductivity (Kirk, 2004). Under anoxic conditions and in the presence of sulfate (or other electron acceptors), the deposition of labile organic matter associated with eutrophication (e.g., phytoplankton, decaying macroalgae, or even marsh primary macrophyte production) may fuel anaerobic decomposition, liberating sulfides, which act as a potent phyto-toxicant (Watson et al., 2014). In contrast, coarse mineral soils tend to be well-oxygenated, meaning that labile C deposited in marshes with these soils is likely remineralized aerobically, rather than contributing to anaerobic respiration and sulfide production. Fine mineral soils often provide a source of reduced iron, which co-precipitates forming insoluble iron sulfides, thereby reducing sulfide toxicity (van der Welle et al., 2006).

Consider, too, the soil matrix. Organic soils typically form in locations where low nutrient concentrations and/or temperatures prevent the organic matter from decomposing (Kirk, 2004). Even if nutrient addition increases aboveground productivity, these nutrients may prime microbial communities, potentially remineralizing the organic soil matrix at

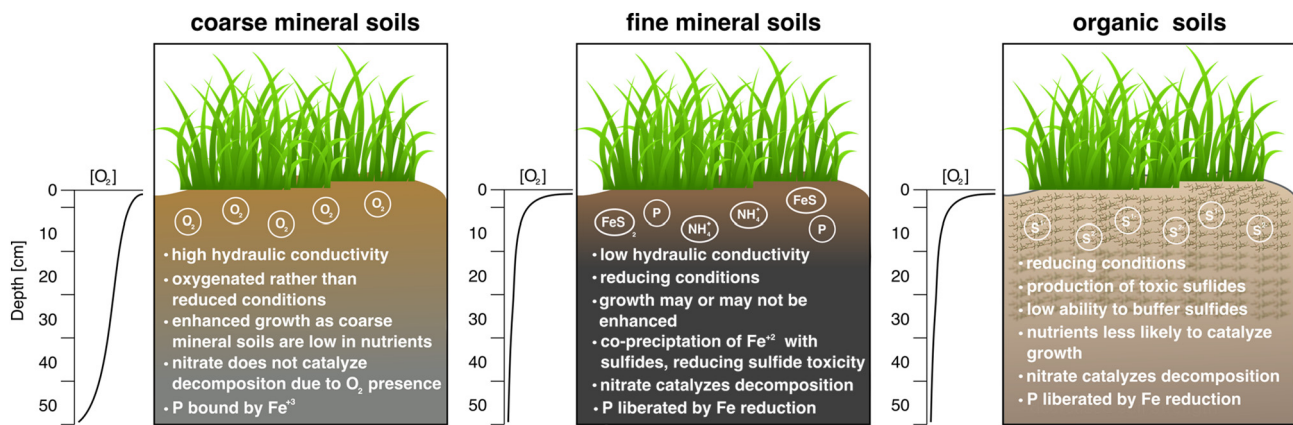


Fig. 2. Effects of nutrient enrichment on marshes and wetlands may vary with soil type. Soils composed of fine mineral sediments tend to have lower hydraulic conductivity than coarse mineral soils. For organic soils, excess inputs of N or P may result in higher respiration, leading to more sapric soils with reduced soil strength.

faster rates than it is replaced. In wetland soils exposed to frequent raw sewage discharges (e.g., Philadelphia and New York City) or where agricultural inputs are combined with tidal restrictions (e.g., Elkhorn Slough, CA), wetland soils are typically sapric, low in oxygen, and rich in iron sulfides (Hartig et al., 2002; Hughes et al., 2011), and similar to the black silts common near sewage outfall points (Papakostidis et al., 1975; Murphy et al., 2004). Where wetland plants are able to oxygenate the root zone with robust rhizomes, these soils may provide an adequate growth environment, but are vulnerable to erosion if the soil matrix lacks cohesiveness of deeper rooting profiles and more fibric soils. In addition to priming microbial communities, added nutrients by themselves may catalyze anaerobic decomposition. This is because NO_3^- also serves as a terminal electron acceptor for both denitrification and dissimilatory nitrate reduction to ammonium. Increasing the availability of terminal electron receptors may also remineralize environmentally relevant amounts of soil organic matter above that from denitrification alone by altering the microbial community to select taxa that are known to reduce nitrate and oxidize more complex forms of organic matter (Bulsecu et al., 2019). Future studies should explicitly consider the role of soil matrix as a driving variable in the response of wetland ecosystems to nutrient enrichment.

Hypothesis 3. Belowground responses cannot be explained solely by plant phenotypic responses.

Organic matter and mineral matter, together with air and water, combine to make up wetland soil volume. Wetland soil structure is important both for maintaining wetland elevation relative to local water level (Fitzgerald and Hughes, 2020; Turner et al., 2002) and through the distribution of macro- and micro-pores, controlling the movement of water and solutes between marsh soil and adjacent surface waters (Harvey et al., 1985). The combined dry mass of organic and mineral matter in wetland soils typically makes up a minor portion of the total soil volume (Fig. 3). Void space, containing varying amounts of gas and water often composes the largest part of the soil volume (Fig. 3, Carey et al., 2017; Craft et al., 1993; Fitzgerald and Hughes, 2020; Nyman et al., 1990; Turner et al., 2002).

How organic matter and mineral matter combine to fill the accommodation space created by sea level rise is essential to understanding the sustainability and health of wetlands and how they respond to perturbations related to higher nutrient loading to ecosystems. Anything that interacts or interferes with how the two solids combine to change the void space and pore size distribution may affect soil elevation, water, and solute movement. Kirwan and Megonigal (2013) provide a conceptual model for how mineral and organic matter build wetland soils (and elevation) that emphasizes belowground production, mainly as a parabolic response function to inundation (Kirwan and Guntenspergen, 2015). However, this approach neglects void space – the largest component by volume – of

wetland soils. Although important, phenotypic responses, such as changes in above- and below-ground production, shifts in communities, or root or rhizome architecture, are only part of the wetland response to nutrient enrichment.

We hypothesize that belowground responses are the most sensitive and consequential to wetland structure and function, as well as resilience to climate change and sustainability, given the growing evidence of nutrient enrichment effects on belowground processes (Deegan et al., 2012; Graham and Mendelsohn, 2016; Langley and Megonigal, 2010; Valiela, 2015). What happens to organic matter quality, and factors that affect how the organic matter breaks down are important response variables (Benner et al., 1985; Benner et al., 1991; Bulsecu et al., 2019). For example, Bulsecu et al. (2019) showed that nitrate additions stimulated decomposition of complex organic matter compounds into more bioavailable forms that could be more easily degraded by a changed microbial community. Against a backdrop of accelerating sea-level rise, changes in porosity may also interact with nutrient exposure. For instance, porosity may increase as plant growth struggles to keep up with sea-level rise, making the marsh organic matter more vulnerable to chemical oxidation, for example by nitrate or sulfate. Conversely, as organic soils decompose, organic matter fractionates into smaller size classes (Swarzenski et al., 2008). This might result in an increased proportion of micropore space and decreased rates of water and solute movement. Sea-level rise could also result in increased mineral sediment deposition (Kirwan et al., 2010). In this case, mineral sediment deposition could buffer negative effects of sulfide toxicity to plants through presence of reduced iron, which co-precipitates with reduced sulfur species forming iron sulfides (FeS , FeS_2) or metal sulfide complexes, and thereby lowering sulfide toxicity to macrophytes (van der Welle et al., 2006).

Hypothesis 4. Shifting zones of redox and salinity gradients modulate nutrient enrichment impacts.

Whether increases in nutrient availability to coastal wetlands will threaten their sustainability is linked to both salinity regimes and nutrient biogeochemical processes (Fig. 4). This variance in source and sinks and throughputs will create multiple kinds of ecosystem outcomes.

Studies have shown that salinity is a master variable that controls nutrient uptake and cycling. Osborne et al. (2015), for example, observed decreases in nitrification and denitrification with increased salinity in tidal wetlands. This coupling was accompanied by reduced oxygen content and increased sulfide in the sediments, presumably due to stimulation of microbial sulfate reduction by seawater sulfate. Soil organic matter losses and a regeneration of soil nutrients also accompanied the increase in microbial sulfate reduction, and these changes seem to be a common feature of salinity incursion into coastal wetlands (Jun et al., 2013; Noe et al., 2013; Weston et al., 2006). Salinity

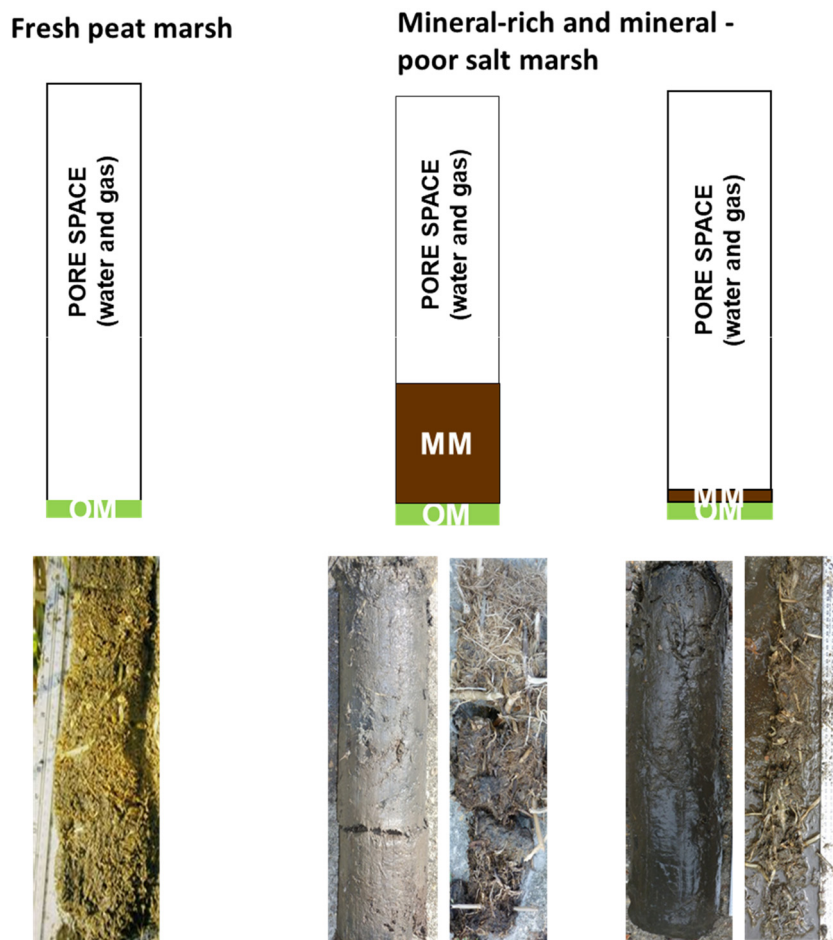


Fig. 3. Percentage of representative soil sods occupied by void space (water and gas) and mass-based mineral matter (MM) and organic matter (OM) in fresh, and in mineral-rich and -poor salt marshes of the inactive portions of the Mississippi River Delta Plain in coastal Louisiana. Note that the mineral-rich salt marsh contains as much as 25% higher OM mass than in the mineral-poor and peat marshes. This difference when adjusted to the entire volume is comparatively minor. OM quality is as much, or more important, than the quantity in its ability to lend structure to the soil.

appears to inhibit uptake of ammonium by wetland plants (Bradley and Morris, 1990) and facilitates release of adsorbed ammonium from sediment surfaces by ion exchange (Giblin et al., 2010), resulting in an accumulation of ammonium in pore water. A buildup of ammonium or higher N inputs to coastal wetlands may inhibit belowground root development, thereby destabilizing coastal wetlands. However, high atomic ratios of available N:P that occur through simultaneous N buildup and P removal (through immobilization with calcium as salinity increases; van Dijk et al., 2015) may tip these systems into P limitation and promote belowground root development as plants scavenge for P (Turner, 2011).

Salinity by itself has been positively correlated with belowground root growth in some salt marshes (Alldred et al., 2017). However, an encroachment of seawater (containing sulfate) will stimulate microbial sulfate reduction that may increase organic soil biodegradation and limit plant uptake of nutrients after sulfide buildup. Chambers et al. (2013) observed organic C loss in both freshwater marshes subject to seawater storm surge and in salt marshes subject to seawater exposure from enhanced microbial respiration (sulfate reduction). However, the freshwater marshes subject to periodic storm surges of seawater appeared more vulnerable to soil C loss and marsh instability. If nutrient inputs to freshwater marshes inhibit belowground growth and are coupled with the effects of storm surge, then these marshes may be especially vulnerable to erosion, and more so considering projected SLR.

The effects of salinity gradients may vary from system to system, linked to the local topography, oceanographic factors (tides), and the

types of wetland environments (mineral sediment or organic soil). Climate change and SLR will likely cause changes in local systems as seawater encroaches into wetland areas and changes existing salinity gradients, with some systems likely to be more resilient than others (Kirwan et al., 2013; Kirwan and Megonigal, 2013).

Hypothesis 5. Eco-evolutionary processes can drive responses to nutrient enrichment.

There is ample evidence that genetic variation within a species can influence C cycle processes including methane emissions (Mozdzer and Megonigal, 2013), C gain (Souza et al., 2011), net primary production (NPP) (Crutsinger et al., 2009; Grady et al., 2011), CO₂ efflux (Walker et al., 2019), net ecosystem CO₂ exchange (NEE) (Breza et al., 2012; Souza et al., 2011), and decomposition (Hines et al., 2014; Schweitzer et al., 2004) in terrestrial and wetland ecosystems. Furthermore, it is also demonstrated that evolutionary processes (i.e., changes in heritable trait variation) can bring about ecological change (Fig. 5; Bassar et al., 2010; Crutsinger et al., 2009; Harmon et al., 2009; Johnson et al., 2009; Palkovacs et al., 2009; Pimental, 1961). Recently, Monroe et al. (2018) hypothesized that C cycling can be influenced by heritable trait variation related to atmospheric carbon dioxide concentrations, and that these traits could potentially induce feedbacks to atmospheric carbon dioxide concentrations. We similarly suggest that nutrient enrichment may also manifest in selection of heritable traits, and that the selection of novel traits may lead to unanticipated outcomes in coastal wetlands.

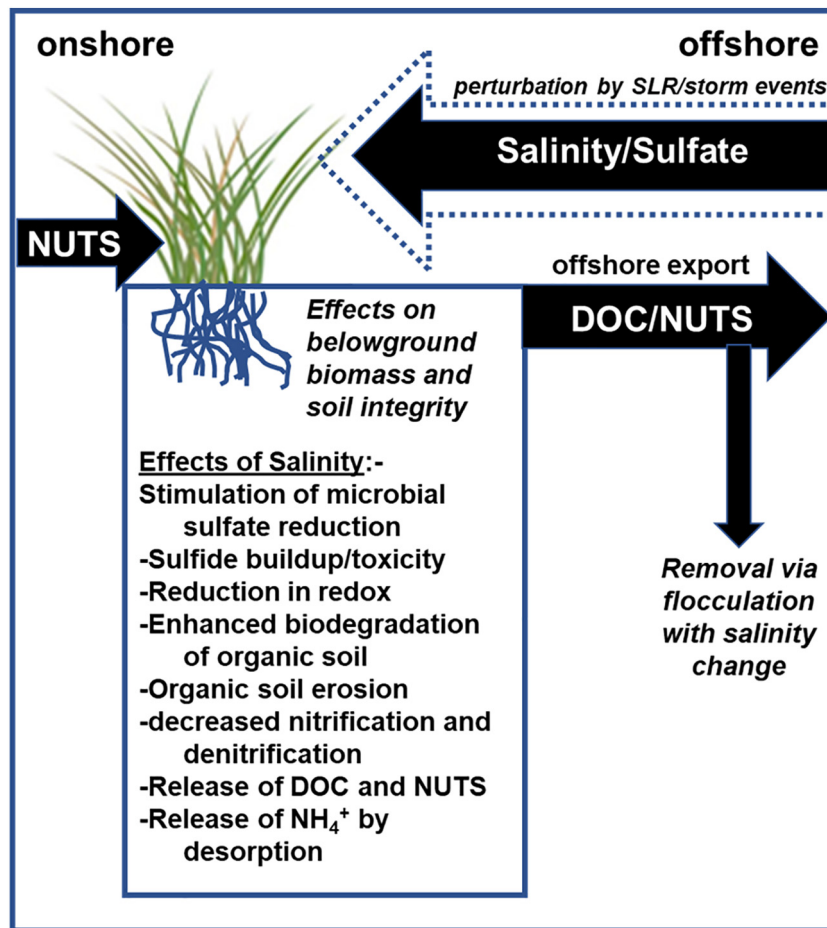


Fig. 4. Effects of salinity (and sulfate) on nutrient (NUTS) biogeochemistry in coastal wetland. Sea level rise (SLR) and increased storm events will likely enhance salinity effects on coastal areas but the precise nature of the perturbation is unknown.

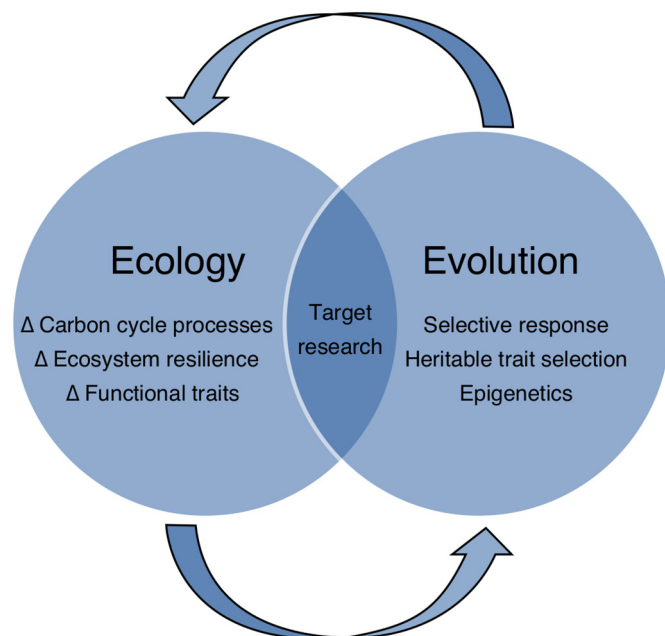


Fig. 5. Hypothesized relationship between ecology and evolution. Future research needs to address the relationship between these fields, with collaborative teams working at the interface of these fields to better understand how selective responses from nutrient enrichment can alter ecosystem processes and outcomes.

We hypothesize that exposure to nutrient enrichment will induce selection of plant functional traits in wetland foundation species. Foundation species within coastal wetlands are demonstrated to harbor a high degree of genetic variation (Blum et al., 2007; Lambertini et al., 2008; Richards et al., 2004; Saltonstall, 2003), which is contrary to our historical understanding of clonal species, which were previously thought to primarily spread via asexual reproduction. Because nutrient enrichment typically induces a strong plant response in wetlands, especially when compared to other factors like elevated CO_2 (Langley and Megonigal, 2010; Mozdzer and Caplan, 2018), the combination of standing genetic variation and a strong selection pressure allows for adaptive responses to occur. What is unknown, however, is what traits will be selected for with nutrient enrichment, and how these traits will influence ecosystem resilience? For example, the potential selection of functional traits to nutrient enrichment (i.e., lower root:shoot ratio) could lower ecosystem resilience due to lower belowground biomass accumulation and roots that stabilize soils, lowering the resilience to relative sea level rise. We must also acknowledge that there is also more to trait variation than the environment, genes, and potential interactions (Bossdorf et al., 2008; Richards et al., 2017). Heritable epigenetic variation (as measured by differential methylation patterns) can similarly explain adaptive variation and evolutionary potential. Future studies need to consider changing levels of genetic diversity, genotypic identity, and epigenetic variation as a driver of change, acknowledging potential feedbacks between evolutionary and ecological processes. Consequently, future studies will require collaborations between ecosystem, evolutionary, and climate scientists to build models that incorporate both phenotypic plasticity and heritable trait variation

(evolutionary processes). This emerging frontier is garnering support within the National Science Foundation with the newly formed cluster, “Bridging Ecology and Evolution.”

Hypothesis 6. Nutrient enrichment leads to multiple changed ecosystem states.

Short-term studies of nutrient enrichment can inform ecological theory, but the results may not capture, or be sufficiently competent, to accurately predict state shifts observed in longer-term studies. Coastal wetlands exposed to nutrient enrichment for decades may persist despite the effects on predator-prey interactions (Denno et al., 2002), changes to aboveground plant growth or stem density (Morris and Bradley, 1999), belowground biomass reduction (Song et al., 2019), higher sediment accumulation because of sediment trapping in denser vegetation (Temmerman et al., 2005), or increased greenhouse gas exchanges (Moseman-Valtierra et al., 2011). Alternatively, the effects of nutrients may force the ecosystem to transition to an alternative unvegetated state if soil strength is reduced profoundly (Howes et al., 2010), wrack deposits smother the marsh (Wasson et al., 2017), the creek bank collapses (Deegan et al., 2012), or snails graze down the plants to a ‘die-back’ condition (Silliman and Bertness, 2002). These tipping points can be a reaction to changes at a cellular or ecosystem level of organization and interaction, and the range of time scales may vary widely, from that of days, as in the case of sulfide toxicity or flooding, to decades, as in the case of evolutionary shifts.

Examples of state shifts drawn from other aquatic systems suggest that crossing critical thresholds can force a change in state from one endpoint, as in some lakes (Fig. 6; Scheffler, 1998), shifts to multiple potential end-points (e.g., Handa and Jefferies, 2000), or frequent fluctuations between end-points in response to multiple disturbances (e.g., Petraitis and Latham, 1999). Some implications of this uncertainty in prediction highlight the value of long-term studies and making multiple comparisons on protected sites across multiple years, if not decades. Further, while long-term studies can provide important guideposts for what to expect in terms of time and extent of change, it is becoming clear, however, that restoration may not return ecosystems changed by nutrient enrichment to their former state (Duarte et al., 2009) with ecosystems showing hysteresis in the path and timing of recovery in function (Ludwig et al., 1997).

Hypothesis 7. Biogeographic origin, or provenance, may be more important than phenotypic plasticity in determining the response of foundation species to nutrient enrichment.

Tidal salt marshes are excellent ecosystems to test this hypothesis for two reasons: 1) there is a broad distribution of clonal foundation species across latitudinal ranges, and, 2) tidal saline wetlands are typically species-poor ecosystems, where intraspecific genetic variation may be as important as genetic diversity (Hughes et al., 2008). Thus, there is a greater ecological importance of intraspecific genetic diversity, and furthermore, small changes in genetic diversity within populations may result in altered ecosystem processes.

The results of several studies provide clear examples of how ecosystem processes can be affected by intraspecific genetic diversity, even at the local scale. Two salt marsh foundation species, *S. alterniflora* and *Schoenoplectus americanus*, exhibit geographically structured genetic variation differing in their longitudinal and latitudinal distribution and diversity (Blum et al., 2007; Summers et al., 2018). There is evidence from these species, and others, from reciprocal transplant experiments that phylogenetic structure can result in heritable traits regardless of growth location (Seliskar et al., 2002; Crosby et al., 2015; Mozdzer et al., 2016). Other studies have suggested that key functional traits (height, biomass, density, nutrient uptake capacity) and phenology are also conserved at the population level (Crosby et al., 2015; Crosby et al., 2017; Mozdzer et al., 2014; Proffitt et al., 2003; Travis and Proffitt, 2016). This intraspecific genetic diversity is a critical function

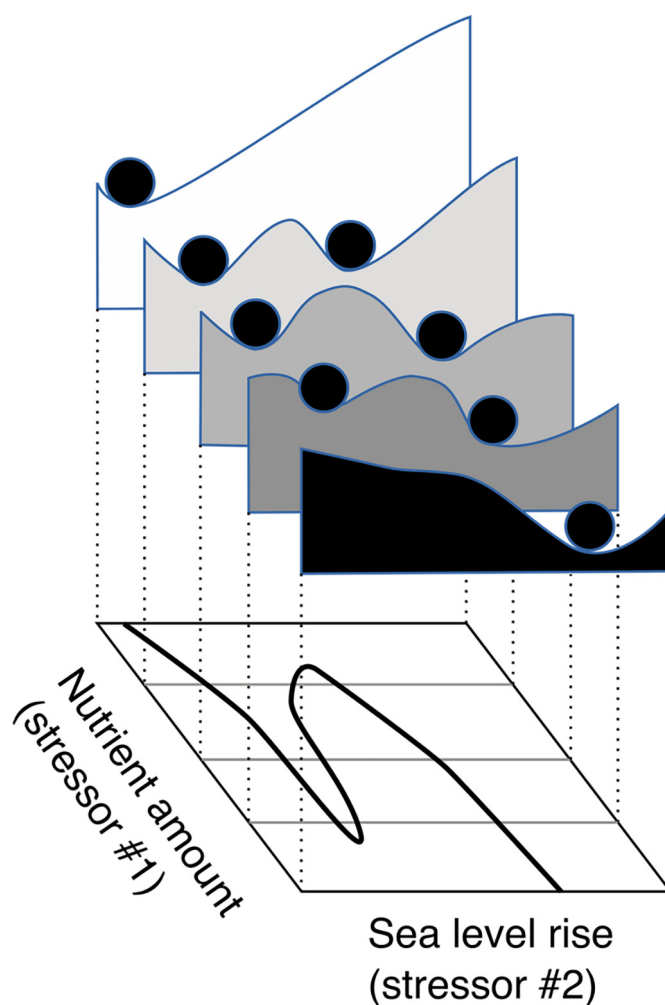


Fig. 6. Conceptual model suggesting how wetlands may reside in several multiple ‘basins of attractions’ or positions of stability that depend on how they respond to multiple stressors when combined with nutrient enrichment. Modified from Scheffler et al. (2001).

of ecosystem resilience (Hughes et al., 2008). For example, the genetic variation in *S. alterniflora* can mediate both soil shear strength and shoreline erosion (Bernik et al., 2018a; Bernik et al., 2018b). Furthermore, genotypic variation in *Phragmites australis* influences decomposition (Hines et al., 2014), primary production (Mozdzer and Megonigal, 2012), nutrient uptake (Mozdzer et al., 2010a, 2010b; Mozdzer and Megonigal, 2012; Mozdzer et al., 2013; Mozdzer et al., 2016), methane emissions (Mozdzer and Megonigal, 2013), and the structure of the rhizosphere community (Bowen et al., 2017). Biogeographic studies have likewise established that herbivory and plant palatability covary with latitude (Pennings et al., 2001), which concomitantly affects food webs (Pennings et al., 2001; Pennings and Silliman, 2005).

There is, therefore, a pressing need for studies that focus on intraspecific genetic variation at the population level, and across biogeographic regions, to better inform understanding of the potential responses and limitations to nutrient enrichment. It is currently impossible to predict if the responses of foundation species to nutrient enrichment are constrained because of long-term evolutionary history, decades to century's exposure to different kinds and amounts of nutrient enrichment (i.e., NH_4^+ vs NO_3^- see Hypothesis 1), local adaptation, or other environmental factors. Although latitudinal differences in productivity have been associated with a plant's plastic responses to temperature (Kirwan et al., 2009), we cannot distinguish if these gradients are due to local adaptation or phenotypic plasticity. For example, northern

S. alterniflora genotypes died when transplanted to warmer temperatures (Crosby et al., 2017), providing strong evidence for local adaptations. Future research and interpretations should not assume that local phenotypic responses would be broadly applicable without acknowledging the importance of local and regional variation, and the associated traits and responses. There are also opportunities to improve ecosystem restoration trajectories. For example, it may be advantageous to identify plant populations across the biogeographic ranges to improve restoration outcomes. However, such admixing should be approached cautiously.

Hypothesis 8. Nutrient-enriched tidal wetlands are more susceptible to these additional anthropogenic changes.

Short-term studies may not adequately highlight the potential feedbacks. Because there may be a decadal lag in marsh loss after the sea level rise thresholds are exceeded (Kirwan et al., 2010), key thresholds and interactions under nutrient enrichment can likewise be difficult to determine. For instance, soil weakening resulting from higher nutrient availability (Deegan et al., 2012; Turner, 2011), might not be apparent until a pulse, such as a hurricane, results in the tearing of the soil fabric in one brief and unobserved catastrophic event (e.g., Kearney et al., 2011). Another example of the complex interactions between sea level rise and nutrient enrichment is from McKee et al. (2007) who studied how changing nutrient availability non-homogeneously affected mangroves in a micro-tidal and mostly autochthonous Caribbean mangrove ecosystem. Due to complex interactions, elevation differences were driven by fine-root growth, species changes from zonation, and nutrient stimulation of organic matter decay.

The challenge of predicting responses of nutrient enrichment alongside changes in temperature and CO₂ is complicated by the mixture of C3 and C4 foundation species in tidal wetlands. These two functional groups respond differently to a wide variety of global change factors, but most especially to the variability in CO₂ concentrations. C3 plants increase ecosystem resilience with elevated CO₂ (Cherry et al., 2009; Langley et al., 2009), but are outcompeted by C4 plants in long term studies under nutrient enrichment even though C4 plants lack the ability to respond to elevated CO₂ (Langley and Megonigal, 2010) due to differences in nutrient uptake (Cott et al., 2018). Although C4 plants can increase short-term aboveground productivity with warming (Gedan and Bertness, 2009; Kirwan et al., 2009), the interaction with nutrients is complex, especially belowground. It is possible that the modest warming (~2 °C) of soils creates a disconnect between plant N demand and N mineralization rates (Noyce et al., 2019), suggesting that modest warming will not result in the anticipated benefits. When possible, long-term studies are critically important to better understand how nutrient enrichment interacts with a growing number of anthropogenic factors.

3. Addressing these hypotheses as a science endeavor

Human population increases in the coastal zone over the last century have either strained or outpaced wastewater infrastructure development (NRC, 1993), and the development of synthetic nitrogen fertilizers and demands of rapid population growth increased nutrient application in agriculture (Tilman et al., 2001). Nutrient loads have increased by 10 to 15 times in some areas (Howarth, 2008), resulting in enhanced nutrient runoff and coastal eutrophication (Baumann and Smith, 2018; Rabalais et al., 2002). Nutrient pollution is a major challenge of this coming century. Developing accurate ways to assess its impacts on coastal ecosystems is a key to maintain and improve environmental conditions as the world population continues to climb.

We assert that while there is no one 'right way' to test these eight hypotheses, a combination of simple highly-replicated and more complex experiments is essential to cutting through the Gordian Knot that currently obscures our understanding of this issue. Several concrete

recommendations can improve our understanding of this issue. An example of a simple, highly replicated study that has provided new insight into ecosystem functions is the Tea Bag experiment (Djukic et al., 2018; Keuskamp et al., 2013; Mueller et al., 2018) where independent investigators across the world collaboratively use the same prescribed protocol to quantify decomposition of two kinds of standardized materials that are readily available. Such efforts may identify important interactions between and among critical processes and functions (e.g., temperature, soil type, tidal range, vegetation type), as well as outliers that might lead to new breakthroughs in understanding. At the other end of the size spectrum are the long-term fertilization experiments at Plum Island (Deegan et al., 2012), Cape Cod, MA (Valiela et al., 1976), and four long term experiments at the Global Change Research Wetland of the Smithsonian Environmental Research Center, Edgewater, MD (Caplan et al., 2015; Langley and Megonigal, 2010; Lu et al., 2019; Noyce et al., 2019) where there are large scale and multi-year global change experiments investigating the role of nutrients, elevated CO₂, warming, and invasive species.

For researchers intimately engaged with this issue, some simple concrete suggestions may also contribute to unraveling this Gordian knot. If nutrient fertilization experiments provided more details regarding soil characteristics and relevant environmental conditions in research studies (redox, soil texture), and bracketed their experiments by what might be expected based on soil type, then synthesis or review studies may more easily untangle modulating factors. Another example is to consider fertilization experiments with multiple nutrient forms and delivery mechanisms, beyond testing N and P fertilization (e.g., ammonium sulfate vs. potassium nitrate or even POM). Another suggestion is to leverage and highlight the insights that have come from long-term studies, but with better acknowledgement of their artifacts. For instance, the long-term fertilization experiment at Waquoit Bay has spawned dozens of scientific studies, but the form of applied nutrients (a solid fertilizer derived from sewage sludge) as well as the soil composition clearly play a role in the generalizability of results.

We do not wish to be prescriptive. Scientists are flexible, inventive and thoughtful in diverse and sometimes unexpected ways. However, consideration of two aspects about how scientists address these hypotheses may be helpful: one involves the necessity of addressing the complexity of the convergent recent stressors in time and space, and another is about how scientists together work successfully.

3.1. Multiple stressors

Song et al. (2019) conducted a meta-analysis of 1119 manipulative ecosystem N addition experiments that included wetlands and described how "Nitrogen addition significantly stimulated plant productivity, biomass, litter mass and ecosystem C fluxes, but not belowground net primary productivity or net ecosystem productivity." They found few results from experiments on multiple stressors (CO₂, precipitation, and temperature) and said: "These contrasting conclusions leave model predictions of such interactions in question, especially given that three- and four-factor studies are too scarce to draw general conclusions." Future research would benefit from a network of geographically diverse and comparable long-term nutrient enrichment field experiments that allow for additional investigator-driven experiments/observations. Some recommended minimum protocols should be created to include a pre-experiment baseline, multiple control sites, and data sharing for a suite of core measurements common to all sites. The protocol might be similar to those of forests and coastal wetlands such as the Coastal Carbon Network (<https://serc.si.edu/coastalcarbon>) Forest Reserves Research Network (COSTE4) <https://www.efi.int/projects/forest-reserves-research-network-coste4>; LTER; biodiversity networks; and Estuarine Research Reserves. Regardless of form, approaches where serendipitous outcomes can thrive must be preserved even while working on comparative studies.

3.2. Working group size

Wu et al. (2019) analyzed 65 million papers, patents and software products for 1954 to 2014, and demonstrated that smaller teams tended to disrupt science and technology with new ideas and opportunities, whereas larger teams tended to develop existing ones. More authors meant, in general, that there was less disruption of ideas. Papers from larger research teams tended to be cited more than from smaller groups, but the highly cited paper isn't necessarily a 'breakthrough' paper. These are more frequently authored by smaller groups. Nobel Prize-winning papers, for example, tended to be from within the top 2% of the most disruptive papers, while review articles fell within the bottom 46%.

A combination of both large and small groups, and both complex and simple experiments, are essential to better understand how wetlands will change and be conserved in our future. Applying the improved understanding in restoration will not necessarily result in a reversal of the trajectory of change; the recovery after restoration will be unclear; things can happen quickly, and recovery may not mirror changes following exposure to the causal stressors (Duarte et al., 2009). Increasing nutrient enrichment to our coastal ecosystems is leading to growing uncertainties. Some questions and approaches are maybe more consequential than others. But the shortest path to find solutions to nutrient enrichment will be understanding. These eight hypotheses will be useful to fulfill those goals.

CRediT authorship contribution statement

Thomas J. Mozdzer: Conceptualization, Writing - original draft, Writing - review & editing. **Elizabeth Burke Watson:** Writing - original draft, Writing - review & editing. **William H. Orem:** Writing - original draft, Writing - review & editing. **Christopher M. Swarzenski:** Writing - original draft, Writing - review & editing. **R. Eugene Turner:** Conceptualization, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of competing interest

There are no conflict of interests to report.

Acknowledgments

We thank Scott Warren and Lauris Hollis for various comments in the development of the workshops, Lena Champlin for artistic preparation of the Gordian knot, and the suggestions by from Tom Doyle and three anonymous reviewers whose suggestions were helpful in improving this manuscript. This research was made possible in part by a grant from the Gulf of Mexico Research Initiative and support from the National Science Foundation (DEB-1557009, DEB 1902712, OCE-1637630). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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