Black Mangrove Range Expansion in Georgia: An Annotated Bibliography

Review papers

Kelleway, J. J., Cavanaugh, K., Rogers, K., Feller, I. C., Ens, E., Doughty, C., and Saintilan, N. (2017). Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology*, 23: 3967–3983.

In this review, the authors assess changes in ecosystem services associated with mangrove encroachment. Based on current understanding of ecosystem structure and function, mangrove encroachment may increase nutrient storage and improve storm protection, but cause declines in habitat availability for fauna requiring open vegetation structure as well as the recreational and cultural activities associated with this fauna. Changes to provisional services such as fisheries productivity and cultural services are likely to be site specific and dependent on the species involved. The authors discuss the need for explicit experimental testing of the effects of encroachment on ecosystem services to address knowledge gaps and present an overview of the options available to coastal resource managers.

Osland, M. J., Hughes, A. R., Armitage, A. R., Scyphers, S. B., Cebrian, J., Swinea, S. H., Shepard, C. C., Allen, M. S., Feher, L. C., Nelson, J. A., O'Brien, C. L., Sanspree, C. R., Smee, D. L., Snyder, C. M., Stetter, A. P., Stevens, P. W., Swanson, K. M., Williams, L. H., Brush, J. M., … Bardou, R. (2022). The impacts of mangrove range expansion on wetland ecosystem services in the southeastern United States: Current understanding, knowledge gaps, and emerging research needs. *Global Change Biology*, 28: 3163–3187.

In this article, the authors review the current understanding of the effects of mangrove range expansion and displacement of salt marshes on wetland ecosystem services in the southeastern United States. They also identify knowledge gaps and emerging research needs regarding the ecological and societal implications of salt marsh displacement by expanding mangrove forests. A consistent theme throughout the review is that there are ecological trade-offs for consideration by coastal managers. Mangrove expansion and marsh displacement can produce beneficial changes in some ecosystem services, while simultaneously producing detrimental changes in other services. Thus, there can be local-scale differences in perceptions of the impacts of mangrove expansion into salt marshes.

Research papers

Adgie, Terese, E. and Chapman, C.K. (2021). Salt Marsh Plant Community Structure Influences Success of *Avicennia germinans* During Poleward Encroachment. *Wetlands,* 41: 82.

Using a semi-natural mangrove planting experiment, the authors investigated the impact of four distinct marsh plant community structures (*Batis maritima, Spartina alterniflora*, mixture of *B. maritima* and *S. alterniflora*, and mudflat) on mangrove survivorship and decomposition rate. In mixed marsh plots, mangrove survivorship was 42% higher compared to mudflat plots, and decomposition rate was 47% greater in mixed marsh plots compared to mudflat. However, percent cover of vegetation differed across treatments, and was highest in mixed marsh plots. This is likely due to increased protection from physical stressors by the dense aboveground cover, and belowground plant root-driven effect. The findings suggest that above and below ground differences in salt marsh plant community structure can have an impact on the survival of encroaching mangroves, which may have implications for predicting future mangrove encroachment and improving mangrove restoration techniques.

Armitage, A. R., Weaver, C. A., Whitt, A. A., and Pennings, S. C. (2021). Effects of mangrove encroachment on tidal wetland plant, nekton, and bird communities in the Western Gulf of Mexico. *Estuarine, Coastal & Shelf Science*, 248: 106767.

This study's goal was to quantify the bottom-up effects of mangrove encroachment into coastal wetlands on associated plant, nekton, and bird assemblages. The results indicate that coastal wetlands dominated by mangroves support different plant and animal assemblages than marsh-dominated areas. Therefore, as woody encroachment continues and mangrove cover gradually increases, this change may lead to complex bottom-up effects on a range of ecosystem processes and services.

Bardou, Rémi, Michael J. Osland, Steven Scyphers, et al. (2023). Rapidly Changing Range Limits in a Warming World: Critical Data Limitations and Knowledge Gaps for Advancing Understanding of Mangrove Range Dynamics in the Southeastern USA. *Estuaries and Coasts,* 46: 1123–1140.

In this study, the authors synthesized existing data and expert knowledge to assess the distribution of mangroves near rapidly changing range limits in the southeastern USA. We used expert elicitation to identify data limitations and highlight knowledge gaps for advancing understanding of past, current, and future range dynamics. Mangroves near poleward range limits are often shorter, wider, and more shrublike compared to their tropical counterparts. Thus, there is need for methodological refinements and improved spatiotemporal data regarding changes in mangrove structure and abundance near northern range limits. Advancing understanding of rapidly changing range limits is critical for foundation plant species such as mangroves, as it provides a basis for anticipating and preparing for the cascading effects of climate-induced species redistribution on ecosystems.

Cahoon, D. R., McKee, K. L., and Morris, J. T. (2020). How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. *Estuaries and Coasts*, 44: 883–898.

This review evaluates the importance of plants and associated biological processes in determining the vulnerability of coastal wetlands to sea-level rise. We explore how plants influence sediment accretion, elevation capital (vertical position in the tidal frame), and compaction or erosion of deposited material in salt marsh and mangrove wetlands. In both

habitats, plants stabilize emergent mudflats and help sustain the wetland position in the tidal frame relative to ocean height through both surface and subsurface process controls on soil elevation. Plants influence soil elevations by modifying (1) mineral sediment deposition and retention, (2) organic matter contributions to soil volume, and (3) resistance to compaction and erosion. Recognition of the importance of plants in coastal wetland resilience to sea-level rise is key to accurate predictions about the future fate of salt marshes and mangrove forests and for development of effective management and restoration plans.

Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Williams, A. P., Parker, J. D., Hayes, M. A., Rodriguez, W., and Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences of the United States of America*, 116: 21602–21608.

The authors combined historical accounts from books, personal journals, scientific articles, logbooks, photographs, and maps with climate data to show that the current ecotone between mangroves and salt marshes in northeast Florida has shifted between mangrove and salt marsh dominance at least 6 times between the late 1700s and 2017 due to decadal-scale fluctuations in the frequency and intensity of extreme cold events. Model projections of daily minimum temperature from 2000 through 2100 indicate an increase in annual minimum temperature by 0.5 °C/decade. Thus, climate projections suggest that the recent trend may represent a more permanent regime shift because of climate change.

Chapman, S. K., Feller, I. C., Canas, G., Hayes, M. A., Dix, N., Hester, M., Morris, J., and Langley, J. A. (2021). Mangrove growth response to experimental warming is greatest near the range limit in northeast Florida. *Ecology*, 102: e03320.

Increasing mangrove biomass in wetlands often increases carbon storage but little is known about how mangrove growth will change in response to warming. To address this knowledge gap, the authors deployed warming experiments at three coastal wetland sites along a latitudinal gradient in northeast Florida where black mangroves, are encroaching into salt marshes. Air temperature warming (+1.6°C during the day) was achieved at all three sites and stem elongation, canopy height and area changes, and leaf and node number were measured. After 2 yr of warming, mangrove growth rate in height increased due to warming. Warming increased stem elongation by 130% over unwarmed control plots after 1 yr at the northern site. Mangrove growth in canopy area did not respond to warming. Site differences in growth rate were pronounced, and mangrove growth in both height and area were lowest at the northern site, despite greater impacts of warming at that site. Also, the area-based relative growth rate was five times higher across all treatments than height-based relative growth rate, indicating that mangroves are growing wider rather than taller in these ecotonal environments. These findings indicate that the growth effect of experimental warming depends on site characteristics and growth parameter measured. Differential mangrove growth across the three sites may also be

driven by biotic factors such as the identity of the salt marsh species into which mangroves are encroaching.

Coldren, G. A., Langley, J. A., Feller, I. C., and Chapman, S. K. (2019). Warming accelerates mangrove expansion and surface elevation gain in a subtropical wetland. *Journal of Ecology*, 107: 79–90.

This study used a large scale in situ warming experiment in a subtropical wetland to increase both marsh and mangrove ecosystem air temperatures to assess how 2 years of continuous warming influenced above- and below-ground plant growth and surface elevation relative to sea level. It was found that chronic warming doubled plant height and accelerated the expansion of mangrove into salt marsh vegetation, as indicated by a sixfold greater increase in mangrove cover in warmed plots compared to ambient temperature plots and a corresponding loss in salt marsh cover. Surface elevation gain, a measure of soil-building capacity, increased due to warming over a 2-year period and these changes in surface elevation were driven by increased mangrove root production in warmed plots. These findings suggest that, in some coastal wetlands, warming can facilitate plant community changes from marsh to mangrove, with corresponding increases in growth that help coastal wetlands to keep pace with sea-level rise.

Dangremond, E. M., Simpson, L. T., Osborne, T. Z., and Feller, I. C. (2020). Nitrogen enrichment accelerates mangrove range expansion in the temperate–tropical ecotone. *Ecosystems*, 23: 703–714.

This study tested the hypothesis that nutrient enrichment enhances the expansion of mangroves into areas historically dominated by saltmarshes by increasing mangrove growth and cover, allowing them to outcompete and overgrow adjacent saltmarsh plants. Nitrogen (N) and phosphorus (P) availability was manipulated and measured the effects on growth, cover, diversity, leaf traits, and nutrient dynamics of black mangroves. Results showed that shrubs grew taller, increased their canopies, and had higher reproductive output when enriched with N compared to control plants and P-enriched plants. Nutrient enrichment did not alter *Sarcocornia perennis* growth and increased *Batis maritima* height but did not alter density or biomass. Nitrogen addition caused an increase in black mangrove cover and decrease in *B. maritima* cover and Simpson's index of diversity, suggesting that N enrichment can hasten the invasion of mangroves into saltmarshes by favoring mangrove growth and reproduction without significantly enhancing saltmarsh plant growth.

Geoghegan, E. K., Langley, J. A., & Chapman, S. K. (2020). A comparison of mangrove and marsh influences on soil respiration rates: A mesocosm study. *Estuarine, Coastal & Shelf Science*, 248: 106877.

Using a full factorial greenhouse mesocosm experiment, the authors investigated the effects of plant type (no plant, black mangroves, or *Spartina*) and soil type (sand, mangrove-derived soil, or marsh-derived soil) on estimated heterotrophic soil respiration rates. While it was predicted that mangrove seedlings would increase heterotrophic respiration, it was found that mangrove seedlings did not increase heterotrophic respiration when compared to control (no plant) treatments. Additionally, heterotrophic respiration was higher in marsh-derived soils than in mangrove-derived soils for both control and mangrove plant treatments. These findings suggest that the stage of mangrove invasion and the level of root development may influence changes in heterotrophic soil respiration.

Glazner, R., Ballard, J., and Armitage, A. R. (2021). Predation refuge values of marsh and mangrove vegetation for the marsh periwinkle *Littoraria irrorata*. *Marine Ecology Progress Series*, 672: 153–162.

A series of field studies compared prey refuge values between marsh and mangrove vegetation for a vertically migrating gastropod, the marsh periwinkle, *Littoraria irrorata*. *Littoraria* were tethered to marsh grasses (*Spartina alterniflora*) or the aerial roots of mangrove arrays that fully crossed vegetation type (*Spartina* vs. *Avicennia*), tether height (base vs. canopy), and wetland location (edge vs. interior marsh platform). After 1 d, acute predation rates were twice as high on *Littoraria* tethered to the base of *Spartina* stems than on those tethered to pneumatophores, suggesting that mangroves provided superior refuge from benthic predators like blue crabs. In the canopy, *Spartina* reduced acute predation rates by 75%, indicating that marsh grasses may provide superior refuge from aerial predators (possibly wetland birds). After 7 d, the effect of vegetation type diminished, but *Littoraria* mortality was 2 times higher on the benthos than in the canopy. Links between vegetation type and predation intensity on this important basal consumer may have broader consequences for trophic dynamics in coastal wetlands that are experiencing mangrove encroachment.

Glazner, R., Blennau, J., and Armitage, A. R. (2020). Mangroves alter predator-prey interactions by enhancing prey refuge value in a mangrove-marsh ecotone. *Journal of Experimental Marine Biology and Ecology*, 526: 151336.

This study investigated how increasing mangrove cover might alter predator-prey interactions involving an important consumer in coastal wetlands, blue crabs, and one of their key prey items, penaeid shrimp. A series of mesocosm experiments were conducted to assess predation rates and prey refuge values in artificial vegetation (AV) matrices simulating flexible marsh grasses (e.g., *Spartina*) and rigid mangrove pneumatophores. In predation experiments within each of these AV matrices, blue crabs captured 50% fewer penaeid shrimp in the rigid mangrove treatment compared to the flexible marsh treatment, and time between captures was 83% longer among the simulated pneumatophores. In a prey refuge experiment that allowed both predator and prey to move freely among the AV matrices, penaeid shrimp occupied the rigid pneumatophore matrix 30% more often than the grass matrix when blue crabs were present but had no preference when the predator was absent. This study suggests that where mangrove and marsh grasses co-occur, the mangroves may provide superior refuge for prey items such as penaeid shrimp. Pneumatophores will likely restrict the mobility of predators such as blue crabs, resulting in

lower predation efficiency. These results suggest that as mangrove stands continue to increase in cover within mangrove-marsh ecotones, there are likely to be consequences for upper trophic level dynamics.

Goeke, J. A., and A. R. Armitage (2021). Coastal woody encroachment reduces food quality for basal consumers. *Ecosphere*, 12: e03511.

This study used interactions between fiddler crabs and the encroaching black mangrove in Gulf of Mexico salt marshes to explore trophic interactions between basal consumers and encroaching shrubs. In a series of food preference trials, fiddler crabs consumed over five times more marsh (*S. alterniflora*) plant matter when given a choice between mangrove and marsh diets. In food quality trials, fiddler crabs stored 50% less energy, as measured by hepatopancreas lipid content, when restricted to a mangrove diet. These results demonstrate that mangrove encroachment may have negative consequences for salt marsh basal consumers, which may lead to deleterious population-level effects and altered ecosystem carbon flows. As fiddler crabs are generalist consumers and mangroves share many physical and chemical characteristics with other encroaching woody species, negative consequences for basal consumers may be widespread in other environments undergoing woody shrub encroachment.

Harris, J. M., James, W. R., Lesser, J. S., Doerr, J. C., and Nelson, J. A. (2020). Foundation species shift alters the energetic landscape of marsh nekton. *Estuaries and Coasts*, 44: 1671–1680.

Using stable isotopes and habitat cover maps, the authors built energetic landscapes (*E*-scapes) for three nekton species to determine how the landscape's ability to produce energy changes with changing habitat cover over a 5-year period. Between 2015 and 2020, 25% (367.26 ha) of marsh habitat converted into mangrove habitat and 10% (144.93 ha) of marsh habitat transitioned into water. An overall decrease in the energetic benefit to all consumers was observed with increasing mangrove cover, due to the fact mangrove detritus is not used as a food source by consumers in the system. Edge habitat had a positive relationship with overall energetic production, likely due to the increase in available area for benthic algal production. The relationship between edge habitat and water habitat suggests that while these areas may initially increase in their ability to support consumer species, continued sea level rise will lead to reductions in the landscape's ability to produce energy for consumers as land is converted to water. As these coastal areas experience rapid habitat cover changes, the reduction in energetic quality of habitats could lead to a reduction in the ability of these systems to support existing consumer species.

Howard, R. J., From, A. S., Krauss, K. W., Andres, K. D., Cormier, N., Allain, L., and Savarese, M. (2020). Soil surface elevation dynamics in a mangrove-to-marsh ecotone characterized by vegetation shifts. *Hydrobiologia*, 847: 1087–1106.

To better understand how soil processes may influence vegetation change, the authors studied soil surface elevation change, accretion rates, and soil subsurface change across a

coastal salinity gradient in Florida, an area with documented mangrove encroachment into saline marshes. Their objective was to identify any variations in the soil variables studied and to document any associated vegetation shifts. They used surface elevation tables and marker horizons to document the soil variables over 5 years in a mangrove-to-marsh transition zone or ecotone. Study sites were located in three marsh types (brackish, salt, and transition) and in riverine mangrove forests. Mangrove forest sites had significantly higher accretion rates than marsh sites and were the only locations where elevation gain occurred. Significant loss in surface elevation occurred at transition and salt marsh sites. Transition marshes, which had a significantly higher rate of shallow subsidence compared to other wetland types, appear to be most vulnerable to submergence or to a shift to mangrove forest. Submergence can result in herbaceous vegetation mortality and conversion to open water, with severe implications to the quantity and quality of wetland services provided.

Kimball, M. E., and W.E. Eash-Loucks (2021). Estuarine nekton assemblages along a marsh-mangrove ecotone. *Estuaries and Coasts*, 44: 1508–1520.

To determine if estuarine nekton assemblages differ along the marsh-mangrove ecotone, a 60-km transition zone within the Guana-Tolomato-Matanzas (GTM) estuary in northeast Florida was divided into 20 sub-zones where nearshore subtidal nekton communities were sampled monthly with trawls for 1 year. A total of 15,750 individuals consisting of 100 species were collected during the study period; 13 species made up 90% of the total catch. Subtidal nekton assemblages in marsh sites were dominated by typical salt marsh species and had little overlap with assemblages in mixed and mangrove sites, which were dominated by structure-oriented species. Despite similar environmental conditions among the zones, there were clear differences in the subtidal nekton community along the marsh-mangrove ecotone, largely driven by fish species. This change in nekton community along the ecotone suggests that ecological processes such as food availability or predator/prey dynamics affected by changes in marsh surface habitats may result in differences in nekton species distribution and abundance across interconnected habitats.

Lewis, D. B., Jimenez, K. L., Abd-Elrahman, A., Andreu, M. G., Landry, S. M., Northrop, R. J., Campbell, C., Flower, H., Rains, M. C., and Richards, C. L. (2021). Carbon and nitrogen pools and mobile fractions in surface soils across a mangrove saltmarsh ecotone. *Science of the Total Environment*, 798: 149328.

In this study, the authors quantified total C and N pools, and mobile fractions including extractable mineral N, extractable organic C and N, and active (aerobically mineralizable) C and N, in surface soils (top 7.6 cm) of adjacent mangrove and saltmarsh vegetation zones in tidal wetlands of west-central Florida. They tested whether surface-soil accumulations of C, N, and their potentially mobile fractions are greater in mangrove than in saltmarsh owing to greater accumulations in the mangrove zone of soil organic matter (SOM) and fine mineral particles (C- and N-retaining soil constituents). Extractable organic fractions were 39–45%

more concentrated in mangrove than in saltmarsh surface soil, and they scaled steeply and positively with SOM and fine mineral particle (silt + clay) concentrations, which themselves were likewise greater in mangrove soil. Elevation may drive this linkage. Mangrove locations were generally at lower elevations, which tended to have greater fine particle content in the surface soil. Active C and extractable mineral N were marginally ($p < 0.1$) greater in mangrove soil, while active N, total N, and total C showed no statistical differences between zones. Extractable organic C and N fractions composed greater shares of total C and N pools in mangrove than in saltmarsh surface soils, which is meaningful for ecosystem function, as persistent leaching of this fraction can perpetuate nutrient limitation. The active (mineralizable) C and N fractions observed constituted a relatively small component of total C and N pools, suggesting that mangrove surface soils may export less C and N than would be expected from their large total C and N pools.

Loveless, J. B., and D. L. Smee (2019). Changes in arthropod communities as black mangroves *Avicennia germinans* expand into Gulf of Mexico salt marshes. *Arthropod-Plant Interactions*, 13: 465–475.

The authors investigated insect community assemblages in wetlands with and without black mangroves to assess potential effects of mangrove expansion on insect fauna in the Gulf of Mexico. Insect abundance, biomass, richness, diversity, community structure, and feeding guild composition were measured in both the spring and the fall across three levels of mangrove abundance. Insect abundance and biomass were larger in both the spring and the fall in wetlands where mangrove abundance was low. Significant differences in community structure were associated with the presence of mangroves. Feeding guild composition was also different in wetlands containing mangrove, having less predator biomass. Shifting vegetation caused by climate change can alter insect communities in coastal wetlands, illustrating the need for a more comprehensive understanding of climate change effects on fauna in response to shifting foundation plant species.

Macy, A., Osland, M. J., Cherry, J. A., and Cebrian, J. (2020). Changes in ecosystem nitrogen and carbon allocation with black mangrove (Avicennia germinans) encroachment into *Spartina alterniflora* salt marsh. *Ecosystems*, 24: 1007–1023.

In this study, the authors compare carbon and nitrogen stocks and relate these findings to the expected effects of mangrove encroachment on nitrogen filtration and carbon sequestration in coastal wetlands. they specifically evaluate the implications of black mangrove encroachment into *Spartina alterniflora*-dominated salt marsh in Louisiana. The results indicate that black mangrove encroachment will lead to increased aboveground carbon and nitrogen stocks. However, we found no differences in belowground nitrogen or carbon stocks between marshes and mangroves. Thus, the shift from marsh to mangrove may provide decadal-scale increases in aboveground nitrogen and carbon sequestration, but belowground nitrogen and carbon sequestration (that is, carbon burial) may not be affected. Lower pore water nitrogen content beneath growing mangroves were measured,

which the authors postulate may be due to greater nitrogen uptake and storage in mangrove aboveground compartments compared to marshes. However, further studies are needed to better characterize the implications of mangrove encroachment on nitrogen cycling, storage, and export to the coastal ocean.

Macy, A., Sharma, S., Sparks, E., Goff, J., Heck, K. L., Johnson, M. W., Harper, P., and Cebrian, J. (2019). Tropicalization of the barrier islands of the northern Gulf of Mexico: A comparison of herbivory and decomposition rates between smooth cordgrass (*Spartina alterniflora*) and black mangrove (*Avicennia germinans*). *PLoS One*, 14: e0210144.

In this study, the authors find mangrove leaves to be preferable to chewing herbivores, but simultaneously, chewing herbivores cause more damage to *S. alterniflora* leaves. Despite higher nitrogen content, mangrove leaves decomposed slower than *S. alterniflora* leaves, perhaps due to other leaf constituents or a different microbial community. Other studies have found the opposite in decomposition rates of the two species' leaf tissue. This study provides insights into basic trophic process, herbivory and decomposition, at the initial stages of black mangrove colonization into *S. alterniflora* salt marsh.

McKee, K. L., Mendelssohn, I. A., and Hester, M. W. (2020). Hurricane sedimentation in a subtropical salt marsh-mangrove community is unaffected by vegetation type. *Estuarine, Coastal, and Shelf Science*, 239: 106733.

In the subtropical climate of the Mississippi River Delta Complex (MRDC), the black mangrove has been expanding and replacing salt marsh (*Spartina alterniflora*). Because these vegetation types differ in structure, their influence on sedimentation may also differ. The authors conducted a survey along 160 km of coastline to determine if the spatial deposition pattern in saline wetlands by Hurricanes Gustav and Ike in September 2008 was differentially influenced by vegetation type. Sampling was initiated two months after landfall at eighteen sites in the MRDC containing side-by-side stands of mangroves and *S. alterniflora* along the shoreline, with *S. alterniflora* marsh landward. Average thickness of hurricane sediment across sites varied from 0.6 to 5.6 cm with an overall mean of 2.6 ± 0.4 cm. Within sites, hurricane-layer thickness varied from 1.3 cm at the shoreline to 4.8 cm in the marsh interior, but this pattern was unaffected by vegetation type. Despite greater canopy height, stem density (including pneumatophores), and leaf area, mangroves did not capture more hurricane sediment than salt marsh nor did they attenuate the delivery of sediment to the marsh interior. Data recorded at thirty-six monitoring stations in Louisiana's Coastwide Reference Monitoring System further showed that rates of accretion, as well as elevation change, in saline wetlands (*S. alterniflora*) of the MRDC were temporarily increased by Hurricanes Gustav and Ike. These findings agree with previous work showing the beneficial effects of hurricane sediments on coastal wetlands, but suggest that a climate-driven shift from *S. alterniflora* to mangroves in the MRDC will not necessarily alter hurricane sediment capture.

Nelson, J. A., Lesser, J., James, W. R., Behringer, D. P., Furka, V., and Doerr, J. C. (2019). Food web response to foundation species change in a coastal ecosystem. *Food Webs*, 21: e00125.

Here, the authors used stable isotopes and Bayesian mixing models to determine the contributions of primary production sources to the food webs in Louisiana saltmarshes currently experiencing rapid mangrove encroachment. In addition, they determined how these contributions are altered as a function of foundation species cover, particularly for white shrimp. Species primarily rely on algae-derived and water-column derived production, not on production derived from the foundational macrophytes themselves. The trophic position of white shrimp increased in areas with higher mangrove cover at some locations; shrimp used more water column-derived production and less algae-derived production. Transition from *Spartina* to mangrove-dominated estuarine areas has little effect on the overall pattern of primary producer contribution to food webs in these areas. However, differences in the structural and substrate properties of these foundational species could be altering the way energy moves through food webs.

Osland, M. J., Stevens, P. W., Lamont, M. M., Brusca, R. C., Hart, K. M., Waddle, J. H., Langtimm, C. A., Williams, C. M., Keim, B. D., Terando, A. J., Reyier, E. A., Marshall, K. E., Loik, M. E., Boucek, R. E., Lewis, A. B., and Seminoff, J. A. (2021). Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*, 27: 3009–3034.

Here, the authors examine the influence of extreme cold events on the northward range limits of a diverse group of tropical organisms, including terrestrial plants, coastal wetland plants, coastal fishes, sea turtles, terrestrial reptiles, amphibians, manatees, and insects. For these organisms, extreme cold events can lead to major physiological damage or landscape-scale mass mortality. Conversely, the absence of extreme cold events can foster population growth, range expansion, and ecological regime shifts. The authors discuss the effects of warming winters on species and ecosystems in tropical–temperate transition zones. In the 21st century, climate change-induced decreases in the frequency and intensity of extreme cold events are expected to facilitate the poleward range expansion of many tropical species. This review highlights critical knowledge gaps for advancing understanding of the ecological implications of the tropicalization of temperate ecosystems in North America.

______, Day, R. H., Hall, C. T., Feher, L. C., Armitage, A. R., Cebrian, J., Dunton, K. H., Hughes, A. R., Kaplan, D. A., Langston, A. K., Macy, A., Weaver, C. A., Anderson, G. H., Cummins, K., Feller, I. C., and Snyder, C. M. (2020). Temperature thresholds for black mangrove (*Avicennia germinans*) freeze damage, mortality, and recovery in North America: Refining tipping points for range expansion in a warming climate. *Journal of Ecology*, 108: 654–665.

To refine temperature thresholds for mangrove freeze damage, mortality and recovery, the authors integrated data from 38 sites spread across the mangrove range edge in the Gulf of Mexico and Atlantic coasts of North America, including data from a regional collaborative network – the Mangrove Migration Network. In 2018, an extreme freeze event affected

60% of these sites, with minimum temperatures ranging from 0 to −7°C. They used temperature and vegetation data from before and after the freeze to quantify temperature thresholds for leaf damage, mortality and biomass recovery of the black mangrove – the most freeze-tolerant mangrove species in North America. For mangrove individuals near their northern range limit, the results indicate that temperature thresholds for leaf damage are close to −4°C, but temperature thresholds for mortality are closer to −7°C. Thresholds are expected to be warmer for more southern mangrove individuals and for the other two common mangrove species in the region (*Laguncularia racemosa* and *Rhizophora mangle*). Regenerative buds allowed mangrove to resprout and recover quickly from above-ground freeze damage. Hence, biomass recovery levels during the first post-freeze growing season were 90%, 78%, 62% and 45% for temperatures of −4, −5, −6 and −7°C, respectively. Due to a combination of vigorous resprouting and new recruitment from propagules, full recovery at most sites within 1–3 years are expected, assuming no further freeze events.

Rogers, K., and K. W. Krauss (2019). Moving from generalisations to specificity about mangrove–saltmarsh dynamics. *Wetlands*, 39: 1155– 1178.

In this paper the spatial variability in mangrove distribution and variability in factors influencing mangrove establishment and survival during the Quaternary period are reviewed, focusing on research at latitudinal limits in Australia and mainland USA. Despite similarities in the response of mangrove to some drivers, the expression of these drivers is both spatially and temporally variable, demonstrating the need for analyses of mangrove-saltmarsh dynamics to move beyond generalisations and incorporate regional and local-scale specificity. The authors propose: i) that precursory recognition that 'correlation does not mean causation' is inadequate and assumptions, caveats, and limitations should be clearly articulated in correlative studies; ii) experimental design in manipulative experiments must also articulate the spatial and temporal scale to which the analysis is relevant; and iii) analyses that draw from a range of methods will provide greater confidence. Integrated research programs that transect spatial and temporal scales and incorporate a range of techniques are essential to improve projections.

Simpson, L. T., Cherry, J. A., Smith, R. S., and Feller, I. C. (2020). Mangrove encroachment alters decomposition rate in saltmarsh through changes in litter quality. *Ecosystems,* 24: 840–854.

This work quantified and compared aboveground litter decomposition of the range-expanding black mangrove and resident saltmarsh cordgrass, *Spartina alterniflora*, and decomposition of a standard substrate belowground, in the saltmarsh and saltmarsh-mangrove ecotone habitat along the Atlantic coast of Florida. Plant and soil fractions were tested for natural abundances of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to elucidate soil nutrient sources. Although aboveground decomposition rates differed between marsh and mangrove species due to differences in litter quality, decomposition rates did not vary between saltmarsh and ecotonal habitats. Decay rates were higher for mangrove leaf litter than for *S. alterniflora* regardless of habitat, which suggests that increasing inputs of mangrove litter with encroachment may increase nutrient availability through rapid turnover. Furthermore, belowground decomposition was similar between habitats, whereas soil $\delta^{13}C$ and $\delta^{15}N$ stable isotopes differed significantly. Collectively, these results suggest that mangrove encroachment may not modify the environmental factors driving decomposition, but alterations in foundation plant species may ultimately alter nutrient cycling within habitats through shifts in litter quality.

Snyder, C. M., Feher, L. C., Osland, M. J., Miller, C. M., Hughes, A. R., and Cummins, K. L. (2021). The distribution and structure of mangroves (*Avicennia germinans* and *Rhizophora mangle*) near a rapidly changing range limit in the northeastern Gulf of Mexico. *Estuaries and Coasts*, 45: 181–195.

In this study, the authors combined field vegetation surveys, historical herbarium records, and analyses of past temperature data to examine the distribution and structure of *Avicennia germinans* and *Rhizophora mangle* in the Apalachicola Bay region. Historical records indicate that mangroves have been present for at least 150 years. However, the abundance and structural data indicate that mangroves are currently reaching heights, densities, and reproductive stages not historically reported. The authors found a surprisingly broad distribution and high number of *R. mangle* individuals, which is unlike *A. germinans*–dominated mangrove range limits in Louisiana and Texas. Using cold temperature tolerance thresholds and gridded temperature data, they show that *A. germinans* and *R. mangle* distributions can be influenced by spatial variation in the frequency of extreme freeze events, which can be used to spatially depict the risk of mangrove cold damage. Given the rapid pace of change and the potential for abrupt landscape-scale transformation, these findings reinforce the pressing need to advance understanding of mangrove expansion dynamics near northern range limits in the southeastern United States.

Steinmuller, H. E., Foster, T. E., Boudreau, P., Hinkle, C. R., and Chambers, L. G. (2019). Tipping points in the mangrove march: Characterization of biogeochemical cycling along the mangrove–salt marsh ecotone. *Ecosystems*, 23: 417–434.

Black mangroves (*Avicennia germinans L.*) are encroaching on saltgrass (*Distichlis spicata L.*) within the Merritt Island National Wildlife Refuge in east central Florida. Nine soil cores collected along three transects captured the transitions of both perceived abiotic drivers (salinity and inundation) and vegetation communities during both high- and low-water seasons to investigate patterns in soil biogeochemical cycling of carbon (C), nitrogen (N), and phosphorus (P). Results showed no change in soil carbon dioxide production along the ecotone during either season, though changes in enzyme activity and mineralization rates of N and P could indicate changes in C quality and nutrient availability affecting C degradation along the ecotone. All parameters, excluding microbial biomass carbon, showed higher rates of activity or availability during the low-water season. Long-term soil nutrient stores (total C, N, P) were greatest in the saltgrass soils and similar between the mangrove and transition zone soils, indicating a ‘tipping point’ in biogeochemical function where the transition zone is functionally equivalent to the encroaching mangrove zone. Indicators of

current biogeochemical cycling showed alterations in activity across the ecotone, with the transition zone often functioning with lower activity than within end members. These indicators of current biogeochemical cycling change in advance of full vegetation shifts. Increases in salinity and inundation were linked to mangrove encroachment.

Sullivan, C. R., Smyth, A. R., Martin, C. W., and Reynolds, L. K. (2021). How does mangrove expansion affect structure and function of adjacent seagrass meadows? *Estuaries and Coasts*, 101: e02916.

The authors surveyed seagrass meadows adjacent to mangroves, salt marshes, and a mixture of the two and asked, do changes in intertidal plant composition influence (1) environmental conditions (subtidal water and sediment characteristics); (2) biogeochemical cycling (net oxygen and nitrogen gas fluxes); (3) seagrass meadow cover, biomass, and productivity; and (4) invertebrate community assemblage? There are clear differences in sediment organic matter and net nitrogen gas (N_2) fluxes between adjacent intertidal habitats, but the magnitude or direction of change differs seasonally. The authors hypothesize that this seasonal pattern is due to outwelling from the intertidal, as mangroves senesce in fall, and marshes senesce later in winter. Therefore, changes in adjacent intertidal habitat can impact the timing of organic matter delivery. This also has implications for seagrass biomass. *Thalassia testudinum* belowground biomass adjacent to mangroves substantially decreased over the winter, suggesting vulnerability to stressors as the intertidal plant community shifts from marsh to mangrove dominance. Epifauna density and diversity did not vary among seagrass meadows based on adjacent intertidal habitats, but subtle differences in community assemblages associated with shifts in intertidal plant community were detected. This work demonstrates that impacts of species range expansions are far-reaching due to connectivity in marine systems.

Vaughn, D. R., Bianchi, T. S., Shields, M. R., Kenney, W. F., and Osborne, T. Z. (2020). Increased organic carbon burial in northern Florida mangrove-salt marsh transition zones. *Global Biogeochemical Cycles*, 34: e2019GB006334.

Blue carbon habitats like salt marshes and mangroves bury large amounts of carbon with limited area; however, they also are increasingly susceptible to current climate change. Combined effects of rising temperatures, decreasing freeze frequencies, and increasing sea level rise rates are resulting in mangrove replacement of salt marshes along the southern United States. Surface soils analyzed here from wetlands along northern Florida Atlantic and Gulf Coasts showed higher apparent sedimentation rates in mangrove-dominated sites and where mangroves are migrating into the marsh (termed transition sites). Average carbon burial rates were higher in transition sites for both coasts compared to the respective mangrove and salt marsh sites. Lignin biomarker data indicated that mangrove and transition sites had higher lignin inputs from woody vascular plants compared to salt marsh sites, which may slow decadal- to centennial-scale decay. Higher amino acid concentrations in mangrove soils relative to mangrove biomass and lower C/N indicated that these mangrove sites receive higher algal inputs than the transition and salt marsh sites, attributed to greater tidal inundation in the mangrove sites given their position near the shoreline. Overall, increased accretion, carbon burial, and lignin in mangrove transition sites indicate that this migration may increase carbon burial and increase the stability and residence time of buried soil carbon. Future studies on mangrove migration in northern Florida can verify this through replication and elevation analysis.

Walker, J. E., Angelini, C., Safak, I., Altieri, A. H., and Osborne, T. Z. (2019). Effects of changing vegetation composition on community structure, ecosystem functioning, and predator–prey interactions at the saltmarsh-mangrove ecotone. *Diversity*, 11: 208.

Decreasing frequency of freeze events due to climate change is enabling the poleward range expansion of mangroves. As these tropical trees expand poleward, they are replacing herbaceous saltmarsh vegetation. Mangroves and saltmarsh vegetation are ecosystem engineers that are typically viewed as having similar ecosystem functions. However, few studies have investigated whether predation regimes, community structure, and ecosystem functions are shifting at the saltmarsh-mangrove ecotone. In this study, the authors manipulated predator access to marsh and mangrove creekside habitats to test their role in mediating vegetation and invertebrate structure and stability in a two-year experiment. They also conducted a survey to evaluate how shifting vegetation is modifying structural complexity, invertebrate communities, and ecosystem functioning at the ecotone. Excluding larger (> 2 cm diameter) predators did not affect vegetation or invertebrate structure or stability in either saltmarsh or mangrove habitats. The survey revealed that the two habitat types consistently differ in structural metrics, including vegetation height, inter-stem distance, and density, yet they support similar invertebrate and algal communities, soil properties, and predation rates. The authors conclude that although mangrove range expansion immediately modifies habitat structural properties, it is not altering larger predator consumptive effects, community stability, community composition, or some other ecosystem functions and properties at the ecotone.