Received: 18 August 2021 | Accepted: 17 January 2022

DOI: 10.1111/gcb.16111

Global Change Biology WILEY

REVIEW

The impacts of mangrove range expansion on wetland ecosystem services in the southeastern United States: Current understanding, knowledge gaps, and emerging research needs

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Funding information
U.S. Geological Survey Southeast Climate Adaptation Science Center; USGS Greater Everglades Priority Ecosystem Science Program; National Academy of Sciences, Engineering, and Medicine Gulf Research Program Healthy Ecosystems Grant; USGS Climate R&D Program

Abstract

Climate change is transforming ecosystems and affecting ecosystem goods and services. Along the Gulf of Mexico and Atlantic coasts of the southeastern United States, the frequency and intensity of extreme freeze events greatly influence whether coastal wetlands are dominated by freeze-sensitive woody plants (mangrove forests) or freeze-tolerant grass-like plants (salt marshes). In response to warming winters, mangroves have been expanding and displacing salt marshes at varying degrees of severity in parts of north Florida, Louisiana, and Texas. As winter warming accelerates, mangrove range expansion is expected to increasingly modify wetland ecosystem structure and function. Because there are differences in the ecological and societal benefits that salt marshes and mangroves provide, coastal environmental managers are challenged to anticipate the effects of mangrove expansion on critical wetland ecosystem services, including those related to carbon sequestration, wildlife habitat, storm protection, erosion reduction, water purification, fisheries support, and recreation. Mangrove range expansion may also affect wetland stability in the face of extreme climatic events and rising sea levels. Here, we 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. We also identify critical knowledge gaps and emerging research needs regarding the ecological and societal implications of salt marsh displacement by expanding mangrove forests. One consistent theme throughout our 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. For very specific local reasons, some individuals may see mangrove expansion as a positive change to be embraced, while others may see mangrove expansion as a negative change to be constrained.

KEYWORDS
climate change, coastal wetland, ecosystem services, mangrove, range expansion, winter climate change

1 | INTRODUCTION

In response to warming air and ocean temperatures, temperate ecosystems are being transformed by tropical organisms whose range limits are expanding poleward (Osland et al., 2021; Vergés et al., 2014). In North America, the transition between tropical and temperate ecosystems is greatly influenced by the frequency and intensity of winter temperature extremes, as the northern range limits of most tropical organisms are governed by extreme freezing temperatures (Boucek et al., 2016; Osland et al., 2021). Climate change is producing warmer winters with fewer extreme freeze events (Carter et al., 2018; USGCRP, 2017), which allows tropical organisms to move north of their current range limits. Coastal environmental managers near tropical-temperate transitions are increasingly faced with making natural resource management decisions related to the range expansion of these tropical organisms. Thus, there is a need to advance understanding of the ecological implications of range expansion. In this communication, we review the literature on the ecological and societal impacts of warming winters and tropical range expansion within coastal wetland ecosystems in the southeastern United States, where tropical mangrove forests are expected to invade and ultimately displace salt marshes as they continue to move north (Cavanaugh et al., 2014; Gabler et al., 2017; Osland et al., 2013).

Mangrove forests and salt marshes are both highly productive coastal wetland ecosystems that occupy very similar geomorphic positions within tidal saline environments (Cahoon et al., 2020). Thus, there are many similarities in the ecosystem goods and services provided by these tree- and grass-dominated coastal wetlands. Both ecosystems are frequently ranked among the most valuable ecosystems on the planet (Costanza et al., 2014). In addition to providing habitat for fish and wildlife species, mangrove forests and salt marshes sequester large quantities of CO_2, protect coastlines from storms, reduce erosion, improve water quality, support productive fisheries, and provide recreational opportunities (Barbier et al., 2011).

Despite the similarities in the ecosystem goods and services provided by mangrove forests and salt marshes (Table 1), there are trade-offs and differences in the magnitude, spatiotemporal scale, and characteristics of the good or service provided (Barbier et al., 2011; Ewel et al., 1998; Kelleway et al., 2017). Research on the ecological effects of mangrove expansion in the southeastern United States has accelerated rapidly in recent years (Figure 1). Here, we synthesize this recent knowledge to review the current understanding of the effects of mangrove range expansion and displacement of salt marsh on the ecosystem services provided by coastal wetlands in the southeastern United States. We begin with a background section that describes the history and expected future of mangrove expansion within this region. Next, based on the current state of knowledge, we review changes in wetland ecosystem services that occur as salt marshes are replaced by mangroves. We also identify critical knowledge gaps and emerging research needs for improving our understanding and management of mangrove expansion and salt marsh displacement in the southeastern United States.

TABLE 1 Mangrove forests and salt marshes are both frequently ranked among the most valuable ecosystems on the planet (Costanza et al., 2014). There are many similarities in the ecosystem goods and services provided by these tree- and grass-dominated coastal wetlands. The left column shows broad ecosystem service categories supported by mangrove forests and salt marshes (partially adapted from Barbier et al., 2011), and the right column provides more specific examples within those categories

Ecosystem services provided by mangrove forests and salt marshes	Examples
Carbon sequestration	Plant carbon storage, soil carbon storage
Land loss avoidance	Elevation gains to offset relative sea-level rise
Erosion control	Shoreline erosion reduction
Water purification	Nutrient and sediment removal
Coastal protection	Wave and wind attenuation
Maintenance of fisheries	Fish, shrimp, and crabs
Maintenance of avifauna	Wading birds, shorebirds, marsh birds, and passerines
Recreation and tourism	Fishing, birdwatching, kayaking
Raw materials and food	Mangrove honey

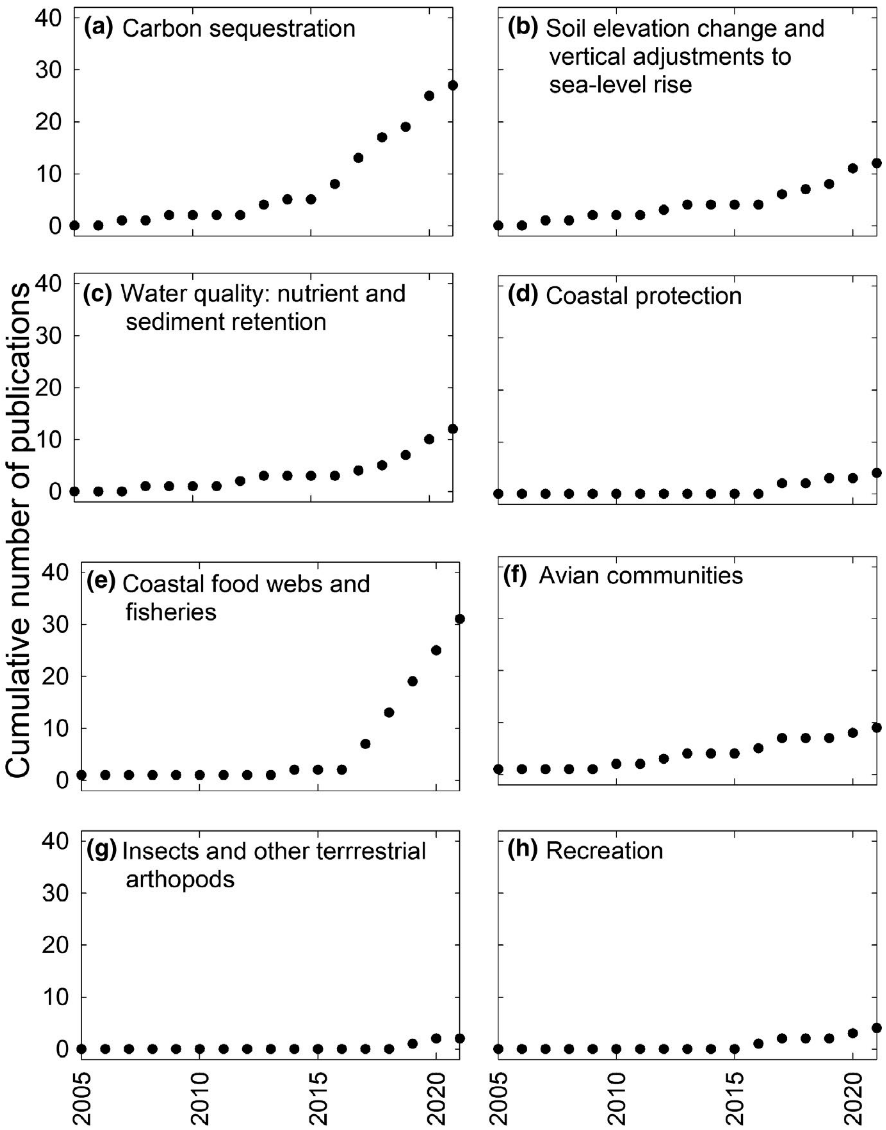

FIGURE 1 The cumulative number of publications investigating the effects of mangrove expansion in the southeastern United States on (a) carbon sequestration; (b) soil elevation change and vertical adjustments to sea-level rise; (c) water quality, specifically nutrient and sediment retention; (d) coastal protection; (e) coastal food webs and fisheries; (f) avian communities; (g) insects and other terrestrial arthropods; (h) recreation

2 | BACKGROUND: MANGROVE RANGE EXPANSION IN THE SOUTHEASTERN United States

The Gulf of Mexico and Atlantic coasts of North America are global hotspots for mangrove range expansion (Cavanaugh et al., 2018; Osland, Feher, et al., 2017; Figure 2). Coastal wetlands are abundant in the southeastern United States due to the region's expansive low-lying coastal plains (Deegan et al., 1986; Enwright et al., 2016). In warmer and more tropical southern coastal reaches, tidal saline wetlands are dominated by mangrove trees and shrubs (Odum et al., 1982), with the three most common mangrove species in the

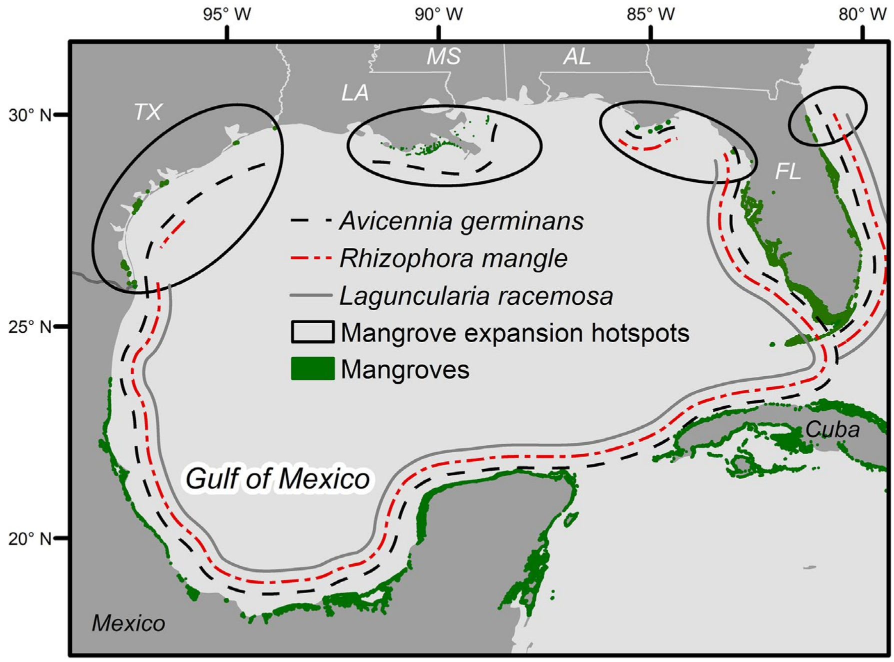

FIGURE 2 Map showing the distribution of mangroves in the southeastern United States. Mangrove expansion hotspots in Texas, Louisiana, and north Florida are shown with the four black ovals. Mangrove species' poleward range limits are shown with the black, red, and grey lines. Mangrove distribution data are from: (1) Mexico: CONABIO (2016); (2) Cuba: Giri et al. (2011); (3) south and central Florida: FDEP (2016); (4) northwestern Florida: Snyder et al. (2021); (5) Louisiana: Day et al. (2020); (6) Texas: Sherrod and McMillan (1981) and Armitage et al. (2015). Map updated and adapted from Osland, Feher, et al., 2018 [Colour figure can be viewed at wileyonlinelibrary.com]

region being *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove). The northern range limits of these mangrove species (Figure 2) are controlled by extreme freeze events, which can lead to physiological damage and/or mortality (Bardou et al., 2021; Cavanaugh et al., 2014; Pickens & Hester, 2011; Sherrod & McMillan, 1985). Thus, along cooler, northern coastal reaches, tidal saline wetlands are dominated by grass-like salt marsh plants (i.e., grasses, sedges, and rushes; Gabler et al., 2017; Osland, Grace, et al., 2019) because salt marsh plants can tolerate freezing temperatures via winter dormancy. Conversely, mangroves outcompete salt marsh plants along southern coastal reaches where temperatures are suitable for mangrove growth and canopy development (Feher et al., 2017; Kangas & Lugo, 1990).

The northernmost mangrove populations in the region are present in Texas (Armitage et al., 2015; Sherrod & McMillan, 1981), Louisiana (Day et al., 2020; Osland, Day, et al., 2017; Osland, Day, Michot, et al., 2020), and the Gulf of Mexico and Atlantic coasts of northern Florida (Simpson et al., 2017; Snyder et al., 2021; Stevens et al., 2006). Isolated mangrove individuals have also been found on Mississippi's barrier islands (Macy et al., 2019; Scheffel et al., 2013, 2017). In the past century, mangrove range limits have expanded across the region during freeze-free years and contracted due to mass mortality during extreme freeze events (Brown et al., 2016; Cavanaugh et al., 2019; Osland, Day, et al., 2017; Sherrod & McMillan, 1985). The last major freeze event resulting in region-wide mass mangrove mortality and range contraction occurred in December 1989 (Lonard & Judd, 1991; Osland, Day, et al., 2017; Stevens et al., 2006). Since then, mangroves have been expanding in parts of northern Florida, Louisiana, and Texas. Although 1989 was the last cold event to affect mangroves across the entire northern Gulf of Mexico, there have been several smaller, less intense cold events (e.g., 1996, 2000, 2001, 2002, 2003, 2010, 2011, 2014, 2018, 2021), which have caused short-term mangrove damage, mortality, and/or local reductions in coverage (e.g., Osland, Day, et al., 2017; Osland, Day, Hall, et al., 2020; Osland, Day, Michot, et al., 2020; Osland, Hartmann, et al., 2019; Osland et al., 2015; Snyder et al., 2021). The most recent event (February 2021) caused varying levels of mangrove damage and mortality across the Texas coast [Anna Armitage (Texas A&M Galveston) and Kathleen Swanson (Mission Aransas National Estuarine Research Reserve), oral communication, March 2021). In response to future warming, mangrove forests are expected to expand farther north and displace salt marshes in much of Texas, Louisiana, and northern Florida (Cavanaugh et al., 2015, 2019; Gabler et al., 2017; Osland et al., 2013).

Inundation and salinity regimes are critical abiotic factors that govern ecosystem structure and function in coastal wetlands (Ibáñez et al., 2012; Twilley & Day, 2012). Thus, across the southeastern United States, there is some variation in the salt marsh plant communities that are being replaced by range-expanding mangrove forests (Gabler et al., 2017; Osland, Grace, et al., 2019; Yando et al., 2016; Figure 3). In general, salt marshes are dominated by grass-like (graminoid) plants (e.g., *Spartina alterniflora*, *Juncus roemerianus*, *Spartina patens*, *Schoenoplectus americanus*) near mangrove range limits in northern Texas, Louisiana, and northern Florida (Brockmeyer et al., 2017; Chapman et al., 2021; Gabler et al., 2017; Osland, Grace, et al., 2019; Yando et al., 2016). Salt marshes in all three of these areas receive comparatively large freshwater inputs that maintain salinities below or near ocean waters (NOAA, 1990; Osland et al., 2014; USEPA, 1999). In contrast, along more arid coasts that receive less rainfall and smaller riverine freshwater inputs, such as the lower and central Texas coast, hypersaline conditions can develop when high evaporation concentrates oceanic salts (Longley, 1995; Montagna et al., 2007; Osland et al., 2014; Withers, 2002b). Halophytic succulent plant species (e.g., *Batis maritima*, *Salicornia depressa*, *Borrichia frutescens*, *Monanthochloe littoralis*) tend to dominate hypersaline

FIGURE 3 The effects of mangrove expansion on ecosystem goods and services are highly dependent upon the structure and composition of: (1) the expanding mangrove forests; and (2) the salt marsh that is being replaced. These photos illustrate some of the variations in marsh and mangrove plant communities near mangrove range limits in the southeastern United States. Upper photo: A mangrove-marsh ecotone in north Florida (near Cedar Key), which contains highly productive grass- and succulent plant-dominated marshes and comparatively tall (>6 m height) mangrove plants. Middle and Lower photos: Mangrove-marsh ecotones along the central and southern Texas coast (within Mustang Island State Park and Lower Rio Grande Valley National Wildlife Refuge, respectively), which contain less productive succulent plant-dominated marshes, comparatively short (<2 m height) mangrove plants, and hypersaline salt flats that lack vascular plants (see right side of lower photo). Photo credits: Michael Osland [Colour figure can be viewed at wileyonlinelibrary.com]

salt marsh plant communities (Gabler et al., 2017; Osland, Grace, et al., 2019; Yando et al., 2016). Limited connectivity with the ocean can also produce hypersaline conditions and halophytic succulent plant-dominated salt marshes, as in parts of the Indian River Lagoon along the Atlantic coast of Florida (Brockmeyer et al., 2017; Chapman et al., 2021; Simpson et al., 2019). These examples show that regional differences in climate- and hydrology-controlled salt marsh plant community composition, structure, and zonation (Gabler et al., 2017) are important to consider as they can influence how wetland ecosystem services change due to mangrove expansion and salt marsh displacement.

How do mangrove range limits in the southeastern United States compare with other mangrove range limits across the world? At the global scale, mangrove range limits are governed by many factors including winter air temperature regimes, aridity, ocean temperatures, and dispersal limitations (Duke et al., 1998; Osland, Feher, et al., 2017; Saenger, 2002; Van der Stocken, Carroll, et al., 2019). Winter air temperatures affect mangrove range limits to varying degrees in Australia, New Zealand, South Africa, Brazil, and China (Quisthoudt et al., 2012; Osland, Feher, et al., 2017). Due to the movement of cold air outbreaks from the arctic across continental land masses in the Northern Hemisphere, mangrove range limits in the Northern Hemisphere (i.e., North America and China) are affected by colder winter air temperature extremes than range limits in the Southern Hemisphere (i.e., Australia, New Zealand, South Africa, Brazil; Osland, Feher, et al., 2017; Osland et al., 2021; Smith & Sheridan, 2020). Thus, mangrove range expansion is more dynamic and more strongly influenced by cold temperature extremes in the southeastern United States (Cavanaugh et al., 2018, 2019; Osland, Day, et al., 2017) and China (Chen et al., 2017) compared to Australia, New Zealand, South Africa, and Brazil (Osland, Feher, et al., 2017).

While mangrove expansion is occurring on several other continents, there is much variation in the environmental settings and the drivers responsible for these changes (Rogers & Krauss, 2019; Saintilan & Williams, 1999; Saintilan et al., 2014). For example, changing rainfall regimes (Diop et al., 1997; Eslami-Andargoli et al., 2009), rapid sedimentation (Asbridge et al., 2015; Lovelock et al., 2010; Walcker et al., 2018), hydrologic alterations (Raabe et al., 2012), and rising sea levels (Howard et al., 2020; Krauss et al., 2011) are all common drivers of mangrove expansion. These drivers and the accompanying differences in environmental setting (e.g., geomorphology, climate, and the ecosystem properties of the interacting salt marshes and mangrove forests) greatly influence the ecological implications of mangrove expansion. Our review focuses primarily on the southeastern United States to avoid confounding interpretations due to such differences.

3 | LOCAL IMPACTS AND TRADE-OFFS

At global and regional scales, coastal wetlands are typically valued for their support of multiple ecosystems services (Barbier et al., 2011; Costanza et al., 2014). However, at local scales (e.g., a specific wetland within a refuge, park, or neighborhood), coastal management actions are sometimes motivated by an interest to maintain or enhance a specific ecosystem good or service. For example, if a

TABLE 2 Mangrove expansion can produce beneficial changes in some ecosystem services while producing detrimental changes in other ecosystem services. Cedar Key (Florida) and Aransas (Texas) are two prominent areas where such trade-offs are observed. The table below shows some of the positive and negative changes associated with mangrove expansion in these two locations

Location	Positive change associated with mangrove expansion	Negative change associated with mangrove expansion
Cedar Key (Florida)	*Improved coastal protection *Storm debris reduction *Enhanced pelican habitat *Increased aboveground carbon storage *Altered food webs and fisheries	*Loss of coastal views *Increased nuisance insects *Increased freeze vulnerability *Altered food webs and fisheries
Aransas (Texas)	*Improved coastal protection *Improved wind protection for fishing *Improved erosion control *Enhanced pelican habitat *Increased aboveground carbon storage *Increased soil carbon storage *Altered food webs and fisheries	*Reduced access to fishing grounds *Reduced whooping crane habitat and food resources *Increased freeze vulnerability *Altered food webs and fisheries

wetland is valued for waterfowl hunting, management actions may be guided primarily by an interest to maintain or enhance waterfowl habitat (Mitchell et al., 2006). Conversely, if an urban municipal wetland provides valuable recreation opportunities, wetland management may be driven by an interest to optimize public recreation (Zedler & Leach, 1998). Across the southeastern United States, there is much variation in the coastal wetland ecosystem services that are prioritized by coastal communities and managers (Engle, 2011; Feagin et al., 2010; Yoskowitz et al., 2012). Thus, there can be local-scale differences in perceptions of the ecological and societal impacts of mangrove expansion into salt marshes. For very specific local reasons, some individuals may see mangrove expansion as a positive change to be embraced, while others may see mangrove expansion as a negative change to be constrained (Table 2; Figure 4). At several points in this communication, we include specific examples that illustrate some of the variations in local perceptions of the impacts and trade-offs associated with mangrove expansion.

4 | CARBON SEQUESTRATION

How will mangrove range expansion and encroachment into salt marshes affect carbon cycling and storage in coastal wetlands? The short answer is that mangrove expansion is expected to universally increase aboveground carbon storage, but the effects of mangrove expansion on soil carbon storage are variable and heavily influenced by site-specific abiotic and biotic conditions, as described below.

One of the most striking and consistent effects of mangrove expansion is an increase in canopy height and aboveground carbon stocks (Feher et al., 2017; Gabler et al., 2017; Simpson et al., 2017; Yando et al., 2016). Mangroves are woody plants that can rapidly accumulate aboveground carbon stocks during the early stages of forest development (Chapman et al., 2021; Kelleway et al., 2016; Lovelock et al., 2010; Osland, Feher, Spivak, et al., 2020; Walcker et al., 2018). In contrast, salt marshes are dominated by herbaceous plants that lose their aboveground biomass each year during winter senescence (Macy et al., 2020). Thus, mangrove forests are typically taller and contain more aboveground biomass than their salt marsh counterparts. Studies conducted in mangrove-marsh ecotones across the southeastern United States have consistently shown that mangrove expansion into salt marsh results in taller plants, more aboveground biomass, and increases in aboveground carbon stocks (Charles et al., 2020; Doughty et al., 2016; Hutchison, 2016; Hutchison et al., 2018; Macy et al., 2020; Perry & Mendelssohn, 2009; Simpson et al., 2019; Yando et al., 2016). However, the magnitude of those increases in aboveground carbon stocks and storage rates can be influenced by other factors, including geomorphic position and interactions between aridity, salinity, and plant productivity (Gabler et al., 2017; Osland, Gabler, et al., 2018; Yando et al., 2016).

What are the implications of mangrove expansion for belowground carbon cycling and storage? Soil carbon burial represents the largest long-term carbon storage pathway within coastal wetlands (Breithaupt et al., 2012; Chmura et al., 2003). Thus, there has been much interest and debate regarding the soil carbon implications of mangrove expansion. Mangrove forests and salt marshes are both highly productive ecosystems that, on a per unit area basis, have the potential to support soil carbon burial rates that are among the highest on the planet (Donato et al., 2011; Mcleod et al., 2011). The factors that contribute to rapid soil organic matter development in both mangrove forests and salt marshes include high rates of primary productivity, prolific belowground root production, low rates of decomposition due to anaerobic conditions, and continued organic matter burial as wetlands trap sediments and build elevation to adjust to rising sea levels (Cahoon et al., 2020). As in terrestrial grasslands, where there is much variation in the edaphic effects of woody plant encroachment due to climate-plant trait interactions (Archer et al., 2017; Barger et al., 2011; Eldridge et al., 2011), studies in coastal wetlands have revealed divergent results regarding the effects of mangrove expansion on soil carbon cycling and storage. While some studies have found no measurable effect of mangrove expansion on soil carbon stocks (Charles et al., 2020; Doughty et al.,

FIGURE 4 Across the southeastern United States, there is considerable variation in perceptions of the ecological and societal impacts of mangrove expansion into salt marsh. For very specific local reasons, some individuals may see mangrove expansion as a positive change to be embraced, while others may see mangrove expansion as a negative change to be constrained. These two photos provide an example of a negative and positive impact of mangrove expansion and salt marsh displacement. Upper photo (negative impact): Along Texas' central coast, mangrove expansion reduces viable fishing areas. While fly fishing is possible within the region's grass and succulent plant-dominated salt marshes, fly fishing for redfish (*Sciaenops ocellatus*) is not possible within dense meter-tall mangrove stands. Lower photo (positive impact): On Louisiana's barrier islands, expanding mangroves provide valuable habitat for brown pelicans (*Pelecanus occidentalis*). Photo credits: Travis Glidden (upper photo) and Louisiana Department of Wildlife and Fisheries (lower photo) [Colour figure can be viewed at wileyonlinelibrary.com]

2016; Henry & Twilley, 2013; Macy et al., 2020; Perry, 2007; Perry & Mendelssohn, 2009; Yando et al., 2018), others have found increases in soil carbon associated with mangrove expansion (Bianchi et al., 2013; Simpson et al., 2019; Vaughn et al., 2020). When viewed collectively, these studies indicate that the edaphic and soil carbon effects of mangrove expansion are highly site-dependent and greatly influenced by the plant traits and ecosystem properties of the interacting salt marshes and mangrove forests (Charles et al., 2020; Osland, Gabler, et al., 2018; Yando et al., 2016; Figure 3). In the subsequent paragraphs, we briefly examine several alternative hypotheses regarding the divergent soil carbon-focused findings in the literature.

Biomass-based hypotheses regarding changes in soil carbon cycling and storage due to mangrove expansion presume that increases in aboveground biomass will be accompanied by concomitant increases in belowground carbon storage. Across some coastal wetland abiotic gradients (e.g., nutrient limitation gradients or extreme salinity gradients), there can be strong positive relationships and positive feedbacks between coastal wetland plant biomass, plant productivity, and soil carbon stocks and cycling (Kauffman & Bhomia, 2017; McKee et al., 2007; Osland, Gabler, et al., 2018; Rovai et al., 2018). However, aboveground biomass increases due to mangrove expansion do not necessarily affect net soil carbon cycling and storage. Indeed, across the tropical-temperate transition zone in eastern North America, which spans productive mangrove forests in the warmer south and productive salt marshes in the colder north, coastal wetland aboveground biomass varies greatly but is not correlated to soil carbon stocks or soil carbon burial (Chmura et al., 2003; Feher et al., 2017; Holmquist et al., 2018; Osland, Gabler, et al., 2018). Under comparable geomorphic conditions, mangrove forests and salt marshes have the potential to support similarly high soil carbon stocks and soil carbon accumulation rates. Thus, instead of being linked directly to aboveground biomass, mangrove-triggered changes in coastal wetland soil properties and soil carbon burial rates, where present, are more likely linked to changes in other processes (e.g., productivity, decomposition). Moreover, where mangrove expansion is occurring across a salinity or elevation gradient (e.g., Krauss et al., 2011; Lewis et al., 2021; Ross et al., 2000), the effects of mangrove expansion may be due to concomitantly changing abiotic conditions that are governed by other drivers (e.g., saltwater intrusion, rising sea levels).

In general, more productive coastal wetland ecosystems tend to support higher soil carbon burial rates and the rapid development of soil carbon stocks (Kauffman & Bhomia, 2017; McKee et al., 2007; Osland, Gabler, et al., 2018; Rovai et al., 2018). Thus, where decomposition rates are similar (e.g., Geoghegan et al., 2020), the soil carbon implications of mangrove expansion may be heavily influenced by the productivity of the interacting salt marsh and mangrove plant communities. Due in part to differences in leaf C:N ratios, aboveground leaf litter decay rates can be higher in *A. germinans* compared to *S. alterniflora* (Perry & Mendelssohn, 2009; Simpson et al., 2020; Smith et al., 2019). However, the belowground abiotic conditions in mangroves and marshes along Florida's Atlantic coast produced similar belowground decomposition rates (Simpson et al., 2020). If a salt marsh and an expanding mangrove forest both support similarly high productivity rates and similar belowground decomposition rates, then there may be no effect of mangrove expansion on soil carbon burial rates. For example, studies conducted within highly productive salt marshes dominated by graminoid plants in Louisiana and Florida have found no changes in soil carbon storage due to mangrove expansion (Doughty et al., 2016; Henry & Twilley, 2013; Macy et al., 2020; Perry, 2007; Perry & Mendelssohn, 2009; Yando et al., 2016, 2018). In contrast, soil carbon burial may increase if the expanding mangrove forest supports higher rates of productivity, especially belowground (root) productivity, compared to the incumbent salt marsh. For example, several studies conducted within salt marshes dominated by succulent plants along the central

Texas coast (Bianchi et al., 2013; Yando et al., 2016) and in Florida (Simpson et al., 2019) have noted soil carbon increases associated with mangrove expansion. Beyond just carbon quantity, soil carbon quality can be affected by mangrove expansion (Breithaupt et al., 2020; Charles et al., 2020; Lewis et al., 2014; Vaughn et al., 2020). For example, along the central Texas coast, succulent marsh plant (*B. maritima*) leaf and root breakdown rates were 1000% and 35% faster, respectively, than *A. germinans* (Charles et al., 2020). The effects of mangrove expansion on autochthonous detrital inputs and allochthonous carbon burial via changes in sedimentation (Charles et al., 2020; Chen et al., 2018; Guo et al., 2017; Kuhn et al., 2021; McKee et al., 2020) also warrant further investigation.

In summary, although mangrove expansion is universally expected to increase aboveground carbon storage, the effects on soil carbon storage are highly variable and warrant closer investigation via field- and greenhouse-based manipulative experiments as well as measurements from a larger number of mangrove-marsh ecotones across the region (Table 3). There is also a pressing need for studies that, instead of measuring carbon stocks, directly measure critical processes (e.g., root productivity, decomposition, sediment deposition) that directly affect soil carbon storage and cycling. Chronosequence designs can be used to advance understanding of the influence of forest developmental stage on carbon cycling and storage, including the potential presence of lag times between mangrove colonization and changes in carbon storage and cycling (Kelleway et al., 2016, 2017). Species-specific effects on soil carbon quality and quantity also warrant further investigation. For example, most studies have focused on the effects of *A. germinans* expansion, but due to differences in plant traits, the edaphic effects of *R. mangle* expansion may differ from *A. germinans* (McKee, 1993). There is also a need for species-specific salt marsh research that moves beyond just *S. alterniflora*. Although there are 24 dominant foundation plant species in tidal saline wetlands across the conterminous United States, 45% of publications have been focused on *S. alterniflora* (Osland, Grace, et al., 2019).

5 | SOIL ELEVATION CHANGE AND VERTICAL ADJUSTMENTS TO SEA-LEVEL RISE

Mangrove forests and salt marshes have the potential to adjust to moderate rates of rising sea levels via soil elevation gains that are driven by positive feedbacks between inundation, plant growth, and sediment deposition (Krauss, McKee, Lovelock, et al., 2014; Morris et al., 2002). Given the vulnerability of coastal wetlands to accelerated sea-level rise, will mangrove expansion increase soil elevation building capacity and the ability of coastal wetlands to adjust to rising sea levels? This question has been investigated through the use

TABLE 3 Level of knowledge and critical research gaps regarding the impacts of mangrove expansion on ecosystem goods and services

Ecosystem good and service	Level of knowledge	Critical research gaps
Carbon sequestration	Better understood	Why is there so much variability in the effects of mangrove expansion on soil carbon storage and cycling? What is the role of site- and species-specific conditions (e.g., geomorphology, environmental variables, and the ecosystem properties of the interacting salt marsh and mangrove forest)? Beyond just stocks, how does mangrove expansion affect key processes?
Soil elevation change and vertical adjustments to sea-level rise	Somewhat understood	What are the effects of mangrove expansion on soil elevation dynamics and the ability of coastal wetlands to adjust to sea-level rise? How are these effects influenced by geomorphology, environmental conditions, and the ecosystem properties of the interacting salt marsh and mangrove forest?
Water quality: nutrient and sediment retention	Somewhat understood	What are the effects of salt marsh replacement by mangroves on nitrogen cycling and storage, and ultimately nitrogen pollution filtration by coastal wetlands? How does mangrove expansion affect sediment retention?
Coastal protection	Poorly understood	How does mangrove expansion affect coastal protection against storms, including wave and wind attenuation? What are the effects of salt marsh replacement by mangroves on soil erosion rates, shear strength, and sediment deposition?
Coastal food webs and fisheries	Better understood	How are the effects of mangrove expansion on coastal food webs and fisheries influenced by site- and species-specific conditions (e.g., geomorphology, environmental conditions, and the ecosystem properties of the interacting salt marsh and mangrove forest)?
Avian communities	Poorly understood	How does mangrove expansion affect communities of wading birds, shorebirds, marsh birds, and passerines? How are the perspectives of coastal resource managers on mangrove expansion influenced by avian conservation priorities of local organizations?
Insects, other terrestrial arthropods, and honey	Poorly understood	How does mangrove expansion affect terrestrial arthropod communities? Can mangrove expansion provide a novel kind of honey for beekeepers?
Recreation	Poorly understood	How does mangrove expansion affect recreation and tourism through changes in water access, viewscapes, birdwatching, and fishing?

of radioisotopes, sediment traps, marker horizons, and surface elevation tables. Many of the processes that affect soil carbon storage and cycling (e.g., root productivity, belowground decomposition, and sediment deposition) are also the primary processes that govern soil elevation change. Thus, given the variable and highly site-specific effects of mangrove expansion on soil carbon storage, we expect that the effects of mangrove expansion on soil elevation change dynamics are also highly context-dependent and governed by site- and species-specific conditions (e.g., geomorphology, abiotic conditions, and the ecosystem properties of the interacting salt marsh and mangrove forest).

The surface elevation table-marker horizon (SET-MH) approach (Cahoon et al., 2002; Lynch et al., 2015) has been used to directly measure shorter-term (e.g., 5–30 years) soil elevation change dynamics and quantify the contributions of critical above and belowground processes (e.g., accretion, erosion, subsurface root zone expansion, subsurface subsidence). There are only a few studies that have directly measured the soil elevation change implications of mangrove expansion using the SET-MH approach. A SET-MH study conducted along the Atlantic coast of Florida within *Distichlis spicata*-dominated marshes found higher elevation gains associated with warming temperatures and mangrove (*L. racemosa*) expansion; vertical accretion was about threefold higher in mangrove plots exposed to a warming temperature treatment compared to salt marshes exposed to the same treatment (Coldren et al., 2019). In contrast, a SET-MH study conducted in Louisiana found similar rates of soil elevation gain in creekbanks dominated by *A. germinans*, *S. alterniflora*, or a mixture of both species (McKee & Vervaeke, 2018). A hurricane sediment-focused study conducted using soil cores from within the same Louisiana mangrove-marsh ecotone found no difference in sediment capture by stands dominated by *S. alterniflora* or *A. germinans* (McKee et al., 2020). A comparison of short-term accretion rates in the Louisiana mangrove-marsh ecotone, measured using sediment traps (biweekly accretion) and feldspar marker horizons (annual accretion), also found no difference in stands dominated by *S. alterniflora* or *A. germinans* (Perry & Mendelssohn, 2009). These results suggest that replacement of marsh by mangroves would have no effect on vertical accretion and soil elevation change within the Louisiana mangrove-marsh ecotone. However, as discussed in these papers and others across the region, the lack of a difference may be unique to the sedimentary setting, the size and developmental stage of the mangroves, and/or to the specific species compared (Charles et al., 2020; Kuhn et al., 2021; McKee et al., 2020; McKee & Vervaeke, 2018; Perry, 2007).

These divergent findings indicate that there is a need to further investigate the effects of mangrove expansion on soil elevation change dynamics (Table 3). Most existing studies have compared adjacent mangroves and marsh stands. However, there is also a need for manipulative experiments in which marsh plots are experimentally planted with mangrove seedlings and compared to marsh plot controls. Such comparisons would enable direct measurements of changes in soil elevation dynamics that may occur when the marsh is replaced by mangroves.

Although several studies have used radioisotope-based methods to compare vertical accretion rates in mangroves and salt marshes near poleward mangrove range limits in eastern North America (Bianchi et al., 2013; Comeaux et al., 2012; Perry & Mendelssohn, 2009; Vaughn et al., 2020), century- and multi-decadal scale mangrove expansion patterns near range limits can be dynamic and include freeze-controlled mangrove-marsh expansion and contraction cycles (Cavanaugh et al., 2019; Osland, Day, et al., 2017). Thus, radioisotope-based approaches should ideally be paired with historical analyses of imagery (e.g., Perry & Mendelssohn, 2009) and climate data to identify freeze event-driven oscillations in mangrove and/or salt marsh coverage during the time periods represented by soil cores.

6 | WATER QUALITY: NUTRIENT AND SEDIMENT RETENTION

How do mangrove expansion and salt marsh displacement affect the water quality-based ecosystem services provided by coastal wetlands? Salt marshes and mangroves lie at the land-ocean interface, where they can improve water quality by filtering pollution inputs both from the ocean (e.g., tidal and wave-driven inputs) and from the inland watershed (e.g., surface and groundwater inputs; Mitsch et al., 2015; Mitsch & Gosselink, 2007). The main mechanisms through which nitrogen inputs are filtered in these coastal wetlands are plant uptake and denitrification (Sparks et al., 2015; Steinmuller et al., 2019). While denitrification represents a net loss of nitrogen from the system, and thus complete filtration, plant uptake only constitutes temporary filtration because the nutrients bound to plant tissues can be delivered back into the coastal environment through decomposition. There have been many studies of nutrient cycling and storage in salt marshes and mangroves (e.g., Craig et al., 2021; Dangremond et al., 2020; Hunter et al., 2015; Martin et al., 2021; Mozdzer et al., 2011; Simpson et al., 2013; Weaver & Armitage, 2018; and references cited therein). In general, those studies show variable rates of nutrient cycling and storage, and thus variable rates of nutrient pollution filtration in salt marshes and mangroves.

Based on the current literature, it is difficult to predict how the replacement of salt marshes by mangroves may affect nutrient pollution filtration in coastal wetlands as the existing studies are spatially and temporally disjointed. Many environmental factors other than changes in dominant vegetation can affect the differences observed between salt marsh- and mangrove-focused studies. Long-term studies that directly record changes in nutrient cycling and storage as mangroves replace salt marshes would be informative; however, we are unaware of such studies. Another alternative is a "space-for-time substitution" approach (Pickett, 1989), where nutrient cycling and storage are compared between contiguous stands of salt marsh and mangroves present across ecotones where the expansion of mangroves and replacement of salt marshes is actually occurring. A few such "space-for-time substitution" studies exist (e.g., Henry, 2012; Macy et al., 2019, 2020; Steinmuller et al., 2019) and provide some indication of the changes that will occur with mangrove expansion. These studies show higher nitrogen content in the aboveground tissues of black mangroves (*A. germinans*) than in marsh smooth cordgrass (*S. alterniflora*; McKee & Rooth, 2008; Macy et al., 2020). Higher aboveground biomass and aboveground nitrogen stocks (Macy et al., 2020) suggest higher nitrogen uptake from the soil by plants in *A. germinans* than in *S. alterniflora* stands, which is consistent with the lower nitrogen concentrations observed in the soil porewater of *A. germinans* in comparison with *S. alterniflora* stands (Macy et al., 2020). Altogether, these results suggest that *A. germinans* individuals, by removing larger quantities of nitrogen from the soil, may be larger filters of nitrogen pollution than *S. alterniflora*. However, more studies are needed for a clear and robust description of the effects of salt marsh replacement by mangroves on nitrogen cycling and storage, and ultimately nitrogen pollution filtration in coastal wetlands.

Sediment and sediment-bound phosphorus retention is another process through which salt marshes and mangroves can improve water quality in coastal ecosystems. Wetlands with more near-surface plant structural complexity (e.g., greater stem density, biomass, flexibility) can be more effective at retaining sediments by slowing down the flow of incoming and outgoing waters (Chen et al., 2018; Feagin et al., 2015; McKee et al., 2020). A hurricane-focused study conducted in Louisiana found that despite differences in plant structure there was no difference in hurricane sediment capture within stands dominated by *S. alterniflora* or *A. germinans* (McKee et al., 2020). Conversely, a study conducted along the central Texas coast within a mangrove-marsh ecotone that included *A. germinans* and succulent plants (e.g., *B. maritima*) found that hurricane sediment accretion decreased with increasing mangrove cover (Kuhn et al., 2021). Despite these two hurricane-focused studies, there are no studies that fully examine how salt marsh replacement by mangroves in this region may alter wetland sediment retention and soil build-up under dynamic conditions ranging from daily tidal cycles to storms. More research is needed to better understand how salt marsh replacement by mangroves alters wetland sediment retention, nutrient retention, and associated water quality-based ecosystem services (Table 3).

7 | COASTAL PROTECTION

Given the high vulnerability of coastal communities to storms, what is the potential for mangrove expansion to enhance the coastal protection benefits provided by coastal wetlands? Mangroves and salt marsh ecosystems both can reduce the height and energy of waves passing through them (Gedan et al., 2011; Marois & Mitsch, 2015), increase soil strength (Jafari et al., 2019; Sasser et al., 2018), and facilitate sediment deposition (Cahoon et al., 2020). These plant-controlled processes can reduce shoreline erosion, decrease flooding extent, and lessen damages to infrastructure (Arkema et al., 2013; Barbier, 2016; Narayan et al., 2019). The ability of wetlands to support these coastal protection ecosystem services is dependent upon multiple factors ranging from the characteristics of the individual wetland plants to landscape-scale ecosystem coverage and configuration. Coastal protection services are also influenced by geomorphology and the types and magnitudes of the hazard forces. The structural differences between mangroves and salt marshes, with mangroves being generally larger, more complex, and rigid, have led to the hypothesis that coastal protection services may increase following mangrove expansion into salt marsh.

Existing data, from a range of modeled computer simulations, natural experiments, wave tank studies, and semi-controlled field experiments indicate that mangroves may provide more coastal protection value than salt marshes. For example, in a recent field study conducted within large experimental mangrove removal plots in Texas, Pennings et al. (2021) found that mangroves are more effective at preventing erosion than succulent plant-dominated salt marshes, presumably due to: (1) the enhanced wave-buffering effects of taller, stiffer mangrove stems and (2) the soil-strengthening effects of greater mangrove root biomass. In a model-based assessment that was parametrized with local field-based measurements of vegetation structure along the Atlantic coast of Florida, Doughty et al. (2017) found that wave attenuation and erosion prevention were greater in mangroves than graminoid-dominated salt marshes, which was attributed to the larger canopy heights and stem diameters of mangrove trees. Similarly, in a model-based comparison of mangroves and graminoid-dominated marshes in Louisiana, Hijuelos et al. (2019) noted that wave attenuation was greater in mangroves than graminoid-dominated marshes. All three of these studies indicate that there may be a gain in coastal protection services associated with mangrove expansion, which is especially important given that climate change is increasing the frequency of major hurricanes (Kossin et al., 2017). However, there is a need for more empirical evaluations of how salt marsh versus mangrove shorelines influence wave attenuation and storm impacts on civic infrastructure.

Within the context of coastal erosion, there is interest in advancing the understanding of mangrove expansion effects on the ability of wetlands to tolerate and recover from extreme events and other disturbances (e.g., droughts, hurricanes, floods, freezes, and oil spills). For example, in the Galveston region, frequent oil spills are a concern for resource managers because they can lead to vegetation dieback (Rozas et al., 2000; Williams et al., 2017). For many coastal wetland practitioners in the Galveston area, there is interest in maximizing the ability of wetlands to recover from potential future oil spills [Cherie O'Brien (Texas Parks and Wildlife Department), oral communication, May 24, 2021]. However, there is some local concern that expanding mangroves (*A. germinans*) may decrease wetland resilience to oil spills [Cherie O'Brien (Texas Parks and Wildlife Department), oral communication, May 24, 2021] (but see: Hughes et al., 2018). Thus, during coastal wetland restoration efforts in the Galveston area within the past decade, *S. alterniflora* has typically been the targeted species, and very few Texas Parks and Wildlife permits (i.e., the Permit to Introduce Fish, Shellfish, or Aquatic Plants into Public Waters) have been granted to plant mangroves [Cherie O'Brien (Texas Parks and

Wildlife Department), oral communication, 24 May 2021]. This example highlights the importance of considering the effects of extreme events on wetland stability and coastal protection benefits. Another example in this arena comes from Louisiana, where landscape-scale marsh and mangrove dieback can be triggered by extreme events. For example, drought can lead to marsh dieback (Alber et al., 2008; McKee et al., 2004), and extreme cold events can lead to mangrove dieback (Osland, Day, et al., 2017). Mangroves (*A. germinans*) may be more drought tolerant than *S. alterniflora* marshes in Louisiana due to lower water use (Krauss, McKee, Hester, et al., 2014). Conversely, extreme freeze events similar to the 1989 freeze could lead to landscape-scale mangrove mass mortality, peat collapse, and accelerated erosion (McBride & Byrnes, 1997; Osland, Day, Michot, et al., 2020; Penland et al., 2003), which would compromise the coastal protection benefits provided by expanding mangrove forests.

8 | COASTAL FOOD WEBS AND FISHERIES

Marshes and mangrove forests support critical coastal food webs and fisheries-based ecosystem services (Beck et al., 2001; Engle, 2011; Minello et al., 2003; Nagelkerken et al., 2008; Rönnbäck, 1999). However, due to the structural and functional differences between the two ecosystems, how will mangrove range expansion and marsh displacement affect coastal food webs, fish communities, and key ecosystem services (e.g., fisheries, fisheries-based recreation)?

Overall, the current evidence suggests that mangrove range expansion may lead to changes in associated fish and invertebrate community composition (Armitage et al., 2021), but there is less evidence that mangroves will substantially alter the major production sources to aquatic food webs. Stable isotope analyses indicate that microphytobenthos and phytoplankton are the dominant energy channels that directly support many aquatic consumer groups (e.g., fishery species, wetland specialists, zoobenthivores, phytodetritovores, and planktivores; Baker et al., 2021). Contributions from both mangrove and marsh plants typically flow through the detrital pathway and play a lesser role in directly supporting food webs (Baker et al., 2021; Nelson et al., 2019). In Louisiana, no detrital inputs from mangroves contributed significantly to the dominant consumers in the food web (Nelson et al., 2019). It is uncertain if mangroves will ultimately replace marsh grass detritus as an energy source (Harris et al., 2020; James et al., 2022; Nelson et al., 2019). However, reductions in marsh habitat as a result of mangrove expansion may lead to a decline in energy supplied to some consumers, as mangrove detritus is not readily used as a food source by the current nekton species in Louisiana (Harris et al., 2020). A study in Texas also noted that differences in leaf nutritive quality (e.g., higher tannin, phenolic, and lignin contents) may be linked to lower fitness for benthic consumers that consume mangrove detritus (Goeke & Armitage, 2021).

Most comparative studies of mangroves and marshes have detected differences in food webs and community structure; however, those differences are not universal and can vary depending on the measured taxonomic group, community metric, or functional attribute (Armitage et al., 2021; Diskin & Smee, 2017; Loveless & Smee, 2019; Walker et al., 2019). For instance, the relative abundance and species richness of nektonic fish and invertebrates in Texas were similar between sites with and without mangroves, though individual species varied considerably across those same sites (Armitage et al., 2021). Differences among areas with and without mangroves can also be masked by abiotic conditions or disturbances that influence associated faunal abundance and diversity (Diskin & Smee, 2017). For example, Smee et al. (2017) found significant differences in nekton and infaunal community structure in stands of smooth cordgrass (*S. alterniflora*) bordered by mangroves (*A. germinans*) versus stands without mangrove. Infaunal organisms, blue crabs (*Callinectes sapidus*), and shrimp (*Farfantepenaeus aztecus*, *Palaemonetes* spp.) were less abundant in marshes bordered by mangroves than in marshes without mangroves, whereas mud crabs (Xanthidae/Panopeidae) and fish were more abundant in marshes bordered by mangroves (Smee et al., 2017). Similarly, macrofaunal communities differed in marsh versus mangrove-dominated vegetation along the Atlantic coast of Florida, due to the influence of fine-scale plant structural differences and stand-level habitat attributes (Johnston & Gruner, 2018). Along the Atlantic coast, studies have noted differences in detrital-based epifaunal communities (Smith et al., 2019) and subtidal nekton communities (Kimball & Eash-Loucks, 2021) associated with mangroves compared to marshes. For example, Smith et al. (2019) found that crabs were 2–7 times more abundant in *S. alterniflora* detritus than *A. germinans* detritus. In an early study comparing nekton communities in marsh and mangroves in Louisiana, Caudill (2005) found that while fishes [e.g., gulf killifish (*Fundulus grandis*) and sheepshead minnow (*Cyprinodon variegatus*)] were more abundant in *S. alterniflora*-dominated marshes, white shrimp (*Litopenaeus setiferus*) were more abundant in *A. germinans*-dominated mangrove stands.

Beyond just the direct effects on animals, mangrove expansion can also affect microbial (Barreto et al., 2018) and rhizosphere communities (Chen et al., 2020), which can affect abiotic conditions, biotic interactions, and biogeochemical cycling. The effects of mangrove expansion on coastal food webs and fisheries may also increase with time due to the influence of the forest developmental stage (Barimo & Serafy, 2003; Scheffel et al., 2018). Linkages to adjacent ecosystems can also be important. For example, along the northwestern coast of Florida, mangrove expansion affects the seasonal delivery of organic matter to adjacent seagrass ecosystems, which can alter epifaunal communities, subtidal environmental conditions, gas fluxes, and seagrass standing biomass (Sullivan et al., 2021).

Mangroves can also impact coastal food webs via changes in habitat complexity that affect key species or predator-prey interactions (Johnston & Smith, 2018; Scheffel et al., 2017). Habitat complexity influences feeding efficiency and predation rates in fishes (Ahrens et al., 2012; Gotceitas & Colgan, 1989), and thus we expect that a shift from salt marsh to mangrove will influence fish foraging and community composition. From the existing studies, the consensus is that grass shrimps (*Palaemonetes* spp.), blue crabs (*C. sapidus*), and some marsh-associated fishes (e.g., *F. grandis*) are more abundant in marshes compared to mangrove habitats (Armitage et al., 2021; Caudill, 2005; Johnston & Caretti, 2017; Smee et al., 2017). However, there are some inconsistencies in findings for penaeid shrimp that may be attributed to the type of predators present at a given location. For example, penaeid shrimp preferred marsh grass over mangroves in experimental trials, likely due to increased protection from a predatory gray snapper (*Lutjanus griseus*; Scheffel et al., 2017). On the contrary, benthic invertebrates, such as penaeid shrimp and the marsh periwinkle (*Littoraria irrorata*), were less vulnerable to predation by blue crabs in the presence of mangroves in mesocosm and field studies, respectively (Glazner et al., 2020, 2021). The aerial root structures of mangroves (i.e., pneumatophores and prop roots) can provide refuge from benthic predators, which could lead to shifts in predator-prey interactions and altered trophic dynamics (Glazner et al., 2020, 2021). In Louisiana, penaeid shrimp foraging in mangroves had higher trophic levels than those foraging in marsh-dominated habitats (Nelson et al., 2019). Increased predation on small benthic infauna could feedback to other parts of the food web with uncertain consequences. Mangroves can have additional negative impacts on blue crabs beyond the crab-shrimp interaction, with juvenile crabs exhibiting a habitat preference for and higher survival in marsh grasses in experimental trials (Johnston & Caretti, 2017).

Much of the existing literature has focused on the effects of *A. germinans* expansion; however, the impacts due to the range expansion of other common mangrove species may be different. For example, the habitat quality characteristics for fishes differ between red mangrove (*R. mangle*) and black mangrove (*A. germinans*), with the former having prop roots and the ability to grow at lower intertidal elevations, thus influencing fish habitat inundation time and depth. In areas where *R. mangle* occurs, overhanging limbs and prop roots can extend fringing shoreline habitat another 10 m into the water. The overhanging vegetation and prop roots support fishes by providing shade and cover (Ley & McIvor, 2002; Ley et al., 1999). Because mangroves are almost always located in shallow water and often in sheltered environments, it can be difficult to isolate the effects of *R. mangle* prop roots as a fish habitat (Ellis & Bell, 2004). A study using an experimental design with artificial mangroves found that the structure provided by *R. mangle* prop roots can support unique juvenile fish assemblages (Nagelkerken & Faunce, 2008). In estuaries of southwestern Florida, *R. mangle*-dominated shorelines provide habitat for larger-bodied species such as common snook (*Centropomus undecimalis*), sheepshead (*Archosargus probatocephalus*), striped mullet (*Mugil cephalus*), gray snapper (*L. griseus*), redfin needlefish (*Strongylura notata*), striped mojarra (*Eugerres plumieri*), and Atlantic spadefish (*Chaetodipterus faber*; Greenwood et al., 2007). The large-bodied species that associate closely with *R. mangle* prop roots are often plastic in their habitat use and may not be fully dependent on mangroves (e.g., Stevens et al., 2018). However, there are other species that exhibit greater dependency on *R. mangle* habitat, such as juvenile smalltooth sawfish (*Pristis pectinata*) and goliath grouper (*Epinephelus itajara*). Studies of fine-scale habitat use show that juvenile smalltooth sawfish feed on shallow flats during the night and occupy protected *R. mangle*-dominated embayments during the day (Huston et al., 2017; Lear et al., 2014), and specific use of *R. mangle* prop roots to avoid predators has been observed (Poulakis et al., 2011). Juvenile goliath grouper are found under overhanging mangroves and associated *R. mangle* prop roots in areas where currents create deep undercuts in creek banks (Koenig et al., 2017). Adult goliath grouper move long distances to aggregate in south Florida during the spawning season, which occurs when mangroves are most flooded and thus most available as habitat for juveniles (Koenig et al., 2017).

In the southeastern United States, mangrove expansion is just one of many dynamic aspects of global change that challenge our ability to predict the future of coastal food webs and fisheries. For example, accelerated sea-level rise is expected to ultimately lead to wetland fragmentation, loss, and the transformation of coastal landscapes (Borchert et al., 2018; Couvillion et al., 2017; Enwright et al., 2016; Kirwan & Megonigal, 2013; Stagg et al., 2020). In the short term, wetland loss and fragmentation could lead to ephemeral increases in fisheries production due to increases in the amount of valuable edge habitat (Baker et al., 2020; Harris et al., 2020). However, in the long-term and under higher rates of sea-level rise, the landscape-scale loss of coastal wetlands (Saintilan et al., 2020; Törnqvist et al., 2020) and the associated edge habitat are expected to have a negative impact on fisheries.

The northward range expansion of tropical fish and invertebrate species is another aspect of climate change that will interact with mangrove expansion to affect coastal food webs and fisheries (Osland et al., 2021; Vergés et al., 2014). Warming winter water temperatures could transform fish and invertebrate assemblages across the southeastern United States. Thus, in addition to shifts in vegetation structure due to mangrove encroachment and sea-level rise, coastal food webs and fisheries in the region may also change as new tropical species migrate northward in response to warming winter water temperatures (Vergés et al., 2014). In North America, the northern distributions of tropical, cold-sensitive fish species are governed by the frequency and intensity of extreme cold-water temperatures (Boucek & Rehage, 2014; Martin & McEachron, 1996; Stevens et al., 2016). For example, the northern limits of common snook (*C. undecimalis*; Howells et al., 1990), gray snapper (*L. griseus*; Hare et al., 2012), and tarpon (*Megalops atlanticus*; Mace et al., 2017) are governed by winter cold temperature extremes, which can lead to mass mortality events (i.e., fish kills). Conversely, warming winters can lead to population growth and range expansion. For example, the common snook expanded northward along Florida's Gulf of Mexico coast (Anderson et al., 2020; Purtlebaugh et al., 2020) after a 2010 cold event that resulted in mass mortality and range contraction (Stevens et al., 2016).

In contrast to mangroves, which rely on passive water transport of propagules for dispersal and migration (Van der Stocken, Carroll, et al., 2019; Van der Stocken, Wee, et al., 2019), fish are actively mobile organisms. The high adaptive capacity of many coastal fish and invertebrate species to warming winter waters indicates that some fish and invertebrate species will move northward at rates that exceed the northward migration of mangroves (Cannizzo et al., 2020; Riley et al., 2014; Stevens et al., 2021). Anthropogenic habitat and microclimatic refugia can aid in the expansion of mangrove fauna. For example, the occupation of warm-water springs allows common snook to overwinter in a climate where coastal water temperatures can still drop below their lethal limits (Stevens et al., 2018). Along the Atlantic coast of North America, the northern range limit of mangrove tree crabs (*Aratus pisonii*) is currently in Georgia (Riley et al., 2014), which is north of mangrove forests' current range limit in Florida. Interestingly, in the absence of mangrove trees, mangrove tree crabs can adapt to suboptimal novel marsh environments by: (1) shifting behavioral strategies from predator evasion (i.e., tree climbing) to autotomy (i.e., leg dropping) to optimize survival (Johnston & Smith, 2018), or (2) using anthropogenic structures like docks (Cannizzo & Griffen, 2018, 2019; Cannizzo et al., 2018, 2019, 2020). Anthropogenic structures such as bridges and docks may also provide habitat for juvenile goliath grouper in the northern Gulf of Mexico where adult spawning sites have been recently documented (Malinowski et al., 2019).

In addition to affecting the distribution and abundance of fish, mangrove expansion can affect the recreational fishing experience in positive and negative ways. For example, along the central Texas coast near San Jose Island, many anglers fly fish for redfish (*Sciaenops ocellatus*; Figure 4), but mangrove expansion has reduced the amount of viable fishing area. While fly fishing is possible within the region's grass and succulent plant-dominated salt marshes, fly fishing is not possible within dense meter-tall mangrove stands [Chuck Naiser, oral communication, 26 May 2021]. However, on windy days, the same mangroves can have a positive effect on the fishing experience by buffering winds (Guo et al., 2017), which can improve boat control, water clarity, and the ability to sight cast [Billy Trimble, oral communication, 24 May 2021]. Interestingly, by hindering airboat access into wetlands, mangroves may also prevent damage to wetland vegetation and sediments, which has the potential to reduce rates of erosion, hydrologic change, and wetland loss in areas with high boat and angler concentrations [Billy Trimble and Chuck Naiser, oral communication, 24 and 26 May 2021].

Although the number of investigations of the effects of mangrove expansion on coastal food webs and fisheries has increased rapidly in the past decade (Figure 1e), there is still a need to advance knowledge on this topic, especially regarding how impacts to coastal food webs and fisheries are influenced by site- and species-specific conditions (e.g., geomorphology, environmental conditions, and the ecosystem properties of the interacting salt marsh and mangrove forest; Table 3).

9 | AVIAN COMMUNITIES

What are the effects of mangrove expansion on avian communities? The response of migratory and resident avifauna is arguably one of the least understood consequences of mangrove expansion in the southeastern United States. However, these responses are likely to have a broad range of consequences for ecosystem functions and services. Birds move between coastal wetlands and adjacent ecosystems and are thus critical and wide-ranging influencers of ecosystem connectivity, including fluxes of energy and nutrients (Buelow & Sheaves, 2015). Mangroves in the Gulf of Mexico are important habitats for foraging, resting, nesting, and migrant avifauna (Burger, 2017). However, many of these birds do not use mangroves year-round, instead relying on a species-dependent matrix of mudflat, marsh, and other coastal habitats during migration, nesting, and wintering. Therefore, the consequences of mangrove expansion into salt marshes for birds could be substantial yet variable across taxa. The following sections address known and hypothesized consequences of mangrove expansion for four major taxonomic groups of coastal birds: wading birds, shorebirds, marsh birds, and passerines.

Wading birds (hereafter waders) are large and conspicuous wetland-dependent birds, including members from Families Ardeidae, Threskiornithidae, and Gruidae. Many waders nest in trees or shrubs, including mangrove stands found across much of the southeastern United States (Burger, 2017; Davis et al., 2005; Portnoy, 1977). Thus, mangrove expansion may improve the nesting habitat for some wading birds. However, the effects of expanding mangroves on foraging behaviors may be less beneficial, as ibis and herons select areas with lower mangrove cover to feed (Guo et al., 2017; see also the whooping crane section below). Wader species richness tends to be lower at encroached sites on the Texas coast, though relative abundances for most common species are generally similar between marsh and mangrove sites (Armitage et al., 2021).

Shorebirds comprise four major families (Scolopacidae, Charadriidae, Recurvirostridae, Haematopodidae) and dozens of genera. These mostly small and often gregarious birds frequently forage and roost in large groups within coastal estuaries. The northern Gulf of Mexico is a particularly important part of the North American central migratory flyway (Withers, 2002a). Although some shorebirds will use mangrove shrubs for nesting or roosting (Zwarts, 1988), mangroves produce extensive aerial root complexes that may reduce the accessibility of tidal flats or ponds, which are the preferred foraging habitat for many shorebird species (Darnell & Smith, 2004; Withers, 2002a). In addition, dense mangrove stands may conceal and attract predators, and nonbreeding shorebirds will actively avoid areas with mangroves in favor of salt marshes, tidal flats, and other coastal habitats (Kelleway et al., 2017; Straw & Saintilan, 2006; Vitale et al., 2021). For example, optimal high-tide shorebird roosts were located far from woody vegetation at a critical wintering and migratory stopover site in Florida's Big Bend (Brush et al., 2017). There could be survival and energy costs associated with antipredator behaviors and increased predation if alternative roosting and foraging habitats are not available (e.g., due to human disturbance or habitat loss; Rogers et al., 2006). Because shorebirds are relatively long-lived, their populations are greatly affected by small changes to demographic parameters, such as adult mortality (Colwell, 2010). One study concluded that mangrove expansion into roosting habitats likely contributed to local declines of wintering shorebird populations and biodiversity (Woodley, 2004). Accordingly, surveys of wintering shorebirds on the Texas coast revealed that diversity and relative abundance are higher in marshes than at sites with high mangrove cover (Armitage et al., 2021; Whitt, 2016).

Marsh birds are coastal marsh-dependent and live at the ecotone between aquatic and terrestrial ecosystems. These often cryptic colored and elusive species include members from the families Rallidae, Troglodytidae, and Passerellidae. Marsh habitat loss, regardless of environmental or anthropogenic drivers, can have detrimental impacts on marsh-dependent species. For example, nearly 50% of marsh birds found in the northern Gulf of Mexico are of conservation concern primarily due to the loss of wetland habitats (Woodrey et al., 2019). Species that are dependent on graminoid marsh plants [e.g., seaside sparrows (*Ammospiza maritima*) or marsh wrens (*Cistothorus palustris*)] are unlikely to utilize mangrove-encroached wetlands (Schwarzer et al., 2020). There could be direct or indirect impacts of mangrove expansion into high marsh habitats that are critical for the eastern black rail (*Laterallus jamaicensis*; Watts, 2016). More information is also needed to understand the migratory ecology of marsh bird species to determine the potential impacts of mangrove expansion in different parts of their geographic range.

The passerine group (Order Passeriformes) includes many species of conspicuous migratory warblers that are highly sought-after targets by birdwatchers and photographers. During migration stopovers, these birds roost on coastal shrubs and trees, sometimes including mangroves. Thus, it is often hypothesized that mangroves could increase migratory stopover habitat quality for warblers and other passerines (Kelleway et al., 2017). However, there is little data from the Gulf of Mexico or Atlantic coast to quantitatively support this hypothesis, largely due to the challenges of accurately censusing populations of these small, active birds. Analyses derived from eBird, a community science data repository, suggest that birdwatchers detect substantially more warblers in marsh than in mangrove habitats on the Texas coast (Whitt, 2016). Additional species- and community-level analyses are needed for a more robust evaluation of whether mangrove expansion will be a net benefit or detriment to passerine assemblages.

Birds are visible and iconic users of coastal wetlands, attracting recreational users and supporting a vigorous ecotourism industry (Barbier et al., 2011) that brings millions of dollars to the southeastern United States' coastal economies each year (Kildow et al., 2008; NRDC, 2010). Mangrove expansion into salt marshes in the southeastern United States may alter the perceived and actual value of coastal wetland habitats for avifauna. For example, in coastal Texas, birdwatchers spend more time visiting coastal marsh sites with fewer mangroves (Armitage et al., 2021; Whitt, 2016). The reasons for that preference may be linked to accessibility or visibility. Identifying the drivers behind this pattern is an area ripe for future study that reaches across social and life science disciplines.

For some coastal parks and refuges, coastal resource managers' perspectives on mangrove expansion can be heavily influenced by their organizations' local avian priorities. For example, on Louisiana's barrier islands, dense mangrove stands provide valuable habitat for nesting colonies of brown pelicans (*Pelecanus occidentalis*; Figure 4), which is the state bird and a species with a rich conservation history. Following pesticide-driven extirpation and reintroduction in the 1960s, brown pelican populations have rebounded to the extent that they were removed from the endangered species list in 2009 (Walter, Carloss, Hess, Athrey, et al., 2013). Nevertheless, barrier island habitat losses in Louisiana have been very high (Martinez et al., 2009), and pelican nesting habitat has become a priority during recent coastal restoration efforts. Pelicans prefer to place nests on mangroves, which provide strong nesting platforms that are tall enough to avoid flooding during island overwash events (Hintgen et al., 1985; Visser et al., 2005; Walter, Carloss, Hess, & Leberg, 2013). Thus, mangrove expansion and growth on these islands is viewed as a positive change for pelicans, and, therefore, is sometimes facilitated during barrier island restoration efforts [Darin Lee (Louisiana Coastal Protection and Restoration Authority), oral communication, 21 May 2021].

Another example of how avian habitat priorities can affect local perspectives on mangrove expansion can be found in the Aransas National Wildlife Refuge (ANWR) in Texas. The salt marshes within and near ANWR provide critical wintering grounds for the rare and endangered whooping crane (*Grus americana*). Whooping crane populations declined during the late 19th and early 20th century to the point where <25 individuals remained in the early 1940s (Allen, 1952; Erickson & Derrickson, 1981). The only self-sustaining population that persists today is the Aransas-Wood Buffalo population, which winters in coastal Texas in the ANWR region and migrates to its summer breeding grounds in north-central Canada. During the winter of 2019–2020, the Aransas-Wood Buffalo population was estimated to contain just 506 individuals (Butler et al., 2020). While wintering in coastal Texas, whooping cranes forage within salt marshes for blue crabs (*C. sapidus*), wolfberries (*Lycium carolinianum*), and other foods (Chavez-Ramirez, 1996; Hunt & Slack, 1989). However, the ANWR region is a recent hotspot for mangrove expansion in Texas (Armitage et al., 2015; Brown et al., 2016), and there is concern that mangrove replacement of salt marsh will negatively affect the habitat and food resources available for whooping cranes (Chavez-Ramirez & Wehtje, 2012; Stehn & Prieto, 2010). Blue crabs are an especially important food source for cranes (Chavez-Ramirez, 1996; Hunt & Slack, 1989), and blue crab abundance may have a positive relationship with whooping crane survival (Pugesek et al., 2013). Thus, mangrove expansion effects on blue crabs and other foods are a concern. Several studies have indicated that blue crab abundance may decrease with mangrove expansion (Glazner et al., 2020; Johnston & Caretti, 2017; Smee et al., 2017). For coastal managers at ANWR, maintaining the region's whooping crane population is a high priority; however, managers are concerned that continued mangrove expansion could have a negative impact [Andrew Stetter and Colt Sanspree (U.S. Fish and Wildlife Service), oral communication, March 30, 2021]. In addition to research that better characterizes the effects of mangrove expansion on whooping cranes, coastal managers in the ANWR region are interested in management strategies for limiting mangrove expansion into the salt marshes used by whooping cranes [Andrew Stetter and Colt Sanspree (U.S. Fish and Wildlife Service), oral communication, March 30, 2021].

10 | INSECTS, OTHER TERRESTRIAL ARTHROPODS, AND MANGROVE HONEY

How might mangrove expansion affect insects, other terrestrial arthropods, and associated ecosystem services (e.g., mangrove honey)? In a study conducted in Texas, insect abundance and biomass decreased with mangrove abundance, whereas insect richness and diversity increased (Loveless & Smee, 2019). An arthropod-focused study conducted along Florida's Atlantic coasts also found distinct arthropod communities in mangrove- and marsh-dominated wetlands, indicating that mangrove expansion may increase habitat heterogeneity, which would produce an increase in arthropod diversity (Nathan, 2020). In marsh-dominated coastal wetlands, mangroves may provide a novel resource for insects and other terrestrial arthropods in the form of nectar-producing flowers (Nathan, 2020). However, more data are needed to evaluate the effects of mangrove encroachment on terrestrial arthropods and the terrestrial portion of coastal wetland food webs (see Loveless & Smee, 2019; Nathan, 2020).

In areas that historically supported salt marsh plants, expansion of mangroves with nectar-producing flowers (Nathan, 2020) may provide a novel kind of honey for beekeepers along the northern coastal reaches of the southeastern United States. Along many tropical coastlines, mangrove forests are popular honey-producing areas for beekeepers and honey hunters (Bradbear, 2009). In Florida, which is one of the largest honey-producing states in the United States, mangroves are a popular source of nectar for honey production (Sanford, 2016). For this reason, in some of the scientific literature and herbarium records from the early 20th century, the common name used for *A. germinans* was honey mangrove (e.g., Penfound & Hathaway, 1938). Currently, mangrove honey in the southeastern United States is produced primarily along the southern and central coasts of Florida. However, as mangroves expand further north, there is the potential for mangrove honey to be produced along Florida's northern coasts. For example, in the Apalachicola region, where freshwater swamps have historically supported tupelo honey-specialty businesses for more than a century, the recent expansion of mangroves on the region's barrier island ecosystems (Snyder et al., 2021) has prompted interest to also produce mangrove honey [George Watkins, oral communication, 24 May 2021].

11 | RECREATION

Generally, the recreational value of coastal wetlands is underpinned by many of the ecological and biophysical characteristics described in previous sections of this review, as well as numerous other socioeconomic factors (Hamilton & Snedaker, 1984). For instance, many of the recreational benefits of mangroves and marshes result from the diverse species and food webs that depend on these habitats (Kelleway et al., 2017). Rare, exotic, and charismatic species can be particularly important for recreation in wetlands. More broadly, the aesthetic appeal or scenery, uniqueness of a site, proximity to population centers, trail, and water access, and overall public awareness are key landscape and socioeconomic factors that influence recreational use, value, and satisfaction of people (Hamilton & Snedaker, 1984; Harty, 2009; Lundquist et al., 2014).

Similar to other ecosystem services, mangrove expansion in marshes is likely to have variable and site-specific impacts on recreation (Kelleway et al., 2017). For instance, shifting assemblages of birds may impact, either positively or negatively, recreational demand and satisfaction among bird watchers (Armitage et al., 2021; Whitt, 2016). Likewise, the same scenario would apply to recreational fishers if expanding mangroves support different fish communities than salt marshes. These impacts are likely to be greatest among highly specialized recreational users who may value specific places or prioritize certain species that could become more or less common (Oh et al., 2013). The expansion of mangroves may also impact water access and viewscapes (Harty, 2009; Kaplowitz, 2001; Lundquist et al., 2014; see also coastal food webs and fisheries section). Both mangroves and marshes are appreciated for their aesthetic or scenic values (Kaplowitz, 2001), but water access is more difficult in areas with dense mangrove forests. In general, recreation-related attitudes, preferences, and behaviors represent a major gap in the literature on mangrove ecosystem services, especially within the context of mangrove expansion into salt marshes.

Where mangrove expansion is occurring near residential areas, mangrove replacement of marsh can have striking effects on residents' recreational activities and interactions with their coast (Harty, 2009; Lundquist et al., 2014). For example, in the 1990s following the major freeze events of the 1980s, many residents in the Cedar Key area of Florida had wide-ranging views that looked out onto expansive wetlands dominated by salt marsh grasses (Stevens et al., 2006). However, expanding mangrove forests have grown to heights greater than 6 m (Yando et al., 2016), which is tall enough to block valuable landscape views of the salt marsh [Andrew Gude (U.S. Fish and Wildlife Service) and Micheal Allen (University of Florida), oral communication, May 19, 2021]. Despite the potential gains in coastal protection supported by mangrove expansion (Doughty et al., 2017; Hijuelos et al., 2019; Pennings et al., 2021), the loss of salt marsh views is a critical and overarching concern for many Cedar Key residents, and some residents are interested in managing the expanding mangrove forests to regain the previously present salt marsh views and access [Andrew Gude (U.S. Fish and Wildlife Service) and Micheal Allen (University of Florida), oral communication, May 19, 2021]. Further, by reducing wind speeds, the mangrove forests can also increase the number of mosquitos and other nuisance insects near residences [Andrew Gude (U.S. Fish and Wildlife Service) and Micheal Allen (University of Florida), oral communication, May 19, 2021]. Conversely, from a practical landscape maintenance perspective, mangrove expansion can reduce the amount of storm debris (i.e., marsh wrack) that is transported and deposited onto waterfront properties [Andrew Gude (U.S. Fish and Wildlife Service) and Micheal Allen (University of Florida), oral communication, May 19, 2021]. Thus, mangroves can be viewed as both positive (shoreline protection) and negative (impeding ocean views and thus reducing property values) by local homeowners.

12 | KNOWLEDGE GAPS AND EMERGING RESEARCH NEEDS

The majority of research regarding the effects of mangrove expansion has focused on coastal food webs and fisheries (Figure 1e; 31 papers) and carbon sequestration (Figure 1a; 27 papers). Less research has examined soil elevation dynamics (Figure 1b; 12 papers), water quality and nutrient cycling (Figure 1c; 12 papers), avian communities (Figure 1f; 9 papers), coastal protection (Figure 1d; 4 papers), recreation (Figure 1h; 4 papers), and insects and terrestrial arthropods (Figure 1g; 2 papers). Within the ecosystem service-focused sections of this review, we have identified knowledge gaps and emerging research needs. In Table 3, we summarize this information to: (1) rank the level of knowledge regarding the impacts of mangrove expansion on specific ecosystem services and (2) summarize the most critical knowledge gaps and research needs. One common research gap that spans several ecosystem services is the need to better investigate and account for the influence of site- and species-specific conditions (e.g., geomorphology, environmental conditions, and the ecosystem properties of the interacting salt marsh and mangrove forest).

Beyond just research gaps in key thematic areas, there is a need for methodological refinements that expand upon findings from local scale inter-habitat comparisons. Most of the studies in this review have employed inter-habitat comparisons or comparative measurements made across mangrove-marsh ecotones, which are valuable approaches that require careful consideration of potentially confounding abiotic gradients (e.g., inundation and salinity gradients). To broaden the significance of results and better account for the influence of site- and species-specific conditions, there is a need for studies that employ innovative experimental designs (see Kelleway et al., 2017 for more details)—for example, field- and greenhouse-based manipulative experiments, space-for-time substitutions, before-after-control-impact designs, and coordinated replicated experiments conducted across environmental gradients by regional collaborative networks.

13 | INTERACTIONS WITH OTHER ASPECTS OF CLIMATE CHANGE

Our review focuses primarily on the ecological effects of mangrove expansion driven by warming winter temperatures. However, coastal wetlands in the southeastern United States are vulnerable to many different aspects of climate change. In addition to warming winter temperatures, coastal wetlands in the region are affected by rising sea levels, saltwater intrusion, and changes in the frequency and intensity of extreme climatic events (Carter et al., 2018; Osland, Feher, et al., 2018; USGCRP, 2017). For example, rising sea levels can lead to wetland conversion to open water (Couvillion et al., 2017; Saintilan et al., 2020; Törnqvist et al., 2020) and the landward migration of wetlands (Borchert et al., 2018; Enwright et al., 2016). Landscape-scale wetland vegetation dieback events can be triggered by extreme drought (Alber et al., 2008; Duke et al., 2017; Lovelock et al., 2017; Sippo et al., 2018), flooding (Stagg et al., 2021), hurricanes (Cahoon et al., 2003; Osland, Feher, Anderson, et al., 2020), and freeze events (Osland, Day, et al., 2017). Macroclimate drivers govern foundation plant communities in the region, which means that changing temperature and precipitation regimes can transform coastal wetlands (Gabler et al., 2017; Osland, Grace, et al., 2019). Climate change is also expected to increase the frequency of major hurricanes, which affects the dispersal of mangroves beyond current range limits (Kennedy et al., 2016, 2020; Van der Stocken, Carroll, et al., 2019). Collectively, these examples show that mangrove range expansion dynamics will be greatly influenced by interactions between many different aspects of climate change.

14 | CONCLUSIONS

In the past two decades, there has been a rapid increase in the number of studies investigating the effects of mangrove range expansion on ecosystem goods and services in the southeastern United States (Figure 1). This review synthesizes that information with an emphasis on impacts to carbon sequestration, wildlife habitat, storm protection, erosion prevention, water purification, fisheries support, and recreation. One consistent theme throughout this work is that there are ecological trade-offs for consideration by coastal scientists and natural resource managers (e.g., Table 2; Figure 4). Mangrove expansion and marsh displacement can produce beneficial changes in some ecosystem services while producing detrimental changes in other services. As a result, there is much variation in opinions regarding the social and ecological consequences of mangrove expansion. For the same location, some individuals may view mangrove expansion as a positive transformation to be fostered, while others may see it as a negative change to be prevented. Such variation in perceptions and impacts highlights the benefits of careful planning and discussion preceding management efforts (e.g., mangrove planting or removal) that could accelerate or constrain the pace of mangrove expansion.

ACKNOWLEDGMENTS

We thank the many individuals across the region that took the time to speak to us about this topic and provide local examples from their coasts. This research was funded by the U.S. Geological Survey Southeast Climate Adaptation Science Center, which is managed by the USGS National Climate Adaptation Science Center. This work was also supported by a National Academy of Sciences, Engineering, and Medicine Gulf Research Program Healthy Ecosystems Grant to ARH, SBS, CCS, and MJO. Additional support for MJO was provided by the USGS Climate R&D Program and the USGS Greater Everglades Priority Ecosystem Science Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

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How to cite this article: 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. https://doi.org/10.1111/gcb.16111