

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

3 **Running Title:** Impacts of mangrove range expansion

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23 **Abstract**

24 Climate change is transforming ecosystems and affecting ecosystem goods and services. Along
25 the Gulf of Mexico and Atlantic coasts of the southeastern United States, the frequency and
26 intensity of extreme freeze events greatly influences whether coastal wetlands are dominated by
27 freeze-sensitive woody plants (mangrove forests) or freeze-tolerant grass-like plants (salt
28 marshes). In response to warming winters, mangroves have been expanding and displacing salt
29 marshes at varying degrees of severity in parts of north Florida, Louisiana, and Texas. As winter
30 warming accelerates, mangrove range expansion is expected to increasingly modify wetland
31 ecosystem structure and function. Because there are differences in the ecological and societal
32 benefits that salt marshes and mangroves provide, coastal environmental managers are
33 challenged to anticipate effects of mangrove expansion on critical wetland ecosystem services,
34 including those related to carbon sequestration, wildlife habitat, storm protection, erosion
35 reduction, water purification, fisheries support, and recreation. Mangrove range expansion may
36 also affect wetland stability in the face of extreme climatic events and rising sea levels. Here, we
37 review current understanding of the effects of mangrove range expansion and displacement of
38 salt marshes on wetland ecosystem services in the southeastern United States. We also identify
39 critical knowledge gaps and emerging research needs regarding the ecological and societal
40 implications of salt marsh displacement by expanding mangrove forests. One consistent theme
41 throughout our review is that there are ecological trade-offs for consideration by coastal
42 managers. Mangrove expansion and marsh displacement can produce beneficial changes in some
43 ecosystem services, while simultaneously producing detrimental changes in other services. Thus,
44 there can be local-scale differences in perceptions of the impacts of mangrove expansion into salt
45 marshes. For very specific local reasons, some individuals may see mangrove expansion as a

46 positive change to be embraced, while others may see mangrove expansion as a negative change
47 to be constrained.

48

49 **Keywords:** climate change, coastal wetland, ecosystem services, mangrove, range expansion,
50 winter climate change

51

52 **Introduction**

53 In response to warming air and ocean temperatures, temperate ecosystems are being transformed
54 by tropical organisms whose range limits are expanding poleward (Vergés *et al.* 2014; Osland *et*
55 *al.* 2021). In North America, the transition between tropical and temperate ecosystems is greatly
56 influenced by the frequency and intensity of winter temperature extremes, as the northern range
57 limits of most tropical organisms are governed by extreme freezing temperatures (Boucek *et al.*
58 2016; Osland *et al.* 2021). Climate change is producing warmer winters with fewer extreme
59 freeze events (USGCRP 2017; Carter *et al.* 2018), which allows tropical organisms to move
60 north of their current range limits. Coastal environmental managers near tropical-temperate
61 transitions are increasingly faced with making natural resource management decisions related to
62 the range expansion of these tropical organisms. Thus, there is a need to advance understanding
63 of the ecological implications. In this communication, we review the literature on the ecological
64 and societal impacts of warming winters and tropical range expansion within coastal wetland
65 ecosystems in the southeastern United States, where tropical mangrove forests are expected to
66 invade and ultimately displace salt marshes as they continue to move north (Osland *et al.* 2013;
67 Cavanaugh *et al.* 2014; Gabler *et al.* 2017).

68 Mangrove forests and salt marshes are both highly productive coastal wetland ecosystems
69 that occupy very similar geomorphic positions within tidal saline environments (Cahoon *et al.*
70 2020). Thus, there are many similarities in the ecosystem goods and services provided by these
71 tree- and grass-dominated coastal wetlands. Both ecosystems are frequently ranked among the
72 most valuable ecosystems on the planet (Costanza *et al.* 2014). In addition to providing habitat
73 for fish and wildlife species, mangrove forests and salt marshes sequester large quantities of
74 CO₂, protect coastlines from storms, reduce erosion, improve water quality, support productive
75 fisheries, and provide recreational opportunities (Barbier *et al.* 2011).

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

89

90 **Background: mangrove range expansion in the southeastern United States**

91 The Gulf of Mexico and Atlantic coasts of North America are global hotspots for mangrove
92 range expansion (Osland *et al.* 2017b; Cavanaugh *et al.* 2018) (Figure 2). Coastal wetlands are
93 abundant in the southeastern United States due to the region's expansive low-lying coastal plains
94 (Deegan *et al.* 1986; Enwright *et al.* 2016). In warmer and more tropical southern coastal
95 reaches, tidal saline wetlands are dominated by mangrove trees and shrubs (Odum *et al.* 1982),
96 with the three most common mangrove species in the region being *Avicennia germinans* (black
97 mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove).
98 The northern range limits of these mangrove species (Figure 2) are controlled by extreme freeze

99 events, which can lead to physiological damage and/or mortality (Sherrod & McMillan 1985;
100 Pickens & Hester 2011; Cavanaugh *et al.* 2014; Bardou *et al.* 2021). Thus, along cooler, northern
101 coastal reaches, tidal saline wetlands are dominated by grass-like salt marsh plants (i.e., grasses,
102 sedges, and rushes) (Gabler *et al.* 2017; Osland *et al.* 2019a), because salt marsh plants can
103 tolerate freezing temperatures via winter dormancy. Conversely, mangroves outcompete salt
104 marsh plants along southern coastal reaches where temperatures are suitable for mangrove
105 growth and canopy development (Kangas & Lugo 1990; Feher *et al.* 2017).

106 The northernmost mangrove populations in the region are present in Texas (Sherrod &
107 McMillan 1981; Armitage *et al.* 2015), Louisiana (Osland *et al.* 2017a; Day *et al.* 2020; Osland
108 *et al.* 2020b), and the Gulf of Mexico and Atlantic coasts of northern Florida (Stevens *et al.*
109 2006; Simpson *et al.* 2017; Snyder *et al.* 2021). Isolated mangrove individuals have also been
110 found on Mississippi's barrier islands (Scheffel *et al.* 2013; Scheffel *et al.* 2017; Macy *et al.*
111 2019). In the past century, mangrove range limits have expanded across the region during freeze-
112 free years and contracted due to mass mortality during extreme freeze events (Sherrod &
113 McMillan 1985; Brown *et al.* 2016; Osland *et al.* 2017a; Cavanaugh *et al.* 2019). The last major
114 freeze event resulting in region-wide mass mangrove mortality and range contraction occurred in
115 December 1989 (Lonard & Judd 1991; Stevens *et al.* 2006; Osland *et al.* 2017a). Since then,
116 mangroves have been expanding in parts of northern Florida, Louisiana, and Texas. Although
117 1989 was the last cold event to affect mangroves across the entire northern Gulf of Mexico, there
118 have been several smaller, less intense cold events (e.g., 1996, 2000, 2001, 2002, 2003, 2010,
119 2011, 2014, 2018, 2021), which have caused short-term mangrove damage, mortality, and/or
120 local reductions in coverage (e.g., Osland *et al.* 2015; Osland *et al.* 2017a; Osland *et al.* 2019b;
121 Osland *et al.* 2020a; Osland *et al.* 2020b; Snyder *et al.* 2021). The most recent event (February

122 2021) caused varying levels of mangrove damage and mortality across the Texas coast [Anna
123 Armitage (Texas A&M Galveston) and Kathleen Swanson (Mission Aransas National Estuarine
124 Research Reserve), oral communication, March 2021). In response to future warming, mangrove
125 forests are expected to expand farther north and displace salt marshes in much of Texas,
126 Louisiana, and northern Florida (Osland *et al.* 2013; Cavanaugh *et al.* 2015; Gabler *et al.* 2017;
127 Cavanaugh *et al.* 2019).

128 Inundation and salinity regimes are critical abiotic factors that govern ecosystem
129 structure and function in coastal wetlands (Ibáñez *et al.* 2012; Twilley & Day 2012). Thus,
130 across the southeastern United States, there is some variation in the salt marsh plant communities
131 that are being replaced by range-expanding mangrove forests (Yando *et al.* 2016; Gabler *et al.*
132 2017; Osland *et al.* 2019a) (Figure 3). In general, salt marshes are dominated by grass-like
133 (graminoid) plants (e.g., *Spartina alterniflora*, *Juncus roemerianus*, *Spartina patens*,
134 *Schoenoplectus americanus*) near mangrove range limits in northern Texas, Louisiana, and
135 northern Florida (Yando *et al.* 2016; Brockmeyer *et al.* 2017; Gabler *et al.* 2017; Osland *et al.*
136 2019a; Chapman *et al.* 2021). Salt marshes in all three of these areas receive comparatively large
137 freshwater inputs that maintain salinities below or near ocean waters (NOAA 1990; USEPA
138 1999; Osland *et al.* 2014). In contrast, along more arid coasts that receive less rainfall and
139 smaller riverine freshwater inputs, such as the lower and central Texas coast, hypersaline
140 conditions can develop when high evaporation concentrates oceanic salts (Longley 1995;
141 Withers 2002b; Montagna *et al.* 2007; Osland *et al.* 2014). Halophytic succulent plant species
142 (e.g., *Batis maritima*, *Salicornia depressa*, *Borrchia frutescens*, *Monanthochloe littoralis*) tend
143 to dominate hypersaline salt marsh plant communities (Yando *et al.* 2016; Gabler *et al.* 2017;
144 Osland *et al.* 2019a). Limited connectivity with the ocean can also produce hypersaline

145 conditions and halophytic succulent plant-dominated salt marshes, as in parts of the Indian River
146 Lagoon along the Atlantic coast of Florida (Brockmeyer *et al.* 2017; Simpson *et al.* 2019;
147 Chapman *et al.* 2021). These examples show that regional variation in climate- and hydrology-
148 controlled salt marsh plant community composition and structure is important to consider as it
149 can influence how wetland ecosystem services change due to mangrove expansion and salt
150 marsh displacement.

151 How do mangrove range limits in the southeastern United States compare with other
152 mangrove range limits across the world? At the global scale, mangrove range limits are governed
153 by many factors including winter air temperature regimes, aridity, ocean temperatures, and
154 dispersal limitations (Duke *et al.* 1998; Saenger 2002; Osland *et al.* 2017b; Van der Stocken *et*
155 *al.* 2019a). Winter air temperatures affect mangrove range limits to varying degrees in Australia,
156 New Zealand, South Africa, Brazil, and China (Quisthoudt *et al.* 2012; Osland *et al.* 2017b). Due
157 to the movement of cold air outbreaks from the arctic across continental land masses in the
158 Northern Hemisphere, mangrove range limits in the Northern Hemisphere (i.e., North America
159 and China) are affected by colder winter air temperature extremes than range limits in the
160 Southern Hemisphere (i.e., Australia, New Zealand, South Africa, Brazil) (Osland *et al.* 2017b;
161 Smith & Sheridan 2020; Osland *et al.* 2021). Thus, mangrove range expansion is more dynamic
162 and more strongly influenced by cold temperature extremes in the southeastern United States
163 (Osland *et al.* 2017a; Cavanaugh *et al.* 2018; Cavanaugh *et al.* 2019) and China (Chen *et al.*
164 2017) compared to Australia, New Zealand, South Africa, and Brazil (Osland *et al.* 2017b).

165 While mangrove expansion is occurring on several other continents, there is much
166 variation in the environmental settings and the drivers responsible these changes (Saintilan &
167 Williams 1999; Saintilan *et al.* 2014; Rogers & Krauss 2019). For example, changing rainfall

168 regimes (Diop *et al.* 1997; Eslami-Andargoli *et al.* 2009), rapid sedimentation (Lovelock *et al.*
169 2010; Asbridge *et al.* 2015; Walcker *et al.* 2018), hydrologic alterations (Raabe *et al.* 2012), and
170 rising sea levels (Krauss *et al.* 2011; Howard *et al.* 2020) are all common drivers of mangrove
171 expansion. These drivers and the accompanying differences in environmental setting (e.g.,
172 geomorphology, climate, and the ecosystem properties of the interacting salt marshes and
173 mangrove forests) greatly influence the ecological implications of mangrove expansion. Our
174 review focuses primarily on the southeastern United States to avoid confounding interpretations
175 due to such differences.

176

177 **Local impacts and trade-offs**

178 At global and regional scales, coastal wetlands are typically valued for their support of multiple
179 ecosystems services (Barbier *et al.* 2011; Costanza *et al.* 2014). However, at local scales (e.g., a
180 specific wetland within a refuge, park, or neighborhood), coastal management actions are
181 sometimes motivated by an interest to maintain or enhance a specific ecosystem good or service.
182 For example, if a wetland is valued for waterfowl hunting, management actions may be guided
183 primarily by an interest to maintain or enhance waterfowl habitat (Mitchell *et al.* 2006).

184 Conversely, if an urban municipal wetland provides valuable recreation opportunities, wetland
185 management may be driven by an interest to optimize public recreation (Zedler & Leach 1998).

186 Across the southeastern United States, there is much variation in the coastal wetland ecosystem
187 services that are prioritized by coastal communities and managers (Feagin *et al.* 2010; Engle
188 2011; Yoskowitz *et al.* 2012). Thus, there can be local-scale differences in perceptions of the
189 ecological and societal impacts of mangrove expansion into salt marshes. For very specific local
190 reasons, some individuals may see mangrove expansion as a positive change to be embraced,

191 while others may see mangrove expansion as a negative change to be constrained (Table 2;
192 Figure 4). At several points in this communication, we have included specific examples that
193 illustrate some of the variation in local perceptions of the impacts and tradeoffs associated with
194 mangrove expansion.

195

196 **Carbon sequestration**

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

202 One of the most striking and consistent effects of mangrove expansion is an increase in
203 canopy height and aboveground carbon stocks (Yando *et al.* 2016; Feher *et al.* 2017; Gabler *et*
204 *al.* 2017; Simpson *et al.* 2017). Mangroves are woody plants that can rapidly accumulate
205 aboveground carbon stocks during the early stages of forest development (Lovelock *et al.* 2010;
206 Walcker *et al.* 2018; Osland *et al.* 2020d; Chapman *et al.* 2021). In contrast, salt marshes are
207 dominated by herbaceous plants that lose their aboveground biomass each year during winter
208 senescence (Macy *et al.* 2020). Thus, mangrove forests are typically taller and contain more
209 aboveground biomass than their salt marsh counterparts. Studies conducted in mangrove-marsh
210 ecotones across the southeastern United States have consistently shown that mangrove expansion
211 into salt marsh results in taller plants, more aboveground biomass, and increases in aboveground
212 carbon stocks (Perry & Mendelssohn 2009; Doughty *et al.* 2016; Hutchison 2016; Yando *et al.*
213 2016; Hutchison *et al.* 2018; Simpson *et al.* 2019; Charles *et al.* 2020; Macy *et al.* 2020).

214 However, the magnitude of those increases in aboveground carbon stocks and storage rates can
215 be influenced by other factors, including geomorphic position and interactions between aridity,
216 salinity, and plant productivity (Yando *et al.* 2016; Gabler *et al.* 2017; Osland *et al.* 2018b).

217 What are the implications of mangrove expansion for belowground carbon cycling and
218 storage? Soil carbon burial represents the largest long-term carbon storage pathway within
219 coastal wetlands (Chmura *et al.* 2003; Breithaupt *et al.* 2012). Thus, there has been much interest
220 and debate regarding the soil carbon implications of mangrove expansion. Mangrove forests and
221 salt marshes are both highly productive ecosystems that, on a per unit area basis, have the
222 potential to support soil carbon burial rates that are among the highest on the planet (Donato *et*
223 *al.* 2011; Mcleod *et al.* 2011). The factors that contribute to rapid soil organic matter
224 development in both mangrove forests and salt marshes include high rates of primary
225 productivity, prolific belowground root production, low rates of decomposition due to anaerobic
226 conditions, and continued organic matter burial as wetlands trap sediments and build elevation to
227 adjust to rising sea levels (Cahoon *et al.* 2020). As in terrestrial grasslands, where there is much
228 variation in the edaphic effects of woody plant encroachment due to climate-plant trait
229 interactions (Barger *et al.* 2011; Eldridge *et al.* 2011; Archer *et al.* 2017), studies in coastal
230 wetlands have revealed divergent, nuanced results regarding the effects of mangrove expansion
231 on soil carbon cycling and storage. While some studies have found no measurable effect of
232 mangrove expansion on soil carbon stocks (Perry 2007; Perry & Mendelsohn 2009; Henry &
233 Twilley 2013; Doughty *et al.* 2016; Yando *et al.* 2018; Charles *et al.* 2020; Macy *et al.* 2020),
234 others have found increases in soil carbon associated with mangrove expansion (Bianchi *et al.*
235 2013; Simpson *et al.* 2019; Vaughn *et al.* 2020). When viewed collectively, these studies indicate
236 that the edaphic and soil carbon effects of mangrove expansion are highly site dependent and

237 greatly influenced by the plant traits and ecosystem properties of the interacting salt marshes and
238 mangrove forests (Yando *et al.* 2016; Osland *et al.* 2018b; Charles *et al.* 2020) (Figure 3). In the
239 subsequent paragraphs, we briefly examine several alternative hypotheses regarding the
240 divergent soil carbon-focused findings in the literature.

241 Biomass-based hypotheses regarding changes in soil carbon cycling and storage due to
242 mangrove expansion presume that increases in aboveground biomass will be accompanied by
243 concomitant increases in belowground carbon storage. Across some coastal wetland abiotic
244 gradients (e.g., nutrient limitation gradients or extreme salinity gradients), there can be strong
245 positive relationships and positive feedbacks between coastal wetland plant biomass, plant
246 productivity, and soil carbon stocks and cycling (McKee *et al.* 2007; Kauffman & Bhomia 2017;
247 Osland *et al.* 2018b; Rovai *et al.* 2018). However, aboveground biomass increases due to
248 mangrove expansion do not necessarily affect net soil carbon cycling and storage. Indeed, across
249 the tropical-temperate transition zone in eastern North America, which spans productive
250 mangrove forests in the warmer south and productive salt marshes in the colder north, coastal
251 wetland aboveground biomass varies greatly but is not correlated to soil carbon stocks or soil
252 carbon burial (Chmura *et al.* 2003; Feher *et al.* 2017; Holmquist *et al.* 2018; Osland *et al.*
253 2018b). Under comparable geomorphic conditions, mangrove forests and salt marshes have the
254 potential to support similarly high soil carbon stocks and soil carbon accumulation rates. Thus,
255 instead of being linked directly to aboveground biomass, mangrove-triggered changes in coastal
256 wetland soil properties and soil carbon burial rates, where present, are more likely linked to
257 changes in other processes (e.g., productivity, decomposition). Moreover, where mangrove
258 expansion is occurring across a salinity or elevation gradient (e.g., Ross *et al.* 2000; Krauss *et al.*
259 2011; Lewis *et al.* 2021), the effects of mangrove expansion may be due to concomitantly

260 changing abiotic conditions that are governed by other drivers (e.g., saltwater intrusion, rising
261 sea levels).

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

283 expansion. Beyond just carbon quantity, soil carbon quality can be affected by mangrove
284 expansion (Lewis *et al.* 2014; Breithaupt *et al.* 2020; Charles *et al.* 2020; Vaughn *et al.* 2020).
285 For example, along the central Texas coast, succulent marsh plant (*B. maritima*) leaf and root
286 breakdown rates were 1000% and 35% faster, respectively, than *A. germinans* (Charles *et al.*
287 2020). The effects of mangrove expansion on autochthonous detrital inputs and allochthonous
288 carbon burial via changes in sedimentation (Guo *et al.* 2017; Chen *et al.* 2018; Charles *et al.*
289 2020; McKee *et al.* 2020; Kuhn *et al.* 2021) also warrant further investigation.

290 In summary, although mangrove expansion is universally expected to increase
291 aboveground carbon storage, the effects on soil carbon storage are highly variable and warrant
292 closer investigation via field- and greenhouse-based manipulative experiments as well as
293 measurements from a larger number of mangrove-marsh ecotones across the region (Table 3).
294 There is also a pressing need for studies that, instead of measuring carbon stocks, directly
295 measure critical processes (e.g., root productivity, decomposition, sediment deposition) that
296 directly affect soil carbon storage and cycling. Species-specific effects on soil carbon quality and
297 quantity also warrant further investigation. For example, most studies have focused on the effects
298 of *A. germinans* expansion, but due to differences in plant traits, the edaphic effects of *R. mangle*
299 expansion may differ from *A. germinans* (McKee 1993). There is also a need for species-specific
300 salt marsh research that moves beyond just *S. alterniflora*. Although there are 24 dominant
301 foundation plant species in tidal saline wetlands across the conterminous United States, 45
302 percent of publications have been focused on *S. alterniflora* (Osland *et al.* 2019a).

303

304 **Soil elevation change and vertical adjustments to sea-level rise**

305 Mangrove forests and salt marshes have the potential to adjust to moderate rates of rising sea
306 levels via soil elevation gains that are driven by positive feedbacks between inundation, plant
307 growth, and sediment deposition (Morris *et al.* 2002; Krauss *et al.* 2014b). Given the
308 vulnerability of coastal wetlands to accelerated sea-level rise, will mangrove expansion increase
309 soil elevation building capacity and the ability of coastal wetlands to adjust to rising sea levels?
310 This question has been investigated through the use of radioisotopes, sediment traps, marker
311 horizons, and surface elevation tables. Many of the processes that affect soil carbon storage and
312 cycling (e.g., root productivity, belowground decomposition, and sediment deposition) are also
313 the primary processes that govern soil elevation change. Thus, given the variable and highly site-
314 specific effects of mangrove expansion on soil carbon storage, we expect that the effects of
315 mangrove expansion on soil elevation change dynamics are also highly context-dependent and
316 governed by site- and species-specific conditions (e.g., geomorphology, abiotic conditions, and
317 the ecosystem properties of the interacting salt marsh and mangrove forest).

318 The surface elevation table-marker horizon (SET-MH) approach (Cahoon *et al.* 2002;
319 Lynch *et al.* 2015) has been used to directly measure shorter-term (e.g., 5 to 30 year) soil
320 elevation change dynamics and quantify the contributions of critical above and belowground
321 processes (e.g., accretion, erosion, subsurface root zone expansion, subsurface subsidence).
322 There are only a few studies that have directly measured the soil elevation change implications
323 of mangrove expansion using the SET-MH approach. An SET-MH study conducted along the
324 Atlantic coast of Florida within *Distichlis spicata*-dominated marshes found higher elevation
325 gains associated with warming temperatures and mangrove (*L. racemosa*) expansion; vertical
326 accretion was about threefold higher in mangrove plots exposed to a warming temperature
327 treatment compared to salt marshes exposed to the same treatment (Coldren *et al.* 2019). In

328 contrast, an SET-MH study conducted in Louisiana found similar rates of soil elevation gain in
329 creekbanks dominated by *A. germinans*, *S. alterniflora*, or a mixture of both species (McKee &
330 Vervaeke 2018). A hurricane sediment-focused study conducted using soil cores from within the
331 same Louisiana mangrove-marsh ecotone found no difference in sediment capture by stands
332 dominated by *S. alterniflora* or *A. germinans* (McKee *et al.* 2020). A comparison of short-term
333 accretion rates in the Louisiana mangrove-marsh ecotone, measured using sediment traps
334 (biweekly accretion) and feldspar marker horizons (annual accretion), also found no difference in
335 stands dominated by *S. alterniflora* or *A. germinans* (Perry & Mendelssohn 2009). These results
336 suggest that replacement of marsh by mangroves would have no effect on sediment capture in
337 the Louisiana mangrove-marsh ecotone. However, as discussed in these papers and others across
338 the region, the lack of a difference may be unique to the sedimentary setting, the size and
339 developmental stage of the mangroves, and/or to the specific species compared (Perry 2007;
340 McKee & Vervaeke 2018; Charles *et al.* 2020; McKee *et al.* 2020; Kuhn *et al.* 2021).

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

347 Although there have been several studies that have used radioisotope-based methods to
348 compare vertical accretion rates in mangroves and salt marshes near poleward mangrove range
349 limits in eastern North America (Perry & Mendelssohn 2009; Comeaux *et al.* 2012; Bianchi *et*
350 *al.* 2013; Vaughn *et al.* 2020), century- and multi-decadal scale mangrove expansion patterns

351 near range limits can be dynamic and include freeze-controlled mangrove-marsh expansion and
352 contraction cycles (Osland *et al.* 2017a; Cavanaugh *et al.* 2019). Thus, radioisotope-based
353 approaches should ideally be paired with historical analyses of imagery (e.g., Perry &
354 Mendelssohn 2009) and climate data to identify freeze event-driven oscillations in mangrove
355 and/or salt marsh coverage during the time periods represented by soil cores.

356

357 **Water quality: nutrient and sediment retention**

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

371 Based on the current literature, it is difficult to predict how the replacement of salt
372 marshes by mangroves may affect nutrient pollution filtration in coastal wetlands as the existing
373 studies are spatially and temporally disjointed. Many environmental factors other than changes in

374 dominant vegetation can affect the differences observed between salt marsh- and mangrove-
375 focused studies. Long-term studies that directly record changes in nutrient cycling and storage as
376 mangroves replace salt marshes would be informative; however, we are unaware of such studies.
377 Another alternative is a ‘space-for-time substitution’ approach (Pickett 1989), where nutrient
378 cycling and storage are compared between contiguous stands of salt marsh and mangroves
379 present across ecotones where the expansion of mangroves and replacement of salt marshes is
380 actually occurring. A few such ‘space-for-time substitution’ studies exist (e.g., Henry 2012;
381 Macy *et al.* 2019; Steinmuller *et al.* 2019; Macy *et al.* 2020) and provide some indication of the
382 changes that will occur with mangrove expansion. These studies show higher nitrogen content in
383 the aboveground tissues of black mangroves (*A. germinans*) than in marsh smooth cordgrass (*S.*
384 *alterniflora*) (McKee & Rooth 2008; Macy *et al.* 2020). Higher aboveground biomass and
385 aboveground nitrogen stocks (Macy *et al.* 2020) suggest higher nitrogen uptake from the soil by
386 plants in *A. germinans* than in *S. alterniflora* stands, which is consistent with the lower nitrogen
387 concentrations observed in the soil porewater of *A. germinans* in comparison with *S. alterniflora*
388 stands (Macy *et al.* 2020). All together, these results suggest that *A. germinans*, by removing
389 larger quantities of nitrogen from the soil, may be larger filters of nitrogen pollution than *S.*
390 *alterniflora*. However, more studies are needed for a clear and robust description of the effects of
391 salt marsh replacement by mangroves on nitrogen cycling and storage, and ultimately nitrogen
392 pollution filtration in coastal wetlands.

393 Sediment and sediment-bound phosphorus retention is another process through which salt
394 marshes and mangroves can improve water quality in coastal ecosystems. Wetlands with more
395 near-surface plant structural complexity (e.g., greater stem density, biomass, flexibility) can be
396 more effective at retaining sediments by slowing down the flow of incoming and outgoing waters

397 (Feagin *et al.* 2015; Chen *et al.* 2018; McKee *et al.* 2020). A hurricane-focused study conducted
398 in Louisiana found that despite differences in plant structure there was no difference in hurricane
399 sediment capture within stands dominated by *S. alterniflora* or *A. germinans* (McKee *et al.*
400 2020). Conversely, a study conducted along the central Texas coast within a mangrove-marsh
401 ecotone that included *A. germinans* and succulent plants (e.g., *B. maritima*) found that hurricane
402 sediment accretion decreased with increasing mangrove cover (Kuhn *et al.* 2021). Despite these
403 two hurricane-focused studies, there are no studies that fully examine how salt marsh
404 replacement by mangroves in this region may alter wetland sediment retention and soil build-up
405 under dynamic conditions ranging from daily tidal cycles to storms. More research is needed to
406 better understand how salt marsh replacement by mangroves alters wetland sediment retention,
407 nutrient retention, and associated water quality-based ecosystem services (Table 3).

408

409 **Coastal protection**

410 Given the high vulnerability of coastal communities to storms, what is the potential for
411 mangrove expansion to enhance the coastal protection benefits provided by coastal wetlands?
412 Mangroves and salt marsh ecosystems both can reduce the height and energy of waves passing
413 through them (Gedan *et al.* 2011; Marois & Mitsch 2015), increase soil strength (Sasser *et al.*
414 2018; Jafari *et al.* 2019), and facilitate sediment deposition (Cahoon *et al.* 2020). These plant-
415 controlled processes can lead to reductions in shoreline erosion, decreases in flooding extent, and
416 avoided damages to infrastructure (Arkema *et al.* 2013; Barbier 2016; Narayan *et al.* 2019). The
417 ability of wetlands to support these coastal protection ecosystem services is dependent upon
418 multiple factors ranging from the characteristics of the individual wetland plants to landscape-
419 scale ecosystem coverage and configuration. Coastal protection services are also influenced by

420 geomorphology and the types and magnitudes of the hazard forces. The structural differences
421 between mangroves and salt marshes, with mangroves being generally larger, more complex and
422 rigid, have led to the hypothesis that coastal protection services may increase following
423 mangrove expansion into salt marsh.

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

442 Within the context of coastal erosion, there is interest in advancing understanding of
443 mangrove expansion effects on the ability of wetlands to tolerate and recover from extreme
444 events and other disturbances (e.g., droughts, hurricanes, floods, freezes, and oil spills). For
445 example, in the Galveston region, frequent oil spills are a concern for resource managers because
446 they can lead to vegetation dieback (Rozas *et al.* 2000; Williams *et al.* 2017). For many coastal
447 wetland practitioners in the Galveston area, there is interest in maximizing the ability of wetlands
448 to recover from potential future oil spills [Cherie O’Brien (Texas Parks and Wildlife
449 Department), oral communication, 24 May 2021]. However, there is some local concern that
450 expanding mangroves (*A. germinans*) may decrease wetland resilience to oil spills [Cherie
451 O’Brien (Texas Parks and Wildlife Department), oral communication, 24 May 2021] (but see:
452 Hughes *et al.* 2018). Thus, during coastal wetland restoration efforts in the Galveston area within
453 the past decade, *S. alterniflora* has typically been the targeted species, and very few Texas Parks
454 and Wildlife permits (i.e., the Permit to Introduce Fish, Shellfish or Aquatic Plants into Public
455 Waters) have been granted to plant mangroves [Cherie O’Brien (Texas Parks and Wildlife
456 Department), oral communication, 24 May 2021]. This example highlights the importance of
457 considering the effects of extreme events on wetland stability and coastal protection benefits.
458 Another example in this arena comes from Louisiana, where landscape-scale marsh and
459 mangrove dieback can be triggered by extreme events. For example, drought can lead to marsh
460 dieback (McKee *et al.* 2004; Alber *et al.* 2008) and extreme cold events can lead to mangrove
461 dieback (Osland *et al.* 2017a). Mangroves (*A. germinans*) may be more drought tolerant than *S.*
462 *alterniflora* marshes in Louisiana due to lower water use (Krauss *et al.* 2014a). Conversely,
463 extreme freeze events similar to the 1989 freeze could lead to landscape-scale mangrove mass
464 mortality, peat collapse, and accelerated erosion (McBride & Byrnes 1997; Penland *et al.* 2003;

465 Osland *et al.* 2020b), which would compromise the coastal protection benefits provided by
466 expanding mangrove forests.

467

468 **Coastal food webs and fisheries**

469 Marshes and mangrove forests support critical coastal food webs and fisheries-based ecosystem
470 services (Rönnbäck 1999; Beck *et al.* 2001; Minello *et al.* 2003; Nagelkerken *et al.* 2008; Engle
471 2011). However, due to the structural and functional differences between the two ecosystems,
472 how will mangrove range expansion and marsh displacement affect coastal food webs, fish
473 communities, and key ecosystem services (e.g., fisheries, fisheries-based recreation)?

474 Overall, the current evidence suggests that mangrove range expansion may lead to
475 changes in associated fish and invertebrate community composition (Armitage *et al.* 2021), but
476 there is less evidence that mangroves will substantially alter the major production sources to
477 aquatic food webs. Stable isotope analyses indicate that microphytobenthos and phytoplankton
478 are the dominant energy channels that directly support many aquatic consumer groups (e.g.,
479 fishery species, wetland specialists, zoobenthivores, phytodetritivores, and planktivores) (Baker
480 *et al.* 2021). Contributions from both mangrove and marsh plants typically flow through the
481 detrital pathway and play a lesser role in directly supporting food webs (Nelson *et al.* 2019;
482 Baker *et al.* 2021). In Louisiana, no detrital inputs from mangroves contributed significantly to
483 the dominant consumers in the food web (Nelson *et al.* 2019). It is uncertain if mangroves will
484 ultimately replace marsh grass detritus as an energy source (Nelson *et al.* 2019; Harris *et al.*
485 2020; James *et al.* 2020). However, reductions in marsh habitat as a result of mangrove
486 expansion may lead to a decline in energy supplied to some consumers, as mangrove detritus is
487 not readily used as a food source by the current nekton species in Louisiana (Harris *et al.* 2020).

488 A study in Texas also noted that differences in leaf nutritive quality (e.g., higher tannin,
489 phenolic, and lignin contents) may be linked to lower fitness for benthic consumers that consume
490 mangrove detritus (Goeke & Armitage 2021).

491 Most comparative studies of mangroves and marshes have detected differences in food
492 webs and community structure; however, those differences are not universal and can vary
493 depending on the measured taxonomic group, community metric, or functional attribute (Diskin
494 & Smee 2017; Loveless & Smee 2019; Walker *et al.* 2019; Armitage *et al.* 2021). For instance,
495 the relative abundance and species richness of nektonic fish and invertebrates in Texas were
496 similar between sites with and without mangroves, though individual species varied considerably
497 across those same sites (Armitage *et al.* 2021). Differences among areas with and without
498 mangroves can also be masked by abiotic conditions or disturbances that influence associated
499 faunal abundance and diversity (Diskin & Smee 2017). For example, Smee *et al.* (2017) found
500 significant differences in nekton and infaunal community structure in stands of smooth cordgrass
501 (*S. alterniflora*) bordered by mangroves (*A. germinans*) versus stands without mangrove.
502 Infaunal organisms, blue crabs (*Callinectes sapidus*), and shrimp (*Farfantepenaeus aztecus*,
503 *Palaemonetes* spp.) were less abundant in marshes bordered by mangroves than in marshes
504 without mangroves, whereas mud crabs (Xanthidae/Panopeidae) and fish were more abundant in
505 marshes bordered by mangroves (Smee *et al.* 2017). Similarly, macrofaunal communities
506 differed in marsh- versus mangrove-dominated vegetation along the Atlantic coast of Florida,
507 due to the influence of fine-scale plant structural differences and stand-level habitat attributes
508 (Johnston & Gruner 2018). Along the Atlantic coast, studies have noted differences in detrital-
509 based epifaunal communities (Smith *et al.* 2019) and subtidal nekton communities (Kimball &
510 Eash-Loucks 2021) associated with mangroves compared to marshes. For example, Smith *et al.*

511 (2019) found that crabs were 2-7 times more abundant in *S. alterniflora* detritus than *A.*
512 *germinans* detritus. In an early study comparing nekton communities in marsh and mangroves in
513 Louisiana, Caudill (2005) found that while fishes [e.g., gulf killifish (*Fundulus grandis*) and
514 sheepshead minnow (*Cyprinodon variegatus*)] were more abundant in *S. alterniflora*-dominated
515 marshes, white shrimp (*Litopenaeus setiferus*) were more abundant in *A. germinans*-dominated
516 mangrove stands.

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

526 Mangroves can also impact coastal food webs via changes in habitat complexity that
527 affect key species or predator-prey interactions (Scheffel *et al.* 2017; Johnston & Smith 2018).
528 Habitat complexity influences feeding efficiency and predation rates in fishes (Gotceitas &
529 Colgan 1989; Ahrens *et al.* 2012), and thus we expect that a shift from salt marsh to mangrove
530 will influence fish foraging and community composition. From the existing studies, the
531 consensus is that grass shrimps (*Palaemonetes* spp.), blue crabs (*C. sapidus*), and some marsh-
532 associated fishes (e.g., *F. grandis*) are more abundant in marshes compared to mangrove habitats
533 (Caudill 2005; Johnston & Caretti 2017; Smee *et al.* 2017; Armitage *et al.* 2021). However, there

534 are some inconsistencies in findings for penaeid shrimp that may be attributed to the type of
535 predators present at a given location. For example, penaeid shrimp preferred marsh grass over
536 mangroves in experimental trials, likely due to increased protection from predatory gray snapper
537 (*Lutjanus griseus*) (Scheffel *et al.* 2017). On the other hand, benthic invertebrates, such as
538 penaeid shrimp and the marsh periwinkle (*Littoraria irrorata*), were less vulnerable to predation
539 by blue crabs in the presence of mangroves in mesocosm and field studies, respectively (Glazner
540 *et al.* 2020; Glazner *et al.* 2021). The aerial root structures of mangroves (i.e., pneumatophores
541 and prop roots) can provide refuge from benthic predators, which could lead to shifts in predator-
542 prey interactions and altered trophic dynamics (Glazner *et al.* 2020; Glazner *et al.* 2021). In
543 Louisiana, penaeid shrimp foraging in mangroves had higher trophic levels than those foraging
544 in marsh-dominated habitats (Nelson *et al.* 2019). Increased predation on small benthic infauna
545 could feedback to other parts of the food web with uncertain consequences. Mangroves can have
546 additional negative impacts on blue crabs beyond the crab-shrimp interaction, with juvenile crabs
547 exhibiting a habitat preference for and higher survival in marsh grasses in experimental trials
548 (Johnston & Caretti 2017).

549 Much of the existing literature has focused on the effects of *A. germinans* expansion;
550 however, the impacts due to the range expansion of other common mangrove species may be
551 different. For example, the habitat quality characteristics for fishes differ between red mangrove
552 (*R. mangle*) and black mangrove (*A. germinans*), with the former having prop roots and the
553 ability to grow at lower intertidal elevations, thus influencing fish habitat inundation time and
554 depth. In areas where *R. mangle* occurs, overhanging limbs and prop roots can extend fringing
555 shoreline habitat another 10 m into the water. The overhanging vegetation and prop roots support
556 fishes by providing shade and cover (Ley *et al.* 1999; Ley & McIvor 2002). Because mangroves

557 are almost always located in shallow water and often in sheltered environments, it can be
558 difficult to isolate the effects of *R. mangle* prop roots as fish habitat (Ellis & Bell 2004). A study
559 using an experimental design with artificial mangroves found that the structure provided by *R.*
560 *mangle* prop roots can support unique juvenile fish assemblages (Nagelkerken & Faunce 2008).
561 In estuaries of southwestern Florida, *R. mangle*-dominated shorelines provide habitat for larger-
562 bodied species such as common snook (*Centropomus undecimalis*), sheepshead (*Archosargus*
563 *probatocephalus*), striped mullet (*Mugil cephalus*), gray snapper (*L. griseus*), redfin needlefish
564 (*Strongylura notata*), striped mojarra (*Eugerres plumieri*), and Atlantic spadefish
565 (*Chaetodipterus faber*) (Greenwood *et al.* 2007). The large-bodied species that associate closely
566 with *R. mangle* prop roots are often plastic in their habitat use and may not be fully dependent on
567 mangroves (e.g., Stevens *et al.* 2018). However, there are other species that exhibit greater
568 dependency on *R. mangle* habitat, such as juvenile smalltooth sawfish (*Pristis pectinata*) and
569 goliath grouper (*Epinephelus itajara*). Studies of fine-scale habitat use show that juvenile
570 smalltooth sawfish feed on shallow flats during the night and occupy protected *R. mangle*-
571 dominated embayments during the day (Lear *et al.* 2014; Huston *et al.* 2017), and specific use of
572 *R. mangle* prop roots to avoid predators has been observed (Poulakis *et al.* 2011). Juvenile
573 goliath grouper are found under overhanging mangroves and associated *R. mangle* prop roots in
574 areas where currents create deep undercuts in creek banks (Koenig *et al.* 2017). Adult goliath
575 grouper move long distances to aggregate in south Florida during the spawning season, which
576 occurs when mangroves are most flooded and thus most available as habitat for juveniles
577 (Koenig *et al.* 2017).

578 In the southeastern United States, mangrove expansion is just one of many dynamic
579 aspects of global change that challenge our ability to predict the future of coastal food webs and

580 fisheries. For example, accelerated sea-level rise is expected to ultimately lead to wetland
581 fragmentation, loss, and the transformation of coastal landscapes (Kirwan & Megonigal 2013;
582 Enwright *et al.* 2016; Couvillion *et al.* 2017; Borchert *et al.* 2018; Stagg *et al.* 2020). In the short
583 term, wetland loss and fragmentation could lead to ephemeral increases in fisheries production
584 due to increases in the amount of valuable edge habitat (Baker *et al.* 2020; Harris *et al.* 2020).
585 However, in the long-term and under higher rates of sea-level rise, the landscape-scale loss of
586 coastal wetlands (Saintilan *et al.* 2020; Törnqvist *et al.* 2020) and the associated edge habitat are
587 expected to have a negative impact on fisheries.

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

602 along Florida's Gulf of Mexico coast (Anderson *et al.* 2020; Purtlebaugh *et al.* 2020) after a
603 2010 cold event that resulted in mass mortality and range contraction (Stevens *et al.* 2016).

604 In contrast to mangroves, which rely on passive water transport of propagules for
605 dispersal and migration (Van der Stocken *et al.* 2019a; Van der Stocken *et al.* 2019b), fish are
606 actively mobile organisms. The high adaptive capacity of many coastal fish and invertebrate
607 species to warming winter waters indicates that some fish and invertebrate species will move
608 northward at rates that exceed the northward migration of mangroves (Riley *et al.* 2014;
609 Cannizzo *et al.* 2020; Stevens *et al.* 2021). Anthropogenic habitat and microclimatic refugia can
610 aid in the expansion of mangrove fauna. For example, the occupation of warm-water springs
611 allows common snook to overwinter in a climate where coastal water temperatures can still drop
612 below their lethal limits (Stevens *et al.* 2018). Along the Atlantic coast of North America, the
613 northern range limit of mangrove tree crabs (*Aratus pisonii*) is currently in Georgia (Riley *et al.*
614 2014), which is north of mangrove forests' current range limit in Florida. Interestingly, in the
615 absence of mangrove trees, mangrove tree crabs can adapt to suboptimal novel marsh
616 environments by: (1) shifting behavioral strategies from predator evasion (i.e., tree climbing) to
617 autotomy (i.e., leg dropping) to optimize survival (Johnston & Smith 2018); or (2) using
618 anthropogenic structures like docks (Cannizzo *et al.* 2018; Cannizzo & Griffen 2018; Cannizzo
619 & Griffen 2019; Cannizzo *et al.* 2019; Cannizzo *et al.* 2020). Anthropogenic structures such as
620 bridges and docks may also provide habitat for juvenile goliath grouper in the northern Gulf of
621 Mexico where adult spawning sites have been recently documented (Malinowski *et al.* 2019).

622 In addition to affecting the distribution and abundance of fish, mangrove expansion can
623 affect the recreational fishing experience in positive and negative ways. For example, along the
624 central Texas coast near San Jose Island, many anglers fly fish for redfish (*Sciaenops ocellatus*)

625 (Figure 4), but mangrove expansion has reduced the amount of viable fishing area. While fly
626 fishing is possible within the region's grass and succulent plant-dominated salt marshes, fly
627 fishing is not possible within dense meter-tall mangrove stands [Chuck Naiser, oral
628 communication, 26 May 2021]. However, on windy days, the same mangroves can have a
629 positive effect on the fishing experience by buffering winds (Guo *et al.* 2017), which can
630 improve boat control, water clarity, and the ability to sight cast [Billy Trimble, oral
631 communication, 24 May 2021]. Interestingly, by hindering airboat access into wetlands,
632 mangroves may also prevent damage to wetland vegetation and sediments, which has the
633 potential to reduce rates of erosion, hydrologic change, and wetland loss in areas with high boat
634 and angler concentrations [Billy Trimble and Chuck Naiser, oral communication, 24 and 26 May
635 2021].

636

637 **Avian communities**

638 What are the effects of mangrove expansion on avian communities? The response of migratory
639 and resident avifauna is arguably one of the least understood consequences of mangrove
640 expansion in the southeastern United States. However, these responses are likely to have a broad
641 range of consequences for ecosystem functions and services. Birds serve as vectors of
642 connectivity between coastal wetland habitats and adjacent systems, and are thus critical and
643 wide-ranging influencers of ecosystem connectivity, including fluxes of energy and nutrients
644 (Buelow & Sheaves 2015). Mangroves in the Gulf of Mexico are important habitat for foraging,
645 resting, nesting, and migrant avifauna (Burger 2017). However, many of these birds do not use
646 mangroves year-round, instead relying on a species-dependent matrix of mudflat, marsh, and
647 other coastal habitats during migration, nesting, and wintering. Therefore, the consequences of

648 mangrove expansion into salt marshes for birds could be substantial yet variable across taxa. The
649 following sections address known and hypothesized consequences of mangrove expansion for
650 four major taxonomic groups of coastal birds: wading birds, shorebirds, marsh birds, and
651 passerines.

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

661 Shorebirds comprise four major families (Scolopacidae, Charadriidae, Recurvirostridae,
662 Haematopodidae) and dozens of genera. These mostly small and often gregarious birds
663 frequently forage and roost in large groups within coastal estuaries. The northern Gulf of Mexico
664 is a particularly important part of the North American central migratory flyway (Withers 2002a).
665 Although some shorebirds will use mangrove shrubs for nesting or roosting (Zwarts 1988),
666 mangroves produce extensive aerial root complexes that may reduce the accessibility of tidal
667 flats or ponds, which are the preferred foraging habitat for many shorebird species (Withers
668 2002a; Darnell & Smith 2004). In addition, dense mangrove stands may conceal and attract
669 predators, and nonbreeding shorebirds will actively avoid areas with mangroves in favor of salt
670 marshes, tidal flats, and other coastal habitats (Straw & Saintilan 2006; Kelleway *et al.* 2017;

671 Vitale *et al.* 2021). For example, optimal high-tide shorebird roosts were located far from woody
672 vegetation at a critical wintering and migratory stopover site in Florida's Big Bend (Brush *et al.*
673 2017). There could be survival and energy costs associated with antipredator behaviors and
674 increased predation if alternative roosting and foraging habitats are not available (e.g., due to
675 human disturbance or habitat loss) (Rogers *et al.* 2006). Because shorebirds are relatively long-
676 lived, their populations are greatly affected by small changes to demographic parameters, such as
677 adult mortality (Colwell 2010). One study concluded that mangrove expansion into roosting
678 habitats likely contributed to local declines of wintering shorebird populations and biodiversity
679 (Woodley 2004). Accordingly, surveys of wintering shorebirds on the Texas coast revealed that
680 diversity and relative abundance are higher in marshes than at sites with high mangrove cover
681 (Whitt 2016; Armitage *et al.* 2021).

682 Marsh birds are coastal marsh-dependent and live at the ecotone between aquatic and
683 terrestrial ecosystems. These often cryptic colored and elusive species include members from the
684 families Rallidae, Troglodytidae, and Passerellidae. Marsh habitat loss, regardless of
685 environmental or anthropogenic drivers, can have detrimental impacts on marsh-dependent
686 species. For example, nearly 50% of marsh birds found in the northern Gulf of Mexico are of
687 conservation concern primarily due to loss of wetland habitats (Woodrey *et al.* 2019). Species
688 that are dependent on graminoid marsh plants [e.g., seaside sparrows (*Ammospiza maritima*) or
689 marsh wrens (*Cistothorus palustris*)] are unlikely to utilize mangrove-encroached wetlands
690 (Schwarzer *et al.* 2020). There could be direct or indirect impacts of mangrove expansion into
691 high marsh habitats that are critical for the eastern black rail (*Laterallus jamaicensis*) (Watts
692 2016). More information is also needed to understand the migratory ecology of marsh bird

693 species to determine potential impacts of mangrove expansion in different parts of their
694 geographic range.

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

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

715 For some coastal parks and refuges, coastal resource managers' perspectives on
716 mangrove expansion can be heavily influenced by their organizations' local avian priorities. For
717 example, on Louisiana's barrier islands, dense mangrove stands provide valuable habitat for
718 nesting colonies of brown pelicans (*Pelecanus occidentalis*) (Figure 4), which is the state bird
719 and a species with a rich conservation history. Following pesticide-driven extirpation and
720 reintroduction in the 1960s, brown pelican populations have rebounded to the extent that they
721 were removed from the endangered species list in 2009 (Walter *et al.* 2013a). Nevertheless,
722 barrier island habitat losses in Louisiana have been very high (Martinez *et al.* 2009), and pelican
723 nesting habitat has become a priority during recent coastal restoration efforts. Pelicans prefer to
724 place nests on mangroves, which provide strong nesting platforms that are tall enough to avoid
725 flooding during island overwash events (Hintgen *et al.* 1985; Visser *et al.* 2005; Walter *et al.*
726 2013b). Thus, mangrove expansion and growth on these islands is viewed as a positive change
727 for pelicans, and therefore is sometimes facilitated during barrier island restoration efforts [Darin
728 Lee (Louisiana Coastal Protection and Restoration Authority), oral communication, 21 May
729 2021].

730 Another example of how avian habitat priorities can affect local perspectives on
731 mangrove expansion can be found in the Aransas National Wildlife Refuge (ANWR) in Texas.
732 The salt marshes within and near ANWR provide critical wintering grounds for the rare and
733 endangered whooping crane (*Grus americana*). Whooping crane populations declined during the
734 late 19th and early 20th century to the point where less than 25 individuals remained in the early
735 1940s (Allen 1952; Erickson & Derrickson 1981). The only self-sustaining population that
736 persists today is the Aransas-Wood Buffalo population, which winters in coastal Texas in the
737 ANWR region and migrates to its summer breeding grounds in north-central Canada. During the

738 winter of 2019-2020, the Aransas-Wood Buffalo population was estimated to contain just 506
739 individuals (Butler *et al.* 2020). While wintering in coastal Texas, whooping cranes forage within
740 salt marshes for blue crabs (*C. sapidus*), wolfberries (*Lycium carolinianum*), and other foods
741 (Hunt & Slack 1989; Chavez-Ramirez 1996). However, the ANWR region is a recent hotspot for
742 mangrove expansion in Texas (Armitage *et al.* 2015; Brown *et al.* 2016), and there is concern
743 that mangrove replacement of salt marsh will negatively affect the habitat and food resources
744 available for whooping cranes (Stehn & Prieto 2010; Chavez-Ramirez & Wehtje 2012). Blue
745 crabs are an especially important food source for cranes (Hunt & Slack 1989; Chavez-Ramirez
746 1996), and blue crab abundance may have a positive relationship with whooping crane survival
747 (Pugesek *et al.* 2013). Thus, mangrove expansion effects on blue crabs and other foods are a
748 concern. Several studies have indicated that blue crab abundance may decrease with mangrove
749 expansion (Johnston & Caretti 2017; Smee *et al.* 2017; Glazner *et al.* 2020). For coastal
750 managers at ANWR, maintaining the region's whooping crane population is a high priority;
751 however, managers are concerned that continued mangrove expansion could have a negative
752 impact [Andrew Stetter and Colt Sanspree (U.S. Fish and Wildlife Service), oral communication,
753 30 March 2021]. In addition to research that better characterizes the effects of mangrove
754 expansion on whooping cranes, coastal managers in the ANWR region are interested in
755 management strategies for limiting mangrove expansion into the salt marshes used by whooping
756 cranes [Andrew Stetter and Colt Sanspree (U.S. Fish and Wildlife Service), oral communication,
757 30 March 2021].

758

759 **Insects, other terrestrial arthropods, and mangrove honey**

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

771 In areas that historically supported salt marsh plants, expansion of mangroves with
772 nectar-producing flowers (Nathan 2020) may provide a novel kind of honey for beekeepers along
773 northern coastal reaches of the southeastern United States. Along many tropical coastlines,
774 mangrove forests are popular honey-producing areas for beekeepers and honey hunters
775 (Bradbear 2009). In Florida, which is one of the largest honey-producing states of the United
776 States, mangroves are a popular source of nectar for honey production (Sanford 2016). For this
777 reason, in some of the scientific literature and in herbarium records from the early 20th century,
778 the common name used for *A. germinans* was honey mangrove (e.g., Penfound & Hathaway
779 1938). Currently, mangrove honey in the southeastern United States is produced primarily along
780 the southern and central coasts of Florida. However, as mangroves expand further north, there is
781 the potential for mangrove honey to be produced along Florida's northern coasts. For example, in
782 the Apalachicola region, where freshwater swamps have historically supported tupelo honey-

783 specialty businesses for more than a century, the recent expansion of mangroves on the region's
784 barrier island ecosystems (Snyder *et al.* 2021) has prompted interest to also produce mangrove
785 honey [George Watkins, oral communication, 24 May 2021].

786

787

788 **Recreation**

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

798 Similar to other ecosystem services, mangrove expansion in marshes is likely to have
799 variable and site-specific impacts on recreation (Kelleway *et al.* 2017). For instance, shifting
800 assemblages of birds may impact, either positively or negatively, recreational demand and
801 satisfaction among bird watchers (Whitt 2016; Armitage *et al.* 2021). Likewise, the same
802 scenario would apply to recreational fishers if expanding mangroves support different fish
803 communities than salt marshes. These impacts are likely to be greatest among highly specialized
804 recreational users who may value specific places or prioritize certain species that could become
805 more or less common (Oh *et al.* 2013). The expansion of mangroves may also impact water

806 access and viewsapes (Kaplowitz 2001; Harty 2009; Lundquist *et al.* 2014; see also coastal food
807 webs and fisheries section). Both mangroves and marshes are appreciated for their aesthetic or
808 scenic values (Kaplowitz 2001), but water access is more difficult in areas with dense mangrove
809 forests. In general, recreation-related attitudes, preferences, and behaviors represent a major gap
810 in the literature on mangrove ecosystem services, especially within the context of mangrove
811 expansion into salt marshes.

812 Where mangrove expansion is occurring near residential areas, mangrove replacement of
813 marsh can have striking effects on residents' recreational activities and interactions with their
814 coast (Harty 2009; Lundquist *et al.* 2014). For example, in the 1990s following the major freeze
815 events of the 1980s, many residents in the Cedar Key area of Florida had wide-ranging views
816 that looked out onto expansive wetlands dominated by salt marsh grasses (Stevens *et al.* 2006).
817 However, expanding mangrove forests have grown to heights greater than 6 m (Yando *et al.*
818 2016), which is tall enough to block valuable landscape views of the salt marsh [Andrew Gude
819 (U.S. Fish and Wildlife Service) and Michael Allen (University of Florida), oral communication,
820 19 May 2021]. Despite the potential gains in coastal protection supported by mangrove
821 expansion (Doughty *et al.* 2017; Hijuelos *et al.* 2019; Pennings *et al.* 2021), the loss of salt
822 marsh views is a critical and overarching concern for many Cedar Key residents, and some
823 residents are interested in managing the expanding mangrove forests to regain the previously
824 present salt marsh views and access [Andrew Gude (U.S. Fish and Wildlife Service) and Michael
825 Allen (University of Florida), oral communication, 19 May 2021]. Further, by reducing wind
826 speeds, the mangrove forests can also increase the number of mosquitos and other nuisance
827 insects near residences [Andrew Gude (U.S. Fish and Wildlife Service) and Michael Allen
828 (University of Florida), oral communication, 19 May 2021]. Conversely, from a practical

829 landscape maintenance perspective, mangrove expansion can reduce the amount of storm debris
830 (i.e., marsh wrack) that is transported and deposited onto waterfront properties [Andrew Gude
831 (U.S. Fish and Wildlife Service) and Michael Allen (University of Florida), oral communication,
832 19 May 2021]. Thus, mangroves can be viewed as both positive (shoreline protection) and
833 negative (impeding ocean views and thus reducing property values) by local homeowners.

834

835 **Knowledge gaps and emerging research needs**

836 The majority of research regarding the effects of mangrove expansion has focused on coastal
837 food webs and fisheries (Figure 1e; 31 papers) and carbon sequestration (Figure 1a; 27 papers).
838 Less research has examined soil elevation dynamics (Figure 1b; 12 papers), water quality and
839 nutrient cycling (Figure 1c; 12 papers), avian communities (Figure 1f; 9 papers), coastal
840 protection (Figure 1d; 4 papers), recreation (Figure 1h; 4 papers), and insects and terrestrial
841 arthropods (Figure 1g; 2 papers). Within the ecosystem service-focused sections of this review,
842 we have identified knowledge gaps and emerging research needs. In Table 3, we summarize this
843 information to: (1) rank the level of knowledge regarding the impacts of mangrove expansion on
844 specific ecosystem services; and (2) summarize the most critical knowledge gaps and research
845 needs.

846

847 **Interactions with other aspects of climate change**

848 Our review focuses primarily on the ecological effects of mangrove expansion driven by
849 warming winter temperatures. However, coastal wetlands in the southeastern United States are
850 vulnerable to many different aspects of climate change. In addition to warming winter
851 temperatures, coastal wetlands in the region are affected by rising sea levels, saltwater intrusion,

852 and changes in the frequency and intensity of extreme climatic events (USGCRP 2017; Carter *et*
853 *al.* 2018; Osland *et al.* 2018a). For example, rising sea levels can lead to wetland conversion to
854 open water (Couvillion *et al.* 2017; Saintilan *et al.* 2020; Törnqvist *et al.* 2020) and the landward
855 migration of wetlands (Enwright *et al.* 2016; Borchert *et al.* 2018). Landscape-scale wetland
856 vegetation dieback events can be triggered by extreme drought (Alber *et al.* 2008; Duke *et al.*
857 2017; Lovelock *et al.* 2017; Sippo *et al.* 2018), flooding (Stagg *et al.* 2021), hurricanes (Cahoon
858 *et al.* 2003; Osland *et al.* 2020c), and freeze events (Osland *et al.* 2017a). Macroclimate drivers
859 govern foundation plant communities in the region, which means that changing temperature and
860 precipitation regimes can transform coastal wetlands (Gabler *et al.* 2017; Osland *et al.* 2019a).
861 Climate change is also expected to increase the frequency of major hurricanes, which affects the
862 dispersal of mangroves beyond current range limits (Kennedy *et al.* 2016; Van der Stocken *et al.*
863 2019a; Kennedy *et al.* 2020). Collectively, these examples show that mangrove range expansion
864 dynamics will be greatly influenced by interactions between many different aspects of climate
865 change.

866

867 **Conclusions**

868 In the past two decades, there has been a rapid increase in the number of studies investigating the
869 effects of mangrove range expansion on ecosystem goods and services in the southeastern United
870 States (Figure 1). This review synthesizes that information with an emphasis on impacts to
871 carbon sequestration, wildlife habitat, storm protection, erosion prevention, water purification,
872 fisheries support, and recreation. One consistent theme throughout this work is that there are
873 ecological trade-offs for consideration by coastal scientists and natural resource managers (e.g.,
874 Table 2; Figure 4). Mangrove expansion and marsh displacement can produce beneficial changes

875 in some ecosystem services, while producing detrimental changes in other services. As a result,
876 there is much variation in opinions regarding the social and ecological consequences of
877 mangrove expansion. For the same location, some individuals may view mangrove expansion as
878 a positive transformation to be fostered, while others may see it as a negative change to be
879 prevented. Such variation in perceptions and impacts highlights the benefits of careful planning
880 and discussion preceding management efforts (e.g., mangrove planting or removal) that could
881 accelerate or constrain the pace of mangrove expansion.

882

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893

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- 1633
- 1634

1635 Table 1. Mangrove forests and salt marshes are both frequently ranked among the most valuable
 1636 ecosystems on the planet (Costanza et al. 2014). There are many similarities in the ecosystem
 1637 goods and services provided by these tree- and grass-dominated coastal wetlands. The left
 1638 column shows broad ecosystem service categories supported by mangrove forests and salt
 1639 marshes (partially adapted from Barbier et al. 2011), and the right column provides more specific
 1640 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

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1642

1643 Table 2. Mangrove expansion can produce beneficial changes in some ecosystem services while
 1644 producing detrimental changes in other ecosystem services. Cedar Key (Florida) and Aransas
 1645 (Texas) are two prominent areas where such trade-offs are observed. The table below shows
 1646 some of the positive and negative changes associated with mangrove expansion in these two
 1647 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

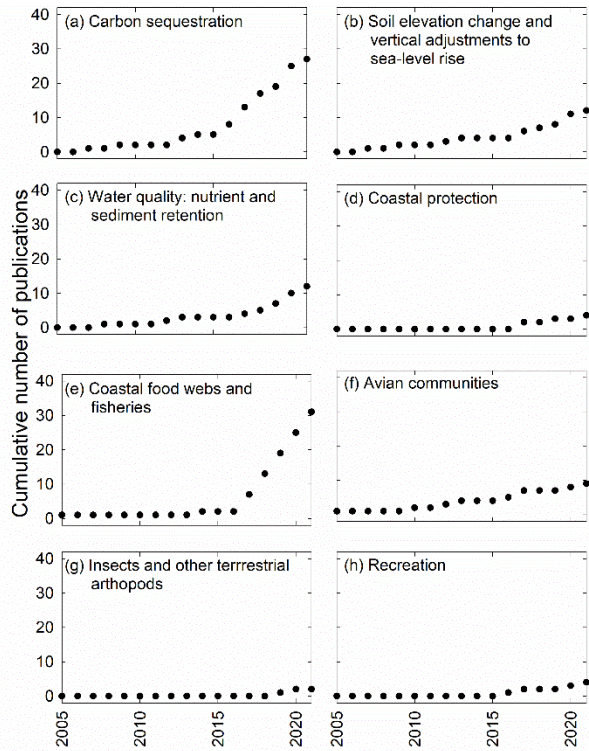
1648

1649 Table 3. Level of knowledge and critical research gaps regarding the impacts of mangrove expansion on ecosystem goods and
 1650 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)?
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?
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, shore birds, 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	Can mangrove expansion provide a novel kind of honey for beekeepers? How does mangrove expansion affect terrestrial arthropod communities?
Recreation	Poorly understood	How does mangrove expansion affect recreation and tourism through changes in water access, viewscales, birdwatching, and fishing?

1651

1652 Figure 1. The cumulative number of publications investigating the effects of mangrove
 1653 expansion in the southeastern United States on (a) carbon sequestration; (b) soil elevation change
 1654 and vertical adjustment to sea-level rise; (c) water quality, specifically nutrient and sediment
 1655 retention; (d) coastal protection; (e) coastal food webs and fisheries; (f) avian communities; (g)
 1656 insects and other terrestrial arthropods; and (h) recreation.



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1660 Figure 2. Map showing the distribution of mangroves in the southeastern United States.

1661 Mangrove expansion hotspots in Texas, Louisiana, and north Florida are shown with the four

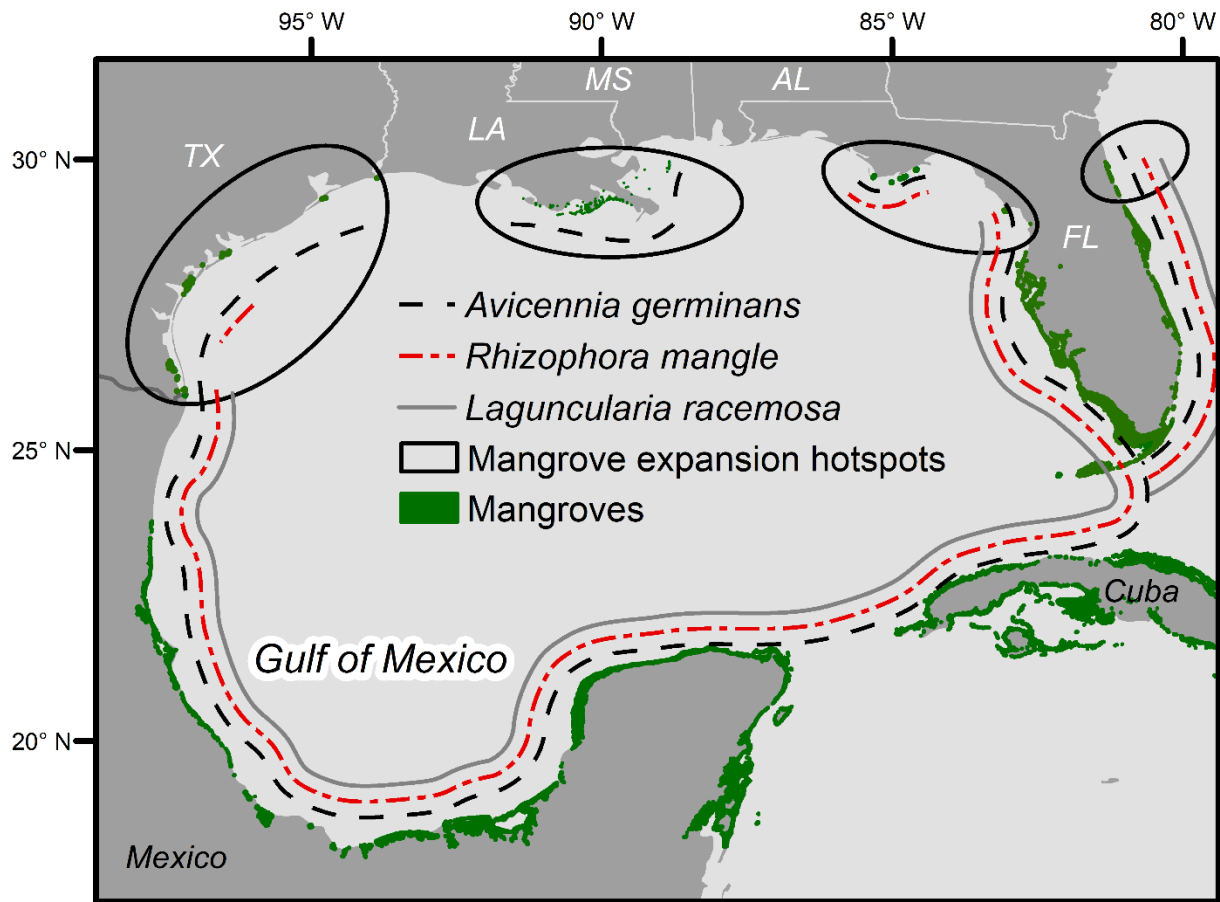
1662 black ovals. Mangrove species' poleward range limits are shown with the black, red, and grey

1663 lines. Mangrove distribution data are from: (1) Mexico: CONABIO (2016); (2) Cuba: Giri et al.

1664 (2011); (3) south and central Florida: FDEP (2016); (4) northwestern Florida: Snyder et al.

1665 (2021); (5) Louisiana: Day et al. (2020); (6) Texas: Sherrod and McMillan (1981) and Armitage

1666 et al. (2015). Map updated and adapted from Osland et al. 2018.



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1668

1669 Figure 3. The effects of mangrove expansion on ecosystem goods and services are highly
1670 dependent upon the structure and composition of: (1) the expanding mangrove forests; and (2)
1671 the salt marsh that is being replaced. These photos illustrate some of the variation in marsh and
1672 mangrove plant communities near mangrove range limits in the southeastern United States.
1673 Upper photo: A mangrove-marsh ecotone in north Florida (near Cedar Key), which contains
1674 highly productive grass- and succulent plant-dominated marshes and comparatively tall (>6 m
1675 height) mangrove plants. Lower photo: A mangrove-marsh ecotone in south Texas (within
1676 Laguna Atascosa National Wildlife Refuge), which contains less productive succulent plant-
1677 dominated marshes, comparatively short (< 2 m height) mangrove plants, and hypersaline salt
1678 flats that lack vascular plants. Photo credits: Michael Osland



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1681 Figure 4. Across the southeastern United States, there is considerable variation in perceptions of
1682 the ecological and societal impacts of mangrove expansion into salt marsh. For very specific
1683 local reasons, some individuals may see mangrove expansion as a positive change to be
1684 embraced, while others may see mangrove expansion as a negative change to be constrained.
1685 These two photos provide an example of a negative and positive impact of mangrove expansion
1686 and salt marsh displacement. Left photo (negative impact): Along Texas' central coast,
1687 mangrove expansion reduces viable fishing areas. While fly fishing is possible within the
1688 region's grass and succulent plant-dominated salt marshes, fly fishing for redfish (*Sciaenops*
1689 *ocellatus*) is not possible within dense meter-tall mangrove stands. Right photo (positive impact):
1690 On Louisiana's barrier islands, expanding mangroves provide valuable habitat for brown
1691 pelicans (*Pelecanus occidentalis*). Photo credits: Chuck Naiser (left photo) and Louisiana
1692 Coastal Protection and Restoration Authority (right photo).
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