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American alligators (*Alligator mississippiensis*) as wetland ecosystem carbon stock regulators

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Blue carbon refers to organic carbon sequestered by oceanic and coastal ecosystems. This stock has gained global attention as a high organic carbon repository relative to other ecosystems. Within blue carbon ecosystems, tidally influenced wetlands alone store a disproportionately higher amount of organic carbon than other blue carbon systems. North America harbors 42% of tidally influenced global wetland area, which has been identified as a critical carbon stock in the context of climate change mitigation. However, quantified associations between vertebrate biota and carbon sequestration within ecosystems are in their infancy and have been incidental, given that microbial trophic levels are thought to drive nutrient dynamics. Here, we assess the relationship between American alligator (*Alligator mississippiensis*) demography and tidally influenced wetland soil carbon stock among habitats at continental, biogeographically-relevant, and local scales. We used soil core profile data from the Smithsonian's Coastal Carbon Network and filtered for continuous core profiles in tidally influenced wetland areas along the Gulf and Atlantic Coasts of the United States. Results indicate that American alligator presence is positively correlated with soil carbon stock across habitats within their native distribution. Further, American alligator demographic variables are positively correlated with soil carbon stock at local scales. These conclusions are concordant with previous findings that apex predators, through trophic cascade theory, play a key role in regulating soil carbon stock and that alligators are functional apex predators in carbon dynamics and a key commercialized natural resource.

Keywords Carbon sequestration, Apex predator, Blue carbon, American alligator

A comprehensive understanding of carbon dynamics paired with rapid and effective climate change mitigation will define the Anthropocene and present modern people's most prominent global challenge. The importance of ecosystem-scale carbon dynamics cannot be understated as a means to open potential agroecological mitigation strategies for global climate change[1]. *Blue carbon*, or organic carbon sequestered by oceanic and coastal ecosystems, has gained global attention as a disproportionately high organic carbon repository relative to other ecosystems[2]. Within *blue carbon* ecosystems, tidally influenced fresh water and low-salinity wetlands alone store a disproportionately higher amount of organic carbon than other *blue carbon* systems, despite their relatively minimal spatial extent around the globe[3]. North America harbors 42% of tidally-influenced global wetlands, which have been identified as a critical carbon stock[4]. Factors influencing tidal wetland carbon include canopy cover (including associated leaf litterfall), salinity, nitrogen and phosphorus accumulation and mineralization, and inundation frequency and depth[5]. However, larger biotic residents have yet to be seriously evaluated for their functional role in influencing carbon flux and the overall biogeochemical dynamics, as top predators may exert a cascading effect that extends beyond their prey, influencing ecosystem nutrient dynamics on a variety of spatial scales[6]. Overlooking this relationship could lead to underestimating the crucial role apex predators play in the ecosystems they inhabit, particularly considering the significance of nutrient cycling as an invaluable ecosystem service.

The understanding of relationships between vertebrate biota and carbon storage within ecosystems is in its infancy and, when quantified, have been incidental, as microbial trophic levels are thought to drive nutrient dynamics[7]. Mechanistically, vertebrates may impact ecosystem carbon storage trophically. Recent research in terrestrial systems has suggested that apex predator presence may causally and positively influence mean soil carbon stocks using a large-scale exclusion design[7]. Similar trends were described between the presence of brown bear (*Ursus arctos*), a key mammalian apex predator, and a corresponding increase in soil nitrogen and N_2O flux[8,9], thus generating further discussion of predator driven nutrient vectors and hotspots in riparian

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and terrestrial systems. Additionally, the idea of predator-mediated herbivore control and increased carbon storage has also been replicated in *blue carbon* systems. Atwood et al. [10,11] observed increased organic carbon sequestration in three strongly predator-mediated coastal marine systems compared to low-predation habitats—a result corroborated in kelp forests with marine mammal predators[10–12].

Tidally influenced *blue carbon* ecosystems are theorized here to be trophically regulated by the apex predator, American alligator (*Alligator mississippiensis*), throughout their native coastal distribution from North Carolina to southern Texas[13,14] in the Southeast United States. Alligator populations have recovered from near extinction across the United States since legislation limited recreational harvest and generated a sustainable, population-dependent industry for meat and hide in 1967[15,16]. Alligators have also been considered ecosystem engineers, either directly modifying hydrology[17,18] or indirectly modifying nutrient distribution through mechanical action[19,20]. The modulation of resource availability via physical state change (i.e., ecosystem engineer[21]) is a definition only met by alligators in a unique and small portion of their distribution. Evidence of alligator influence on biotic and abiotic physical state change throughout their entire range remains to be seen.

Here, we assess the relationship between American alligator demography and tidally-influenced wetland soil carbon stock among habitats at continental (Eastern United States), bio-geographically relevant (alligator native range [i.e., distribution]), and local (State of Louisiana) scales. We used soil core profile data from the Smithsonian's Coastal Carbon Network and filtered for continuous core profiles in tidally influenced wetland areas along the Gulf and Atlantic Coasts of the United States. We hypothesize that American alligator presence is positively associated with soil carbon stock both continentally and within the distribution of the species among habitats. Further, we hypothesize that American alligator demographic variables are positively associated with soil carbon stock at local scales. These hypotheses are consistent with existing evidence that apex predators regulate soil carbon stock via the mechanism of trophic cascade. However, in this research we novelly apply mechanistic theory to large reptiles in tidally-inundated wetland systems across spatial scales and habitats.

Methods

Carbon data

We used the Smithsonian Coastal Carbon Network (https://serc.si.edu/coastalCarbon), a global soil core data repository, to assemble carbon core data[22]. In November 2023, we downloaded a total of 3,445 tidally influenced wetland cores collected between 1994 and 2019 and published between 2011 and 2022. We removed incomplete cores (no location, associated habitat, or the parameters required to calculate carbon storage as described below), marine cores, and cores < 10 cm in length, providing 649 usable soil cores from 13 states (Fig. 1; Appendix 1). For complete cores, we used dry bulk density (dry mass per cm^2 of a soil sample) and the fraction of carbon (dimensionless carbon mass relative to sample dry mass) from the Coastal Carbon Network to calculate carbon storage (CC_A) for each cm^2 of soil within each core, following Hillman et al.[23]:

$$CC_A = (Z_A) \ * \ (BD_A) \ * \ (C_{SOIL\,A} \ / \ 100) \tag{1}$$

in which A is the depth interval, CC represents grams of carbon per square centimeter (g/cm^2; Carbon Content), Z indicates slice thickness (max–min depth; cm), BD is dry bulk density, and C_{SOIL} is the fraction of carbon[23]. Of the 26,204 available core sections, 17,873 lacked parameters to calculate CC_A in Eq. (1), leaving 8,331 to be analyzed.

Alligator data

We acquired alligator presence/absence (i.e., detection/non-detection) data from the following state resources: North Carolina[24], South Carolina[25], Georgia[13,26], Florida (A. Woodward, Florida Fish and Wildlife Conservation Commission; unpublished), Louisiana, and Texas (C. M. Murray; unpublished). For the Louisiana regional assessment, the Alligator Program director of Louisiana, J. Linscombe, provided nest data (hectares per nest; the number of hectares flown in an ariel survey between transect nest sightings) and estimated alligator density[27,28]. We assigned data for hectares per nest and alligator density to individual cores by overlaying the geographic coordinates of the cores on the parish transect section and habitat type in the alligator data. Our statistical evaluation then accounted for clustered cores.

Statistical analyses

We analyzed data and created figures using Posit and R[29]. Before analyzing the data, we removed outliers that fell outside the 99th percentile that were median-unbiased regardless of distribution in the carbon storage data (more conservative than the Type 8 quantile algorithm[30,31]), as only four data points were subjectively higher than the others and omitted. We selected the best-fit distribution to the data for each model using the *fitdistrplus* package[32]. We used the *glmmTMB* package[33] to fit all mixed-effects models. All other models were fit using the *stats* package[29]. After fitting each model, we ensured the residuals were normally distributed and compared the predicted beta estimates with the raw data means to assess model fit. Specifically for the mixed-effects models, we assessed fit and validated parameter estimates using non-parametric bootstrapping—a robust alternative to traditional parametric tests like F-tests. We determined statistical significance using an alpha value of 0.05.

We first used all available carbon storage data (continental) for analyses (Fig. 1). Then, we focused on carbon storage data from states within the biogeographic range of alligators—North Carolina, South Carolina, Georgia, Florida, Louisiana, and Texas. Sample size limitations prevented us from using an interactive effect representing states that fall within and outside of the alligator native range in our mixed-effects models, which is why we used separate datasets (i.e., continental and native range) to investigate our hypotheses. For each of the datasets, we investigated carbon storage in two ways: (1) carbon summation of the top 10 cm in the core sample, referred to hereafter as *top-10 carbon*, which reflects the approximate time since alligators were listed as endangered (~ 60

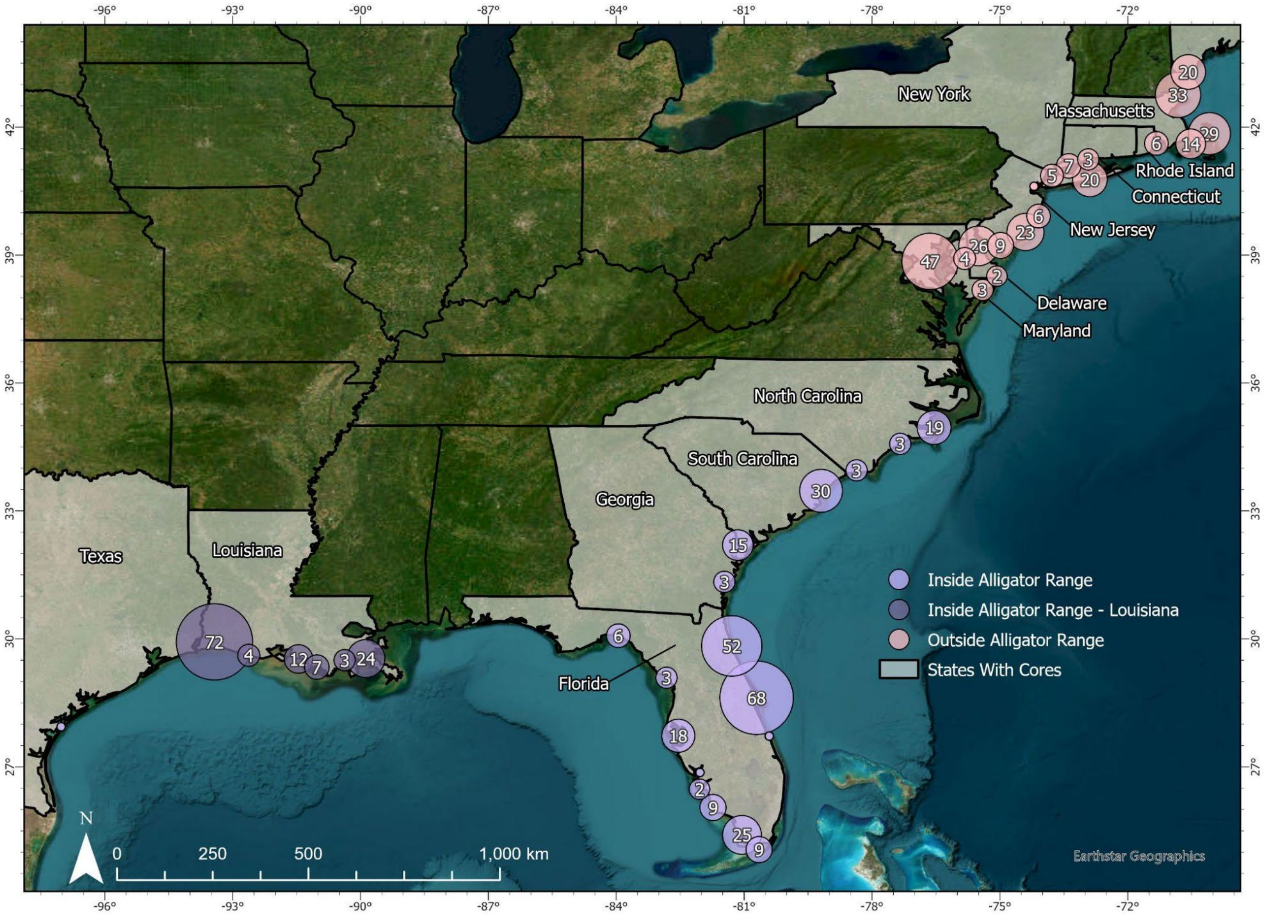

Fig. 1. A bubble plot map—where each bubble represents a sample—of the Coastal Carbon Network soil cores used for the continental analysis of tidally-influenced blue carbon. *Pink* bubbles are cores outside of the alligator distribution, which ranges along the coast from northern North Carolina to southern Texas[13,14]. *Lavender* bubbles represent cores within the alligator distribution. *Dark purple* bubbles represent regional cores within Louisiana. The size of the bubble increases with the number of cores in the study area. We made the map in ArcGIS Pro version 3.4[51]—main map satellite imagery is the World Imagery basemap within ArcGIS Pro version 3.4 software (http://www.esri.com/data/basemaps), see Service Layer Credits.

years, though dates are variable; data obtained from the Coastal Carbon Network [see Appendix 1, 2]) and (2) carbon per cm of the entire core sample by averaging carbon content across all sections within a core, referred to hereafter as *total carbon*.

Continental The first two models we fit were generalized linear mixed-effects models with a Gaussian sampling distribution for the two types of carbon storage data. Each model included alligator presence or absence (binary categorical variable) as a fixed effect and random effects of habitat type and site. The habitat type random effect allowed the model to account for variation in carbon storage based on habitat characteristics and site accounted for spatial variation in carbon storage (sacrificial pseudoreplication).

Due to sample size limitations within habitats, we could not include an interactive effect in the original model to allow each habitat type to have a slope (i.e., effect size estimate). Therefore, to observe within-habitat effects of alligator presence on carbon storage, we fit generalized linear mixed-effects models with a Gaussian sampling distribution to the two types of carbon storage data for each habitat type that had enough data for comparisons—mangrove, marsh, scrub-shrub, and swamp. Each model included alligator presence or absence as a fixed effect and site as a random effect.

Alligator Biogeographic Range Using only the data included in the alligator native range, we first fit a generalized linear mixed-effects model with a Gaussian sampling distribution to analyze the effect of alligator presence on *top-10 carbon*, including the fixed effect of alligator presence and random effects of habitat type and site, like above. However, when assessing *total carbon*, we could not include random effects of habitat type and site due to the small sample size of alligator absent data. Therefore, we fit a generalized linear model with a Gaussian sampling distribution to examine the effect of alligator presence on *total carbon*.

We investigated within-habitat effects of alligator presence on both measurements of carbon storage using generalized linear models for mangrove and scrub-shrub, the only two habitats with enough data for successful

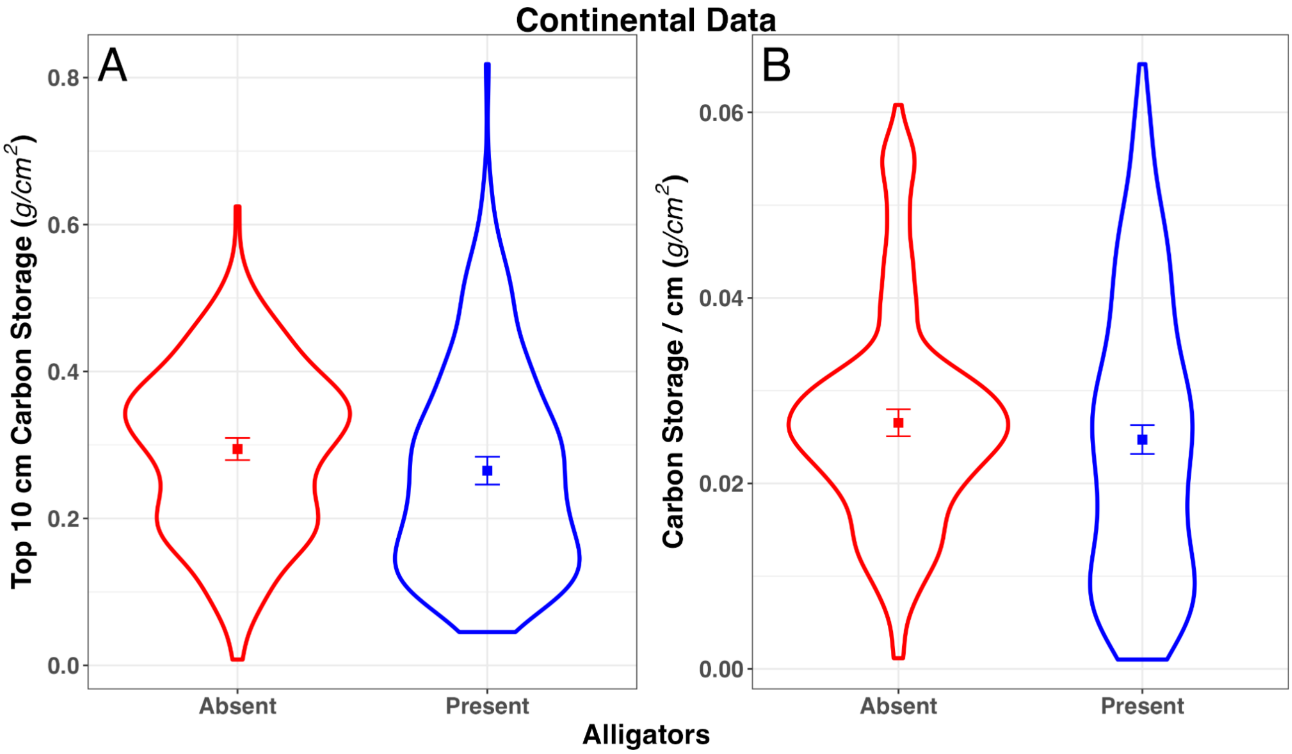

Fig. 2. Violin plots of the summed top 10 cm of carbon storage in the core sample (A) and the carbon storage per cm of the entire core sample (B) data when alligators were absent (red) and present (blue) in the continental dataset. The square and error bars represent the data's mean and 95% confidence intervals.

Habitat	Effect size	SE	*p*-value
Mangrove	0.20	0.073	0.0071
Marsh	– 0.012	0.026	0.64
Scrub shrub	– 0.058	0.066	0.38
Swamp	0.081	0.072	0.26

Table 1. Effect size estimates and the corresponding standard error (SE) and p-values for the models that analyzed carbon summation of the top 10 cm in the core sample dependent on alligator presence or absence and included site as a random effect. Each row represents a specific habitat and how different (i.e., effect size) the carbon storage was when alligators were absent versus present. A positive effect size estimate shows that carbon storage was that value greater when alligators were absent than when they were present.

model convergence. We used a Gaussian sampling distribution and the fixed effect of alligator presence in these four models (two models for each carbon measurement).

Regional: Louisiana Using only Louisiana data, we observed the effects of alligator density (calculation described above) and then the number of hectares per alligator nest on top-10 and *total carbon*. We used a generalized linear mixed-effects model with a Gaussian sampling distribution for all four models, with site included as the random effect in each.

Results

Continental

We observed no significant effect of alligator presence on *top-10 carbon* ($Z_{90,428}$ = 0.21; $p = 0.84$), where carbon storage in the absence of alligators was an insignificant 0.0050 g/cm^2 (± 0.047; 95% CI) greater than when alligators were present (Fig. 2A). Similarly, alligator presence did not affect *total carbon* ($Z_{102,612}$ = – 0.34; $p = 0.73$; Fig. 2B). *Total carbon* was an insignificant 0.00080 g/cm^2 (± 0.0045; 95% CI) greater when alligators were present than when absent (Fig. 2B). We found that *top-10 carbon* was significantly affected by the presence of alligators in the mangrove habitat type ($Z_{11,49}$ = 2.694; $p = 0.0071$), such that carbon storage was 0.20 g/cm^2 (± 0.14; 95% CI) greater when alligators were present versus absent (Table 1; Fig. 3). However, alligator presence did not significantly influence *top-10 carbon* of marsh ($Z_{66,341}$ = – 0.47; $p = 0.64$), scrub-shrub ($Z_{2,6}$ = – 0.88; $p = 0.38$), or swamp ($Z_{6,17}$ = 1.13; $p = 0.26$) habitat types (Table 1; Fig. 3). As for *total carbon* in the same four habitat types,

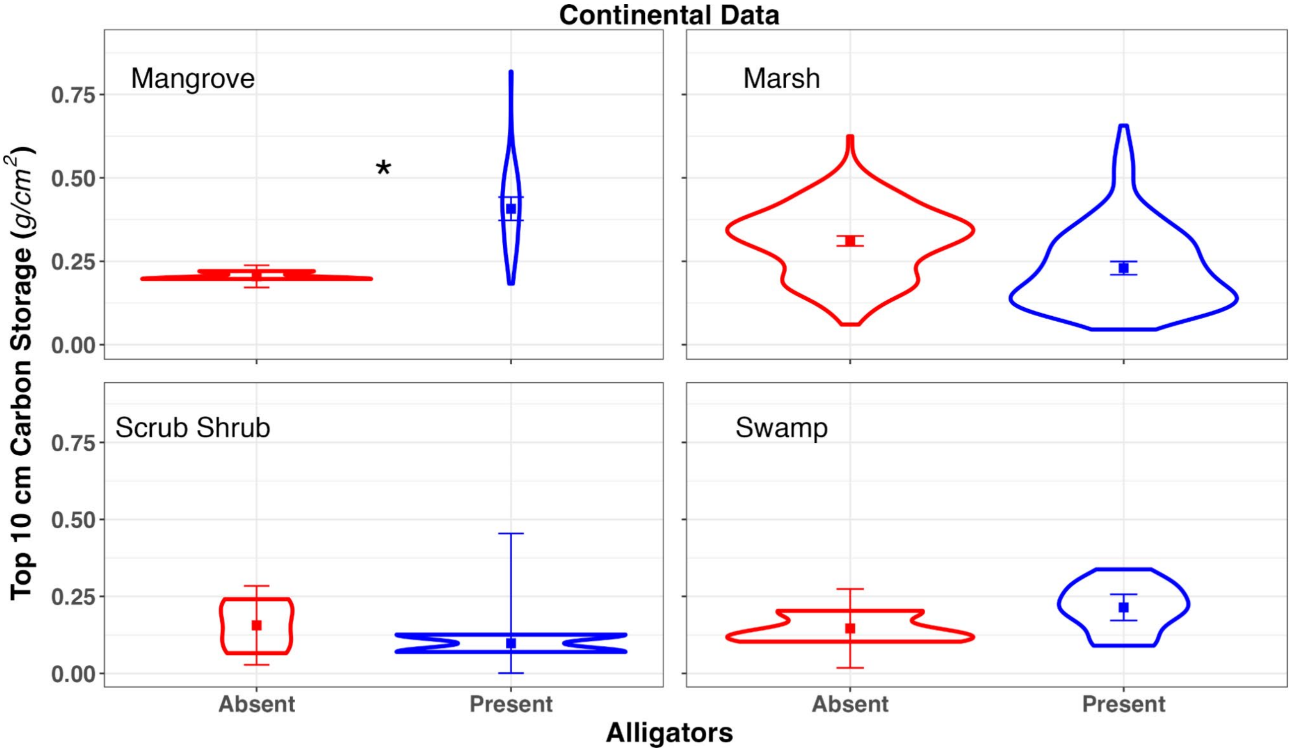

Fig. 3. Violin plots of the summed carbon storage in the top 10 cm of the core sample data in four unique habitats (mangrove, marsh, scrub shrub, and swamp) when alligators were absent (red) and present (blue) in all states. We needed to obtain more data from the other three habitats for comparison. A star represents a statistically significant effect of alligator presence on carbon storage (see Table 1 for exact values).

we did not detect an effect of alligator presence on carbon storage (mangrove [$Z_{15,74}$ = – 0.51; $p=0.61$], marsh [$Z_{75,438}$ = 0.59; $p=0.55$], scrub-shrub [$Z_{5,32}$ = -0.013; $p=0.99$], or swamp [$Z_{7,47}$ = – 0.12; $p=0.90$]; Fig. 4).

Alligator native range

In the alligator native range dataset, we found that *top-10 carbon* was significantly 0.16 g/cm² (± 0.13; 95% CI) greater when alligators were present compared to when they were absent ($Z_{56,219}$ = 2.50; $p=0.013$; Fig. 5A). However, alligator presence did not affect *total carbon* ($F_{1,380}$ = 0.0036; $p=0.95$; Fig. 5B). In the mangrove habitat, we detected that *top-10 carbon* was significantly 0.21 g/cm² (± 0.14; 95% CI) greater when alligators were present compared to absent ($F_{1,48}$ = 8.44; $p=0.0055$; Fig. 6). *Top-10 carbon* was not significantly affected by alligator presence in the scrub-shrub habitat ($F_{1,3}$ = 0.049; $p=0.85$; Fig. 6). Alligator presence did not significantly affect *total carbon*, regardless of habitat (mangrove: $F_{1,72}$ = 0.043, $p=0.84$; scrub-shrub: $F_{1,30}$ = 0.027, $p=0.87$; Fig. 7).

Regional: Louisiana

We detected a significant effect of alligator density on *top-10 carbon* ($Z_{16,97}$ = 5.67; $p<0.005$), where carbon increased by 0.012 g/cm² (± 0.0040; 95% CI) for each 10,000 alligator increase in density (Fig. 8). We also observed a significant effect of hectares per nest on *top-10 carbon* ($Z_{16,97}$ = – 6.93; $p<0.005$), where carbon decreased by 0.050 g/cm² (± 0.014; 95% CI) for each increase of 100 hectares between nests (Fig. 8). We observed the same trends for *total carbon*. *Total carbon* increased by 0.0023 g/cm² (± 0.00044; 95% CI) for each 10,000 alligator increase in density ($Z_{16,97}$ = 10.21; $p<0.005$; Fig. 9). *Total carbon* decreased by 0.0086 g/cm² (± 0.0014; 95% CI) for each increase of 100 hectares between nests ($Z_{16,97}$ = – 12.14; $p<0.005$; Fig. 9). Given the home range size of an alligator (minimum 0.12 hectares for a nesting female over two months, maximum 5,024 hectares for an adult male[34]), these data suggest that a single adult alligator may contribute 14.4 g to 602.8 kg of *top-10 carbon* and 2.76 g to 115.5 kg *total carbon* in Louisiana.

Discussion

These data suggest that alligator presence and population density positively correlate with tidally influenced carbon sequestration at the regional scale and within the alligator's native range. At the continental scale, we discovered no difference in tidally influenced carbon sequestration between alligator presence and absence, aside from the mangrove habitat where sequestration benefitted from alligator presence. Two important characteristics influence carbon storage in mangroves. The first involves increases in belowground productivity in response to several environmental variables, many of which relate to inundation stress with mangrove responses relating to ameliorating inundation influences through root-mediated soil volume expansion[35]. The second is sea-level rise. Mangroves do not tolerate submergence passively but instead build surface elevations in various ways[36]; nearly

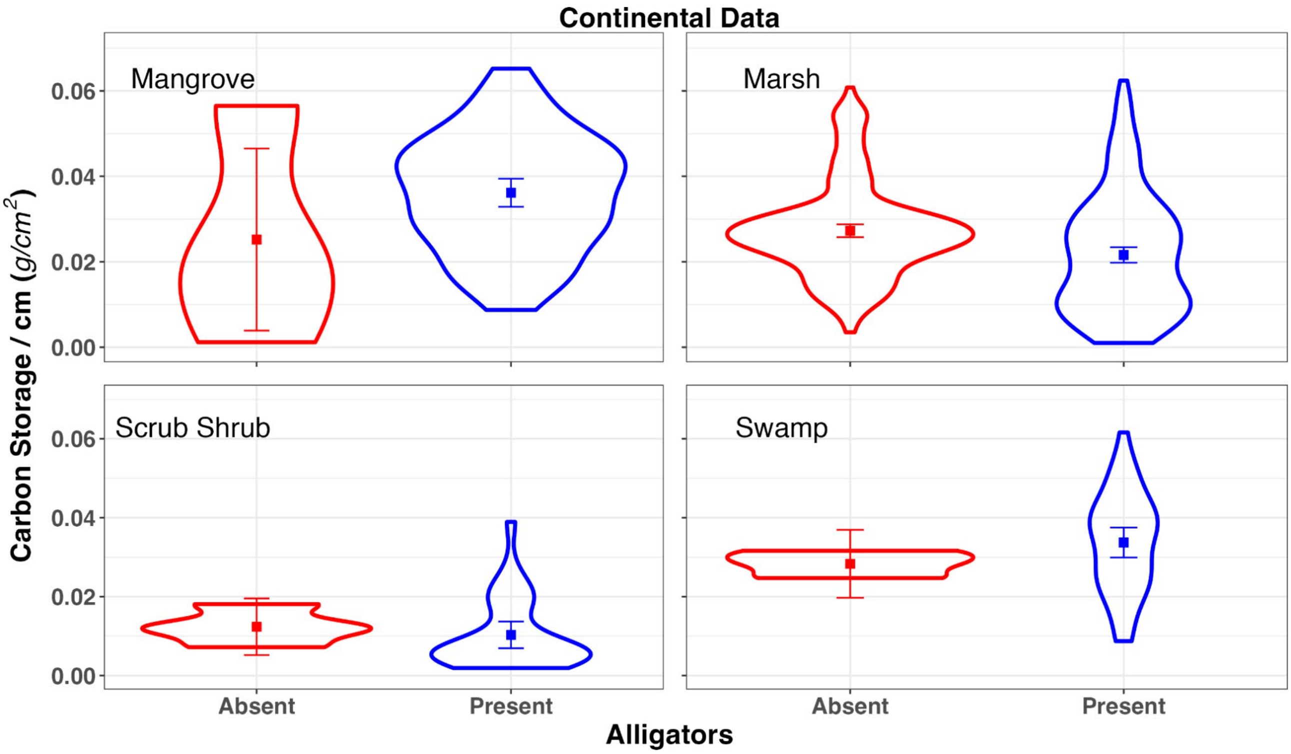

Fig. 4. Violin plots of the *total carbon* storage per cm of the core sample in four unique habitats (mangrove, marsh, scrub shrub, and swamp) when alligators were absent (red) and present (blue) in all states. We needed to obtain more data from the other three habitats for comparison. We did not detect a statistically significant effect of alligator presence on carbon storage in any habitats.

all mechanisms mangroves use relate to increased carbon storage. In fact, without sea-level rise, mangroves cannot build soil carbon stocks because no accommodation space is available, and therefore, mangrove soil volume expansion is not triggered biologically or through inundation-facilitated sedimentation[37]. These factors likely overwhelmed any benefit of having alligators modify the environment at the continental scale. Within the distribution of alligators, however, we recovered a positive association between alligator presence and recent (top-10) tidally influenced blue carbon sequestration overall. This relationship extends to specific habitat types, where mangroves with alligators benefit more than scrub shrub wetlands, a finding that reveals habitat-specific complexities. Regionally, we detect strong positive relationships between alligator demographic metrics and both carbon sequestration metrics. These results suggest that alligators serve as apex predators that positively influence ecosystem carbon storage and sequestration within their native habitat.

The positive correlation between alligator demography and soil carbon at the regional scale elucidates data points above and below the line best fit (Fig. 8). Points above the line indicate that alligators are *not* choosing high-productivity areas that are inherently rich in carbon storage because many of the highest carbon cores are from sites lacking alligators. Data points below the line may indicate a causal inability to increase carbon sequestration, either by variation in trophic chain structure or abiotic constraints. A carefully designed, long-term exclusion experiment could help identify the strength of the causal relationships between alligator abundance and soil carbon storage. Nevertheless, our detected relationship between alligator abundance and *top-10 carbon* identifies alligators as apex predators that may significantly contribute to blue carbon dynamics.

The mechanistic effects of apex predators on carbon accumulation, metabolic capture, and preservation have been theorized and empirically corroborated, indicating that predators play a critical role in carbon cycling and sequestration at the ecosystem level[6,10]. Predator trophic regulation of herbivore and bioturbator abundance and behavior releases plant and microbial assemblages from trophic pressures that otherwise impede carbon cycling[38]. Evidence of this phenomenon includes coastal ecosystems in which salt marsh, seagrass, and mangrove habitats show higher carbon sequestration rates when predators of herbivores and bioturbators are present and abundant. Such trophic pressure mediates herbivory and prevents the reduction of primary productivity that can either reallocate carbon within the plant[39] or allow propagation of fast-growing, low-carbon stock species[40]. Results presented here indicate that alligators function as predators within this trophic cascade mechanism and, therefore, likely play a critical role in carbon sequestration in wetland ecosystems where they reside.

Trophic cascade theory, however, predicts differential carbon outcomes given the number of trophic levels present in the food chain, whereby predators in trophic chains with an odd number of levels negatively affect primary production by consuming second-order consumers and subsequently hinder carbon sequestration[41,42]. This notion was attributed to alligators in mangrove habitats that consumed predatory crabs[43]. In stark contrast, our data find that carbon sequestration is highest in mangrove habitats when alligators *are* present at continental

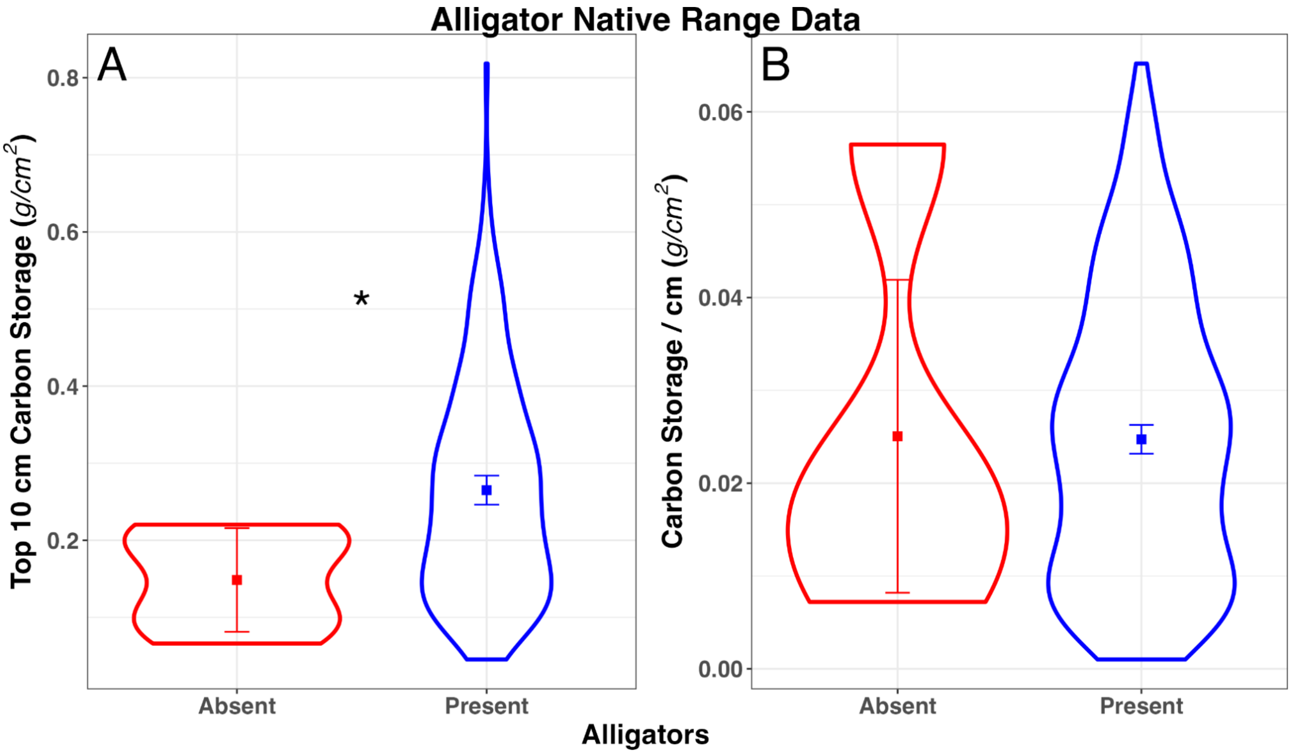

Fig. 5. Violin plots of the summed top 10 cm of carbon storage in the core sample (A) and the carbon storage per cm of the entire core sample (B) data when alligators were absent (red) and present (blue) in states that fall within the native range of alligators. The square and error bars represent the mean and 95% confidence intervals of the data. The black star represents a statistically significant difference of carbon storage when alligators are absent compared to present.

and biogeographic distribution scales, indicating a more complex trophic chain than previously recognized or a negligible amount of crab predation by alligators in such ecosystems. Furthermore, our data suggest that alligators may be active apex predators in even-numbered trophic chains, consuming common diets consisting of herbivores like blue crabs (*Callinectes sapidus*[44]), Nutria (*Myocastor coypus*[45]), waterfowl, herbivorous insects, and feral hogs[46], or are potentially preying on tertiary consumers like large piscivorous fishes[46] at the regional scale, as opposed to secondary order consumers whose consumption may hinder carbon sequestration.

Our analysis shows no difference in carbon storage metrics at the continental scale (i.e., between the alligator geographic distribution vs. non-native distribution), likely due to differential carbon dynamics among plant assemblages across latitude and longitude. For example, *Spartina cynosuroides* produces rhizomes 15–20 cm below the soil, directing a propensity to add little carbon to surface soils, and these plants are more common in coastal South Carolina than in Louisiana[47]. In contrast, *Spartina patens* allocate relatively more biomass to surface soils and are common in Alligator-occupied marshes of Louisiana. Controlling for plant growth strategy is more tenable at smaller analysis scales. Our data, to this effect, encompass differing plant assemblages and habitats among the northern Atlantic seaboard, South Atlantic, and Gulf Coastal Plains of the U.S., contributing to spatial and habitat-specific variation. Hypothesized differences in carbon storage among habitats (particularly salt marsh, mangroves, and seagrass) include differing rates of primary production, carbon allocation to root biomass, nutrient content of plant tissues, and subsequent decomposition rates, ability to capture carbon, sediment retention, and sediment microbial and animal communities (for complete review see Atwood et al.[10]). As such, a comparison of carbon sequestration between sites within the alligator distribution versus those far removed may be misguided in that the ecology of these systems may support different plant, herbivore, and predator assemblages. Furthermore, results across the alligator native range indicate that the relationship between alligators and carbon storage varies among habitats such that the relationship cannot be generalized and is potentially subject to habitat-based complexities.

Top-10 carbon (the sum of carbon content [g/cm^2] in the most recent 10 cm of cores) and *total carbon* (the carbon content per cm of the entire core) present different stories. *Top-10 carbon* elucidates recent (last ~ 60 years; Appendix 2) carbon capture from soil core data. This corresponds temporally to the recovery and subsequent management of stable alligator populations since listing under the Endangered Species Act of 1973 (16 U.S.C. § 1531 et seq.), while *total carbon* elucidates carbon capture, on average, per cm of core sample. Core depths varied from 10 cm to over 200 cm, so the *total carbon* variable lacks temporal applicability among sites and can be interpreted as spatial variation in carbon capture regardless of temporally dynamic processes. Here, *top-10 carbon* may better reflect the relationship between carbon stock and alligators because populations of alligators were both spatially and temporally reduced during the mid 1900's, a period captured in the *total carbon*

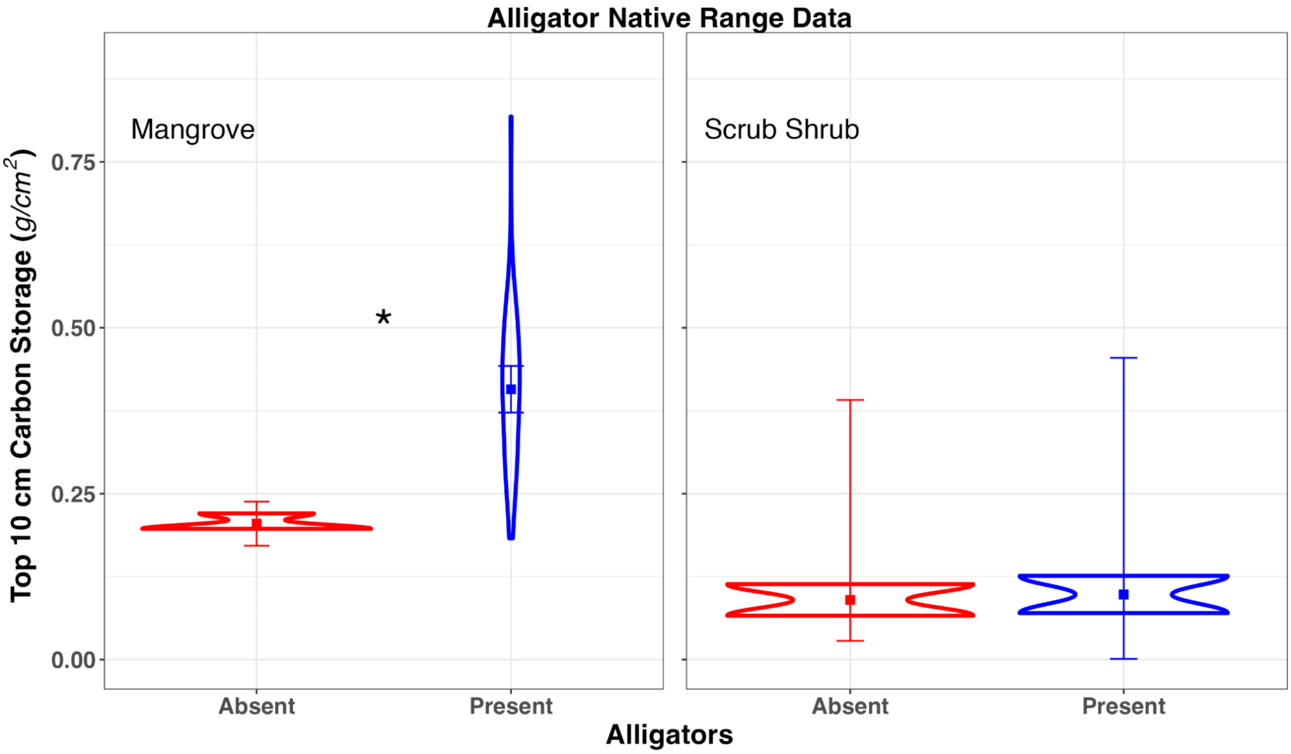

Fig. 6. Violin plots of the summed carbon storage in the top 10 cm of the core sample data in two unique habitats (mangrove and scrub shrub) when alligators were absent (red) and present (blue) in all states that fall within the alligator native range. We did not obtain enough data from the other habitats for comparisons. A star represents a statistically significant effect of alligator presence on carbon storage.

variable. A temporal correlation between alligator endangerment, recovery, and representative soil core carbon data would be a valuable step toward revealing the nature of this relationship; however, few cores are dated, so this analysis is not possible currently.

Limitations to this study are a function of available soil core data across space. Micro-variation in plant assemblage (i.e., fringe versus scrub mangroves), geomorphological and hydrological variation, and levels of land protection versus degradation potentially play driving roles in our carbon data spatially. We utilized all available continuous cores within tidally inundated coastal systems but were unable to factor in the aforementioned variables analytically at the broad spatial resolution of this study. Each of the limitations described may contribute to variation in carbon stock data and should be considered in future studies. Understanding of these confounding variables can be improved by higher soil core resolution across space, from which a robust sample size may be used to tease them apart.

Implications

Vegetated coastal habitats have decreased by as much as 50% over the past 50 years[48], and marine predator populations by as much as 90%[49]. Given that predation pressure influences tidal wetland carbon sequestration, and our data reveal strong links between alligators and carbon stock, conservation priorities could reflect such. As Atwood et al. (2015) demonstrate, conserving herbivores and bioturbators has negative consequences for carbon sequestration, while conservation of carbon initiatives, wetland habitat, and predator populations combined has the utmost positive implications for global carbon stock[10]. Alternatively, consider that any initiative to conserve wetlands, through carbon program incentives or otherwise, benefits the ecosystem as alligator habitat.

The American alligator was monetized as a natural resource for an industry reliant on sustained wild populations[16]. The response and management approach to sustaining these populations rescued the species from extinction in perhaps the most successful natural resource strategy ever implemented. Additionally, the industry utilizing this strategy is clearly a critical player in tidally influenced wetland carbon sequestration and continues focusing on expanding the conservation of these animals through successfully balancing the relationship between economic choices and potential impacts on natural ecosystem interactions[50]. Given that the industry is reliant on and responsible for the propagation of alligators in tidally influenced coastal wetlands—a vital carbon stock habitat—and that alligators are functional apex predators in carbon dynamics, the alligator industry may be one of the most effective commercial practices in resource-based carbon sequestration, assisting with climate change mitigation globally.

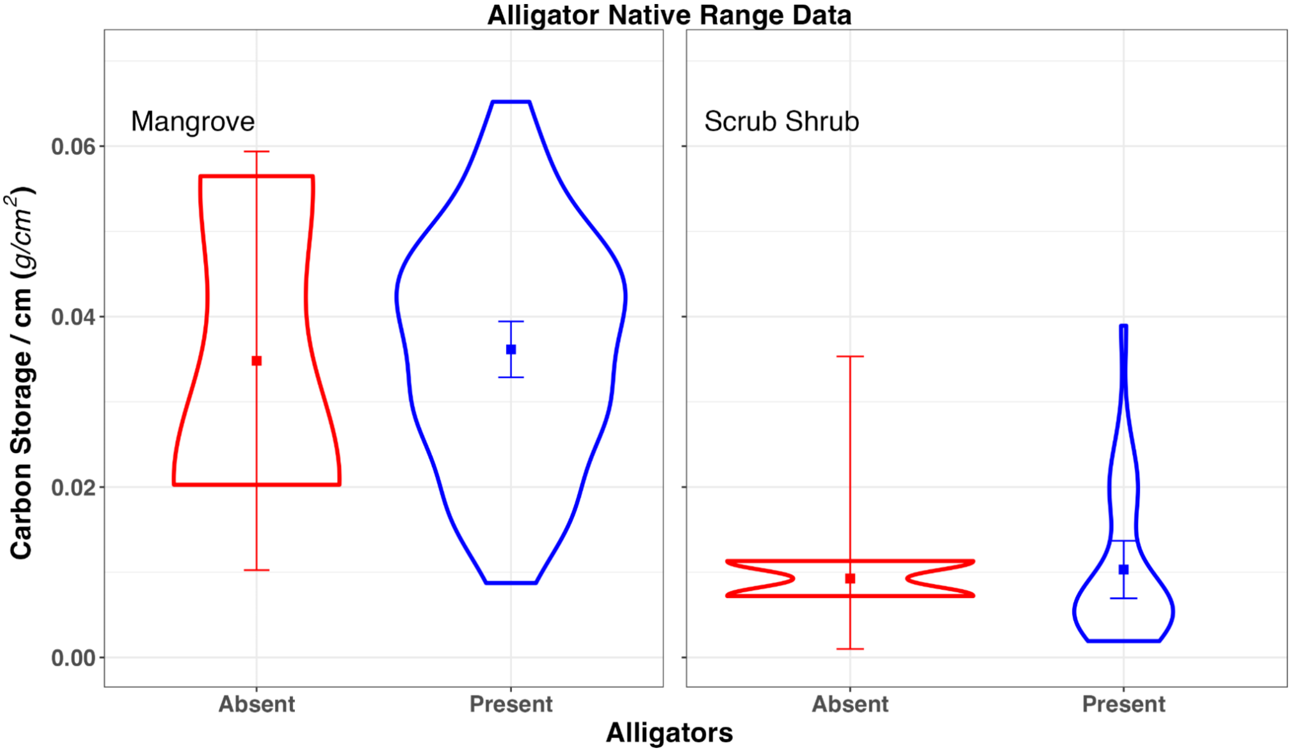

Fig. 7. Violin plots of the *total carbon* storage per cm of the core sample in two unique habitats (mangrove and scrub shrub) when alligators were absent (red) and present (blue) in all states that fall within the alligator native range. We did not obtain enough data from the other habitats for comparisons. We did not detect a statistically significant effect of alligator presence on carbon storage in any of the habitats.

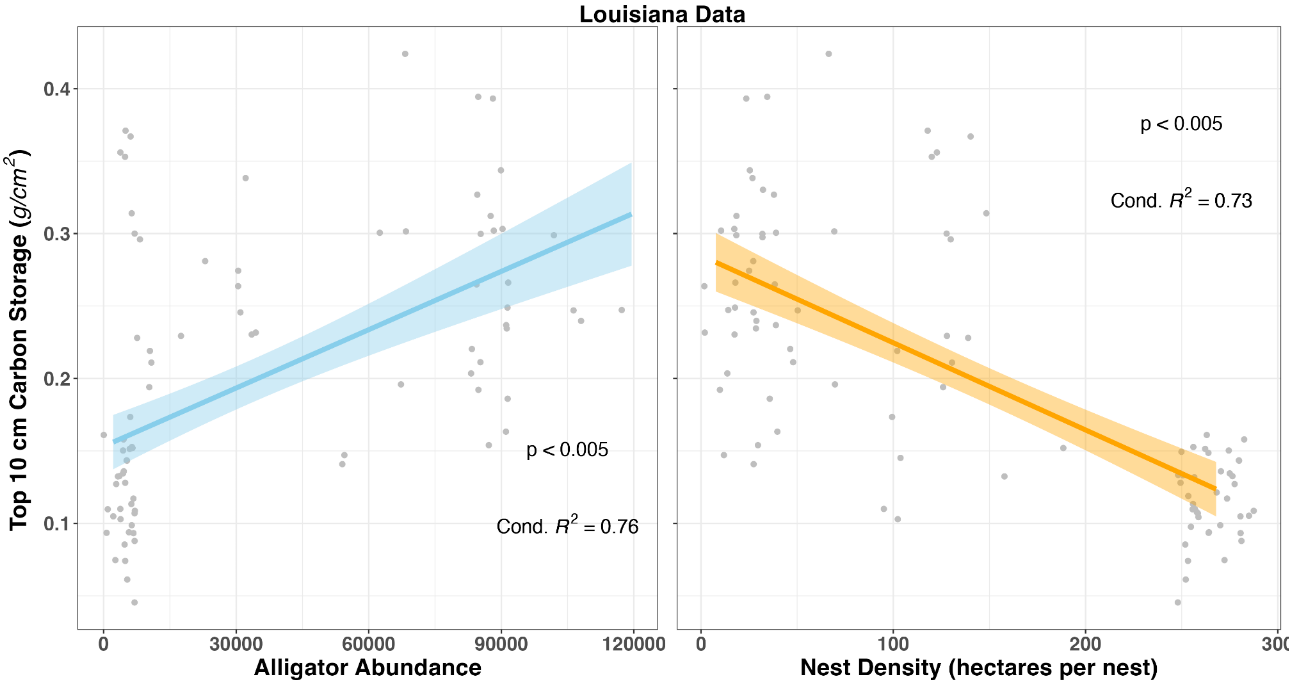

Fig. 8. Generalized linear mixed-effect model trends depicting the effect of alligator density (left; blue) and alligator nest density (right; orange) on the top 10 cm of carbon storage in the core sample of Louisiana data. The corresponding color fill around the line represents the standard errors. The associated conditional R^2 and p-values are reported for each plot. Grey points are jittered raw data points.

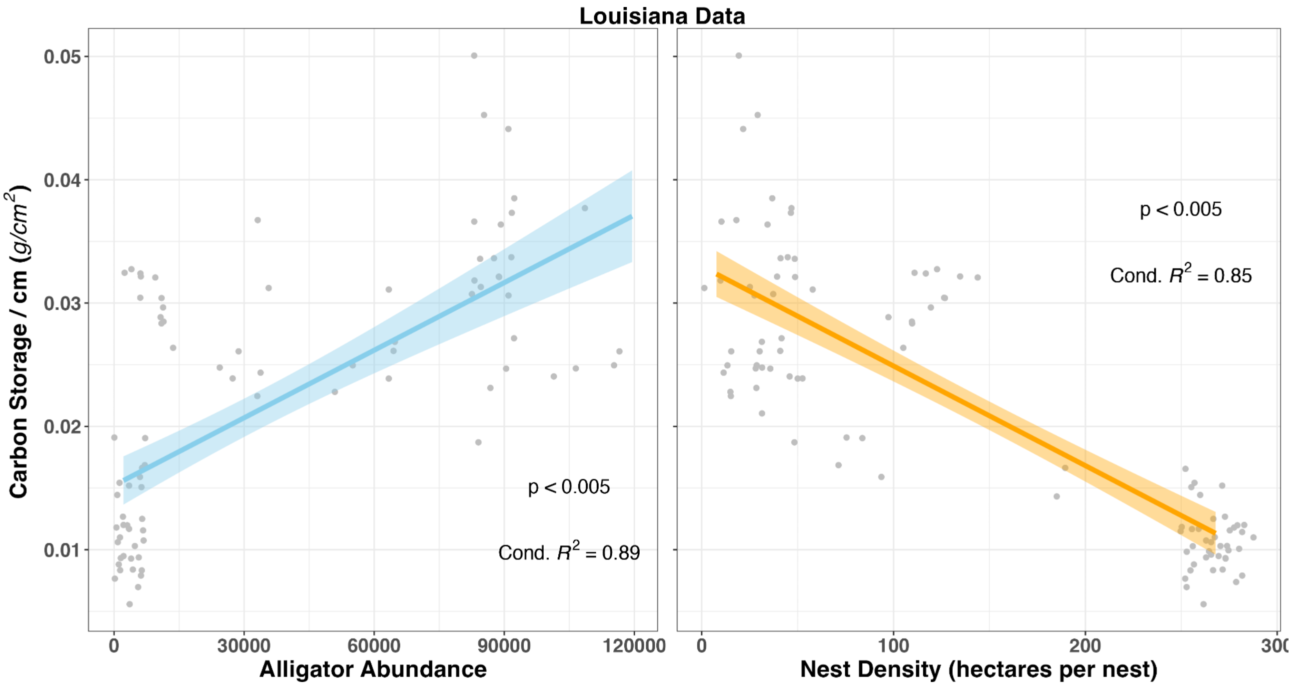

Fig. 9. Generalized linear mixed-effect model trends depicting the effect of alligator density (left; blue) and alligator nest density (right; orange) on the *total carbon* per cm of the entire core sample in Louisiana data. The corresponding color fill around the line represents the standard errors. The associated conditional R^2 and p-values are reported for each plot. Grey points are jittered raw data points.

Data availability

The Smithsonian Coastal Carbon Network data are available here: https://serc.si.edu/coastalCarbon and the sp ecific filtered carbon data are available on GitHub: *DBPR GitHub link available after acceptance*. The USGS data release is available here: Murray, C., Coleman, T.S., Wray, G., Krauss, K.W., and From, A.S., 2024, Determining the role of the American Alligator (*Alligator mississippiensis*) in coastal wetland carbon dynamics of the east and gulf coasts of the USA (1994–2019): U.S. Geological Survey data release, https://doi.org/10.5066/P1BDUJCA.

Code availability

Code is available on GitHub: *DBPR GitHub link available after acceptance*.

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References

1. Srivastava, P., Singh, R., Tripathi, S., Singh, H. & Raghubanshi, A. S. Soil carbon dynamics and climate change: current agro-environmental perspectives and future dimensions. *Energy Ecol. Environ.* **1**, 315–322 (2016).
2. Macreadie, P. I. et al. The future of blue carbon science. *Nat. Commun.* **10**, 1–13 (2019).
3. Krauss, K. W. et al. The role of the upper tidal estuary in wetland blue carbon storage and flux. *Glob Biogeochem. Cycles* **32**, 817–839 (2018).
4. Poulter, B. et al. A review of global wetland carbon stocks and management challenges. *Wetl. Carbon Environ. Manag.* **2021**, 1–20 (2021).
5. Noe, G. B., Krauss, K. W., Lockaby, B. G., Conner, W. H. & Hupp, C. R. The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. *Biogeochemistry* **114**, 225–244 (2012).
6. Schmitz, O. J., Hawlena, D. & Trussell, G. C. Predator control of ecosystem nutrient dynamics. *Ecol. Lett.* **13**, 1199–1209 (2010).
7. Morris, T. & Letnic, M. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proc. R. Soc. B Biol. Sci.* **2017**, 284 (2017).
8. Hilderbrand, G. V., Hanley, T. A., Robbins, C. T. & Schwartz, C. C. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* **121**, 546–550 (1999).
9. Holtgrieve, G. W., Schindler, D. E. & Jewett, P. K. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecol. Res.* **24**, 1125–1135 (2009).
10. Atwood, T. B. et al. Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Change* **5**, 1038–1045 (2015).
11. Atwood, T. B. et al. Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Front. Ecol. Evol.* **6**, 4785 (2018).
12. Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L. & Konar, B. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Front. Ecol. Environ.* **10**, 409–415 (2012).
13. Sutton, W. & Newman, B. Geographic distribution and habitat requirements of the American alligator. In *American Alligators: Habitats, Behaviors, and Threats* 15–46 (Nova Science Publishers, Inc., 2018).

14. Somma, L. A. *Alligator mississippiensis* Daudin, 1802: U.S. Geological Survey, nonindigenous aquatic species database, Gainesville, FL (2024, accessed 28 Nov 2024). https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=221.
15. Joanen, T. & McNease, L. Management of the alligator as a renewable resource in Lousiana. In *Proc. 5th Work. Meet. Croc. Spec. Group. IUCN-The World Conservation Union. Gland, Switzerland* 298–314 (1982).
16. Eversole, C. B. & Henke, S. E. The conservation history of the American alligator. In *American Alligators: Habitats, Behaviors and Threats* 1–14 (Nova Science Publishers, Inc., 2018).
17. Craighead, F. C. *The Role of the Alligator in Shaping Plant Communities and Maintaining Wildlife in the Southern Everglades* (Florida Audubon Society, 1969).
18. Kushlan, J. A. Observations on the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. *Copeia* **1974**, 993–996 (1974).
19. Rosenblatt, A. E. & Heithaus, M. R. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.* **80**, 786–798 (2011).
20. Strickland, B. A. et al. An apex predator engineers wetland food-web heterogeneity through nutrient enrichment and habitat modification. *J. Anim. Ecol.* **92**, 1388–1403 (2023).
21. Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **1994**, 373–386 (1994).
22. Holmquist, J. R. et al. The Coastal Carbon Library and Atlas: open source soil data and tools supporting blue carbon research and policy. *Glob. Change Biol.* **30**, 7485 (2024).
23. Hillmann, E. R., Rivera-Monroy, V. H., Nyman, J. A. & La Peyre, M. K. Estuarine submerged aquatic vegetation habitat provides organic carbon storage across a shifting landscape. *Sci. Total Environ.* **717**, 712 (2020).
24. Gardner, B., Garner, L. A., Cobb, D. T. & Moorman, C. E. Factors affecting occupancy and abundance of American alligators at the northern extent of their range. *J. Herpetol.* **50**, 541–547 (2016).
25. Bennett, S. H. & Buhlmann, K. A. *South Carolina's Species Wildlife Action Plan 2015: American Alligator. Supplemental Volume: Species of Conservation Concern.* 1–275 (2015). https://www.dnr.sc.gov/swap/main/2015StateWildlifeActionPlan-chaptersonly.pdf.
26. Skupien, G. M. & Andrews, K. M. Factors influencing the abundance of American alligators (*Alligator mississippiensis*) on Jekyll Island, Georgia, USA. *J. Herpetol.* **51**, 89–94 (2017).
27. Taylor, D. & Neal, W. Management implications of size-class frequency distributions in Louisiana alligator populations. *Wildl. Soc. Bull. 1973–2006* **12**, 312–319 (1984).
28. Taylor, D., Kinler, N. & Linscombe, G. Female alligator reproduction and associated population estimates. *J. Wildl. Manag.* **55**, 682–688 (1991).
29. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2024).
30. Hyndman, R. J. Sample quantiles 20 years later. https://robjhyndman.com/hyndsight/sample-quantiles-20-years-later/ (2016).
31. Hyndman, R. J. & Fan, Y. Sample quantiles in statistical packages. *Am. Stat.* **50**, 361–365 (1996).
32. Delignette-Muller, M. L. & Dutang, C. Fitdistrplus: an R package for fitting distributions. *J. Stat. Softw.* **64**, 1–34 (2015).
33. Brooks, M. E. et al. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).
34. Joanen, T. E. D. & McNease, L. L. Ecology and physiology of nesting and early development of the American alligator. *Am. Zool.* **29**, 987–998 (1989).
35. McKee, K. L., Cahoon, D. R. & Feller, I. C. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob Ecol. Biogeogr.* **16**, 545–556 (2007).
36. Krauss, K. W. et al. How mangrove forests adjust to rising sea level. *New. Phytol.* **202**, 19–34 (2014).
37. Rogers, K. et al. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature* **567**, 91–95 (2019).
38. Schmitz, O. J. et al. Animating the carbon cycle. *Ecosystems* **17**, 344–359 (2014).
39. Strickland, M. S., Hawlena, D., Reese, A., Bradford, M. A. & Schmitz, O. J. Trophic cascade alters ecosystem carbon exchange. *Proc. Natl. Acad. Sci.* **110**, 11035–11038 (2013).
40. Lavery, P. S., Mateo, M. Á., Serrano, O. & Rozaimi, M. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PloS One* **8**, e73748 (2013).
41. Atwood, T. B. et al. Predator-induced reduction of freshwater carbon dioxide emissions. *Nat. Geosci.* **6**, 191–194 (2013).
42. Atwood, T. B., Hammill, E. & Richardson, J. S. Trophic-level dependent effects on CO2 emissions from experimental stream ecosystems. *Glob. Change Biol.* **20**, 3386–3396 (2014).
43. Nifong, J. C. & Silliman, B. R. Impacts of a large-bodied, apex predator (*Alligator mississippiensis* Daudin 1801) on salt marsh food webs. *J. Exp. Mar. Biol. Ecol.* **440**, 185–191 (2013).
44. Nifong, J. C. et al. American alligator digestion rate of blue crabs and its implications for stomach contents analysis. *Copeia* **2012**, 419–423 (2012).
45. Valentine, J. M. Jr, Walther, J. R., McCartney, K. M. & Ivy, L. M. Alligator diets on the Sabine National Wildlife Refuge, Louisiana. *J. Wildl. Manag.* **1972**, 809–815 (1972).
46. Saalfeld, D. T., Conway, W. C. & Calkins, G. E. Food habits of American alligators (*Alligator mississippiensis*) in East Texas. *Southeast. Nat.* **10**, 659–672 (2011).
47. Gallagher, J. L. & Plumley, F. G. Underground biomass profiles and productivity in Atlantic coastal marshes. *Am. J. Bot.* **66**, 156–161 (1979).
48. Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I. & Marbà, N. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Change* **3**, 961–968 (2013).
49. Myers, R. A. & Worm, B. Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283 (2003).
50. Coleman, T. S. et al. The spatial ecology of nuisance crocodiles: movement patterns of relocated American crocodiles (*Crocodylus acutus*) in Guanacaste, Costa Rica. *Animals* **14**, 339 (2024).
51. Esri ArcGIS Pro Version 3.4. (2024).
52. Hill, T. D. & Anisfeld, S. C. Coastal Wetland response to sea level rise in Connecticut and New York. *Estuar. Coast Shelf Sci.* **163**, 185–193 (2015).
53. Elsey-Quirk, T., Seliskar, D. M., Sommerfield, C. K. & Gallagher, J. L. Salt marsh carbon pool distribution in a mid-atlantic lagoon, USA: sea level rise implications. *Wetlands* **31**, 87–99 (2011).
54. St-Laurent, P. et al. Relative impacts of global changes and regional watershed changes on the inorganic carbon balance of the Chesapeake Bay. *Biogeosciences* **17**, 3779–3796 (2020).
55. Arriola, J. M. & Cable, J. E. Variations in carbon burial and sediment accretion along a tidal creek in a Florida salt marsh. *Limnol. Oceanogr.* **62**, S15–S28 (2017).
56. Breithaupt, J. L., Smoak, J. M., Smith, I. I. I., Sanders, C. J. & T. J. & Temporal variability of carbon and nutrient burial, sediment accretion, and mass accumulation over the past century in a carbonate platform mangrove forest of the Florida Everglades. *J. Geophys. Res. Biogeosci.* **119**, 2032–2048 (2014).
57. Breithaupt, J. L. et al. Partitioning the relative contributions of organic matter and mineral sediment to accretion rates in carbonate platform mangrove soils. *Mar. Geol.* **390**, 170–180 (2017).
58. Breithaupt, J. L. et al. Increasing rates of carbon burial in southwest Florida coastal wetlands. *J. Geophys. Res. Biogeosci.* **125**, 785 (2020).

59. Doughty, C. L. et al. Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries Coasts* **39**, 385–396 (2016).
60. Fell, C., Adgie, T. & Chapman, S. Dataset Carbon sequestration across Northeastern, Florida Coastal Wetlands (2021).
61. Marchio, D. A. Jr, Savarese, M., Bovard, B. & Mitsch, W. J. Carbon sequestration and sedimentation in mangrove swamps influenced by hydrogeomorphic conditions and urbanization in Southwest Florida. *Forests* **7**, 116 (2016).
62. Sanderman, J. et al. A global map of mangrove forest soil carbon at 30 m spatial resolution. *Environ. Res. Lett.* **13**, 125 (2018).
63. O'Keefe Suttles, J. A. E., Mann, M. J., Smith, A. G., Kroeger, C. & Kevin, D. *Collection, Analysis, and Age-Dating of Sediment Cores from Mangrove and Salt Marsh Ecosystems in Tampa Bay, Florida, 2015* (2021).
64. Osland, M. J. et al. Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems* **15**, 848–866 (2012).
65. Vaughn, D. R., Bianchi, T. S., Shields, M. R., Kenney, W. F. & Osborne, T. Z. Increased organic carbon burial in northern Florida mangrove-salt marsh transition zones. *Glob Biogeochem. Cycles* **34**, 369 (2020).
66. Craft, C. Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and U.S. tidal marshes. *Limnol. Oceanogr.* **52**, 1220–1230 (2007).
67. Abbott, K. M., Elsey-Quirk, T. & DeLaune, R. D. Factors influencing blue carbon accumulation across a 32-year chronosequence of created coastal marshes. *Ecosphere* **10**, 78 (2019).
68. McClellan, S. A., Elsey-Quirk, T., Laws, E. A. & DeLaune, R. D. Root-Zone carbon and nitrogen pools across two chronosequences of coastal marshes formed using different restoration techniques: dredge sediment versus river sediment diversion. *Ecol. Eng.* **169**, 106326 (2021).
69. Piazza, S. C. et al. *Geomorphic and Ecological Effects of Hurricanes Katrina and Rita on Coastal Louisiana Marsh Communities* (2011).
70. White, J. R., Sapkota, Y., Chambers, L. G., Cook, R. L. & Xue, Z. Biogeochemical properties of sediment cores from Barataria Basin, Louisiana, 2018 and 2019 (Version 1) [Data set]. In *Biological and Chemical Oceanography Data Management Office (BCO-DMO)* (2020).
71. Drake, K., Halifax, H., Adamowicz, S. C. & Craft, C. Carbon sequestration in tidal salt marshes of the Northeast United States. *Environ. Manage.* **56**, 998–1008 (2015).
72. Ensign, S. H., Noe, G. B., Hupp, C. R. & Skalak, K. J. Head-of-tide bottleneck of particulate material transport from watersheds to estuaries. *Geophys. Res. Lett.* **42**, 10–671 (2015).
73. Keshta, A., Yarwood, S. & Baldwin, A. Dataset: Soil redox and hydropattern control soil carbon stocks across different habitats in tidal freshwater wetlands in a sub-estuary of the Chesapeake Bay (2020).
74. Pastore, M. A., Megonigal, J. P. & Langley, J. A. Elevated CO2 and nitrogen addition accelerate net carbon gain in a brackish marsh. *Biogeochemistry* **133**, 73–87 (2017).
75. Giblin, A. & Forbrich, I. PIE LTER high marsh sediment chemistry and activity measurements, Dataset, Nelson Island Creek marsh, Rowley, MA (2018).
76. Gonneea, M., O'Keefe Suttles, J. & Kroeger, K. Collection, analysis, and age-dating of sediment cores from salt marshes on the south shore of Cape Cod, Massachusetts, from 2013 through 2014: US Geological Survey data release (2018).
77. Luk, S. Y. S., Eagle, A. C., Suttles, M. J. O. & Jennifer, A. Collection, analysis, and age-dating of sediment cores from a salt marsh platform and ponds, Rowley, Massachusetts, 2014-15 (2020).
78. Unger, V., Elsey-Quirk, T., Sommerfield, C. & Velinsky, D. Stability of organic carbon accumulating in Spartina alterniflora-dominated salt marshes of the Mid-atlantic US. *Estuar. Coast Shelf Sci.* **182**, 179–189 (2016).
79. McTigue, N. et al. Dataset: Carbon accumulation rates in a salt marsh over the past two millennia (2020).
80. Rodriguez, A., Miller, C. & Bost, M. Salt marsh radiocarbon and loss on Ignition data: Dataset (2022).
81. Drexler, J. Z. et al. A long-term comparison of carbon sequestration rates in impounded and naturally tidal freshwater marshes along the lower Waccamaw River, South Carolina. *Wetlands* **33**, 965–974 (2013).
82. Noe, G. B., Hupp, C. R., Bernhardt, C. E. & Krauss, K. W. Contemporary deposition and long-term accumulation of sediment and nutrients by tidal freshwater forested wetlands impacted by sea level rise. *Estuaries Coasts* **39**, 1006–1019 (2016).
83. Bianchi, T. S. et al. Enhanced transfer of terrestrially derived carbon to the atmosphere in a flooding event. *Geophys. Res. Lett.* **40**, 116–122 (2012).

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C. M. M. was responsible for project conception, analysis and writing. T. S. C. and W. G. analyzed data, prepared figures and wrote portions of the main text. K. W. K. assisted in project conception and writing. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Ethics declarations

The authors declare no competing interests.

Additional information

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