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Predators help protect carbon stocks in blue carbon ecosystems

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Predators continue to be harvested unsustainably throughout most of the Earth's ecosystems. Recent research demonstrates that the functional loss of predators could have far-reaching consequences on carbon cycling and, by implication, our ability to ameliorate climate change impacts. Yet the influence of predators on carbon accumulation and preservation in vegetated coastal habitats (that is, salt marshes, seagrass meadows and mangroves) is poorly understood, despite these being some of the Earth's most vulnerable and carbon-rich ecosystems. Here we discuss potential pathways by which trophic downgrading affects carbon capture, accumulation and preservation in vegetated coastal habitats. We identify an urgent need for further research on the influence of predators on carbon cycling in vegetated coastal habitats, and ultimately the role that these systems play in climate change mitigation. There is, however, sufficient evidence to suggest that intact predator populations are critical to maintaining or growing reserves of 'blue carbon' (carbon stored in coastal or marine ecosystems), and policy and management need to be improved to reflect these realities.

Climate change is an urgent societal issue that can be addressed by a combination of reduced emissions and climate mitigation strategies, including those based on natural carbon (C) stores (that is, biosequestration). The need to reduce atmospheric CO_2 concentrations combined with global interest in C trading and pricing has intensified research on the C storage capacity of natural ecosystems. To date, most C conservation programs have focused on managing and/or restoring terrestrial ecosystems, such as tropical forests, to maintain/boost their role in climate change mitigation. Recent studies[1–3] suggest, however, that despite their small global extent, vegetated coastal habitats (seagrass meadows, mangroves and salt marshes) play a disproportionately large role in the global capture and storage of C.

Biosequestration in vegetated coastal habitats, a process that takes up atmospheric CO_2 and stores it for millennia in plant biomass and sediments (that is, blue C), is emerging as one of the most effective methods for long-term C storage[4,5]. Vegetated coastal habitats bury C 40 times faster than tropical forests and contribute 50% of the total C buried in ocean sediments[6]. The quantity of C (up to 25 billion tonnes) estimated to be stored in vegetated coastal habitats makes them the most C-rich ecosystems in the world (Table 1)[2,4]. Because of the remarkable capacity of vegetated coastal habitats to sequester and store C for millennia, they should be prominent in our strategies to combat climate change[7]. Yet our ability to conserve these natural C sinks is hampered by our limited understanding of the mechanisms that are conducive to high C accumulation and preservation rates.

There is growing evidence that trophic downgrading, the disproportionate loss of species high in the food chain, can have far-reaching effects on ecosystem function[8,9]. This research has revealed that predators play important and potentially irreplaceable roles in C cycling[10,11], and that their presence may be beneficial for biosequestration[9,10,12,13]. Predators alter ecosystem C cycling largely through their indirect effects on plant or microbial community composition and structure (for example biomass, density, diversity and chemical composition). These effects are mediated through predator-induced changes in the life-history traits, morphology, behaviour and/or abundance of intermediate trophic levels (that is, herbivores and bioturbators). The relationship between predators and herbivores/bioturbators is an important determinant of the contribution of plants and microbes to photosynthetic C fixation, storage and remineralization.

In vegetated coastal habitats, the capture and storage of C, both in sediments and plant biomass, can vary significantly depending on the structure and function of the plant community[5,14,15]. Hypotheses to explain differences in C storage capacity among habitats include differences in: (1) rates of primary production; (2) C allocation to root biomass; (3) nutrient content of plant tissues, which influences decomposition rates of organic matter[5,15,16]; (4) effectiveness of the vegetation in capturing and retaining sediments and associated C, which is strongly influenced by canopy height (in salt marshes and seagrass meadows) and aerial root (mangroves) and shoot density[17,18]; and (5) microbial and macrofaunal (for example worms, crabs, and other bioturbators) communities in sediments, which influence remineralization rates of sediment C stocks[5,19,20]. Because many of these mechanisms and processes can be influenced by biotic interactions between predators, herbivores/bioturbators, and plants, these hypotheses predict that recent global reductions in marine predator populations by up to 90%[21] could generate cascading effects on C sequestration and even C stocks in vegetated coastal habitats.

Best available estimates put the loss of vegetated coastal habitats at 25–50% over the past 50 years[4,22]. These declines have largely been

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Table 1 | Global organic carbon (OC) burial and stock within the top 1 m of sediment in vegetated coastal ecosystems.

	Global OC burial rate (Tg yr^{-1})	Global soil OC stocks (Pg)
Salt marsh	4.8–87.3 (ref. 2)	0.4–6.5 (ref. 4)
Seagrass	48–112 (ref. 2)	4.2–8.4 (ref. 3)
Mangrove	22.5–24.9 (ref. 2)	9.4–10.4 (ref. 4)

attributed to land-use changes, climate change and eutrophication[22]. As a result, most studies have focused on how these stressors influence the accumulation and preservation of C stocks in vegetated coastal ecosystems. These approaches, however, are based on the implicit assumption that the C storage capacity of vegetated coastal ecosystems is largely controlled by bottom-up processes. Yet many studies support the idea that one of humankind's most pervasive effects on ecosystem function has been changes to biodiversity at higher trophic levels[8,9,11]. Indeed, overgrazing, defoliation events and extreme incidences of bioturbation have been reported globally in vegetated coastal ecosystem, with many of these events being at least in part linked to loss of predators (Fig. 1). Although data come from a limited number of studies, they suggest that predators may influence C accumulation and preservation (Fig. 2) in vegetated coastal ecosystems as a result of increased herbivory or bioturbation.

Predator depletion is a global problem shared by many ecosystems[8]; however, we choose to focus our discussion on vegetated coastal ecosystems for three main reasons: (1) together, vegetated coastal ecosystems represent the largest contributor to C storage in the ocean, and have thus become focal ecosystems in climate change mitigation and marine conservation[4,7] (Table 1); (2) coastal vegetated ecosystems and coastal predators are highly threatened because of their proximity to human activities[23,24]; and (3) the potential magnitude of release of C stocks as CO_2 to the atmosphere and the loss of C sequestration capacity when vegetated coastal ecosystems are converted or degraded is unparalleled in other ecosystems[24]. Despite these important roles of vegetated coastal ecosystems, the potential for changes in food webs to result in reductions in sequestration rates and the release of C stocks from these systems has been largely overlooked. Here, we discuss how the decline of predators in vegetated coastal ecosystems could be altering the accumulation and preservation of C stocks in the blue C habitats of salt marshes, seagrasses and mangroves. We focus on how predators indirectly influence particle trapping, C accumulation, and preservation of C stocks in sediments and plants, and how understanding patterns of top-down control in these ecosystems is important for developing effective management practices to aid in climate change mitigation.

Trophic cascades in vegetated coastal ecosystems

Trophic cascades in vegetated coastal ecosystems have been identified in a number of ecosystems, but most studies have involved small-scale experiments and/or focused on small-bodied animals. In seagrass ecosystems, such studies have demonstrated that predators indirectly and positively affect plant growth through predation on small-bodied invertebrates that cause seagrass fouling[25]. Multiple empirical studies have revealed that top predators can also initiate trophic cascades in seagrass ecosystems and that, in general, trophic cascades appear to be important in these systems[26]. In a subtropical seagrass ecosystem in Western Australia, large tiger sharks induce shifts in foraging habitat use of the dominant grazers — dugongs (*Dugong dugon*) and green turtles (*Chelonia mydas*) — as well as changes in foraging tactics (see Heithaus *et al.*[27] for a review). These foraging shifts aid the development of high-biomass seagrass beds dominated by slow-growing species and higher C stocks in habitats dangerous to grazers (Fig. 2). In habitats that are safer for grazers, low-biomass beds dominated by fast-growing species[28] support lower C stocks. These findings suggest that herbivore and predator conservation need to be considered in concert to avoid degradation of seagrass beds and cascading effects on blue C[13].

As in seagrass ecosystems, trophic cascades are increasingly being identified in salt marshes, and top-down control of community structure seems to be a feature of these ecosystems. For example, control of grazing snails by predatory crabs is critical to the persistence of some salt marshes[29]. Indeed, loss of predatory crabs can result in the complete loss of salt marshes[29,30]. In other marshes, overfishing of predators has led to increases in populations of herbivorous crabs that can lead to marsh overgrazing, collapse and reduced C sequestration[31,32] (Fig. 2). It is, however, important to acknowledge that in salt marshes as well as other blue C ecosystems, the magnitude and direction of predator effects is context-dependent[33,34]. For example, in some marsh systems, predatory crabs can actually have negative indirect impacts on marsh grasses by inducing snails to climb higher where their grazing has a stronger negative impact on plant production[35].

Evidence for trophic cascades in mangrove ecosystems is scarce, especially involving top predators. For example, fisheries closures in an Australian mangrove ecosystem increased the abundance of large-bodied predators three-fold, but no effect was detected on the abundance of planktivores, scavengers or detritivores in broad-scale monitoring[36]. Indirect evidence, however, suggests that reductions to predator populations in mangroves could have cascading effects on C capture and storage in some cases. Small-bodied predators (for example predatory ants and birds) can directly and indirectly protect mangroves from insect herbivory[37,38], which would otherwise negatively affect the photosynthetic capacity of mangroves. Shore crabs also seem to be a major driver of recruitment, tree density and distribution, and size structure in mangrove and other coastal tropical forests[39,40], and are a major dietary constituent for many declining species of predators (sting rays, shore birds and fish)[41,42]. Furthermore, bioturbating crabs appear to have major influences on C sequestration, as mangrove ecosystems with large crab populations have lower C sequestration rates than those with no or few crabs (Fig. 2). Although further research on the occurrence of trophic cascades in mangroves is needed, there is indirect evidence suggesting that C capture, accumulation and preservation in mangroves is likely to be influenced by top-down processes.

As mentioned above, the specific direction of predator impacts on their ecosystems is context-dependent, and can be influenced by several factors including food web structure, the number of trophic levels present, and the diversity of species[43–45]. Trophic cascade theory predicts that the removal of predators from odd-numbered food chains will have negative effects on primary producers and aspects of C storage, while removal of predators from even-numbered food chains will have the opposite effect[11,12,45]. For example, recent findings that American alligators (*Alligator mississipiensis*) can consume a considerable biomass of predatory blue crabs in coastal marshes and mangroves[46] indicate that it is possible that historical declines in alligator populations may trigger trophic cascades that benefit blue carbon processes in marshes of the southeastern United States. Omnivory and highly reticulate species networks can also reduce the magnitude of, alter the direction of, or eliminate cascading predator effects on lower trophic levels and ecosystem processes[44,45]. For example, time-series analyses from a temperate seagrass ecosystem suggest that recolonizing sea otters promoted the expansion of seagrass beds by reducing crab populations that in turn led to increases in micrograzer prey, which reduced the biomass of epiphytic algae, increasing seagrass productivity[47]. This four-trophic-level cascade initiated by otters is in contrast to that observed by the loss of large predatory fish in temperate seagrasses of Sweden, which led to increases in mesopredators, declines in small herbivores and increases in epiphytic algae that triggered seagrass decline[48]. As a result, predicting the effects of predator loss on blue C *a priori* may be challenging in ecosystems for which we lack sufficient knowledge of food web structure. Food web theory and behavioural ecological theory, however, provides a basis for making robust predictions that seem to apply across ecosystem types[33].

Effects of predators on particle trapping and C accumulation

Most of the C stored in vegetated coastal ecosystems is in the form of organic material trapped in the anoxic sediments underlying vegetation[1,3,49]. This organic matter may originate outside the ecosystem and can be trapped within the ecosystem in tidal currents; for example terrestrial plant material in seagrass beds[15] or seagrass material in mangrove sediments[50]. Deposited detritus is trapped within vegetated coastal ecosystems because of the enhanced friction offered by the vegetation structure[50–52]. Here, the height and density of canopies, aerial roots and tree trunks are key factors that promote sediment deposition as they dampen waves and currents and increase benthic surface area[53,54], allowing organic C to be buried under low- or no-oxygen conditions that slow decomposition[55,56]. Disturbances, such as herbivory, can alter the friction offered by vegetation by directly altering canopy height and shoot/root density, or indirectly via changes in the community composition of the vegetation.

Predation can alter the capacity of vegetated coastal ecosystems to trap particles by indirectly influencing canopy height, or shoot/root density via effects on herbivores. In some cases herbivores can alter canopy height or density through direct consumption of plant material[28,57,58]. For example, the sudden appearance of a grazing limpet in seagrass meadows of Monterey Bay, US, resulted in the reduction of shoot densities by 68% and the conversion of over 50% of the meadow to bare sand[58]. Under more extreme settings, such as those seen in the salt marshes of Cape Cod, US, and seagrass meadows of Bermuda and Indonesia, relaxed predation on herbivores can result in the removal of 90–100% of the aboveground vegetation in a patch, reducing the canopy height to zero[13,59–61]. Removal of the canopy can result in far lower sedimentation rates compared with vegetated areas[62,63], and overall negative impacts on sediment accretion rates[64,65]. Risk of predation, however, can alter the feeding behaviour of some herbivores to less destructive modes[66]. In the seagrass meadows of Shark Bay, Western Australia, dugongs trade-off food quality for vigilance in habitats with high predation risk by only cropping seagrass blades rather than excavating[66,67]. Although the effects of cropping on canopy height are context-dependent[28], cropping is less destructive than excavation because it leaves both rhizomes and leaf blades more intact. Intense cropping in the absence of predators, however, can have substantial impacts on the complexity of the meadow. Indeed, reductions to canopy height by more than 50%, as seen in the case of green sea turtles[60], can lead to as much as a 10-fold reduction in sediment accumulation rates and sediment re-suspension[68].

Herbivory may also indirectly alter canopy height and shoot/root density via indirect changes in plant species composition. For example, under low predation risk, dugongs and sea turtles forage by excavating the nutrient-rich rhizomes of seagrasses[59,66,69]. This foraging mode creates conditions that favour fast-growing seagrass species that are associated with lower sedimentary C stocks[14,70]. Similarly, herbivory of the dominant marsh plant *Spartina densiflora* by crabs and wild guinea pigs affects secondary succession of salt marsh in Argentina by allowing structurally different subordinate species (*Sarcocornia perennis* and *Cress truxillensis*) to establish[71]. Alterations to the community composition of primary producers will affect sediment accumulation rates in vegetated coastal ecosystems because differences in canopy/root height, blade flexibility and shoot/root density influence sediment dynamics[14,15]. In general, large reductions in annual sedimentation rates mediated through top-down changes in plant community composition pose a serious threat to sediment C accretion rates of vegetated coastal habitats, as this is one of the major processes by which these systems accumulate C.

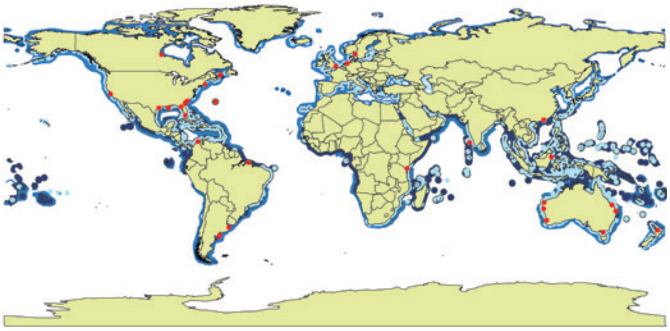

Figure 1 | Global distribution of vegetated coastal ecosystems and documented cases of overgrazing, defoliation, and extreme bioturbation events in these systems. Global distribution of salt marsh (mid-blue) seagrass (light blue) and mangroves (dark blue). Areas represent coastlines with confirmed blue carbon ecosystems; they do not represent the actual area covered by those ecosystems. Red dots represent documented cases from the literature of overgrazing, defoliation or extreme bioturbation events in vegetated coastal ecosystems. This map does not include overgrazing events in salt marshes caused by cattle, sheep or horses. See Supplementary Table 1 for references on overgrazing, defoliation or extreme bioturbation events. Habitat coverage for salt marsh, seagrass and mangroves are from the United Nations Environmental Programme World Conservation Center.

Effects of predators on metabolic C capture

The proportion of outside material that is trapped in a vegetated coastal ecosystem can be high, for example 70% of the total organic carbon in seagrass[72], but in many instances *in situ* production of roots and wood contributes the majority of the organic C within vegetated coastal ecosystems sediment[73–75]. Thus, overall rates of primary production of the plant community and the proportional allocation of biomass to roots over time are important to determining rates of C sequestration, and in some cases may constitute the main component of C sequestered. Historically, plant production in vegetated coastal ecosystems was thought to be solely controlled by bottom-up processes. However, recent research in vegetated coastal ecosystems suggests that primary production, plant growth and plant recruitment are heavily influenced by higher order trophic interactions[13,30,76].

Herbivores have a large influence on primary production and recruitment in all vegetated coastal ecosystems. Herbivores reduce primary production through removal of leaf area, which reduces the potential for photosynthesis and can redirect C allocation to roots[77,78]. Although average rates of herbivory in many mangrove, salt marsh and seagrass ecosystems are comparable to rates seen in terrestrial systems (removal rates of <10% of leaf area)[79,80], release from predation pressure can cause spectacular rates of herbivory in vegetated coastal ecosystems. For example, 40–80% reductions in predatory blue crab and fish populations along the east coast of the United States have led to cascading effects on marsh plant production, with some locations losing 80–100% of the aboveground biomass due to overgrazing by crabs and snails[29,31]. Above- and below-ground biomass in salt marshes is also heavily grazed by several species of geese, suggesting that declines in terrestrial predators could also have implications for marine C cycling[81–83]. Similar to crabs and snails in salt marshes, caterpillars, which are preyed on by many species of shore birds, can devastate mangrove canopies[84], and sea urchins, dugongs and sea turtles under relaxed predation pressure can remove up to 100% of aboveground biomass in seagrass meadows[13,59,70,85]. In some cases, grazers can reduce primary production, and thus C capture, even if there is little visible damage to foliage. For example, exclusion of mesopredators in eelgrass beds of San Diego Bay, US, resulted in a 300–1,000% increase

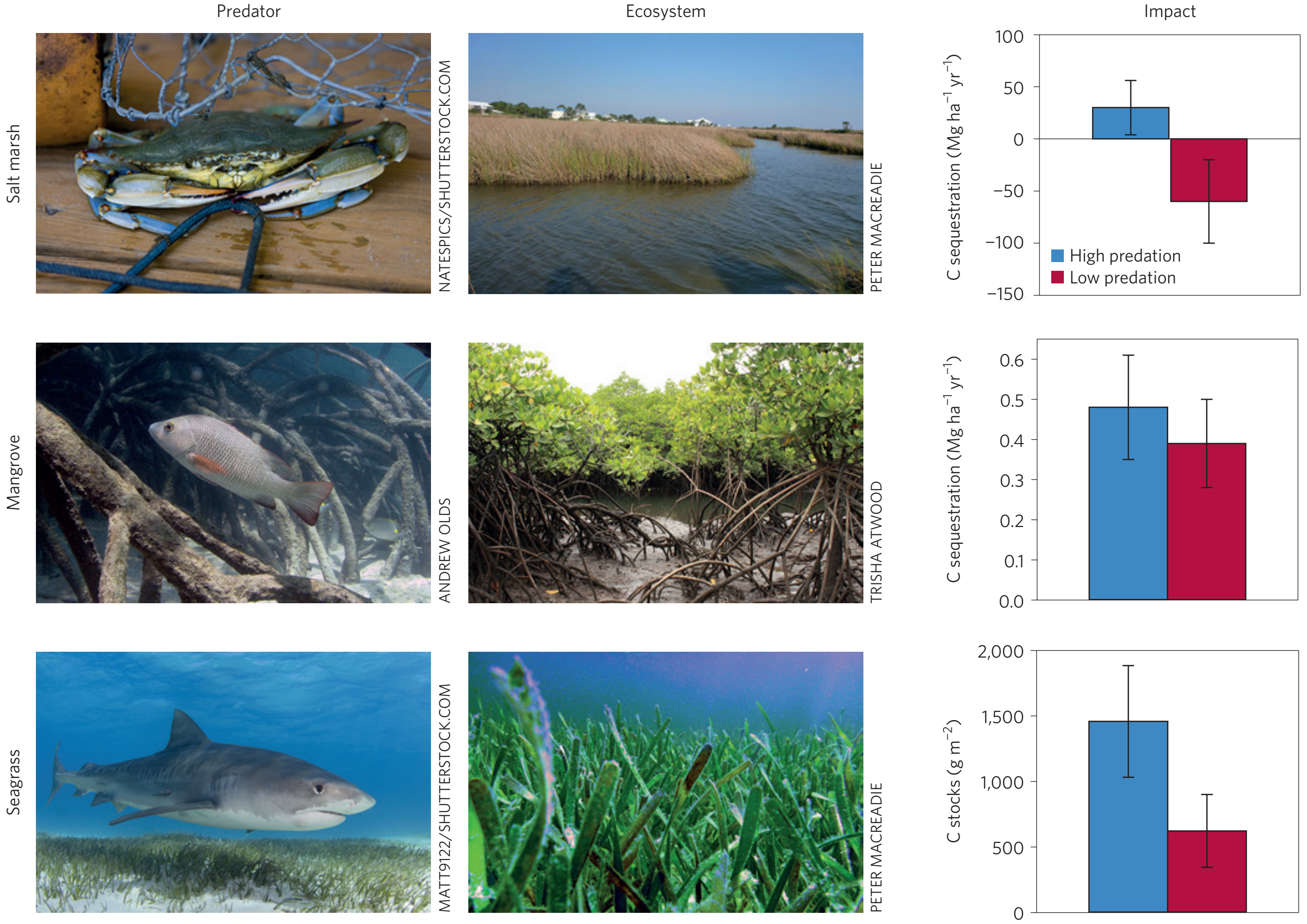

Figure 2 | Indirect effects of reduced predation pressure on C sequestration rates in salt marshes and mangroves, and C stocks in seagrass ecosystems. Plots show mean ± 1 standard deviation. Reductions in predatory blue crabs in New England salt marshes (top panel) and in predatory fish (that is, mangrove jack) in Australian mangroves (middle panel) resulted in increased abundances of bioturbators (for example sesarmid crabs) and ultimately reductions in the C sequestration capacity of these ecosystems. Non-consumptive effects of tiger sharks (bottom panel) in Shark Bay, Western Australia, create a landscape of fear where sea turtles and dugongs preferentially forage in seagrass microhabitats that are low in predation risk. Seagrass microhabitats associated with low predation risk have lower C stocks than do microhabitats associated with high predation risk. Because sedimentation rates for seagrass microhabitats with low predation rates are unknown, we quantified the effects of tiger shark predation on C stocks as opposed to C sequestration rates. Calculations for mean (±SD) effects of predators on blue C responses can be found in the Supplementary Information.

in seagrass epifauna (tube-building crustaceans and limpets) and a 50% reduction in eelgrass production[25].

In addition to the consumption of leaves and wood, some herbivores eat reproductive stages of plants, affecting establishment and the regeneration of forests and meadows, as well as the distribution of plant species. In mangrove forests, scolytid beetles that colonize propagules prior to release from the parent tree severely reduce propagule viability[86]. Once released from the parent tree, propagules are consumed by crabs and insects, which can reduce the establishment of preferred species by up to 70%[87]. In seagrass meadows and salt marshes, seed predators are also common and can remove up to 50% of seeds[88] and suppress the recovery of dominant plant species[71,89]. Despite propagule predators having large influences on new plant growth, no studies have investigated the influence of top-down control on propagule consumers in vegetated coastal habitats. Yet many propagule consumers constitute a substantial proportion of stingray, shore bird and fish diets. The strong effects of herbivores on plant production suggests that in areas where top-down control is high, trophic cascades would alter aboveground C stocks as well as *in situ* material for C burial, although the rapid recovery of biomass after herbivory events may lessen the impact[80].

Effects of predators on C preservation

The structural complexity of plants (root systems and leaves) in vegetated coastal ecosystems allows these systems to be highly effective at retaining trapped particles[2,15]. This promotes their ability to accumulate >1 m thick deposits of ancient C (refs 1,3). Under moderate or low densities, herbivores and bioturbators can aid in the health and growth of vegetation, and thus C preservation, by creating favourable conditions for plant growth[39,40]. However, at high densities bioturbators and herbivores can reduce C preservation through enhanced microbial remineralization of C to CO_2 (ref. 90) or through destabilization of sediment deposits (that is, erosion and re-suspension) from burrowing activities[32]. For example, sediment mixing from bioturbation can increase electron receptor (for example oxygen, nitrate) availability to deeper microbial communities[91], increasing microbial abundance (>tenfold)[92] and CO_2 production (twofold)[90]. Several recent studies have suggested that abnormally high numbers of bioturbators or herbivores seen in some vegetated coastal ecosystems are at least in part due to loss of top-down control[31,32].

One good example of loss of predator control on C preservation within vegetated coastal habitats is in the salt marshes of Cape Cod, Massachusetts, US, where recreational overharvesting of predatory fish and crabs has triggered marsh die-off and major erosion through a trophic cascade[31]. Fish surveys and catch rates show that local predator biomass in areas of die-off is about 50% of that elsewhere. Experimental exclusion of predators from marsh habitat results in large increases in densities of grazing sesarmid crabs[31], as it does for other grazing species such as gastropods on marshes elsewhere[29]. In areas with low predator biomass, densities of grazing crabs are six-fold higher, as is grazing intensity on marsh plants[31]. The high densities of grazing crabs in Cape Cod led to complete loss of vegetation at the marsh edge and subsequent weakening of the sedimentary structure of the marsh, causing the action of moving water to erode the marsh surface. Over periods of several years, the entire marsh edge was removed to a depth of more than 1 m. Ultimately, the loss of top-down control resulted in the total loss of hundreds of years of C stocks from the system, and reduced the sequestration capacity of the Cape Cod marshes by an estimated 17 thousand tonnes of CO_2 per year (equivalent to the annual CO_2 emissions of ~3,000 cars).

Opportunities for management

Alterations to predator–prey relationships in vegetated coastal ecosystems have the potential to modify local and global C cycles in two primary ways: sequestration capacity and preservation of C stocks. As described in our above sections, predators can indirectly alter annual C burial in vegetated coastal ecosystem sediments and CO_2 uptake through primary production. Although salt marshes, seagrass meadows and mangroves have high global net primary productions of 0.18, 0.06 and 0.17 PgC yr^{-1}, respectively, this only offers short-term storage[4]. Conversely, C buried in the sediments of these systems can be stored for millennia[2,4,7], meaning that reductions in this capacity could have significant and costly effects on the global C cycle. Using the 20% decrease in C burial observed in our mangrove example (Fig. 2), if only 10% of vegetated coastal ecosystems were affected by predator loss (far less than would be expected from a 90% reduction in marine predators[21]), the global CO_2 uptake by natural ecosystems could be reduced by ~9.5 million tonnes (cost of US$390 million, based on a market value of US$41 per tonne). If those same ecosystems had a 50% or 90% reduction in annual C burial (as was seen in the Cape Cod salt marsh), this could reduce the global CO_2 uptake by ~23.7–42.7 million tonnes at a cost of US$972 million to 1.8 billion. These losses in annual C sequestration under the 20%, 50% and 90% reduction scenarios are equivalent to the C sequestration capacity of a forest the size of Belgium (20% scenario), Panama (50% scenario) or Greece (90% scenario). Second, vegetated coastal ecosystems hold a significant amount of C in their sediments (Table 1). Disturbances that result in the loss of vegetation and bank erosion can lead to the release and eventual remineralization of C stocks down to 1 metre in the sediment[24,32]. We currently lack estimates of the global area affected by overgrazing and bioturbation; however, even if only 1% of vegetated coastal ecosystems were exposed to trophic cascades that resulted in the loss of the top metre of sediment, this could result in ~460 million tonnes of CO_2 being released. These emissions are equivalent to the annual CO_2 production of ~97 million cars, or the total number of cars registered in 2010 in the United Kingdom, Spain and France combined. Despite the large potential for trophic cascades to degrade vegetated coastal ecosystems and alter C accumulation and preservation, they are currently not incorporated in estimates of global habitat loss[24] nor are they addressed in blue C initiatives[7].

Optimizing C sequestration and the protection of C stocks within vegetated coastal ecosystems will need to involve careful consideration and proactive management of predator populations and their effects on herbivores/bioturbators. Conceptually, various management scenarios can be viewed as a continuum that transitions between three ecosystem states (Fig. 3). Scenario (1) represents an ecosystem state where management either prioritizes herbivore/bioturbator populations (for example green sea turtles) or allows overharvesting of predators. In this scenario, predator populations (for example, large sharks) are greatly reduced, resulting in the release of herbivores (such as sea turtles) or bioturbators (crabs, for example) from predation, intensified removal and destruction of vegetation and depressed C storage potential. To envisage the full implications of intense grazing pressure, consider the case of green turtles. Long-term historic declines in green turtles numbers are thought to have occurred since the fifteenth century through harvesting[93] and, in most places, turtle numbers have probably not recovered to pre-exploitation levels. But in some cases strong conservation programs and declining predator numbers may have led to green turtle densities overshooting historical levels, with consequent seagrass destruction[13,59]. The seagrass meadows of Shark Bay, Western Australia, can help to provide insight as to how an altered predator–prey relationship could potentially shape C storage. Currently, Shark Bay has an intact food web with large populations of both predators and herbivores. Natural predator–prey dynamics across the bay has resulted in both areas with high and areas with low predation pressure[27]. Areas of the bay with high predation pressure have ~60% greater C stocks than areas of the bay with low predation pressure (Fig. 2; see Supplementary Information). If the entire 160 km^2 of seagrass habitat in the Eastern Gulf of Shark Bay had been historically converted to low-predation-pressure habitat from overfishing, it could have resulted in the loss of up to 134 thousand tonnes of CO_2.

Scenario (2) represents an ecosystem state where management prioritizes C storage and sequestration. In this situation predator populations are protected or remain intact, resulting in decreased

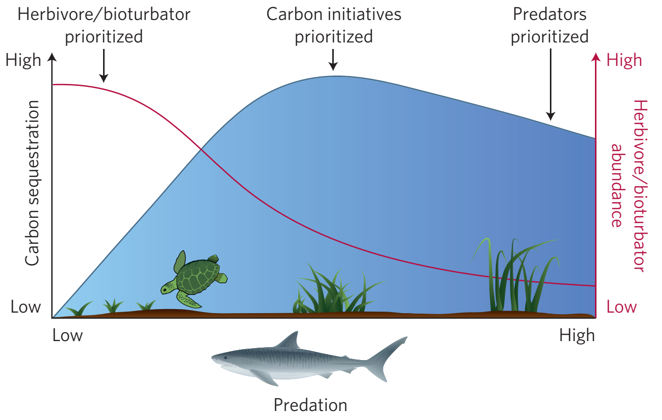

Figure 3 | Different priorities. Conceptual diagram showing how changes to predation pressure as a result of different conservation prioritization are likely to influence herbivore and bioturbator effects on plant growth and the C sequestration capacity of vegetated coastal habitats (for example salt marsh, seagrass and mangroves). Three different conservation needs are shown: (1) Conservation of herbivores/bioturbator (for example turtles, dugong) is the highest priority: has large negative implications for habitat complexity, and C sequestration. (2) Conservation of C initiatives is highest priority: has positive implications for habitat complexity and C sequestration, and intermediate to small negative implications for predators and herbivore/bioturbators. (3) Conservation of predator species is highest priority: has large negative implications for herbivore/bioturbator species and no or small negative implications for habitat complexity and C sequestration. This diagram represents situations in which the loss of predators directly or indirectly results in the increase (abundance or foraging behaviour) of herbivores/bioturbators. In a situation where loss of predators directly or indirectly resulted in the decrease of herbivores/bioturbators, the effects would be reversed. Shark image: DavidSzabo/iStock/Thinkstock; sea turtle image: Michael McClure/iStock/Thinkstock.

herbivore/bioturbator abundance and increased C storage or sequestration. Under this scenario, predators directly or indirectly suppress herbivores/bioturbators, such that overgrazing of vegetation or extensive bioturbation is avoided, but herbivore/bioturbator numbers remain sufficient to maintain vigorous plant growth through grazing/cropping or sediment aeration. Maintaining vegetation in a vigorous growth phase will enhance the amount of C fixed in plant tissues and deposited in sediments.

In scenario (3), management would prioritize protection of predators (for example fishing bans on sharks), but that protection would not extend to all of their food sources. In both scenarios (1) and (3), management efforts would take a species-based approach to conservation as opposed to a more ecosystem-based approach as in scenario (2). A state shift, from (2) to (3), would require heavy predation combined with other anthropogenic or natural effects that result in greatly depressed herbivore/bioturbator populations (for example harvesting or a disease outbreak). Although there are few examples of this scenario in marine systems, wolves and woodland caribou in British Columbia, Canada, provide a good example of how the protection of a predatory species can interact with other global change drivers to decrease a herbivore's population to near extinction[94]. The long-term persistence of this scenario is plausible without future declines in predator populations because many predators have a generalist diet that can allow for prey switching[95]. Furthermore, extinctions of functionally dominant marine herbivores, with or without high predator abundance, as a result of global change (such as establishment of an invasive predator) or overharvesting could present a similar situation for C sequestration to that shown in scenario (3). In scenario (3), vegetation will either remain stable or shift from a vigorous growth and C-fixing state to increasingly senescent. For example, in all three vegetated coastal ecosystems, intermediate levels of bioturbation allow aeration of the sediment and the removal of toxic sulphates on roots, promoting higher growth rates[76,96]. As a result, C storage and sequestration under scenario (3) would either remain constant or be slightly reduced.

The above three scenarios highlight that balancing the conservation of individual species, both herbivores/bioturbators and predators, in conjunction with trying to maximize C storage, will inevitably require trade-offs, because not all can be maximized simultaneously (Fig. 3). Under management scenarios (2) and (3), C capture and storage is likely to be high. But in order to effectively maintain high C accumulation and preservation long-term, two additional factors must be considered. First, the strength and direction of predator effects on C capture and storage depend on food-chain length, and some situations may exist in which high predation pressure results in reduced C capture and storage. Focusing efforts on only top-down processes and ignoring bottom-up and context-dependent relationships can lead to further degradation of these ecosystems. Thus, efforts focused on C storage in vegetated coastal ecosystems need to be viewed at the ecosystem level and incorporate adaptable management of local food web dynamics. Second, many large predators have extensive home ranges that not only extend beyond the boundaries of a focal vegetated coastal ecosystem, but across national or international boundaries. In order to maintain high C stocks and sequestration rates within a focal vegetated coastal ecosystem, management efforts must combine ecosystem-level conservation at a local scale with species-level protection at a spatial scale that is related to the predator species involved.

Conclusions

We are now firmly entrenched in the Anthropocene, Earth's sixth recognized mass species extinction event[97]. There is little doubt that substantial biodiversity loss will greatly alter the structure and function of ecosystems[8,98,99]. From freshwater and terrestrial studies we know that predator losses and their cascading effects on community structure and composition can have negative effects on the capacity of natural ecosystems to sequester atmospheric CO_2 (refs 11,77). If the role of predators on C cycling proves to be similar in vegetated coastal habitats to their role in other ecosystems, as we argue, the implications of their loss on the global C cycle are concerning, considering the significant contributions such ecosystems provide in long-term C storage. Here we have shown that top-down control in vegetated coastal ecosystems seems widespread, and there are multiple pathways by which predators influence accumulation and preservation of C in the sediments and plants of these ecosystems.

Although we have focused our discussion on vegetated coastal ecosystems because of their importance in the oceanic C cycle, predators probably influence C cycling in many other marine ecosystems such as kelp forests[9], coral reefs and open oceans. In order to provide a global synthesis of the effects of predators on C cycling in marine environments, further research in other marine systems is urgently needed. There is still hope that stronger conservation efforts and stricter fishing regulations can ameliorate anthropogenic effects on marine predator populations[100]. It is alluring to think that these efforts could help to remedy our extinction footprint and defend us against climate change and its impacts simultaneously. The future role that vegetated coastal ecosystems play in climate change mitigation will in part depend on the preservation of marine predators, and therefore, policy and management need to reflect this important realization as a matter of urgency.

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Author contributions

All authors helped to conceive the manuscript. T.B.A. led the writing with contributions from all authors. T.B.A., R.C., C.L. and J.F. contributed to data analyses.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence should be addressed to T.B.A.

Competing financial interests

The authors declare no competing financial interests.