


Opinion

Whales in the carbon cycle: can recovery remove carbon dioxide?

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The great whales (baleen and sperm whales), through their massive size and wide distribution, influence ecosystem and carbon dynamics. Whales directly store carbon in their biomass and contribute to carbon export through sinking carcasses. Whale excreta may stimulate phytoplankton growth and capture atmospheric CO₂; such indirect pathways represent the greatest potential for whale-carbon sequestration but are poorly understood. We quantify the carbon values of whales while recognizing the numerous ecosystem, cultural, and moral motivations to protect them. We also propose a framework to quantify the economic value of whale carbon as populations change over time. Finally, we suggest research to address key unknowns (e.g., bioavailability of whale-derived nutrients to phytoplankton, species- and region-specific variability in whale carbon contributions).

Whales and the oceanic carbon cycle

The ocean is an important **carbon sink** (see [Glossary](#)), absorbing approximately 22% of anthropogenic carbon emissions during 2010–2019 [1], some of which is exported to the deep sea [2]. A better understanding of the role of its largest biota, the **great whales**, in the **carbon cycle** is needed to better inform ocean management and **carbon dioxide removal (CDR)** strategies. We discuss the importance of whales to marine ecosystems and their role in the **biological carbon pump (BCP)**, assess their potential to contribute to **carbon storage** and **carbon sequestration**, and consider how whale **carbon services** could play a role in climate-change mitigation strategies.

Whales and marine ecosystems

Blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales are the two largest animals to ever exist on Earth [3,4]. The gigantism of filter-feeding baleen whales results from high energetic efficiency facilitated by feeding on dense, high-energy prey patches with physical adaptations that allow them to engulf large amounts of prey [5,6]. Their size and longevity allow great whales to exert strong effects on the carbon cycle by: (i) storing carbon more effectively than small animals [7], (ii) ingesting extreme quantities of prey [7], and (iii) producing large volumes of waste products [8]. Considering that baleen whales have some of the longest migrations on the planet [9], they potentially influence nutrient dynamics and carbon cycling over ocean-basin scales [10–12].

Industrial whaling is estimated to have reduced great whale biomass by 81% (L.B. Christensen, MSc thesis, The University of British Columbia, 2006), resulting in the removal of an estimated 0.017 Gt carbon stored in baleen whale biomass [7]. In addition, depletion of the great whales may have altered **top-down forcing** [13–15], which further impacted carbon-cycling dynamics [8,16–18]. Whereas industrial whaling had the largest impact on great whale population

Highlights

As climate change accelerates, there is increasing interest in the ability of whales to trap carbon (i.e., whale carbon), yet it is currently undetermined if and how whale carbon should be used in climate-change mitigation strategies.

Restoring whale populations will enhance carbon storage in whale biomass and sequestration in the deep sea via whale falls, though the global impact will be relatively small.

Whale-stimulated primary productivity via nutrient provisioning may sequester substantially more carbon, though there is uncertainty regarding the carbon fate in these food webs.

Recovery of whale populations via reduction of anthropogenic impacts can aid in carbon dioxide removal but its inclusion in climate policy needs to be grounded in the best available science and considered in tandem with other strategies known to directly reduce greenhouse gas emissions.

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abundance [19] and body size [20], modern populations continue to face threats from fisheries entanglement [21], climate-change-induced shifts in prey distribution and abundance [22], noise pollution [23], ship strikes [24], marine debris [25], and, in some areas, continued commercial whaling [26].

The BCP

The ocean's carbon pump is a complex combination of biological, chemical, and physical processes that control the transfer of carbon into the ocean interior where it is removed from exchange with the atmosphere for long time periods [27,28]. The BCP dominates the total sequestration of carbon in the ocean [29] and it can vary regionally by nearly an order of magnitude.

Carbon export generally decreases from the poles to the equator and nearshore to the ocean gyres. The BCP can be further separated into the **gravitational export pump** and **particle injection pumps** [27], which in aggregate are estimated to transfer 4–12 Gt C year⁻¹ to the deep sea [2,30,31].

Diel vertical migrations (DVMs) of mesopelagic fishes and zooplankton drive the **mesopelagic-migrant pump** (one component of the particle injection pump), comprising the largest migration of animals on Earth in terms of abundance and biomass [32]. Consequently, the DVM of mesopelagic nekton can actively transport nutrients and organic matter between the **epipelagic** and deep ocean [32,33]. DVM transport of carbon and nitrogen from the epipelagic, where many copepods, euphausiids, and salps feed at night in shallow, phytoplankton-rich waters, to depths where they excrete waste products can be a large component of carbon and nitrogen export [34,35]. Nonetheless, in some circumstances, the fluxes of organic matter and nutrients may be upward. For example, Antarctic krill (*Euphausia superba*) can forage on the benthos and then migrate into surface waters, releasing high concentrations of new and remineralized iron into the **photic zone** [34,36,37]. Further, marine mammals (e.g., whales), seabirds, and large fishes forage extensively on vertically migrating zooplankton and mesopelagic fish [38,39], releasing nutrient-rich excreta into surface waters and stimulating primary production [40,41]. These connections comprise a potentially important feedback for carbon export and storage.

Carbon persistence

The nomenclature of **carbon persistence** differs by timescale. Carbon storage refers to short-term carbon retention in organismal tissues [42]. For longer-lived animals such as whales, carbon storage can be on the order of decades to centuries. For organisms in the great whale food web (phytoplankton, zooplankton, forage fish, and squid), carbon storage is days to years.

Carbon sequestration, however, extends beyond the time horizon of carbon storage and it often follows from more complex dynamics. For example, great whale excreta are highly enriched in **limiting nutrients**, including nitrogen, phosphorus, and trace metals (e.g., iron) that baleen whales recycle within the epipelagic (see Whale pump section; Figure 1A) [11,40,43–48]. In the case of sperm whales (*Physeter macrocephalus*), the transport of these limiting nutrients from the deep ocean can enhance phytoplankton production in the photic zone. A portion of this whale-stimulated primary and secondary productivity is recycled within the upper-ocean detrital food web. The amount that escapes recycling within the upper ocean can be exported below the maximum mixing depth and sequestered on timescales of centuries to millennia. As such, deep carbon export leading to sequestration is an important sink for CO₂, yet the influence of whales on deep carbon export and the BCP is largely unknown. **Export efficiency** (which can lead to long-term sequestration) spans three orders of magnitude (range: 0.0001–0.24 [49,50]) due to variability in productivity across the global ocean. It is also a process particularly difficult to influence and measure.

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Direct and indirect carbon pathways of whales

Direct pathways

Biomass

In the **pelagic** ocean, animals comprise the vast majority of the biomass capable of storing carbon from one year to the next [51]. Because whales are among the longest-lived animals, they may constitute one of the largest stable living carbon pools in the pelagic ocean. The singularly large size of the great whales means that they interact with the carbon cycle in unique ways. While it is obvious that whaling reduced the amount of carbon stored in populations of great whales, it is not clear if whaling was a net source of CO₂ to the atmosphere.

Pershing *et al.* [7] proposed that because metabolic rates scale with individual biomass raised to a power less than one (typically assumed to be $\frac{3}{4}$ [52]), the large size of whales makes them more efficient at storing carbon. Using $\frac{3}{4}$ scaling, they calculated that removing one 92-ton blue whale would provide enough uneaten krill to support seven minke whales (*Balaenoptera acutorostrata*) or 1800 Adelie penguins (*Pygoscelis adeliae*). However, the new minke whales would have only 50% of the biomass of the missing blue whale, while the new penguins would have only 8% of the biomass. This relationship suggests that the reduction of blue whales and other baleen whales in the Southern Ocean has led to an ecosystem that maintains a lower total biomass of living carbon and releases a greater amount of CO₂ for a given amount of ingested krill, than prior to industrial whaling.

Whale falls

Large body size means that whales are particularly efficient at transferring carbon to the deep sea via **whale falls** [7,53]. The overall reduction in the number of whales and, specifically, the loss of larger species and larger individuals, has altered the flux of whale carbon to the deep sea and caused extinctions of **whale-fall specialists** in the North Atlantic [20].

Indirect pathways

Whale excreta released in surface waters are rich in limiting nutrients. These nutrients, released across both vertical and horizontal gradients, may stimulate **carbon fixation** by phytoplankton, enhancing ecosystem productivity and potentially stimulating carbon storage, export, and sequestration (Figure 1) [11,40,54,55]. Two indirect pathways are discussed next: the whale pump and the great whale conveyor belt.

Whale pump

Buoyant fecal plumes released by whales can provide limiting nutrient concentrations three to seven orders of magnitude higher than background seawater concentrations [40,45–47,56] and can persist at the surface, allowing nutrients to leach into the surrounding seawater and become bioavailable to phytoplankton [40,45,46,57]. Nutrient recycling and transport by whales and other top predators may push planktonic food web structure toward systems dominated by large-celled, quickly sinking diatoms and krill that could affect carbon export [44,58]. DVM by whale prey (e.g., krill) and other nekton provides a particle injection pump that increases export efficiency relative to gravitational flux of particles alone [27]. In locations of high productivity and whale abundance, zooplankton fecal material, exuviae, and carcasses provide considerable pulses of carbon to the deep sea, thereby demonstrating the importance of whale prey to deep carbon export [50,59–61].

Whales unlock nutrients in prey through their feeding behavior and digestive processing. Specifically, **allochthonous nutrients** promote new primary production, carbon storage, export, and potentially, sequestration, while **autochthonous nutrients** promote recycled primary production

Glossary

Additionality: carbon benefits, accrued from a policy/management intervention, exceeding the *status quo*.

Allochthonous nutrients: nutrients originating outside a defined system.

Autochthonous nutrients: nutrients recycled within a defined system.

Biological carbon pump (BCP): sum of all biological and physical processes by which biologically derived organic carbon is transported to the ocean depth.

Blue carbon: carbon naturally captured by marine biota, originally used in reference to coastal mangroves, salt marshes, and seagrasses [83].

Capital breeder: animal that feeds and stores energy before the breeding season, relying on accumulated energy stores to reproduce.

Carbon cycle: sum of processes comprising the flux of carbon atoms between the atmosphere, oceans, soils, and sediments, and the organisms living therein.

Carbon dioxide removal (CDR): capture or retention of CO₂, either naturally or artificially, so that it is taken from the atmosphere for a defined period of time.

Carbon export: flux of organic carbon, derived from CO₂ via photosynthesis, from the upper water column to depth (often considered below the maximum annual surface mixed layer depth).

Carbon fixation: conversion of inorganic carbon (CO₂) into organic carbon (i.e., photosynthesis).

Carbon persistence: tendency for carbon to remain in a reservoir and out of atmospheric contact.

Carbon sequestration: removal of atmospheric organic carbon, generally via photosynthesis, for geologic timescales ≥ 100 years.

Carbon service: natural processes that remove organic carbon, derived from CO₂ via photosynthesis, from the atmosphere.

Carbon sink: process that removes more carbon (generally derived from CO₂ via photosynthesis) from the atmosphere than it emits.

Carbon storage: removal of carbon, derived from CO₂ via photosynthesis, from the atmosphere for <100 years.

Diel vertical migration (DVM): daily movement of zooplankton, fish, and cephalopods (e.g., squid, octopus) to feed nocturnally in surface waters before returning to depth during the daytime.

(Figure 1A [62]). Deep-diving cetaceans, such as sperm whales, feed almost exclusively on cephalopods living well below the **surface mixed layer** [63,64] and thus are presumed to release allochthonous fecal nutrients at the surface (Figure 1A) [43]. In contrast, shallow-diving cetaceans, such as baleen whales, often feed within the surface mixed layer [8,64] and thus are presumed to generally release autochthonous nutrients at the surface [44].

The distinction between new versus regenerated nutrients has implications for carbon cycling and, importantly, export calculations. Nonetheless, observations that overall ecosystem productivity has declined in regions with depleted whale populations (e.g., the Southern Ocean) suggest that the role of whales in nutrient cycling is critical to ecosystem functioning and their associated carbon sequestration potential [8,10,11,40,44].

Great whale conveyor belt

Many great whales are **capital breeders**, migrating from high-latitude, nutrient-rich feeding grounds where they spend the summer to low-latitude, nutrient-poor breeding grounds where they spend the winter (Figure 1B) [65]. Whales usually fast on the breeding grounds, metabolizing lipid-rich blubber for maintenance and, in females, for lactation [10]. Allochthonous nutrient inputs via carcasses, excreta (e.g., urine, placentas), and other byproducts (e.g., sloughed skin) derived from nutrients ingested on the feeding grounds have the potential to stimulate new productivity, carbon export, and carbon sequestration when they are released on the breeding grounds [65]. For species such as humpback (*Megaptera novaeangliae*), right (*Eubalaena* spp.), and gray (*Eschrichtius robustus*) whales, breeding grounds tend to be shallow, with lower nutrient concentrations and higher densities of breeding whales. The nutrient subsidies that migratory whales bring into these systems also support fish, scavengers, and benthic macroinvertebrates [66].

Quantifying the carbon roles of whales

To date, five studies have quantified the role of the great whales in direct or indirect carbon pathways (Table 1). However, we caution that current estimates do not represent the total direct and indirect carbon contributions from all great whale species across all oceans. Specifically, global biomass and whale-fall carbon values did not consider sperm whales [7], the whale pump was examined for just five great whale species in the Southern Ocean [8,43,44], and examination of the great whale conveyor belt was limited to Southern Hemisphere blue whales [10]. Thus, the values in Table 1 represent a fraction of the total contribution of the great whales to the carbon cycle. It should be noted that some estimates report wide confidence intervals spanning multiple orders of magnitude. We have a higher level of confidence in the direct carbon pathway estimates, such as biomass and whale falls, than the indirect carbon pathway estimates. Nonetheless, the great whale populations studied to date (Table 1) currently produce an estimated 2.0×10^{-3} Gt C storage [7], 6.2×10^{-5} Gt C year⁻¹ sequestration, 2.2×10^{-2} Gt C year⁻¹ fixation [8,10], and 4.0×10^{-4} Gt C year⁻¹ export [43].

As industrial whaling devastated great whale populations and their associated carbon benefits by an order of magnitude or more (Table 1), these values should be considered a lower bound because the full carbon values of the great whales have yet to be restored. This may provide an opportunity to enhance CDR from the great whales. Still, the currently known carbon contributions from the great whales are small compared with carbon stored in all marine animals (~1.4 Gt C [67]) or exported via the BCP [2,30,31].

Recently, an outsized role for great whales in carbon fixation, storage, and sequestration was suggested (e.g., carbon contribution of a single blue whale valued at \$1.4 million [68,69]). These estimates, based on assumptions beyond our understanding of whale ecology and

Earth system model: model that simulates carbon movement through atmospheric, terrestrial, and marine environments.

Epipelagic: open ocean waters from the surface to approximately 200 m depth.

Export efficiency: portion of primary productivity (PP) sinking from the upper water column (oftentimes defined as below the maximum annual surface mixed layer depth), quantified as export flux/PP.

Gravitational export pump: downward flux of carbon in the ocean due to gravitational sinking of biologically derived particles.

Great whales: baleen and sperm whales.

Limiting nutrient: nutrient required by phytoplankton for photosynthesis but typically present in small quantities and which limits phytoplankton rate processes and/or standing stocks.

Mesopelagic-migrant pump: type of particle injection pump through which vertically moving biota can directly, by grazing, and indirectly, by boundary layer drag, move particles from the surface ocean to depth.

Nature-based solution (NBS): action that conserves and sustainably manages ecosystems that also promotes biodiversity and human well-being.

Particle injection pump: physical processes that actively transport biologically derived carbon to ocean depths.

Pelagic: open ocean waters.

Photic zone: sunlit portion of the upper water column where photosynthesis occurs.

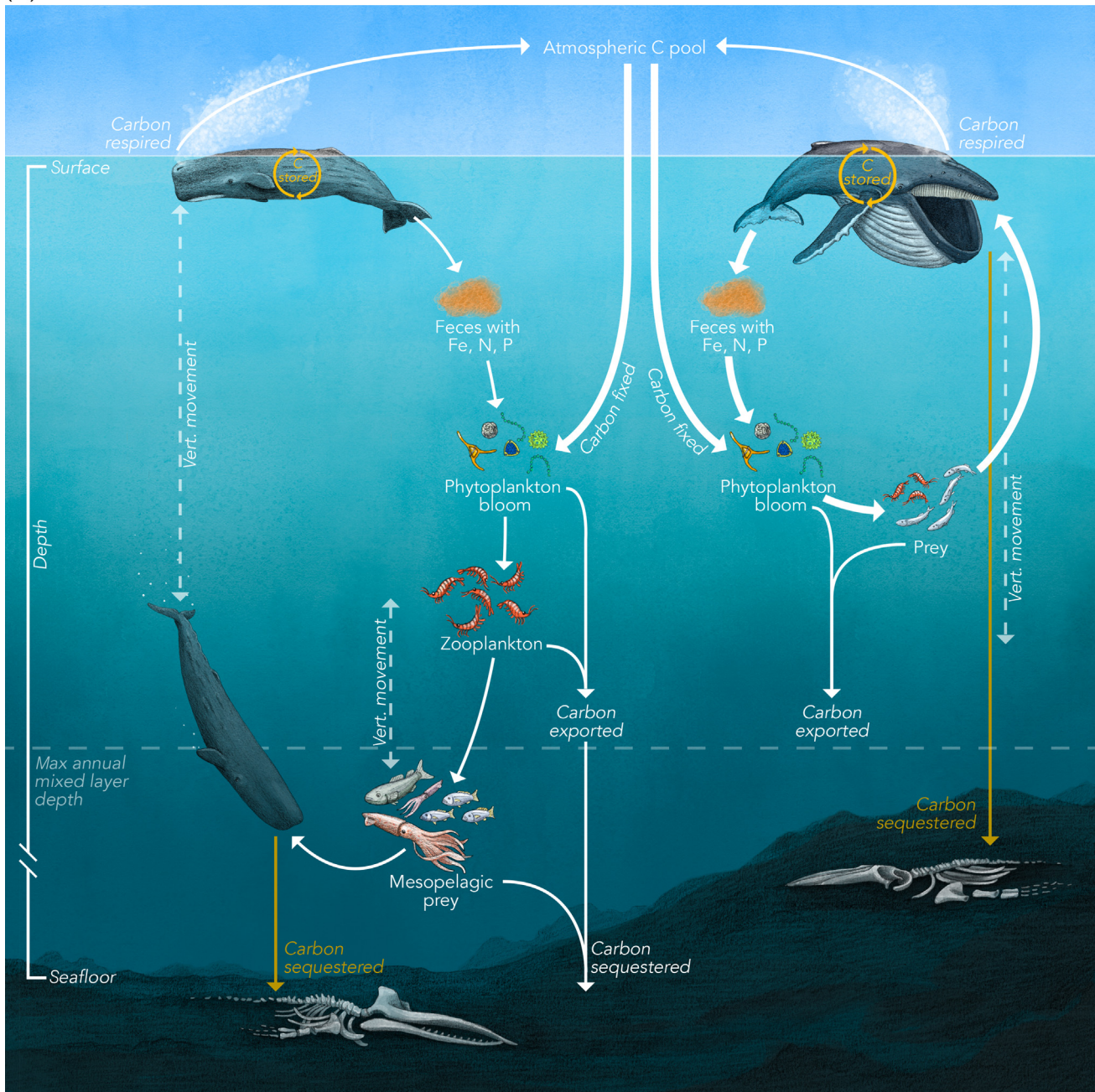
Surface mixed layer: uppermost, unstratified layer of the water column.

Top-down forcing: ecosystem effects arising from upper-trophic level changes.

Whale fall: whale carcasses that sink to the deep sea.

Whale-fall specialists: fauna relying on deep-sea whale carcasses to complete their life cycles.

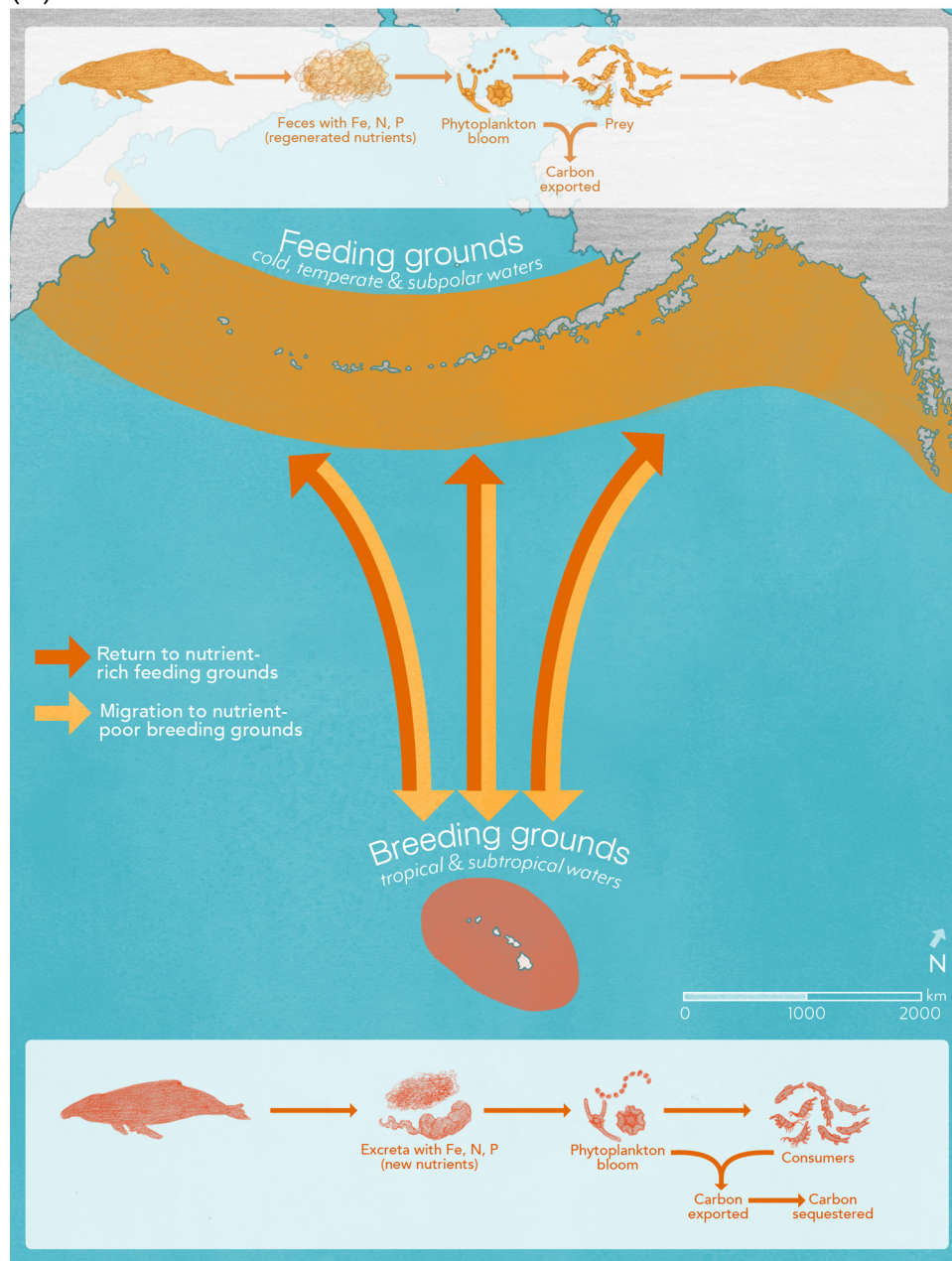
(A)



Trends in Ecology & Evolution

Figure 1. Great whales' direct and indirect nutrient and carbon cycling pathways. (A) A hypothetical Southern Ocean, demonstrated by two endmembers (deep-diving sperm whale, *Physeter macrocephalus*, left, vs. shallow-diving mysticete, right) that share the same direct carbon pathways (i.e., biomass carbon, whale falls) but differ in their indirect carbon pathways (i.e., the whale pump). Sperm whales, feeding below the mixed layer, release new nutrients at the surface, stimulating new primary production, carbon export, and carbon sequestration. Mysticetes, feeding within the mixed layer, release regenerated nutrients at the surface, stimulating recycled primary production and carbon export. Arrow thickness indicates relative magnitude of the carbon flux. Arrow color indicates direct (orange) versus indirect (white) pathways. (B) The great whale conveyor belt, an indirect carbon pathway depicting nutrient and carbon fluxes between humpback whale (*Megaptera novaeangliae*) feeding and breeding grounds in the North Pacific Ocean. Nutrients released on the breeding grounds are assumed to be new nutrients to the system, thus stimulating new primary production, carbon export, and carbon sequestration. Nutrients released on the feeding grounds will follow a pathway similar to the mysticete in panel A. While not shown, direct carbon pathways (see panel A) will also occur on both the feeding and breeding grounds. Illustrations by Alex Boersma.

(B)



Trends in Ecology & Evolution

Figure 1 (continued).

biological oceanography, give values for whales that do not acknowledge the complexity and spatiotemporal variability inherent to whale ecosystem effects (Box 1). We recommend an economic framework for quantifying the carbon values of great whales that is grounded in whale ecology and biological oceanography (Box 2). **Earth system models** may aid in quantifying indirect carbon pathways by simulating the impact of whale-derived nutrients on phytoplankton

Table 1. Estimated carbon (C) fate (fixed, stored, exported, sequestered) in pre-industrial whaling and modern-day great whale populations

Mechanism	Species	Region	Pre-whaling C estimate ^a (N)	Modern C estimate (N, year)	C fate	Refs
Biomass	8 Baleen whale taxa ^b	Global	1.1×10^{-2} Gt C (2.9×10^6)	2.0×10^{-3} Gt C (1.1×10^6 , 2016)	Stored ^c	Updated from [7] ^d
Whale falls	All baleen whales	Global	3.6×10^{-4} Gt C/year (2.9×10^6)	6.2×10^{-5} Gt C/year (1.1×10^6 , 2016)	Sequestered	Updated from [7,95] ^e
Whale pump	Blue whale	Southern Ocean	1.3×10^{-1} Gt C/year, range: 5.2×10^{-2} Gt C/year to 2×10^2 Gt C/year (2.4×10^5)	2.8×10^{-3} Gt C/year, range: 1.2×10^{-3} to 4.5×10^{-3} Gt C/year (5.2×10^3 , 2012)	Fixed	[44]
Whale pump	Blue, fin, humpback, and Antarctic minke whales	Southern Ocean	2.2×10^{-1} Gt C/year; range: 2.7×10^{-2} to 1.5 Gt C/year	2.2×10^{-2} Gt C/year; range: 2.7×10^{-3} to 1.5×10^{-1} Gt C/year	Fixed	[8]
Whale pump	Sperm whale (<i>Physeter macrocephalus</i>)	Southern Ocean	2.4×10^{-3} Gt C/year ($\sim 1.2 \times 10^5$)	4×10^{-4} Gt C/year (1.2×10^4 , 2001)	Exported	[43]
Great whale conveyor belt	Blue whale	Southern Hemisphere	1.4×10^{-4} Gt C/year (3.3×10^5)	5.1×10^{-7} Gt C/year (1.2×10^3 , 2001)	Fixed	[10]

^aAll C values are gross and do not account for the amount of C respired by great whales.

^bMinke (*Balaenoptera acutorostrata*), Antarctic minke (*Balaenoptera bonaerensis*), sei (*Balaenoptera borealis*), Bryde's (*Balaenoptera brydei*), blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), bowhead (*Balaena mysticetus*), gray (*Eschrichtius robustus*), right (*Eubalaena* spp.), and humpback (*Megaptera novaeangliae*) whales.

^cWhile some great whales can live >100 years, most known lifespans of these species are <100 years; thus, the C is considered stored.

^dValues calculated per Pershing *et al.* [7] using updated pre-whaling and modern population estimates from Smith *et al.* [20].

^ePershing *et al.* [7] was the first attempt to calculate C export by whale falls. They used a conservative assumption that 50% of rorqual and gray whale carcasses are exported while only 10% of right and bowhead whale carcasses are exported. Smith and Baco [95] suggested that a high proportion of whale deaths occur during migration. Even for North Atlantic right whales (*Eubalaena glacialis*), a coastal species with a robust monitoring network, the observed number of carcasses is much lower than the estimated number of whale deaths. For this paper, we used higher percentages: 90% for rorquals and gray whales, 50% for right and bowhead whales. This increases the export flux estimates by a factor of 1.8 compared with the original values.

and zooplankton communities and their associated carbon export. As data become available, the economic framework can be populated to estimate whale carbon values for different whale populations and the predicted impact of conservation interventions.

Can great whale recovery be a nature-based solution to climate change?

Two-thirds of signatories to the Paris Agreement have committed to **nature-based solutions (NBS)** to meet the goal of limiting global air temperature rise to $\leq 1.5^\circ\text{C}$ above pre-industrial levels [70,71]. Protection of **blue carbon** ecosystems is a nature-based climate mitigation and adaptation solution declared in the nationally determined contributions (NDCs) of 45 nations [72]. Whereas these NDCs pertain to coastal blue carbon, quantification of carbon values in other marine biota has expanded the concept to include noncoastal or oceanic systems [42,73–79]. For marine vertebrates, however, based on currently available data, there remains significant uncertainty about their carbon sequestration potential and the ability to effectively manage their role in CDR remains debated [80]. As more data become available, it is likely this level of uncertainty will decrease.

There have been several studies examining the impact of whales on the carbon cycle that hold promise for including whales in blue carbon schemes (Table 1), though whether they achieve the criteria outlined by Lovelock and Duarte remains to be seen [73]. Although it is clear that great whales are capable of CDR through direct pathways (Table 1), the many unknowns in the indirect pathways (Figure 1, see Outstanding questions) preclude quantification at this time of the full magnitude of whale-CDR required for integration into NBS calculations (e.g., *sensu* [80,81]) or NDCs. For comparison, coastal blue carbon systems sequester $0.08\text{--}0.2$ Gt C year⁻¹ [82] and marine vertebrates (including great whales) assessed so far sequester $0.03\text{--}0.05$ Gt C year⁻¹ (though this covers a limited number of species across limited regions) [54]. The global potential for CDR via marine ecosystem recovery is likely to be <0.3 Gt C year⁻¹ [65].

Box 1. Monetizing whale carbon

Whales provide numerous ecosystem services such as tourism in the form of whale watching, enhanced primary productivity, and carbon sequestration, along with cultural benefits such as education, aesthetics, and existence value [89]. Recent attempts to monetize whales have garnered attention by valuing an ‘average’ whale at \$2 million for carbon-capture and other services [68,69]. As the authors of several foundational papers cited in these reports, we feel the scientific support for this valuation is lacking [90,91]. Here, we present five concerns regarding the monetary valuations of carbon dioxide removal (CDR) by whales as proposed by Chami *et al.* [69].

1. Whales are proposed to increase primary productivity globally by 1%, with no supporting empirical data. Whales can increase primary productivity, but the magnitude of this varies by species, location, and season [66]. Whales are absent from vast areas, with no indication that they could increase phytoplankton productivity by 1%.
2. Organisms’ lifespan influences the duration of carbon storage. Whereas whales can store carbon for decades or longer, phytoplankton and zooplankton typically store carbon for days to months (see ‘Carbon persistence’). Such short-term storage is generally not considered applicable for carbon-mitigation schemes, which seek storage for ≥ 100 years [65]. Carbon must be transported into the deep ocean, or buried in sediments, to achieve centennial sequestration times [86]. One method used to calculate export efficiency assumes that 10% of net primary production is exported and 10% of that is sequestered below 1000 m, but export and sequestration efficiencies vary considerably by location [65,86]. Regional variation in carbon-storage time and efficiency could reasonably reduce the estimated CDR resulting from whale stimulation of phytoplankton production by 100-fold.
3. Baleen whales often feed and defecate in the mixed layer, yielding primary production from nutrient regeneration [92]. Although surface-feeding whales can play an important role in nutrient recycling, they would have little effect on new production, carbon export, or CDR, further reducing the values proposed.
4. The model relies on overly simplistic assumptions about whale population growth. Age and size structure should be considered due to influences on carbon-storage duration (Box 2).
5. The most advanced work on whales and carbon sequestration (see ‘Whale falls’) was not included.

Whales contribute to vital ecological functions and ecosystem services, including CDR in whale falls, yet recent valuations go beyond our current understanding of their role in the carbon cycle [68,69]. To be viable for CDR strategies, carbon removal by whales should be measurable and long-term, similar to the Verified Carbon Standard on land (verra.org). Field experiments and models (e.g., Earth system models) could provide the requisite data, but recently proposed monetary values should not be implemented in CDR or other policy strategies before such scientific documentation.

A key component of blue carbon is the ability to manage and protect ecosystems for climate-change mitigation [73,83]. The full CDR role of great whales (and other organisms) will only be realized through robust conservation and management interventions that directly promote population increases (e.g., bycatch mitigation, including entanglement reduction; vessel speed and noise reductions in whale hotspots; creation of marine protected areas). We emphasize that for whales to aid in CDR, **additionality** needs to occur [84].

Noting this, natural enhancement of the oceanic carbon sink via whale recovery could be an effective ‘low-regret’ [85] CDR strategy with less risk, longer permanency, and higher efficiency than geoengineering solutions (e.g., direct carbon injection into the ocean interior [86]). While the artificial enhancement of the BCP may be ‘leaky’, with effects persisting for a few decades to approximately 150 years [86], the lifespans of great whales range from at least 50 to 200 years [87,88]. When carbon persistence via reproduction is considered [54], whale recovery has the potential for long-term self-sustained enhancement of the ocean carbon sink by increasing the standing stock of stored carbon and carbon sequestered in the deep sea via direct pathways and enhancing the BCP via indirect pathways (Figure 1). Indeed, ecosystem functions (including carbon services) of whales have already been formally recognized by resolutions to the International Whaling Commission and the Convention on Migratory Species [66].

Concluding remarks

Understanding the role of whales in the carbon cycle is a dynamic and emerging field that may benefit both marine conservation and climate-change strategies. However, while whales are capable of some degree of CDR, there are numerous knowledge gaps (see Outstanding questions) [66] that must also be addressed by policy makers seeking to incorporate whale conservation

Outstanding questions

How effective are whales at creating and maintaining primary productivity hotspots leading to enhanced carbon sequestration? Quantification of cetacean foraging depth with respect to the annual mixed layer depth is needed to determine the contribution of fecal nutrients to carbon recycling versus export. The proportion of carbon derived from whale-stimulated productivity that persists in the food web versus exported, and potentially sequestered, likely varies by location and season.

How bioavailable are whale-derived nutrients? Phytoplankton uptake rate of whale-derived nutrients depends on numerous poorly understood factors (e.g., whale defecation depth, persistence of whale excreta in the photic zone, nutrient leaching rate, organic ligand presence, variation by whale and phytoplankton species, microbial loop remineralization). Estimates from previous studies should be empirically tested; incubation experiments may help.

What is the carbon flux from cetaceans to the atmosphere? Carbon flux from cetaceans to the atmosphere via respiration is needed to provide cetaceans’ net capacity for CO₂ removal. Few studies have included estimates of CO₂ loss to the atmosphere via respiration. Empirical data on breathing rates, respiratory tidal volume, and CO₂ exchange rates in the lungs are needed.

How does cetaceans’ impact on the carbon cycle vary by species and region? Cetaceans’ carbon effects likely have a patchy spatiotemporal distribution and spatial variability in sequestration timescales prohibits a single model of whale-mediated carbon sequestration for the global ocean. Caution must be exercised when extrapolating findings across species or regions, especially if both direct and indirect pathways are not included.

strategies as part of their climate policy. Persistence of carbon stored in whale bodies and exported to the deep sea as whale falls via direct pathways are the best resolved and most precise, yet the largest carbon benefits may result from the indirect pathways, which are also currently the least understood. Elucidating these key unknowns, including realizing the full potential for whales to sequester carbon, presents rich opportunities for further study. Achieving this goal will require interdisciplinary collaboration between marine ecologists, oceanographers, biogeochemists, carbon-cycle modelers, and economists.

Box 2. A bioeconomic framework for carbon valuation of a whale population

A simple framework to establish the carbon value of whales requires at least three components: (i) species-specific whale population dynamics, (ii) carbon dynamics, and (iii) economic valuation. The first component addresses how a whale and its offspring can capture carbon over their lifetimes. The second component addresses the processes by which whales directly and indirectly contribute to the fixation, storage, and sequestration of carbon. Both of these components will require species- or population-specific parameters. The third component aggregates these dynamics and connects them to the social cost of carbon. This intergenerational sequestration potential allows us to quantify the total and marginal carbon sequestration potential of whale populations. This framework allows for clear comparisons of different population trajectories and can also accommodate more complex modeling approaches that tackle parameter uncertainty and complex processes. A visual representation of this framework is shown in Figure 1, with a hypothetical business-as-usual (BAU) scenario and two alternative policy interventions.

Model

We use bold symbols to denote matrices and vectors and Greek letters to denote parameters in the model. When relevant, we use subindices to denote specific times or age classes.

Component 1: species-specific population dynamics

The discrete-time, density-dependent model of an age-structured population builds on [93] and is given by:

$$N_{t+1} = N_t + \delta(M - I)N_t \quad [I]$$

N_t is a $\alpha \times 1$ vector of age-specific population sizes at time t . Parameter α denotes the terminal age class of the population. The scalar δ induces density dependence in the form $\delta = \frac{K-N}{K}$, where N is the total population size (or total mass) and K is the carrying capacity. Finally, M is an $\alpha \times \alpha$ Leslie matrix and I is the identity matrix. Indexing age class with the letter i , and letting μ_i and σ_i be the age-specific fecundity and survival, respectively, M is given by:

$$M = \begin{bmatrix} \mu_1 \sigma_0 & \mu_2 \sigma_1 & \dots & \mu_\alpha \sigma_{\alpha-1} & 0 \\ \sigma_0 & 0 & \dots & 0 & 0 \\ 0 & \sigma_1 & \dots & 0 & 0 \\ 0 & 0 & \dots & \sigma_{\alpha-1} & 0 \end{bmatrix} \quad [II]$$

Component 2: carbon dynamics

The stock of whale carbon at time t is then given by:

$$\bar{C}_t = \underbrace{\sum_{i=1}^{\alpha} N_{it} M_i C^b}_{\text{In-body carbon}} + \underbrace{\sum_{i=1}^{\alpha} N_{it} M_i C^p}_{\text{Stimulated}} + \underbrace{\sum_{i=1}^{\alpha} (1 - \sigma_i) N_{it} M_i C^s}_{\text{Whalefall}} \quad [III]$$

C^b , C^p , and C^s represent the per-kilogram parameters of in-body storage of carbon, carbon storage via productivity enhancement, and sequestration due to death and sinking, respectively. These parameters can be obtained from theoretical and field studies [7,8,94]. Finally, M_i is the mass-at-age.

Component 3: valuation

The present value of whale carbon over a horizon of time T is given by:

$$V = \sum_{t=1}^T \frac{\theta_t \bar{C}_t \psi}{(1 + \rho)^t} \quad [IV]$$

θ_t represents the social cost of carbon (\$ per ton CO_2), ρ is the social discount rate, and ψ is the molecular weight ratio of CO_2 to C. Using a BAU scenario, where whale populations evolve with no additional interventions, allows us to estimate the current value of whale carbon, V^{BAU} . Simulating different interventions, like reducing or increasing mortality (e.g., mitigating entanglement or increasing fisheries activity in whale hotspots, respectively), one can calculate the net value of said intervention, V^{net} . The difference, $V^{\text{net}} - V^{\text{BAU}}$, is the relative value of carbon sequestered under the intervention. Figure 1 shows a comparison of two hypothetical alternative recovery paths and their value in relation to BAU.

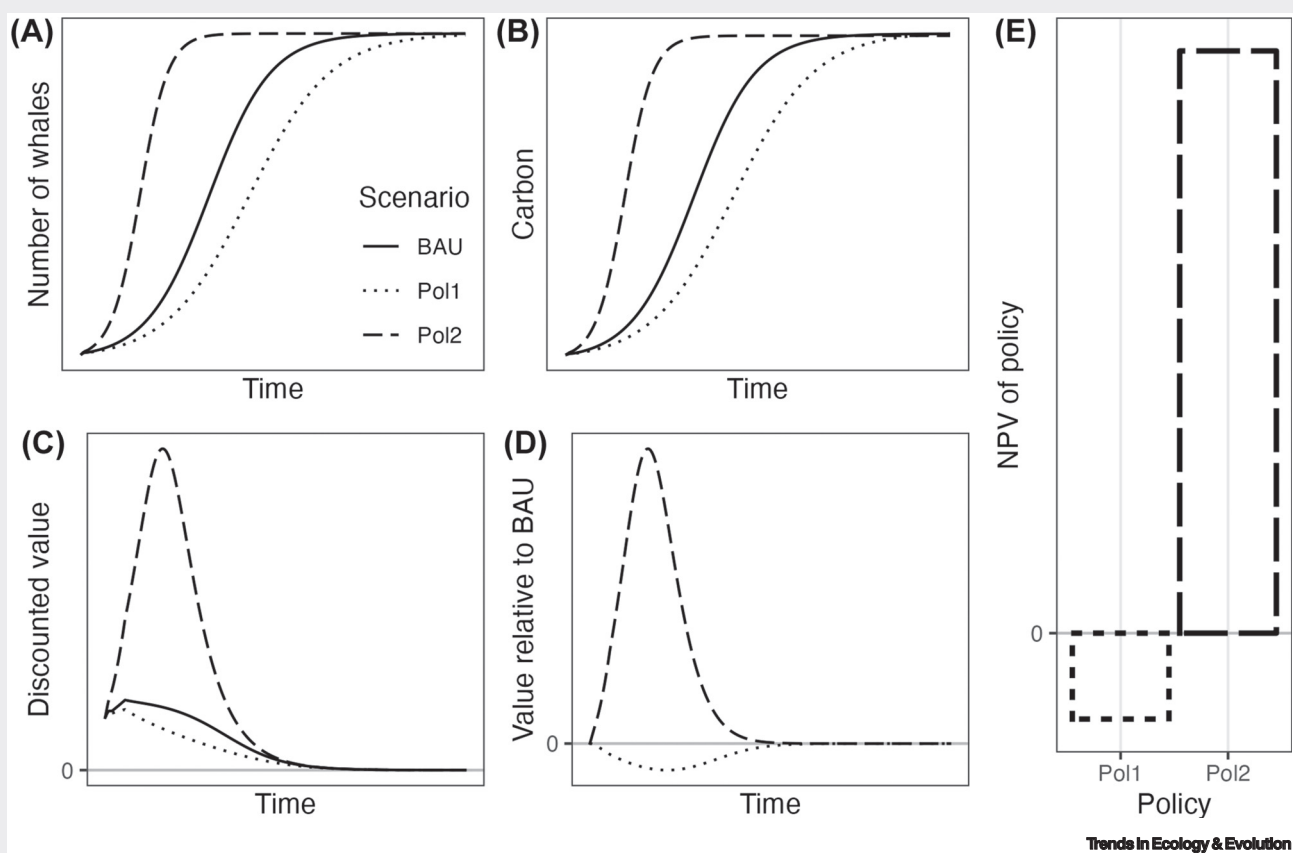


Figure 1. Stylized representation of the proposed bio-economic framework. Business-as-usual (BAU) represents the BAU scenario, while Pol1 and Pol2 represent recovery paths that are slower and faster at recovering the population, respectively. (A) Three population trajectories, (B) whale carbon associated with each trajectory, (C) discounted value of carbon through time, (D) the difference value relative to BAU, and (E) the net present value (NPV) of each policy.

Given the high uncertainty in many of the processes described earlier, and for many natural climate solutions in the ocean, we advocate for calculations of nature-based carbon sequestration that explicitly tackle this uncertainty. Importantly, considering the severe and escalating nature of the climate crisis, we feel it necessary that any consideration of whale recovery as a climate-change mitigation strategy be carefully assessed and considered in tandem with other mitigation strategies, particularly those that directly reduce greenhouse gas emissions. NBS grounded in a whole-ecosystem perspective, which includes natural abundances of species in protected ecosystems, will be essential to these approaches, as will better understanding of the ecological functions provided by whales and other marine species [65]. We suggest that the precautionary principle be applied to promote recovery of whale populations as a holistic ecosystem goal. This is likely to garner multiple benefits to combat the biodiversity and climate crises of the Anthropocene, including enhanced ecosystem health, productivity, and resilience [8,10], with CDR being a co-benefit [84]. There is power in the totality of actions taken concomitantly to meet the climate challenge.

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Declaration of interests

No interests are declared.

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