Historical and Potential Future Importance of Marine Megafauna Subsidies to Terrestrial Ecosystems

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Abstract

Marine megafauna exert tremendous influence on the structure and function of ocean ecosystems, yet mounting evidence shows that their ecological impacts also cross the land-sea interface and modify terrestrial ecosystem dynamics. Marine megafauna connect land and sea by serving as large, calorically-rich food sources for terrestrial consumers and by transferring marine-derived nutrients onto land as carrion, eggs, placentas, and excreta. We synthesize empirical studies from around the world to characterize the broad suite of terrestrial consumers that exploit marine megafauna as food and the ecological impacts arising from these cross-ecosystem resource subsidies. We identified 224 megafauna-consumer species pairs and diverse ecological effects impacting terrestrial consumers, populations, communities, and ecosystems. Given that commercial exploitation has decimated marine megafauna populations globally, land-sea linkages once mediated by these animals have declined from historical periods to the present day, yet megafauna recoveries hold potential to restore these marine-terrestrial connections and reshape coastal ecosystem dynamics.

In a Nutshell

- Marine megafauna facilitate the transfer of nutrients from marine to terrestrial ecosystems by serving as both food sources for land-based consumers and vectors of marine-derived nutrients.
- Megafauna-mediated nutrient flows can drive substantial changes to the structure and function of terrestrial ecosystems. Such effects have likely been diminished due to megafauna declines, yet could be restored through population recoveries.
- Advancing understandings of how marine megafauna alter terrestrial ecosystem dynamics can help us anticipate the cross-ecosystem consequences of megafauna declines and recoveries in order to inform coastal conservation, restoration, and management strategies.

Open Research Statement: The data and code used in this study are publicly available at https://github.com/fgerraty/Marine_Megafauna_Subsidies and via Zenodo at https://doi.org/10.5281/zenodo.15635282.

Introduction

Human exploitation has decimated populations of large-bodied animals (hereafter "megafauna") in most of the world's ecosystems, leading to cascading ecological consequences and pronounced shifts in ecosystem structure and function (Estes et al. 2011, Dirzo et al. 2014, Young et al. 2016). Megafauna are known to play critical ecological roles as predators, ecosystem engineers, and vectors of nutrient redistribution within and across ecosystems (Estes et al. 2016, Doughty et al. 2016). However, most megafauna declines predate and precondition modern ecological studies, such that contemporary understandings of the ecological roles played by megafauna have likely been underestimated due to their drastically reduced abundance and distributions (Jackson et al. 2001, Silliman et al. 2018, Lotze and Worm 2009). Fortunately, far fewer human-caused megafauna extinctions have occurred in the ocean than on land, and some marine megafauna groups—particularly marine mammals—have begun to exhibit strong population recoveries in recent decades (Panel 1, McCauley et al. 2015, Ingeman et al. 2022). These recoveries offer unique opportunities to examine how ecosystem dynamics, functions, and services differ among intact and defaunated land- and seascapes.

Marine megafauna are increasingly being recognized as important vectors of nutrient transport and ecosystem connectivity due to their large sizes, high consumption rates, and widespread movement patterns. Prominent examples include whales pumping nutrients consumed deep in the water column to the ocean's surface (Roman and McCarthy 2010), conveying nutrients laterally from temperate feeding regions to tropical breeding regions (Roman et al. 2025), and providing the nutritional foundation for diverse biotic assemblages as "whale falls" in nutrient-poor seafloor ecosystems (Smith et al. 2015). However, while most research has examined the role of marine megafauna in nutrient cycling within oceanic ecosystems, growing evidence suggests that the ecological impacts of marine megafauna also cross the land-sea interface and modify terrestrial ecosystem dynamics (Roffler et al. 2023, Lin et al. 2023).

Marine megafauna link land and sea by serving as large, calorically-rich food sources for terrestrial consumers and by egesting and excreting marine-derived nutrients into terrestrial ecosystems when they come ashore (Figure 1). Despite that these subsidies can drive diverse and impactful ecological consequences and are likely increasing in magnitude with megafauna recoveries, the global extent and significance of marine megafauna mediated resource subsidies to terrestrial ecosystems remains largely unquantified.

Here, we review the role of marine megafauna (marine animals with >45 kg maximum reported body mass; Estes et al. 2016)—particularly marine mammals and sea turtles—as connectors of land and sea along global coastlines. We compile published literature to describe the diversity of terrestrial consumers that exploit marine megafauna as a food source, as well as descriptions of documented ecological impacts resulting from megafauna-mediated nutrient subsidies (see Appendix S1:Figure S1, Appendix S1:Panel S1, Appendix S1:Panel S2, and Appendix S1:Panel S3 for detailed review methods and taxonomic inclusion criteria). By synthesizing relationships among marine megafauna and terrestrial wildlife and ecosystems, we can better understand and anticipate the cross-ecosystem consequences of megafauna declines and recoveries along future coastlines. These insights can inform the integration of land-sea connectivity into coastal conservation policies, management strategies, and restoration efforts.

Marine Megafauna Connect Land and Sea

Our synthetic literature review revealed four primary pathways through which marine megafauna mediate marine-to-terrestrial nutrient flows (Figure 1). The first three are all pathways by which marine megafauna serve as a food source for terrestrial consumers: predation, in which terrestrial predators hunt marine megafauna; scavenging, in which terrestrial consumers scavenge dead megafauna carrion; and terrestrial wildlife consumption of marine megafauna placenta, eggs, and/or excreta (e.g., feces). The final pathway involves marine megafauna providing a bottom-up subsidy by fertilizing terrestrial ecosystems with excreta (e.g., feces), unhatched eggs, and decomposing carrion.

Our review revealed 224 unique combinations between a marine megafauna species and a terrestrial vertebrate consumer species (Figure 2a, Appendix S1:Panel S2). We categorized these consumer-resource relationships based on the type(s) of consumption documented in source literature: (1) predation, (2) carrion scavenging, (3) consumption of marine mammal placenta, (4) consumption of feces or other excreta, and (5) consumption of sea turtle eggs (Figure 2b-e). Many megafauna-consumer species combinations involved multiple consumption categories, such as black-backed jackals (*Canis mesomelas*) hunting Cape fur seal (*Arctocephalus pusillus*) pups in addition to scavenging carcasses and placentas (Hiscocks and Perrin 1987, Oosthuizen et al. 1996), or Northern raccoons (*Procyon lotor*) consuming sea turtle eggs and hunting hatchlings (Bouchard and Bjorndal 2000).

Marine Megafauna as Prey

We documented 53 unique predator-prey species pairs, with the majority of prey being sea turtles (n=27) and pinnipeds (n=18) (Figure 2b). Pinnipeds and sea turtles are particularly vulnerable to land-based predators when they haul out onshore to rest, breed, molt, thermoregulate, or nest. They also often exhibit strong site fidelity, leading to spatially and temporally predictable prey aggregations that can influence predator behavior, abundance, and species interactions (Gerraty et al. 2025, Lin et al. 2023).

All documented vertebrate predators were mammals (n=30) or birds (n=23), with carnivores (Carnivora, n=27) being the most common class and canids (Canidae, n=11) and ursids (Ursidae, n=9) being the most common families. Predators varied widely in body size and trophic role, from rodents hunting sea turtle hatchlings (Caut et al. 2008) to African lions hunting adult seals (Stander 2019). Megafauna juveniles, particularly sea turtle hatchlings and seal pups, were targeted by terrestrial predators with a broad range of body sizes whereas adults were usually only vulnerable to lethal predation by large-bodied consumers. Not all predation records necessarily led to megafauna mortality—large colonies of vampire bats (*Desmodus rotundus*) have been documented living primarily off the blood of South American sea lions (*Otaria flavascens*) along the hyper-arid Peruvian coast (Catenazzi and Donnelly, 2008), and Española mockingbirds (*Mimus macdonaldi*) also drink blood from Galapagos sea lion (*Zalophus wollbaeki*) adults and placentas (Curry and Anderson 1987).

Marine Megafauna Carcass Scavenging

The land-sea interface is a hotspot of carrion availability in coastal ecosystems, and a diverse suite of coastal scavengers routinely exploit and sometimes depend heavily upon beach-cast marine megafauna carrion (Hyndes et al. 2022, Moleón et al. 2019). As some of the largest parcels of organic matter on the planet, megafauna carcasses—such as those of whales—can provide scavengers nourishment for months to years. However, the frequency and magnitude of carcass stranding events vary across space and time, with input characteristics strongly dependent on subsidy taxonomic group, and has likely been substantially reduced due to anthropogenic exploitation (Panel 1, Laidre et al. 2018, Quaggiotto et al. 2022).

Our review identified 89 unique marine megafauna and terrestrial scavenger species pairs, with published records more commonly documenting scavenging of marine mammal carcasses (n=82) rather than sea turtles (n=7; Figure 2c). Similar to predation, most documented scavengers were carnivores (n=44) and birds (n=41), but other taxa were also documented scavenging sea turtle carrion (e.g., deer, iguanas, and opossums), including jaguar-killed turtle carcasses (Escobar-Lasso et al. 2016, Morera et al. 2022). There were several records of endangered and threatened wildlife scavenging marine mammals, such as polar bears (*Ursus maritimus*) and California condors (*Gymnogyps californianus*), respectively highlighting how marine megafauna subsidies can either help (e.g., by boosting scavenger populations; Laidre et al. 2018) or hinder (e.g., by exposing scavengers to marine-derived contaminants; Kurle et al. 2016) coastal conservation actions (Twining et al. 2025). However, despite the broad diversity of scavenging interactions documented, we hypothesize that our data vastly underrepresent the global diversity of scavengers that exploit marine megafauna carrion due to a mismatch between anecdotal and published records. Studies leveraging camera traps or other remote sensing technologies to catalog marine megafauna carcass scavenging assemblages hold promise to fill in these data gaps (e.g., Escobar-Lasso et al. 2016).

Marine Mammal Placenta and Excreta Consumption

Relative to carcass scavenging records, there was much less documentation of terrestrial vertebrates consuming pinniped placenta and excreta (n=14). Placenta and excreta consumers consisted of birds (n=11), carnivores (n=8), and the Galapagos marine iguana (*Amblyrhynchus cristatus*) (Figure 2d) (Wikelski & Wrege 2000). Pinniped placentas are often rapidly scavenged and birthing observation opportunities are limited, so we again hypothesize that our data significantly underrepresents the global diversity of megafauna placenta and excreta consumers.

Sea Turtle Nest Predation

We documented 88 unique species pairs involving all seven sea turtle species and their terrestrial vertebrate egg predators (Figure 2e). These egg predators were taxonomically diverse, spanning 22 families of mammals, birds, and reptiles. The most common nest predators were canids (n=20), mustelids (Musetelidae, n=11), monitor lizards (Varanidae, n=8) and colubrid snakes (Colubridae, n=7). Despite excluding invertebrate predators of sea turtle nests from our records, our dataset substantially expands the known diversity of sea turtle nest predators (Stokes et al. 2024).

Most studies assessing sea turtle nest predation have focused on determining the identity of sea turtle nest predators and their harmful impacts on nesting success. Far fewer studies have assessed the importance of sea turtle eggs in the diet of such predators and the ways these marine subsidies influence consumer and food web dynamics in sandy beach and terrestrial food webs. Sea turtle egg subsidies can alter consumer behavior and increase consumer abundance, so understanding and anticipating these subsidy effects can guide invasive predator eradication projects and predator management strategies (Lin et al. 2023). Sea turtle nests are also commonly exploited by terrestrial wildlife of conservation or cultural concern, generating wicked conservation problems with significant social and ecological trade-offs (Behrendorff et al. 2023). Deeper understanding of the causes and cross-ecosystem consequences of sea turtle nest predation can inform holistic sea turtle conservation strategies that balance multi-species conservation objectives.

Marine Megafauna as Nutrient Vectors

Pinniped feces and unhatched sea turtle eggs subsidized beach and terrestrial ecosystems in 32 case studies. In 28 of these, pinniped subsidies triggered bottom-up effects through increased nutrient availability, higher primary production and decomposition rates, and altered invertebrate assemblages (Smith, 2008). In one case, seal-mediated nutrient subsidies to terrestrial vegetation on Sable Island, Canada, influenced the foraging behavior and movement patterns of feral horses (*Equus ferus caballus*; McLoughlin et al. 2016). Sea turtle nesting produced similar bottom-up effects in 4 studies, enriching nutrient content in beach sediments and shoreline vegetation and altering meiofaunal assemblages, plant community composition, and potentially impacting dune stability (Bouchard & Bjorndal, 2000, Diane et al. 2017, Hannan et al. 2007, Vander Zanden et al. 2012).

<u>Ecological Impacts</u>

We identified 63 case studies that documented one or more ecological consequence of marine megafauna subsidies to terrestrial ecosystems, which were categorized into five effect types: changes to consumer health, consumer behavior, consumer abundance, community and/or ecosystem dynamics, or other effects (Figure 3). Over half (57%, n=36) of the case studies described impacts on community- or ecosystem-level processes such as shifts in predator-prey relationships, increases or decreases in ecosystem productivity, or other ecological effects. A quarter (25%, n=16) of the case studies documented changes in consumer behavior, such as altered movement patterns and changes in consumer sociality, including increased conspecific tolerance and territorial breakdown (Leighton et al. 2010). Of the remaining case studies, 16% of the case studies (n=10) documented changes in consumer health, including increases in consumer body condition and elevated exposure to marine-derived contaminants (Kurle et al. 2016, González-Solís et al. 2000), and 13% of the case studies (n=8) documented increases in consumer abundance (consumer population size, density, or persistence) (Figure 3). Other documented effects included megafauna carcasses serving as habitat (e.g., for invertebrates, algae, and lichens; Catenazzi et al. 2009, Nývlt et al. 2016) and megafauna indirectly influencing terrestrial ecosystems via marine ecosystem engineering (Anthony et al. 2008).

Cross-ecosystem nutrient subsidies often operate as bottom-up processes in recipient communities, with subsidies enhancing primary production or boosting low trophic level consumers and then subsequently being integrated into higher trophic levels. The marine megafauna subsidy case studies we compiled also influenced terrestrial food webs via bottom-up processes—especially when megafauna served as nutrient vectors—but our results also show that megafauna-mediated nutrient subsidies enter terrestrial food webs at a wide variety of trophic levels, from vegetation and insects all the way to top predators (Figure 2). Subsidized predators can consequently transform terrestrial ecosystem dynamics through top-down impacts, with knock-on ramifications for coastal conservation strategies and human-wildlife conflict (Roffler et al. 2023, Lin et al. 2023).

Subsidy impacts were most frequently documented in subpolar and temperate regions, with a geographic bias towards the western hemisphere (Figure 3b). This pattern may reflect global research biases, megafauna distributions, and the fact that marine subsidies generally cause stronger and longer-lasting ecological effects in low-productivity recipient ecosystems such as those at high latitudes (Oliver et al. 2021, Polis et al. 1997). On Somerset Island in the High Arctic, for example, nutrients from prehistoric bowhead whale bones used for whaler dwellings still elevate nutrient levels and diatom assemblages in nearby freshwater ponds centuries later (Douglas et al. 2004).

Factors Underpinning Subsidy Effects

The ecological impacts of marine megafauna subsidies are often strongest where marine productivity is high and terrestrial productivity is low—such as high-latitude regions and coastal deserts (Polis et al. 1997). Indeed, our review identified striking examples from subpolar regions and arid coastlines (Catenazzi and Donnelly 2008, Laidre et al. 2018, Stander 2019). Subsidy effects are also amplified on islands, especially small islands with high perimeter-to-area ratios (Polis et al. 1997). Other key drivers of subsidy effect sizes include the magnitude and frequency of nutrient inputs, with larger or more frequent inputs having stronger effects (Subalusky & Post, 2019). We hypothesize that the taxonomic group of the marine megafauna is a primary determinant of subsidy input magnitude and frequency. For example, whale carcasses provide rare but high-value subsidies, whereas sea turtle nesting offers predictable annual inputs with a smaller nutritional value. Our case studies qualitatively support these proposed drivers of subsidy impact, but future studies should try to rigorously quantify the ecological factors that underpin subsidy effect sizes and how these drivers interact with coastal human activity and development.

Conservation Implications

Conservation actions such as whaling moratoria, marine protected area establishment, and habitat restoration have produced impactful, positive steps towards marine megafauna population recoveries (Ingeman *et al.* 2022). However, anthropogenic stressors including climate change, overfishing, vessel traffic, and pollution remain severe and accelerating threats (McCauley et al. 2015). Our results suggest that marine megafauna conservation and restoration efforts can produce ecological impacts that extend beyond the marine realm by reconnecting land and sea along global coastlines, reinforcing the critical importance of addressing such anthropogenic threats. Beyond megafauna recoveries, understanding how anthropogenic infrastructures and activities on land influence marine megafauna subsidy dynamics—such as by altering terrestrial consumer behavior, abundance, and species interactions—remains a pressing research gap that can inform coastal conservation strategies and advance human-wildlife coexistence.

Conclusions

Marine megafauna have long served as powerful ecological connectors between ocean and land, delivering nutrient subsidies that reshape coastal food webs and ecosystem processes. Our synthesis highlights the diversity of terrestrial consumers that exploit marine megafauna as a food source and reveals the often-overlooked ecological consequences of the marine subsidies that these megafauna deliver. Our research can serve as a launching point for deeper investigations into the causes and consequences of marine megafauna subsidies from local to global scales. Broadening understanding of the cross-ecosystem impacts of marine megafauna losses and recoveries will be critical to the management of future coastlines and the integration of land-sea connections into holistic coastal conservation approaches.

Panel 1: Status of Marine Megafauna

Humans have dramatically reduced the global abundance of marine megafauna in the last few centuries, largely due to commercial exploitation, industrial fishing, and the rapid expansion of coastal human populations (Dirzo et al. 2014, McCauley et al. 2015, Young et al. 2016). Although marine megafauna defaunation is relatively recent and has led to fewer extinctions than on land, it is projected to rapidly intensify with climate change and increasing ocean industrialization (McCauley et al. 2015). Many of the most threatened marine megafauna are those that come into direct contact with land during some portion of their life history (McCauley et al. 2015). These species are also the most likely to interact with land-based predators, including humans, and deliver marine nutrient subsidies to terrestrial ecosystems.

Lotze and Worm (2009) compiled published records documenting long-term changes (spanning hundreds to thousands of years) in the abundance of marine megafauna populations worldwide, including 68 marine mammal and sea turtle populations. Their analysis included historical baselines, lowest recorded population sizes, and recent abundance estimates (see Lotze and Worm 2009 for detailed methods). These data reveal that marine mammal and sea turtle populations declined by approximately 87% from historical baselines to their lowest observed levels, though some cetacean and pinniped populations have recently begun to recover (Figure 4). However, these marine megafauna recoveries have been uneven—limited to particular species, taxonomic groups, and geographic regions—which carries important implications for which terrestrial consumers and ecosystems are likely to be impacted by renewed marine resource subsidies, and which are not.

Panel 2: Insights from Historical Ecology

While it is impossible to fully reconstruct the ecological consequences of prehistoric and more recent marine megafauna declines, historical ecology approaches—such as analyses of stable isotopes, historical records, Indigenous knowledge, and archaeological and paleontological resources—offer valuable insights into their past roles in land-sea connectivity. For instance, stable isotope analyses of ancient and historical samples have revealed that California and Andean condors extensively scavenged marine mammals in the Pleistocene (Chamberlain et al. 2005, Lambertucci et al. 2018), and that these subsidies may have enabled California condors to persist into the Holocene (Fox-Dobbs et al 2006). However, in both hemispheres condor diets have shifted more towards terrestrial resources in the Holocene, a transition attributed to overexploitation of marine megafauna and increased availability of anthropogenic carrion (Chamberlain et al. 2005, Lambertucci et al. 2018).

Historical records and anecdotal accounts also provide glimpses into past relationships between marine megafauna and terrestrial consumers. For example, Bjorndal (2020) compiled historical accounts suggesting that black bears in Florida, USA, regularly consumed sea turtle eggs before humans drastically reduced black bear populations in the region. Such records highlight the need to incorporate multiple lines of evidence to better understand the historical significance of marine megafauna to land-sea connectivity.

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Figures

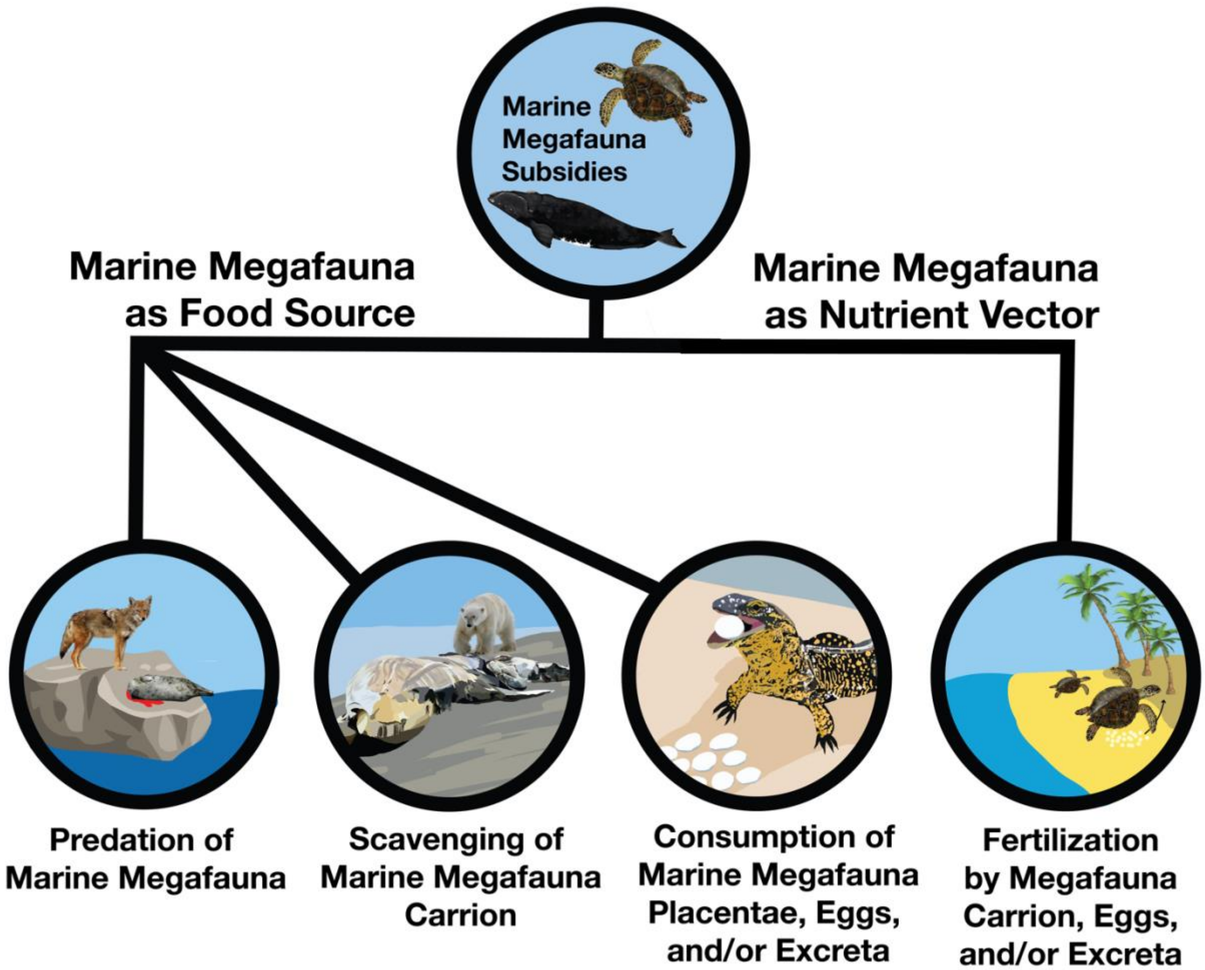


Figure 1. We identified four primary pathways through which marine megafauna facilitate marine-to-terrestrial nutrient subsidies. Marine megafauna serve as a food source for terrestrial consumers through three of these pathways (predation; carrion scavenging; and the consumption of placenta, eggs, and excreta), whereas megafauna serve as a nutrient vector in the fourth pathway.

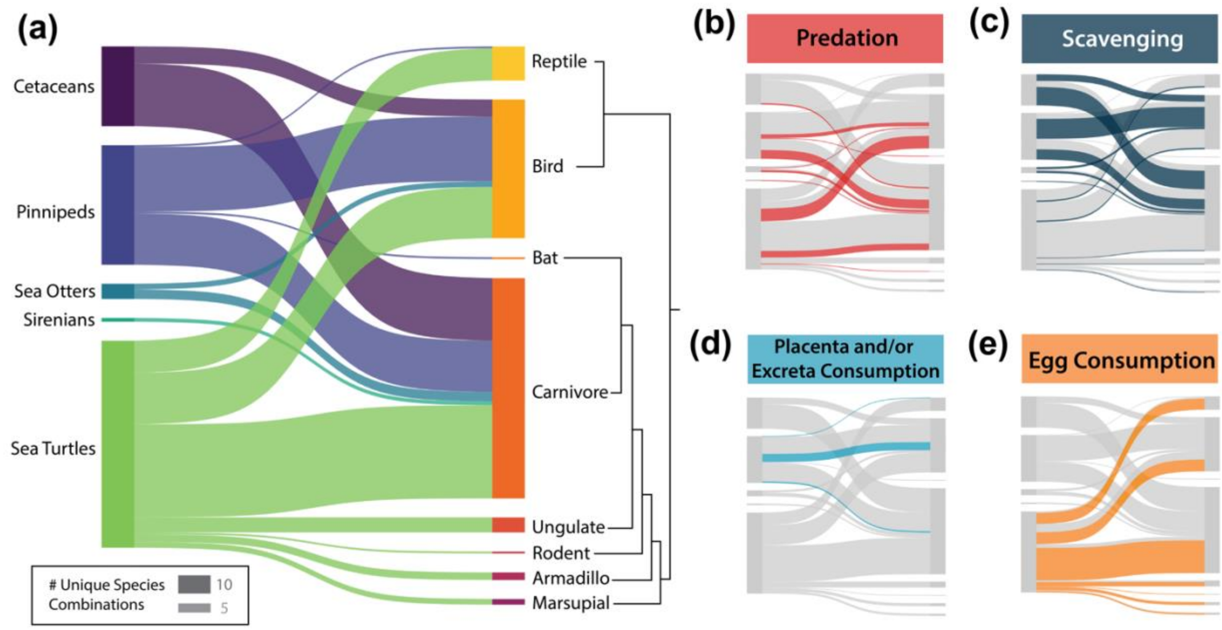


Figure 2. The diversity of marine megafauna and consumer species interactions identified in our synthetic review. The width of each colored flow represents the unique number of species combinations for (a) all consumption types, (b) predation, (c) carrion scavenging, (d) pinniped placenta and/or excreta consumption, and (e) sea turtle egg consumption. Consumer species were identified to class for reptiles (Reptilia) and birds (Aves), or order for mammals (Chiroptera, Carnivora, Artiodactyla, Rodentia, Cingulata, Didelphimorphia).

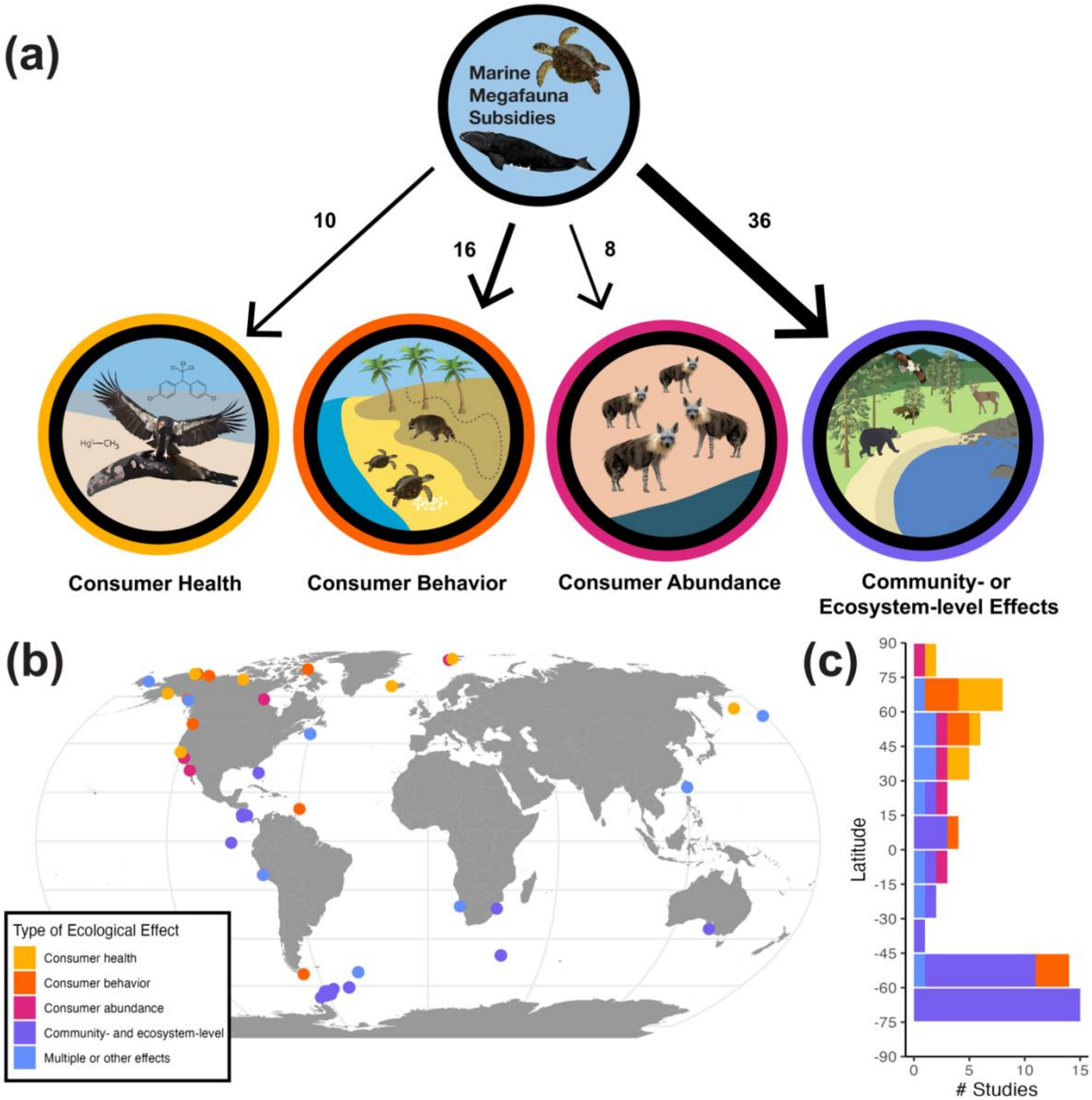


Figure 3. **(a)** Diagram of the number of case studies (number next to arrow) documenting the four primary categories of ecological effects resulting from marine megafauna subsidies to terrestrial consumers and ecosystems: changes to consumer health, consumer behavior, consumer abundance, or community and/or ecosystem dynamics. Case studies documenting multiple types of ecological effects were tallied in all relevant ecological effect categories. **(b)** Map and **(c)** latitudinal histogram illustrating the distribution of studies documenting ecological effects resulting from marine megafauna subsidies. Note the large aggregation of studies on subantarctic islands in panels (b) and (c) investigating community- and ecosystem-level consequences of pinniped-vectored nutrient subsidies.

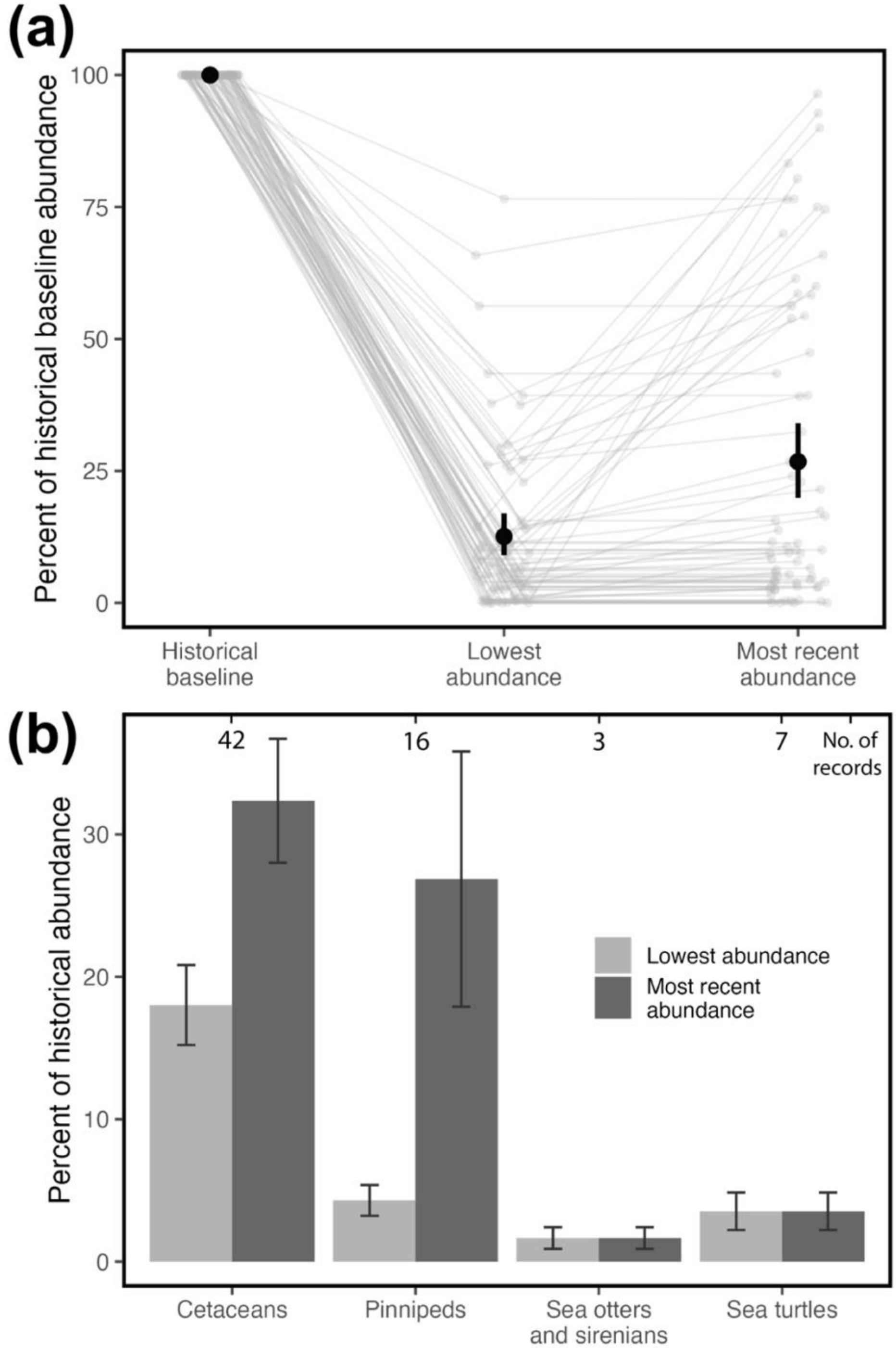


Figure 4. Long-term changes in the abundance of marine megafauna populations (adapted from Lotze and Worm, 2009). Panel **(a)** compares abundance estimates among historical baseline values, lowest recorded population sizes, and recent abundance estimates. Panel **(b)** shows the taxonomic distribution of megafauna recoveries from the lowest recorded abundance to the most recent abundance estimates.

Appendix S1

Supplement to:

Historical and potential future importance of marine megafauna subsidies to terrestrial ecosystems

FD Gerraty *et al.*

Figure S1. Steps of inclusion and exclusion of references in our systematic literature review based on a PRISMA flow diagram.

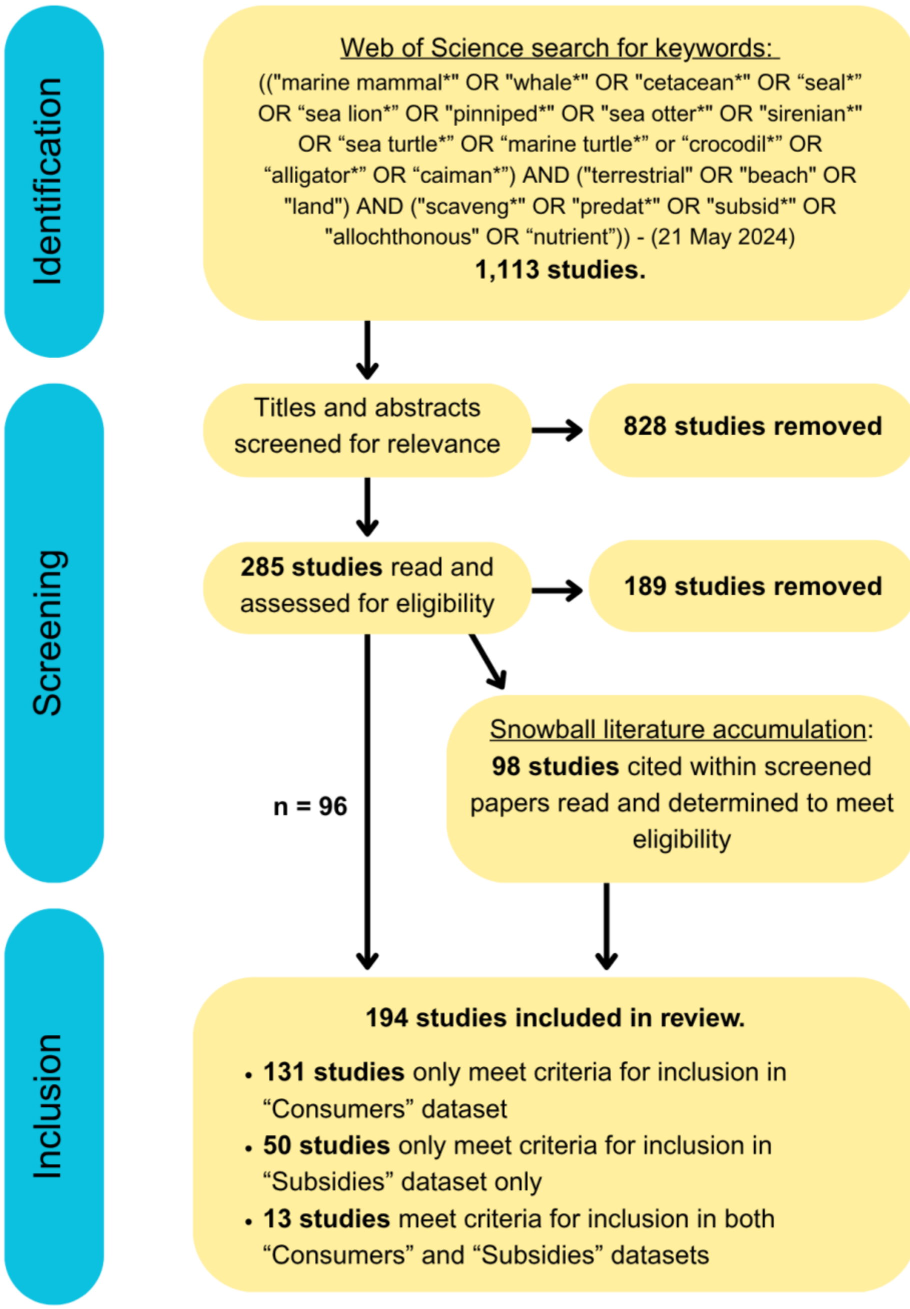
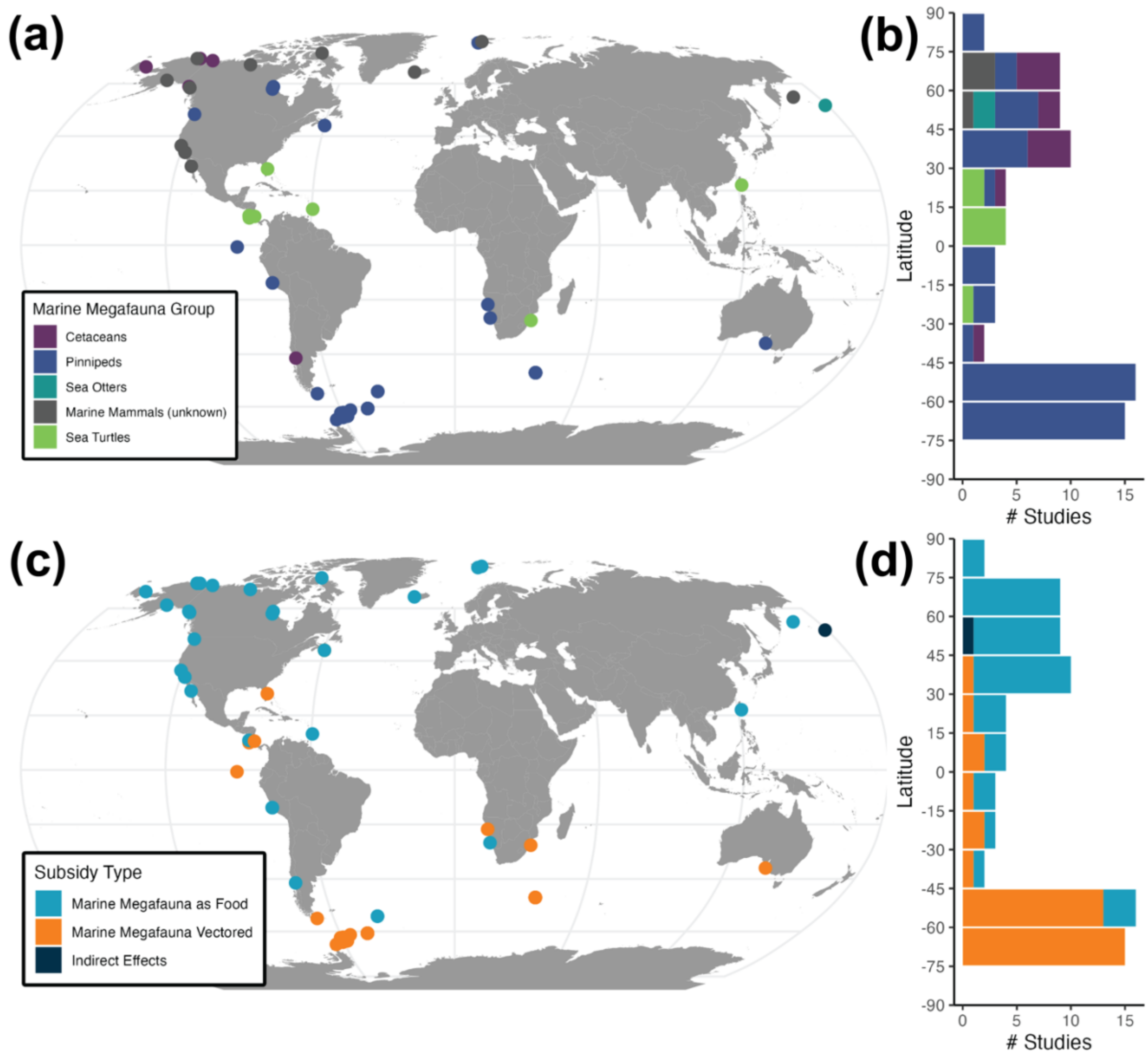


Figure S2. Maps (a,c) and latitudinal histograms (b,d) illustrating the distribution of studies documenting ecological effects resulting from marine megafauna subsidies colored by marine megafauna group (a,b) and subsidy type (c,d).



Panel S1. Systematic Literature Review Scope and Search Procedure

We conducted a systematic literature search (English language) to capture a representative range of case studies through which marine megafauna influence marine-to-terrestrial nutrient transfer.

We follow Estes et al. (2016) to define marine megafauna as marine animals with >45kg maximum reported body mass, a measure originally derived from Lyons et al. (2004) to distinguish body sizes of terrestrial animals that exhibited elevated rates of Pleistocene extinctions. While there are many species of marine megafauna across diverse phyla (Estes et al. 2016), we narrowed the taxonomic focus of our review to marine megafauna categorized as marine mammals (including cetaceans, pinnipeds, sea otters, and sirenians, excluding polar bears and humans) and sea turtles. These taxa were selected because many species within these groups have a shared history of commercial exploitation and subsequent population recovery, and also because many of these species visit intertidal or terrestrial ecosystems as part of their life history (e.g., for breeding, birthing, molting, nesting, resting, and/or thermoregulation). This taxonomic narrowing excludes marine megafaunal fishes, molluscs, cnidarians, emperor penguins, polar bears, and humans.

We conducted a systematic literature review with two primary aims: (1) Identify the diversity of terrestrial consumers that utilize marine megafauna (i.e., only marine megafaunal mammals and reptiles) as a food source and (2) describe the pathways and ecological consequences of marine megafauna mediated nutrient transfer to terrestrial ecosystems. We conducted one systematic literature search to capture literature addressing both of these questions, but had different inclusion criteria and catalogued different information from each paper to address each of these questions (see Panels S2 and S3).

Search and Review Procedure:

- Web of Science search for keywords: (("marine mammal*" OR "whale*" OR "cetacean*" OR “seal*” OR “sea lion*” OR "pinniped*" OR "sea otter*" OR "sirenian*" OR “sea turtle*” OR “marine turtle*” or “crocodil*” OR “alligator*” OR “caiman*”) AND ("terrestrial" OR "beach" OR "land") AND ("scaveng*" OR "predat*" OR "subsid*" OR "allochthonous" OR “nutrient”)) – (date: 21 May 2024). This search produced 1,113 studies.
- Titles and abstracts from the Web of Science search were screened for relevance, resulting in 285 potentially relevant studies that were read. From these, we identified studies that met the inclusion criteria for Aim 1 and/or Aim 2 (see inclusion criteria in Appendix S1:Panel S2 and Appendix S1:Panel S3).
- To capture additional studies within our research scope, we also identified all relevant papers cited by studies included in our review. We continued this snowball search method until we could no longer identify additional relevant studies.
- See Appendix S1:Figure S1 for PRISMA flow diagram outlining inclusion and exclusion steps in systematic review.

References

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Panel S2. Systematic Literature Review Inclusion Criteria and Results: Aim 1

Aim 1: Identify the diversity of terrestrial vertebrate consumers that utilize marine megafauna as a food source.

<u>*Inclusion criteria:*</u>

- Study provides some evidence of a vertebrate, terrestrial consumer (excluding humans and crocodilians, including polar bears and all birds) ingesting organic matter (i.e., flesh, carrion, eggs, placenta, and excreta) derived from marine megafaunal mammals and/or reptiles.
- Studies that only provide indirect evidence of marine megafaunal consumption (e.g., stable isotope evidence) were included, but these studies and their methods were flagged in the "indirect evidence" column of the resultant datasets.
- Because there were numerous cases in which many articles documented the same species interaction in different locations, we only included the first three studies we encountered for each combination of a marine megafauna food source, a terrestrial consumer, and an interaction type (i.e. predation, carrion scavenging, placenta consumption, excreta consumption, egg consumption). After cataloguing three studies of each consumer-resource-interaction type, we excluded further studies documenting the same interaction from the dataset addressing Aim 1. However, this did not exclude such studies from inclusion in the review addressing Aim 2.

<u>*Catalogued from each study:*</u>

- Taxonomic categories of all marine megafauna and terrestrial consumers.
- Each of five pathways scored "TRUE" when documented among marine megafauna and consumer species: (1) predation, (2) scavenging, (3) consumption of marine megafauna placenta, (4) consumption of marine megafauna feces or excreta, (5) consumption of marine megafauna eggs.
- Type of indirect evidence when no direct evidence was presented. All stable isotope evidence was categorized as indirect evidence. Direct observations, camera trap observations, and fecal analysis (excluding stable isotope analysis of fecal material) were categorized as direct evidence.

<u>*Results:*</u>

- We identified 224 unique species pairs of terrestrial vertebrate consumers and marine megafauna. 42 species pairs involved cetaceans as a food source, 8 species pairs involved fissipeds (sea otters) as a food source, 63 species pairs involved pinnipeds (seals and sea lions) as a food source, 109 species pairs involved sea turtles as a food source, and 2 species pairs involved sirenians (manatees and dugongs) as a food source.
- We identified 96 unique terrestrial consumer species in 35 families. The families with the most number of unique consumer species were Canidae (11 species), Mustelidae (9 species), Colubridae (7 species), and Laridae (7 species).

- A table of megafauna-consumer species pairs, additional results, and associated data and code are available at https://github.com/fgerraty/Marine_Megafauna_Subsidies and archived at Gerraty (2025).

References

Gerraty, F.D. (2025). fgerraty/Marine_Megafauna_Subsidies: Historical and Potential Future Importance of Marine Megafauna Subsidies to Terrestrial Ecosystems (v.0.0.1). Zenodo. https://doi.org/10.5281/zenodo.15635282.

Panel S3. Systematic Literature Review Inclusion Criteria and Results: Aim 2

Aim 2: Describe the pathways and ecological consequences of marine megafauna subsidies to terrestrial ecosystems.

Inclusion criteria:

- Study provides some evidence of one or several ecological consequences of marine megafauna mediated nutrient subsidies in terrestrial ecosystems. We used a liberal inclusion criteria for such ecological consequences, but excluded studies that solely documented terrestrial animals consuming marine megafauna (which, apart from invertebrate consumers, were captured in the literature review for Aim 1). Ecological consequences we considered included changes in terrestrial organism behavior, health, abundance (population size, density, and/or persistence), and community or ecosystem dynamics (including shifts in species interactions, community structure, or ecosystem functions and processes).

Catalogued from each study:

- Pathway(s) of marine megafauna-mediated nutrient transfer: (1) marine megafauna predation by terrestrial consumers, (2) marine megafauna scavenging by terrestrial consumers, (3) marine megafauna vectored nutrient transfer.
- Taxonomic categories of all marine megafauna and terrestrial consumers.
- Category of documented ecological effect(s): consumer health, consumer behavior, consumer population, species interactions, community- or ecosystem-level effects.
- Brief (1-3 sentence) description of documented ecological effect.
- Geographic location (latitude, longitude, country) of each study.

Results:

- We identified 63 case studies that met our inclusion criteria and documented one or more ecological consequences of marine megafauna subsidies to terrestrial ecosystems.
- 36 case studies documented impacts on community- or ecosystem-level processes, 16 case studies documented changes in consumer behavior, 10 case studies documented changes in consumer health, 8 case studies documented changes in consumer abundance, and 3 case studies documented terrestrial consequences outside of these categories (e.g., marine megafauna carcasses serving as habitat). 55 of these studies documented only one category of ecological effect, whereas 8 studies documented ecological effects in multiple effect categories.
- Marine megafauna served as food for terrestrial consumers in 29 of these studies. Marine megafauna vectored nutrients into terrestrial ecosystems in 32 of these studies. 2 studies documented indirect effects of marine megafauna influencing terrestrial ecosystem dynamics (e.g., via marine ecosystem engineering).
- A table of ecological effect descriptions and associated data and code are available at https://github.com/fgerraty/Marine_Megafauna_Subsidies and archived at Gerraty (2025).

References

Gerraty, F.D. (2025). fgerraty/Marine_Megafauna_Subsidies: Historical and Potential Future Importance of Marine Megafauna Subsidies to Terrestrial Ecosystems (v.0.0.1). Zenodo. https://doi.org/10.5281/zenodo.15635282.