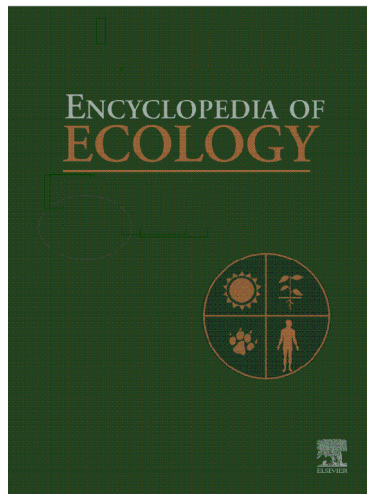


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Introduction**Importance of Calcium to Ecosystems****The Global Calcium Cycle****Ecological Consequences of Anthropogenic****Perturbations to the Calcium Cycle****The Future****Further Reading****Introduction**

Although all of Earth's major biogeochemical cycles have been impacted by human activities, the calcium cycle has been one of the first to display significant changes. Harvesting of crops and the presence of acids and increased levels of carbon dioxide in rainwater from the burning of fossil fuels have altered the weathering rates of minerals and stripped calcium ions from soils, altering the primary sources of microbe- and plant-available calcium and upsetting community structures. The carbon dioxide is also depressing the saturation state of seawater with respect to calcium biominerals like aragonite and calcite, affecting the growth of organisms such as corals, coccolithophores, and pteropods. The ensuing shifts in limiting nutrients and competitive advantages within terrestrial communities, alteration of food webs, shifts in the balance between calcareous and noncalcareous plankton in the ocean, and diminishment of the reef-building ability of corals will in turn alter the delivery and cycling of nutrients and other elements in the terrestrial and marine biospheres and provide further perturbations to atmospheric concentrations of CO₂. As a result, anthropogenic impacts on the calcium cycle have ecological consequences that reach far beyond those ecosystems which are proximally impacted.

Importance of Calcium to Ecosystems**Terrestrial Ecosystems**

Calcium is an element whose careful regulation within every living organism is critical to its survival. Eukaryotic cells use calcium ions as intracellular messengers, signaling environmental stresses and inducing changes in gene expression. Calcium is also an important structural component of cells, present in cell walls and membranes, and is a counterion for anions in cell vacuoles. The presence of too much calcium is, however, problematic and organisms have evolved ways to manage excess calcium. For example, earthworms contain calciferous glands that excrete calcium carbonate when too much calcium has been ingested and certain tree species (e.g., Norway spruce (*Picea abies* (L.) Karst.)) are thought to incorporate excess calcium into extracellular calcium oxalate crystals in their foliage.

Calcium is categorized as a major mineral nutrient for plants, and deficiencies of calcium affect plant health. Studies have demonstrated correlations between calcium availability and susceptibility of trees to insect, drought, frost damage, and disease. Tree species, such as sugar maples (*Acer saccharum* Marsh.), with greater requirements for calcium are more readily damaged due to low calcium availability. Accordingly, Ca deficiency in ecosystems can lead to shifts in plant species composition that may in turn

have effects on the entire food web. Generally speaking, while both monocots (e.g., grasses, corn, and other grains) and dicots require calcium, monocots need less of it than dicots. Legumes, on the other hand, need roughly twice as much calcium as grasses. Plants can be classified into two groups, calcifuges (e.g., rhododendrons, heaths, and azaleas), which grow in acid soils with low calcium, and calcicoles (e.g., the Brassicaceae family including cabbage, broccoli, and kale), which require calcium-rich soils.

Invertebrates such as snails and mollusks use calcium to build their shells. Wood lice and millipedes prefer Ca-rich soils and serve as sources of calcium for their predators. Freshwater crayfish require at least a month of exposure to calcium-rich water after molting or their exoskeletons and claws fail to harden. Predatory birds can be affected if their prey and main calcium source becomes scarce due to inadequate levels of calcium; specifically, studies have demonstrated that egg shells become more fragile as prey (caterpillars, snails, arthropods) populations decline in areas of calcium depletion. Higher organisms, such as birds and humans, require calcium for more cellular structures and biochemical processes than the aforementioned; most of their calcium is contained within bones, but it is also used in nerve impulses, muscle contractions (e.g., heart contractions), DNA transcription, and blood clotting.

The calcium needs of organisms within lakes are the same as any other organism. The most basic difference between land and water terrestrial ecosystems is that organisms in lakes are submerged in water and the calcium content is linked with lakewater pH and, therefore, the survivability of an organism. Bodies of water with low relative concentrations of calcium are usually oligotrophic and can be dystrophic. Dystrophic lakes often have high concentrations of decaying organic matter, high concentrations of organic acids, and a low pH (e.g., bog lakes). The low abundance of calcium arises because the lakes are in an area with Ca-poor rocks or the dissolved organic matter has reacted with all of the available calcium (or both).

Marine Ecosystems

In addition to playing critical roles in the biochemistry of living cells, the major role calcium plays within marine ecosystems is as a major component of biominerals such as calcium carbonate (CaCO_3). Corals, mollusks, including the pelagic pteropods, and the green alga, *Halimeda*, produce aragonite, the more soluble polymorph of calcium carbonate. Coccolithophores, most foraminiferans, coralline algae, many crustaceans, and echinoderms produce the more stable polymorph, calcite.

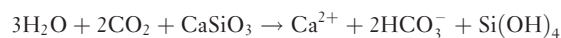
Calcium-biomineralizing organisms play no small role in ocean ecosystems. Coccolithophores are one of the main types of phytoplankton in the ocean and their production of calcium carbonate significantly diminishes the

effectiveness of the biological pump for sequestering carbon dioxide (CO_2) in the deep ocean. Pteropods are a major source of food for carnivorous zooplankton, fishes such as cod, salmon, and herring, and baleen whales. Corals and *Halimeda* and other calcareous algae together form tropical reefs which serve as habitat and food for a diverse community of microbes, invertebrates, and fish. Echinoderms such as sea urchins, brittle stars, and sea stars are important predators, grazers, and scavengers in benthic ecosystems from tropics to poles, shallow waters to deep.

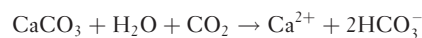
The Global Calcium Cycle

Sources of Calcium to Terrestrial and Marine Ecosystems

Ultimately, calcium inputs to global ecosystems come from the chemical weathering of calcium-containing minerals (Figure 1). Weathering of silicate, carbonate, phosphate, and sulfate minerals in rocks, sediments, and soils releases calcium ions into solution. The two most important of these weathering reactions can be generalized, for calcium-bearing silicates, as



and for carbonates as



The activities of plants are known to increase mineral weathering rates, and studies have suggested that in soils, plants involved in symbiotic relationships with mycorrhizal fungi might also directly access mineral-bound calcium before it enters the soil solution.

Calcium is also deposited into Earth surface ecosystems via wet and dry deposition. Calcium from sea salt and soil dust present as atmospheric particulate matter can be deposited by both these mechanisms. Anthropogenic contributions of calcium to atmospheric deposition come from biomass and fuel burning and the manufacturing of cement. The overall amount and relative contribution from each atmospheric source to an area varies seasonally and with factors such as the proximity of the area to the ocean.

Calcium is stored in biological materials, and calcium can be recycled in ecosystems via the breakdown of organic matter and biominerals containing calcium. Large amounts of calcium are generally exported from terrestrial ecosystems into the ocean through groundwater and surface waters. These ground- and surface waters supply $2\text{--}3 \times 10^{13} \text{ mol Ca yr}^{-1}$ to the oceans versus the $0.3 \times 10^{13} \text{ mol Ca yr}^{-1}$ supplied strictly to the oceans through deep-sea hydrothermal vents.

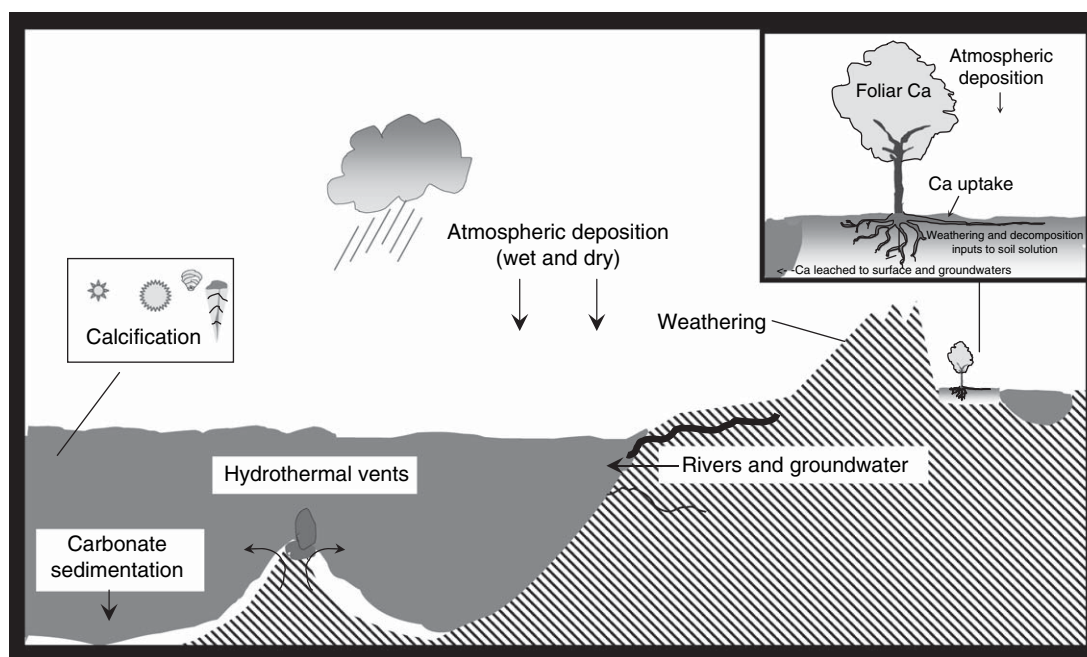


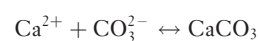
Figure 1 Schematic representation of the calcium cycle. Calcium is liberated in continents by the weathering of calcium-containing minerals, common constituents of most rocks. Calcium pools in terrestrial ecosystems include reservoirs in soils and soil minerals, organisms, and decomposing organic matter. Riverine and groundwater inputs transfer calcium in its ionic form from continents to the oceans. Hydrothermal vents also serve as calcium inputs in the oceans. In marine ecosystems, calcium ions are abundant in seawater. Marine organisms use calcium to make shells and hard parts. Calcium is removed from the oceans primarily by the sedimentation of these calcified organisms. Atmospheric deposition, both wet and dry, contributes calcium throughout both terrestrial and marine ecosystems. Anthropogenic effects including acid deposition, changes in land use (e.g., desertification), harvesting, and increased atmospheric carbon dioxide concentrations influence this natural calcium cycle.

The Production and Solubility of Calcium Biominerals in the Ocean

Approximately balancing the input of $2\text{--}3 \times 10^{13}$ mol Ca yr^{-1} to the ocean is the output of calcium as calcium biominerals formed by marine organisms. In shallow waters, aragonitic corals dominate the production of these minerals, providing 20% of the total output of calcium from the ocean. Calcitic foraminiferans and coccolithophores and aragonitic pteropods form the majority of the output sedimenting to the deep sea, with foraminiferans comprising somewhere between 20% and 60% of the total calcium output from the oceans and pteropods contributing only a few percent of it.

Despite the heavy biological usage of calcium, the relatively high abundance of Ca^{2+} in seawater means that Ca^{2+} concentrations are relatively invariant and never limiting to the growth of organisms. However, the concentration of Ca^{2+} together with the carbonate ion (CO_3^{2-}) concentration defines the saturation state of seawater with respect to calcite and aragonite. The saturation state of seawater is an integral part of the global Ca cycle and has profound implications for biota producing Ca biominerals.

Both the production of calcium carbonate biominerals and their dissolution can be summarized by the simple, reversible reaction



The product of the calcium ion and carbonate ion concentrations in seawater (i.e., $[\text{Ca}^{2+}] \times [\text{CO}_3^{2-}]$) determines whether conditions are supersaturated or undersaturated with respect to the carbonate mineral in question. When the ion activity product is higher than the saturating value, conditions are favorable for mineral formation and dissolution does not occur. The lower the ion activity product below the saturating value, the more difficult it is to precipitate the minerals and the quicker the dissolution of the mineral.

Because the concentration of Ca^{2+} is relatively invariant in the oceans, it is the variability in the carbonate ion concentration in seawater (along with temperature) that affects biological calcification and the dissolution of carbonate minerals. Carbonate ion concentrations drop with pH, as the increasing H^+ concentration favors the protonation of CO_3^{2-} to form bicarbonate ion (HCO_3^-). Aragonite and calcite also become increasingly more

soluble at cooler temperatures. Thus warm, tropical surface waters with their relatively low pH are supersaturated with respect to both aragonite and calcite. Cooler waters require greater carbonate ion concentrations to sustain saturating conditions, making polar waters less saturated than tropical waters. The pH of cold deep waters is relatively low due to the addition of CO_2 from the decay of sinking organic matter, and so these waters contain lower concentrations of carbonate ion and may be undersaturated with respect to both calcite and aragonite. As a result, production of massive, shallow water reefs by corals occurs only in the tropics, polar waters favor noncalcareous phytoplankton, and carbonate sediments do not accumulate below depths of several thousand meters.

Ecological Consequences of Anthropogenic Perturbations to the Calcium Cycle

Acid Deposition

Sulfate (SO_4^{2-}) and NO_x , anthropogenically emitted to the atmosphere, are oxidized and hydrolyzed to form sulfuric (H_2SO_4) and nitric (HNO_3) acids which are then introduced to ecosystems through precipitation or condensation of water vapor on foliage. These acids drive terrestrial ecosystems toward or into calcium limitation. Contact between acid fog and foliage leaches calcium directly out of leaf membranes, causing tissue damage and calcium depletion in plants. The deposition of extra anions (SO_4^{2-} and NO_3^-) causes the increased formation of calcium salts, such as CaSO_4 , in soils and these neutral compounds are easily leached from soils. Acid deposition also increases the concentration of hydrogen ions (H^+) in soil solutions. These excess protons, in turn, compete with other cations (especially Ca^{2+}) for space on the negatively charged surfaces (cation exchange sites) of soil particles. Calcium ions that are not bound to particles are easily removed from the soil and lost to the ecosystem by leaching.

As the concentration of H^+ rises in a soil, weathering rates of aluminosilicates and other minerals increase, inflating concentrations of total soluble Al and soluble free Al^{3+} . This leads to the increasing displacement of Ca^{2+} and other cations from the cation-exchange sites of soils. Eventually, the concentration of H^+ reaches a point where the protons outcompete Al^{3+} . The aluminum ions then become mobile in the soil solution where they may directly interact with plants. This compounds the problem of the depletion of soil Ca^{2+} , because, by damaging root tissue and displacing Ca^{2+} from exchange sites on the xylem walls of plants, Al^{3+} diminishes the ability of plants to take up calcium.

Acid deposition also affects terrestrial bodies of water. The main source of calcium for streams and lakes is runoff

and groundwater; as the minerals and soils surrounding these bodies of water become increasingly depleted in Ca^{2+} , so does the water. A lowering of calcium ion concentrations affects the acid-neutralizing capacity (ANC) of waters, resulting in greater pH fluctuations with changes in proton fluxes and increasing the effects of acidic deposition. The runoff will also contain increasing concentrations of Al^{3+} , potentially delivering lethal doses for some aquatic organisms and severely impacting or destroying local food webs.

Anthropogenic Impacts on the Atmospheric Dry Deposition of Calcium

As noted above, calcium is added to both terrestrial and marine ecosystems via the deposition of particulate matter from the atmosphere. Humans make significant contribution to these fluxes via industry (e.g., the manufacturing of cement) and biomass and fuel burning. An equally large, and in some localities much larger, anthropogenic influence is found in the abundance of dust. Land-use changes that result in desertification and dry soils at construction sites increase the amount of Ca-containing dust in the atmosphere. These inputs may sometimes temporarily offset the effects of acid deposition, but when these inputs are stopped, calcium depletion resumes.

Effects of Increased Carbon Dioxide on Terrestrial Ecosystems

Higher atmospheric concentrations of carbon dioxide eventually lead to higher mineral weathering rates, resulting in the enhanced leaching of calcium and other elements from soils. Such changes in weathering rates are not balanced by the natural recharge rate of soil calcium. Increased carbon dioxide concentrations also increase plant growth rates. Relieved of a carbon dioxide limitation, the plants will grow until they are limited by some other nutrient, often calcium. The increased plant growth could translate into a faster biological cycling of calcium, a process that has unpredictable results.

Carbon Dioxide, Calcium Biominerals, and Marine Ecology

Anthropogenic effects on the marine calcium cycle primarily occur through the acidification of seawater by carbon dioxide. The resultant lowering of pH and carbonate ion concentrations decreases the saturation state of seawater with respect to calcite and aragonite, thus making it more difficult for marine organisms to produce and maintain calcium biominerals.

Since the beginning of the industrial revolution, CO_2 concentrations in the atmosphere have increased by

90 μatm (i.e., by more than a third) and show no signs of slowing down. The CO_2 added to atmosphere will eventually be absorbed by the ocean, acidifying it. The pH of surface waters has already dropped by 0.1 units (a significant amount), and within 40 years carbonate ion concentrations below aragonite saturation will begin to occur in polar waters, spreading eventually into lower latitudes. If CO_2 emissions continue unabated, the pH of the ocean will eventually sink to levels lower than it has been for hundreds of millions of years.

A drop in ocean pH has implications for the existence and ecology of coral reefs because a decrease in the saturation state of seawater with respect to calcium biominerals will have a corresponding decrease in the rate of calcification of coral reefs. Calcification rates in the tropics have already dropped by 10% since the beginning of the industrial revolution and a doubling of atmospheric CO_2 from pre-industrial levels could diminish coral calcification rates by as much as 50%. Such decrease in calcification rates will result in reefs shrinking in size and structural integrity, as reef size and strength result from the balance struck between calcium carbonate production and erosion. A decrease in the areal extent of coral reefs in turn, diminishes the habitat and food available for the hundreds of thousands of species of organisms that dwell within coral reef ecosystems. This is true for both the familiar warm water coral reefs of the tropics whose productive ecosystems are an important resource for subsistence fishers and billion-dollar tourism economies alike, and the deeper-dwelling, cold-water coral reef ecosystems that provide habitat and nursing grounds for numerous species including commercially important fish like rockfish and orange roughy.

The reduced saturation state of seawater with respect to calcium biominerals may also affect the production and maintenance of shells and exoskeletons of organisms like mollusks, echinoderms, and crustaceans. The first impacts will be seen in polar ecosystems whose cold waters may become undersaturated with respect to aragonite at the doubling of pre-industrial CO_2 expected by 2050. Experiments and material collected in sediment traps have shown that the shells of the aragonitic pteropod mollusks become rapidly pitted and begin to dissolve upon exposure to undersaturated waters. Even the shells of live pteropods begin to dissolve under conditions equivalent to those expected for polar waters at the end of this century. Pteropods should not survive if they cannot maintain their shells, and their disappearance from polar waters would have a significant impact on polar ecosystems. Pteropods are important prey for many zooplankton, fish, and baleen whales and their fecal pellets and mucous feeding webs are important vectors for the sinking of organic matter to deep-sea ecosystems and sediments.

The lowering of the saturation state of seawater for calcium carbonate minerals will also make it thermodynamically less favorable for the calcitic plankton, foraminiferans, and coccolithophores to biomineralize. If the lowering of carbonate ion concentrations means that the high internal pHs required for calcite precipitation take more energy to maintain, these organisms will have a lesser portion of their total energy budget available for growth and reproduction. Although, experimentally, the response of coccolithophore species to increased acidification is mixed, an acidification-driven shift in the phytoplankton toward noncalcareous forms such as diatoms would have an impact on the cycling of CO_2 , nutrients, and alkalinity in the ocean by altering efficiency of the biological pumping of particulate organic matter and biominerals into the deep sea. If the ratio of particulate organic carbon to calcium carbonate sinking into the deep sea were to increase due to the lesser production of calcium biominerals by foraminiferans and coccolithophores, the biological pump would be more effective at sequestering CO_2 in the deep sea, lowering atmospheric concentrations at the expense of more quickly lowering the pH of the deep sea.

Tracking Calcium Cycling in Biogeochemical Systems

Changes in the calcium cycle due to pollution and other anthropogenic influences and their impact on ecosystems make unraveling and quantifying the fluxes of calcium through ecosystems a pressing concern. Three types of tools have been employed, trace element ratios, such as Sr/Ca, ratios of nonradioactive isotopes of strontium or calcium (e.g., $^{87}\text{Sr}/^{86}\text{Sr}$, $^{44}\text{Ca}/^{42}\text{Ca}$, $^{44}\text{Ca}/^{40}\text{Ca}$), and, less commonly, studies of artificially enriched stable (e.g., ^{48}Ca) and radioactive (e.g., ^{45}Ca) isotopes. Such tracers reflect sources of Ca to ecosystems and, when reconstructed from the wood of long-lived trees, may serve as a means of reconstructing the acidification of environments over the past century or so.

The use of Sr/Ca in terrestrial ecosystems takes advantage of the fact that different minerals serving as sources of Ca^{2+} contain different Sr/Ca signatures. Studies employing this method rely on the assumption that Sr^{2+} and Ca^{2+} ions are not fractionated as they cycle through ecosystems because of their comparable charge and size. The Sr/Ca of different calcium reservoirs (e.g., soil waters, soils, and vegetation) should thus reflect it of their sources of calcium. Complicating the use of Sr/Ca, however, are data suggesting that Sr/Ca is fractionated during uptake by and internal cycling within plants and the fact that all Sr/Ca inputs to ecosystems (specifically, mineral pools) have not been identified.

Strontium and calcium isotopic signatures may also usefully identify the sources of Ca to terrestrial

environments. Strontium isotopes, which have the advantage of not being biologically fractionated, are used based on the assumption that Sr and Ca in terrestrial environments have been derived from the same sources. The source of calcium to plants, for example, is identified from their $^{87}\text{Sr}/^{86}\text{Sr}$ because it reflects the bulk $^{87}\text{Sr}/^{86}\text{Sr}$ of the materials from which the strontium came. Calcium isotopes provide a more direct way of investigating Ca cycling through ecosystems. Solutions enriched in the stable calcium isotope with the lowest natural abundance (^{48}Ca) or a radioactive isotope of calcium (^{45}Ca) have been released to study the movement of calcium through the environment. Natural abundances of Ca isotopes provide a way to directly study the calcium cycle in ecosystems. Such work is in its infancy and studies are underway to characterize the Ca isotopic composition of minerals, natural waters, and vegetation and to define Ca isotopic fractionation during weathering, soft tissue formation, biomineralization, and between different plant tissues. Such studies pave the way for this new tracer to be universally applied.

In marine systems, such trace elements and isotopic systems are not as useful for tracking anthropogenic changes to the calcium cycle as direct measurements of pH, alkalinity, and calcification rates. Reconstructions of the depth distributions of calcite sediments and the calcium isotopic composition of marine sediments, however, help to identify past perturbations in the calcium cycle and their links to climatic and ecological events.

The Future

Quantifying the effects of anthropogenic perturbations on calcium cycling and ecosystems is challenging because the effects are not instantaneous. Outcomes, such as deteriorating tree health (or die-offs) and declining bird populations due to calcium-depleted eggshells, may only be obvious after years of cumulative damage to the environment. On a hopeful note, grave and large-scale impacts such as these can inspire shifts in industrial practices; in response to the problems acidification was causing to terrestrial ecosystems, care has been taken in recent years by industrialized nations to lower emissions of sulfate and NO_x (although emissions have not ceased entirely). Unfortunately, decreases in calcium-containing emissions have diminished the unintended anthropogenic amelioration of the calcium depletion caused by acidification.

Land-use changes also have mixed effects. Re-vegetation of areas may decrease their production of dust, but reforesting an area after repeated harvesting of crops accelerates the calcium depletion of the area as the calcium contained in the removed biomass has been lost. Accordingly, attempts at environmental remediation have

been made through the application of calcium-rich compounds, such as lime or wollastonite. Although forest-scale manipulations have been set up to assess the effectiveness of these applications, these experiments are ongoing and, thus, conclusions about the effectiveness of these treatments cannot yet be made. Ecosystem models have also been employed to understand and predict impacts of these ecological manipulations on the terrestrial calcium cycle, but as our understanding of the complexities of the terrestrial calcium cycle is currently limited, these models primarily serve to provide broad guesses of future impacts.

As in terrestrial ecosystems, although the impacts of anthropogenic perturbations of the calcium cycle on marine ecosystems have been predicted and modeled, the extent of the impact of ocean acidification on ocean ecosystems remains uncertain. On one hand there are undoubtedly effects and variables that have not been considered, and on the other hand it is an open question to what extent calcifying organisms will adapt to and cope with the lower pHs, lower carbonate ion concentrations, and lesser degrees of saturation with respect to calcium carbonate minerals. Already stressed by pollution and overfishing, ecosystems centered around calcareous organisms like corals may collapse under the additional burden of acidification. Alternatively, although the rate of pH change is occurring at an unprecedentedly rapid timescale relative to evolution, genetic adaptation to the more acidic conditions could occur before widespread alteration of the ecosystems occurs. At the moment no experiments on appropriately long time frames have been conducted, in terms of either pollution or remediation, for the outcomes to be clear. Even where we immediately cease to perturb the calcium cycle, we have still made significant changes to the global calcium cycle and it will take some while for the full consequences of our inadvertent global-scale experiment on the calcium cycle to unfold.

See also: Acidification; Anthropospheric and Anthropogenic Impact on the Biosphere; Climate Change 2: Long-Term Dynamics; Deforestation; Forest Management; Global Change Impacts on the Biosphere; Pelagic Predators.

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Cannibalism

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Introduction

Taxonomic Distribution

Contexts of Cannibalism

Effects of Cannibalism on the Dynamics of Populations and the Structure of Communities

Evolution of Cannibalism: Evaluating the Costs and Benefits

Cannibalistic Polyphenism

Summary

Further Reading

Introduction

The ecology and evolution of numerous organisms may be strongly influenced by cannibalism, the killing and consumption of all or part of an individual of the same species. This phenomenon has been documented in a diversity of taxa in a variety of habitats, including bacteria, octopus, dinosaurs, and humans. Cannibalism occurs in a broad array of ecological contexts and has played a strong role in the evolution of parental care and alternative mating systems. Acts of cannibalism can potentially incur significant costs, such as impairing a cannibal's inclusive fitness by consuming close relatives. Despite such potential disadvantages, cannibalism can also be adaptive, and has even led to the evolution of specialized morphologies (cannibalistic polyphenism) in individuals of some species.

The causes and consequences of cannibalism can be explored in many ways. The dynamic nature of this behavior is strongly influenced by ecological, social, and

psychological contexts. Individual morphology, survival, and evolutionary fitness are modified by cannibalistic actions and choices. Populations subject to density-dependent regulation, as well as entire ecological communities, can be strongly influenced by cannibalism. Elucidation of selective factors leading to the evolution of this behavior remains an active field of scientific investigation.

Taxonomic Distribution

Cannibalism is widespread in nature. It occurs in bacteria, protozoans, invertebrates, and vertebrates, including humans. A varying number of accounts have been published for most groups. Our review of 1000 published papers for the period 2001–05 revealed a wide disparity in attention to this behavior in these taxa. In our brief survey, we found that 0.3% of the papers were on cannibalism in bacteria, 0.5% on protozoans, 0.3% on