The efficiency paradox: How wasteful competitors forge thrifty ecosystems

Geerat J. Vermeij[a,1]

Organic waste, an inevitable byproduct of metabolism, increases in amount as metabolic rates (per capita power) of animals and plants rise. Most of it is recycled within aerobic ecosystems, but some is lost to the system and is sequestered in the crust for millions of years. Here, I identify and resolve a previously overlooked paradox concerning the long-term loss of organic matter. In this efficiency paradox, high-powered species are inefficient in that they release copious waste, but the ecosystems they inhabit lose almost no organic matter. Systems occupied by more efficient low-powered species suffer greater losses because of less efficient recycling. Over Phanerozoic time, ecosystems have become more productive and increasingly efficient at retaining and redistributing organic matter even as opportunistic and highly competitive producers and consumers gained power and became less efficient. These patterns and trends are driven by natural selection at the level of individuals and coherent groups, which favors winners that are more powerful, active, and wasteful. The activities of these competitors collectively create conditions that are increasingly conducive to more efficient recycling and retention of organic matter in the ecosystem.

ecosystems | metabolic power | competition | efficiency | Phanerozoic

Every living thing converts matter and energy into biological work. As long as they are alive, organisms create material and energy waste that they themselves cannot use. This waste, together with the organism's body when it is no longer alive, becomes available to other organisms in principle. Individual-level efficiency—the quantity of waste produced divided by the organism's mass—is an inevitable consequence of metabolism. It can be very high and costly, as in fast-growing plants that lose water through transpiration while capturing carbon dioxide during photosynthesis (1, 2), plants that seasonally drop leaves or twigs (3, 4), arthropods that molt their exoskeleton as they grow (5), mast-fruiting trees (6), mass-spawning and mucus-producing reef corals (7–9), pelagic tunicates that construct throw-away mucus houses (10, 11), and endothermic vertebrates that shed copious heat as they generate and maintain high body temperatures (12). These organisms have high metabolic rates (energy used by the whole body per unit time), and are therefore described as high-powered. Their wastefulness—large amount of unusable organic matter produced for a given whole-body mass—is a price these organisms pay for competitive power and easy access to abundant resources.

At the opposite extreme are low-powered species that recycle waste efficiently: the island palm *Lodoicea* that recycles water and nutrients by channeling rain water to the roots (13), litter-collecting plants (14), plants with C_4 photosynthesis or crassulacean acid metabolism that reduce water loss by opening stomata during cool nights (15), hermit crabs that reuse shells (5), termites that oxidize a large fraction of the methane produced by their symbionts when digesting wood (16), and small herbivorous mammals that reingest their own feces (17).

Inefficiency also prevails in other ecological functions, including interception of light by photosynthesizing plants and phytoplankters (18, 19), the capture of prey by predators (20), particle retention by suspension-feeders (21, 22), securing mates (23), pollination (24), and other activities subject to adaptive evolution. These inefficiencies are important, but the emphasis here is on long-term loss of nutrients.

The concept of efficiency also applies to ecosystems (25, 26), defined here as total biomass in the

[a]Department of Earth and Planetary Sciences, University of California, Davis, CA 95616

system relative to the quantity of biomass exported to sediments, where it is buried or tectonically sequestered for millions of years. Inefficient ecosystems include contemporary tundra and permafrost in the Arctic (27–29), peat bogs (30), white-sand tropical forests and the black-water rivers that drain them (31, 32), anoxic and euxinic zones in lakes and oceans (33, 34), and the coal swamps of the Carboniferous and Permian periods (35–37). Other systems keep permanent losses of degraded biomass to a minimum through storage in long-lived organisms or through highly efficient recycling. In forests, storage in trees can result in depletion of soil nutrients (38, 39), perhaps as the consequence of the removal of abundant large herbivores (40). Efficient systems include tropical and temperate forests on fertile soils (41, 42), grasslands, and coral reefs (7–9, 43). Large-scale efficiency is achieved through exchange of waste between adjacent ecosystems by mobile animals (44). Such exchanges are known between the pelagic zone of the ocean and the benthos (45–47), rivers and their banks (48, 49), coral reefs and mangroves (50), and reefs and offshore waters (51).

Today's biosphere loses less than 0.1% of waste to burial (52), 50 to 90% of it originating in the oceans (53). This very high efficiency, however, obscures spatial and temporal variation indicated by the geological record. Stanley (54) identified 26 major fluctuations in carbon isotopic ratios over the last 540 My, implying that long-term losses of organic carbon to geological reservoirs often exceeded inputs from ecosystems. Where and when ecosystems are inefficient and how adaptive evolution affects nutrient losses are key questions that are increasingly urgent at a time when humans are fundamentally altering both the adaptive landscape for species and the flow of nutrients in ecosystems.

A previously underappreciated pattern, which I call the efficiency paradox, emerges from these considerations. This counterintuitive idea is that highly effective but inefficient organisms with rapid metabolism and large power budgets thrive in ecosystems that are highly efficient in redistributing and recycling material resources and keeping losses of those resources to geological reservoirs small. Conversely, ecosystems dominated by low-powered organisms are inefficient because they do not develop or maintain the ecological networks that are necessary for the retrieval and recycling of waste products.

It was already known that the carbon-use efficiency of land plants rises as the carbon-use efficiency of microbes that decompose organic matter in the soil falls (55), but this finding refers to nutrients accumulating and being temporarily stored in the soil, not permanent loss of material resources. Storage of resources in sediments or in the bodies of long-lived organisms on time scales from decades to centuries slows the flow of nutrients among organisms, but does not necessarily imply sequestration at time scales of millions of years.

Insofar as long-term losses were considered in previous studies, the conditions that promote the long-term accumulation of coals, peats, and marine black shales were thought to be generated by processes beyond the primary control of organisms. These conditions—especially anoxia associated with the accumulation of organic matter that is not oxidized—were thought to prevail during periods of global warming, sluggish ocean circulation (and reduced exchange between bottom and surface water because of a stratified water column), and externally imposed mass extinction (35, 54, 56–58). The role of organisms in creating and maintaining conditions favorable to high ecosystem-level efficiency has generally not been emphasized.

Related to the efficiency paradox is a long-term historical trend toward greater ecosystem-level and global efficiency and productivity. As increasingly powerful (and wasteful) competitors replaced less active equivalents in different clades over Phanerozoic time, ecosystems supporting these high-powered producers and consumers became increasingly effective at retrieving, retaining, and recycling material resources (carbon, nitrogen, phosphorus, and metals). Evidence for increased efficiency and productivity comes from 1) deepening and intensification of bioturbation (sediment disturbance and oxygenation by organisms), both in the oceans and on land, which promotes exchange of buried organic matter with the aerobic part of the biosphere (59, 60); 2) increased photosynthetic capacity (and oxygen production) by land plants (61) and phytoplankton (62); 3) redistribution of nutrients vertically and horizontally in the water column by increasingly active swimming animals and vertically migrating planktonic organisms, which entrain water and nutrients as they move (63–65); 4) a long-term decrease in the formation of coal, marine black shale, and shelf carbonates precipitated by organisms, all sinks for organic carbon on geological time scales (66, 67); 5) deepening of anoxic zones in the oceans, which decreases the size and extent of carbon sinks over time (66, 68); 6) increasing extraction of inorganic nutrients by land plants aided by fungi that chemically break down previously unavailable minerals in rocks (69–72); 7) progressively intense and deep bioerosion of rock and wood, again unlocking nutrients (5); and 8) expansion of energy sources tapped by organisms (73).

Brief reversals (0.5 to 10 Mya in duration) have occurred throughout the Phanerozoic, as indicated by carbon-isotopic excursions that were particularly intense during times of high sea level and during or following mass extinctions (68), but these did not alter the overall trajectory of increasing efficiency and productivity. The input of inorganic nutrients and of oxidized carbon (as carbon dioxide) from the mantle through volcanic activity (74) further stimulated product ion and efficiency by adding raw materials, increasing weathering, and reducing transpiration costs for plants on a global scale, especially during the later Mesozoic era.

These trends increased the rate of turnover of organic matter and oxygen within aerobic ecosystems and promoted exchanges of nutrients among ecosystems, speeding up and spatially expanding the utilization of essential nutrients that were previously buried and unavailable to most organisms. The higher turnover and more effective uptake of resources by increasingly powerful and productive ecosystems indicate greater ecosystem efficiency over time as well as the spread of oxygenated conditions (63, 75), because fewer nutrients became sequestered in sediments where biological activity was reduced or absent (68). Note that the increased recycling and production of organic matter within aerobic ecosystems are not reflected in the carbon-isotopic record because this organic matter is not fossilized. It is unclear whether these trends have resulted in a global increase in biomass, which would imply a long-term concentration of carbon in Earth's outermost layer. This possibility is countered by Hayes and Waldbauer (74), who infer a steady-state flux of carbon between the mantle and the crust.

Here, I propose a mechanistic link between the above empirical trends in ecosystem-level efficiency and productivity on the one hand and the universal evolutionary process of natural selection, which operates at the level of individuals and coherent groups, on the other. In a conceptual analysis, I show how

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selection leading to increasingly powerful competitors makes competitive winners less efficient but the ecosystems they inhabit more efficient. Long-term increases in ecosystem-level efficiency emerge from the cumulative effects of selection among competitors and from the stimulating effects of powerful agents on the efficiency of recycling by other members of the system.

Conceptual Model

The key to an ecosystem's efficiency is accessibility of organic matter to remineralization by organisms. Organic matter becomes inaccessible when it is deeply buried in sediments (33), bound to clay particles (76, 77), or chemically resistant to breakdown (31, 78). Remineralization is also inhibited by low temperature, an abundance of sulfides, and a lack of oxygen. Accessibility increases by at least 3 mechanisms: the evolution of appropriate enzymes with high catalytic activity for breaking down refractory compounds (lignin, suberin, and cutin) produced by land plants (79, 80); bioturbation, which exposes organic matter to aerobic respiration (81, 82); and interception by consumers such as herbivores, suspension-feeders, and predators before organic matter reaches the soil or sediment (83).

All 3 mechanisms—enzymes, bioturbation, and interception—are energetically expensive. They are therefore most effective when an organism's power budget is large, that is, when allocation to expensive functions such as breaking down or retrieving resources without interfering with other essential functions becomes feasible. A large power budget is enabled when temperatures and metabolic rates are high. Rapid metabolism, in turn, is enabled by a system in which productivity—the rate at which biomass is fixed from inorganic sources—is high. Efficient recycling in the presence of inefficient powerful producers and consumers should therefore be associated with high productivity.

These processes and conditions are affected by the ways in which co-occurring species that differ in competitive status acquire and defend resources and by the interactions among these species. Grime (84) recognized 3 classes of species: opportunists, which exploit temporarily plentiful resources by growing and reproducing quickly during a short period of activity; competitive dominants, which are superior at capturing and retaining resources over a long lifespan by expending high power as the need arises; and low-powered species, which exist as long-lived individuals that take up resources slowly and protect them with constitutive defenses in settings of chronically low resource supply thanks to low competitive status, an infertile environment, or low temperatures, all associated with slow metabolism. Selection favors high power in species of the first 2 categories. Opportunists and competitive dominants produce abundant wastes that decomposers and other consumers can rapidly recycle (41, 62, 85, 86). Wastes released by low-powered species tend to resist degradation and recycling because organisms either cannot break them down or do so very slowly; they therefore tend to accumulate on long time scales (62, 85, 86). An efficient ecosystem in which high-powered species thrive therefore depends on diffuse collusion or evolved cooperation between wasteful competitors and more efficient recyclers.

The 3 mechanisms of increasing access to previously unavailable resources all involve adaptive evolution, and all entail increased metabolic costs. Remineralization will be slow, and ecological efficiency will be low, if the metabolic rates of recyclers are constrained by low temperatures or scarce resources; however, if mineralization takes place inside, or in close association with, productive high-powered organisms such as endothermic animals or fast-growing plants, it will be rapid despite the high metabolic costs. This explains the efficiency paradox.

The fossil record offers ample evidence for increasing performance among opportunists and dominant competitors. Older, lower powered opportunists and dominants were displaced to more marginal environments by higher powered species in different clades in land plants (61), phytoplankton (62), suspension-feeders (5), sediment-dwelling animals (59, 87), swimmers (65), predators (5), herbivores (83), and wood-digesting organisms (85). The evolution of endotherms permitted faster recycling of nutrients even in the cold, and therefore reduced losses of organic matter at low temperatures.

Under exceptional circumstances, ecosystems become inefficient when resident organisms are unable to capture or recycle a sudden increase in resource supply. This can happen under conditions of mass mortality, when decomposers are overwhelmed by dead organisms; during floods, when primary producers cannot capture a large influx of raw materials; and, most importantly, when previously sequestered organic matter is released at high rates, as happened during massive intrusions of magma and collisions between Earth and extraterrestrial bodies, exposing carbon-rich deposits to chemical weathering and erosion. Such releases are documented for crises at the end of the Permian (88–90), Triassic (91), and Cretaceous (92, 93). Ecosystem inefficiency also increased during crises because of the extinction of high-powered predators, herbivores, and suspension-feeders, whose loss would imply lower productivity and turnover.

I speculate that the elimination of high-powered swimmers, vertically migrating plankton, and active suspension-feeders during mass extinction events likely led to a decrease in biologically generated water movement and oxygen distribution (63, 64), adding to the reduction in oxygen concentration in the oceans due to a high influx of nutrients from the land and to ocean warming (34, 94) characteristic of past oceanic anoxic events and the present Anthropocene (95).

Conclusions

The role of natural selection and history in explaining previously overlooked patterns in the efficiency of resource retrieval, retention, and recycling in ecosystems is critical to a deeper understanding and mitigation of the destructive human footprint on the biosphere. The conceptual model proposed here opens the door to a more complete integration of ecosystem science and evolutionary biology, disciplines that have largely gone their separate ways. By highlighting a comparative approach to ecosystems, adaptive types, and successive phases in Earth history, the model also points to promising directions for measuring resource flows and for tests of hypotheses about the effects of evolution on resource dynamics. Like so much else in biology and economics, sustainability depends on evolution and on the ways in which life modifies its own environment.

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