The Simulated Evolution of Biochemical Guilds: Reconciling Gaia Theory and Natural Selection

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Abstract Gaia theory, which states that organisms both affect and regulate their environment, poses an interesting problem to Neo-Darwinian evolutionary biologists and provides an exciting set of phenomena for artificial-life investigation. The key challenge is to explain the emergence of biotic communities that are capable, via their implicit coordination, of regulating large-scale biogeochemical factors such as the temperature and chemical composition of the biosphere, but to assume no evolutionary mechanisms beyond contemporary natural selection. Along with providing an introduction to Gaia theory, this article presents simulations of Gaian emergence based on an artificial-life model involving genetic algorithms and guilds of simple metabolizing agents. In these simulations, resource competition leads to guild diversity; the ensemble of guilds then manifests life-sustaining nutrient recycling and exerts distributed control over environmental nutrient ratios. These results illustrate that standard individual-based natural selection is sufficient to explain Gaian self-organization, and they help clarify the relationships between two key metrics of Gaian activity: recycling and regulation.

Keywords
Gaia theory, emergence, genetic algorithms, artificial life, geophysiology

1 Introduction

In the quest to understand the general principles of life's "bio-logic" [11], artificial life (alife) research spans a wide spectrum of natural phenomena, from cellular metabolisms and microcosms to macroscopic populations and ecosystems. A diverse array of models are employed for this task, ranging from the very abstract to the excruciatingly exact. But regardless of the natural scale or modeling approach, the presence of self-organization, emergence, and self-regulation is common to the vast majority of alife experiments, thus fueling our belief that bio-logic does exist and can be deciphered.

This work examines these same alife characteristics in the context of an extremely large-scale natural process but via a very abstract model of metabolism, growth, and environmental interaction. The phenomenon itself is the controversial Gaia theory [15, 16, 19], which, in a nutshell, states that (a) the interactions between the biological and physicochemical realms are bidirectional, and (b) via the feedback loops composed of these interactions, the biota can indirectly control the environmental conditions in which they live.

Some of the key evidence for Gaia involves the chemical fingerprints of life found in the atmosphere, hydrosphere, and lithosphere. Classic among these are (a) the far-from-equilibrium concentrations of gases such as oxygen, methane, and carbon-dioxide in Earth's atmosphere versus the near-equilibrium conditions of lifeless planets such as Mars, and (b) the nearly constant ratios of nitrogen and phosphorus in all the world's oceans and in the bodies of all marine phyto- and zooplankton. These and other examples hint that organisms may have huge impacts on their chemical environments, and in ways that indirectly but effectively sustain life on Earth.

Another interesting sign of life is the intensity of nutrient recycling in the biosphere via the circulation of inorganic and organic compounds among different organisms and the abiotic environment [27]. For example, an atom of phosphorus is, on average, transferred back and forth between plants and detritus-consuming (and phosphate-producing) microbes 46 times before exiting the soil as river runoff. This recirculation creates transfer fluxes among the biota that far exceed the input/output fluxes to the ecosystem. Essentially then, nutrients of high organic utility but low external supply tend to be efficiently recycled, leaving yet another fingerprint of life within and on its physicochemical environment. Hence, both recycling efficiency and regulatory efficacy are promising metrics of Gaian activity. Both appear to capture the essence of Gaia: the ability of life to change its surroundings in a manner favorable to life.

Investigations into the mechanisms underlying the emergence of recycling and regulation place Gaia squarely within the focus of alife research, and in this case, the entire planet is the "living system" in question. However, the evolution of coordinated environment-altering behavior among a host of diverse species runs counter to many Neo-Darwinian intuitions, such as adaptationism and competition-based survival of the fittest. But a review of the Gaia literature, in combination with our simulation results, indicates the fallacy in these apparent incongruities between Gaia and Neo-Darwinism.

We develop a very abstract model of the evolution of biochemical guilds (i.e., groups of microorganisms that perform similar chemical activities). Simulations of this model show that (a) competition for resources leads to rapid diversification and hence the formation of many biochemical guilds, (b) these guilds create pathways for nutrient recycling, and (c) the combined effects of guild biochemistry and frequency-dependent selection can regulate global chemical ratios. Hence, our results show that both Gaian perspectives, recycling and control, are quite compatible with natural selection.

2 Signs of Life

In the early 1960s, James Lovelock [15, 18], a NASA atmospheric chemist, was trying to determine whether there was life on Mars. From infrared spectrometer readings of the distant martian atmosphere, he found that the concentrations of several key chemicals such as oxygen, carbon-dioxide, and methane were very near equilibrium, whereas the Earth's atmosphere was far from equilibrium. Life, Lovelock argued, drove the Earth's atmosphere to low entropy and kept it there. This idea, that the biota could effect large-scale environmental changes, was somewhat controversial, but the central dogma of Lovelock and Margulis's Gaia theory [19], that the biota indirectly regulate the environment for their own benefit, caused an incredible stir among biologists, chemists, and geophysicists alike.

By analyzing the Earth from a Gaian perspective, scientists have found several planetary homeostatic loops that appear to involve climatic, geochemical, and biological factors. These include the short-term regulation of local climate by dimethylsulfide (DMS)-producing algae [6, 21], the long-term regulation of global temperatures by photosynthetic organisms [30], and the maintenance in the oceans of relatively constant salinity [9] and nitrogen-phosphorus (N:P) ratios [13, 22, 27] by marine microorganisms.

The invariance of the N:P ratio at a value near 6.7, known as the Redfield ratio [22], is particularly intriguing. With few exceptions, Redfield ratios are found both in water concentrations and in the biomasses of algae and zooplankton at all depths in all the world's oceans. The big question is whether the biota have adapted their internal concentrations to the biosphere, or whether they have caused global changes in N:P ratios to suit their needs for the magical 6.7, which may represent some physiological optimum. As Volk points out [27], if the biota are passively adapting to the oceanic concentrations, then why do other chemical elements not have matching ratios in marine organisms and waters? He argues that negative feedbacks between populations of nitrogen-fixing and denitrifying bacteria could lead to emergent control of the Redfield ratio. Furthermore, Lenton [13] uses difference equations for these two populations within coupled atmospheric-oceanic compartmental models to show that these regulatory loops do indeed produce water-column N:P ratios near 6.7. So there is mounting evidence that, indeed, local biotic mechanisms can regulate global chemical concentrations.

Another intriguing example of life's ability to create favorable conditions for more life involves the creation of efficient recycling pathways for poorly supplied nutrients. As detailed by Volk [27], the external supplies of critical elements such as carbon (C), nitrogen (N), and phosphorus (P) to terrestrial and aquatic ecosystems are far below the amounts actually required by the biota. The deficit is filled by recycling processes wherein C, N, and P atoms are shuttled among different compounds that are ingested and expelled by various organisms.

For example, carbon is taken up by photosynthesizing plants as carbon dioxide and used to build organic carbon compounds such as carbohydrates, which are then transferred to herbivores or detritus-consuming microorganisms, only to be returned to the atmosphere as carbon dioxide by respiration in plants, animals, bacteria, and fungi. A small percentage of the carbon sinks out of aquatic and terrestrial ecosystems as organic detritus and the calcium-carbonate shells of buried microorganisms, returning millions (to hundreds of millions) of years later via geophysical processes such as volcanism, deep-sea thermal ventilation, and rock weathering [25]. In the case of weathering, the biota have been shown to accelerate this key step of the C, N, and P cycles significantly [26], so many links of the circuit feel the biotic presence.

Nitrogen follows similar cycles from nitrogen gas to ammonium, via the activity of nitrogen-fixing microorganisms, to nitrates, via bacterial nitrification processes, to protein biomass in a wide spectra of organisms, to ammonia waste products, and finally back to nitrogen gas via denitrifying bacteria. A small percentage is also buried as organic detritus, which, again, returns millions of years later via geophysical processes.

The net result of these recycling loops is that the biota annually consume 200 times more carbon, 500–1,300 times more nitrogen, and 200 times more phosphorus than is supplied by external fluxes [25, 27]. These numbers represent the "cycling ratios" for the three elements (computed as the intra-biota transfer rate divided by the external flux). Without this amplification, the total size of the biota would be restricted to a fraction of one percent of Earth's total biomass. Without the biota, there would be no amplification.

In short, the coordination of biochemical processes across a diverse range of organisms enables life to thrive to a degree that dwarfs that of an uncoordinated, low-recycling environment. Furthermore, the abundance of critical nutrients adds stability to the environment, enabling the biota to endure periods of fluctuating external inputs. Once again, life begets life via its effects upon the physicochemical environment.

If we classify organisms by the chemicals that they consume and produce (i.e., by their metabolisms), then each group constitutes a "biochemical guild" [27]. The formation of recycling loops is therefore dependent upon the emergence of the proper complement of biochemical guilds such that the waste products of one guild are the nutrients of another.

3 Neo-Darwinism Versus Gaia Theory

The essential question, from both a Gaian and an alife perspective, is how global recirculation and regulation emerge. Although Gaian homeostatic networks would appear to be near-optimal arrangements for the organisms involved, their evolution is far from inevitable. In fact, some of the most ardent opponents to Gaia theory are Neo-Darwinian biologists.

A common complaint of the Neo-Darwinians is that the evolution of Gaian networks appears to require metaselectional concepts such as group selection, at best, or teleology, at worst. However, geophysiologists (i.e., scientists who study Gaia) invoke nothing beyond standard individual selection in explaining possible pathways of Gaian emergence.

A second difference is one of fundamental principles: Whereas Gaians contend that over the past 3.5 billion years, living organisms have made our planet more livable through their influences, the Adaptationist wing of Neo-Darwinism claims that organisms simply adapt to whatever environment the physical forces of nature present to them.

Finally, Neo-Darwinians argue that the selfish behavior of organisms will preclude the formation of wide-scale coordinated environment-altering activities, since "cheaters" would evolve to reap the benefits of the alterations without paying the cost of exerting their small influence (e.g., secreting a particular chemical). By saving this production cost, the cheaters would have higher fitness and eventually dominate the population, thereby breaking an essential link in the feedback loop.

Gaians counter these attacks by postulating that the environment-altering activities, although potentially costly and of only long-term benefit, have primary local effects that garner immediate selective advantages to the organism. For example, certain marine microorganisms build protective shells out of calcium carbonate, but by dying and sinking into the sediments, these organisms sequester carbon in the sediments and thereby help to regulate atmospheric CO_2 levels, and hence climate (See loops 3 and 4 in Figure 1). These arguments bring Gaia theory back into the Neo-Darwinian, reductionist fold: In their struggle for survival, organisms perform certain fitness-enhancing local activities that have the side-effect of altering large-scale geochemical processes, often to the benefit of life itself.

4 Daisyworld

Watson and Lovelock's classic Daisyworld model [18, 28] has served as Gaia theory's prototype for over a decade. Hence, understanding Daisyworld is a key prerequisite to understanding Gaia theory. Since most proposed Gaian phenomena are very complex, involving geophysical factors and population dynamics spread over an entire planet, operational computer models of Gaian activity are scarce. Daisyworld is the notable exception, since it illustrates the emergence of distributed planetary temperature regulation via an extremely simple differential-equation model. Unfortunately, Daisyworld has done little to reinforce the tenuous connection between Gaia and evolution.

In the classic Daisyworld, two species of daisy, black and white, are grown on a simulated planet. Both species have the same preferred temperature, 22.5 °C, at which their growth rates are maximal. The black variety has low albedo and therefore creates higher local temperatures than the ambient, whereas the white daisies and their high albedo create local temperatures below the ambient. This simple combination of two

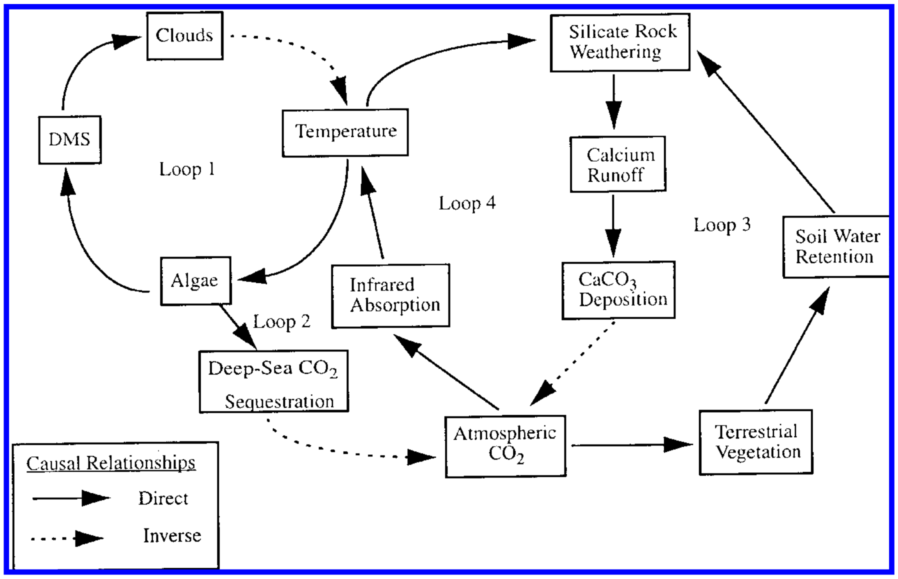


Figure 1. Gaian homeostatic networks. Note that each loop includes an odd number of inverse relationships and is therefore a negative-feedback circuit. *Loop 1*: Algae release dimethylsulfide (DMS) precursors into the atmosphere, which are chemically transformed into DMS. These molecules serve as condensation nucleii for cloud formation, and clouds reduce temperature by increasing planetary albedo. In nutrient-rich waters, temperature normally has a positive influence on algae growth. *Loop 2*: Algae photosynthesis takes up carbon dioxide to build carbon-based biomass. Although most of this biomass-bound carbon is quickly returned to the oceans and atmosphere via the respiration processes of algae or organisms further up the food chain, a small percentage of marine biomass is not immediately recycled and sinks to the ocean depths, where it is eventually respired by microorganisms but where mixing rates are extremely low and currents move very slowly. Hence, the released CO_2 may not return to surface waters for several centuries, often via equatorial outgassing. Thus, the net effect of the marine food chain is atmospheric CO_2 reduction over rather large time scales, with algae functioning as the biota-biosphere interface. *Loop 3*: Carbon dioxide positively influences terrestrial vegetation, whose roots increase soil water retention. The presence of water (and certain soil microorganisms that live in symbiosis with plants) increases the weathering of silicate rocks [26], a process that releases calcium into the soil and increases the supply of calcium to the oceans, via river runoff. Marine calcium and CO_2 are combined to form calcium carbonate, $CaCO_3$, which is used by marine microorganisms to build shells. The death and sinking out of these organisms removes considerable CO_2 from short-term circulation, thus reducing atmospheric CO_2 and temperature via the greenhouse effect. *Loop 4*: Increased temperature also promotes rock weathering via various inorganic and organic mechanisms.

daisy types with the same optimal temperature leads to self-organized regulation of global temperature in the face of a slow but steady increase in solar input.

Briefly, at low temperatures, black daisies proliferate due to their ability to raise local temperatures closer to 22.5. A globe nearly covered in low-albedo black daisies absorbs a high percentage of the incoming solar energy, thereby increasing global temperature to 22.5 at a much faster rate than could the increasing solar input alone. Global temperature is then maintained near 22.5 even as the solar input soars, due to the effect of the white daisies, whose high albedo enables them to create local temperatures near 22.5 and outcompete the black daisies, whose local temperatures are too high. The white daisies thus take over the planet and their collective albedo keeps global temperatures near 22.5 for a long period of time. Eventually, however, the solar input is too great and even the white daisies succumb to heat death, at which point global temperatures rise unabated. However, across a wide range of solar inputs, one of the two daisy populations keeps the planetary temperature nearly constant, thus providing key evidence that simple local interactions among the biota can have global regulatory consequences. The invisible hands of teleology are unnecessary, and Gaia theory thereby takes a huge step away from the mysticism that was unduly attributed to it by a host of renowned scientists.

However, Gaia theory is still very vulnerable on the evolutionary flanks, and Daisyworld provides only minor fortification. From the evolutionary standpoint, the main critique of Daisyworld is the lack of significant genetic diversity for color (i.e., albedo) and preferred temperature. Saunders [24] shows that if black and white daisies have preferred temperatures of 27.5 °C and 17.5 °C, respectively, then the regulatory range (of solar inputs) is reduced. He further claims that if preferred temperature were under genetic control, then cold-loving species would dominate under reduced solar input but quickly give way to heat-loving species as solar forcing increased. In short, the species whose combination of preferred temperature and albedo best matched the current solar trend would dominate. This "greedy" acceptance of the ambient conditions destroys the global regulatory behavior.

Our own Daisyworld extension confirms Saunder's beliefs. In this model, daisy genotypes code for a wide range of albedos and preferred temperatures that can randomly mutate during the simulation. The results show that at any time during the run, the dominant daisy species are those that either have (a) preferred temperatures T^* that match the ambient conditions T and which have albedos A^* close to that of the Earth A, or (b) $T^* < T$ and $A^* > A$, or (c) $T^* > T$ and $A^* < A$. As solar input increases, T rises and new waves of heat-adapted species periodically invade the population. Consequently, temperature regulation never occurs. Robertson and Robinson [23] use a similar model, but with only preferred temperatures in the genome. They also witness a breakdown in regulation as heat-loving species invade. They conclude that this "suggests a tradeoff between the ability of organisms to collectively regulate the environment and the abilities of evolving genotypes to adapt to it" (p. 129).

In our model, if only albedo is under genetic control and the daisies are restricted to a tight range of preferred temperatures, then regulation returns via the early dominance of darker variants and the later spreading of lighter species. Using a similar Daisyworld extension with only albedos in the genotype, Lenton [12] achieves comparable behaviors. However, he parlays these results into a claim that Daisyworld indeed supports the compatibility of natural selection and Gaia theory. He explains away preferred temperature as an unlikely candidate for genetic control, since (a) the physical environment will often decide the best conditions for growth, and (b) physiological adaptations will have to work within those tight limits. For example, ocean temperatures above 10 °C lead to strong thermocline formation and a reduction in upwelled nitrates, whereas temperatures below 0 °C can considerably slow metabolic rates in many organisms. These constraints greatly reduce the range of temperatures over which nitrate-consuming marine microorganisms can thrive. Hence, even if the temperature rose to 25 °C and microorganism physiology were geared toward optimal growth at that temperature, the physical environmental could still enforce 10 °C as the "in vivo" optimum. Daisyworld-type dynamics would then enable the biota to regulate temperatures back down toward 10 °C.

By showing that large-scale regulation can emerge from only local interactions, Daisyworld helped debunk many of the Neo-Darwinian attacks on Gaia, particularly those involving group selection or teleology. However, Daisyworld and its many extensions [18] involve extremely small genotype spaces, with differential equations defined for each possible species. The dynamics are such that one dominant species (of daisy) tends to handle global temperature regulation (in the face of continuously intensifying solar irradiation) for a period before giving way to another species. Thus, the emergence of Gaian homeostatis is essentially hard-wired, since each species is explicitly represented in the model and lies "waiting in the wings" for the global temperature to move into the range that will allow it to invade the population and assume temporary control. So Daisyworld does prove that global control can emerge from local interactions, thus disproving any teleological misinterpretations of Gaia theory, but it refutes the group-selection claims only by showing that coordination among different species is not required for Gaian homeostasis: A single species at a time will suffice.

5 Evolving Coordination

Gaian interactions involve the coordination of many biological, chemical, and physical activities, as illustrated by the networks of microbial guilds involved in the global nitrogen, phosphorus, and carbon cycles. Reconciling the emergence of these multispecies, distributed controllers with Neo-Darwinian evolution is no simple task, since the evolution of coordination is far from inevitable, even when coordinated strategies are clearly the best for all organisms.

The problem is greed: Populations evolve in directions that garner the highest fitness for their individual members, and as countless game-theoretic analyses and alife simulations indicate, when greedy individual behaviors yield higher payoffs than cooperation, global coordination fails to evolve. Or if a coordinated pattern does emerge, it is often susceptible to invasion by greedy individuals, often called “parasites” or “cheaters.”

At first glance, many Gaian phenomena appear susceptible to cycle-breaking greed. For instance, the homeostatic interactions between marine phytoplankton, DMS, cloudcover, and climate (See loop 1 of Figure 1) rely on the willingness of plankton to create dimethylsulphoniopropionate (DMSP), the precursor to DMS. There must be a selective advantage to expending the energy needed to produce DMSP, but Caldeira [5] shows that the climatic benefit pales, by 9 orders of magnitude, in comparison to the metabolic cost. So why do the non-DMSP-producing species not proliferate, thus breaking the Gaian loop? Further biological investigation [14] reveals that internal DMSP concentrations reduce the osmotic gradient in phytoplankton, thus preventing water loss. So DMSP has a critical local function that enhances fitness; the global influence on DMS and climate is merely a happy side effect that connects phytoplankton to climate in a manner that gives added (albeit very small) benefit to the individual organisms but potentially huge advantages to their populations, communities, and ecosystems with respect to long-term stability.

5.1 Coincidental Global Effects

Additional support for the compatibility of Gaia and natural selection comes from Volk [27]. Examples such as the plankton-DMS-climate cycle and another interesting Gaian circuit (See loop 3 of Figure 1) involving terrestrial plants, rock weathering, and climate [20] motivate Volk’s focus on the incidental large-scale consequences of individual traits whose selective advantages come from local actions and immediate payoffs. Daisyworld itself embodies this principle, since the albedos of local populations can give immediate growth advantages by combating an unpleasant ambient to create a more desirable local temperature. The fortuitous global consequence involves changes to the ambient due to the cumulative albedos of all daisies, but the selective advantage stems almost exclusively from the local effect. As Volk [27] states:

> What organisms do to help themselves survive may affect the planet in enormous ways that are not at all the reasons those survival skills were favored by evolution. For the organisms, the survival strategies virtually always carry a metabolic cost. The Gaian side effects come for free. (p. 239)

Volk's crowning illustration of this viewpoint is nutrient recycling, where excretion serves the purely egoistic purpose of removing harmful compounds from the body, but since other guilds have evolved to consume that excrement, it has the pleasant side-effect of supporting a complex ecosystem, to the mutual benefit of all organisms involved.

Coordination is therefore the result of egocentric behavior, competition, and natural selection. Neither sacrifices for a common good nor local behaviors with only long-term payoffs come into play. Everything is as Neo-Darwinian theory would predict, with fortuitous large-scale homeostatic side-effects.

6 The Guild Model

This research combines abstract models of chemistry, biological growth, and natural selection to simulate the emergence of both (a) nutrient recycling networks and (b) the regulation of global chemical ratios. We borrow one key mechanism from Daisyworld: the ability of organisms to create local buffers against the global environment, where the combined buffering effects of many organisms can then exert an influence on the global situation. However, we avoid much of Daisyworld's hard-wiring by providing an extremely large genotype space, defined by a genetic-algorithm (GA) chromosome.

The simulations are seeded with a single species, so all additional genotypes must arise by mutation and crossover. Furthermore, the regulatory task is one involving the coordinated effort of a wide range of temporally co-existent genotypes; a single dominant species cannot do the job alone. Hence, it is the biotic community as a whole that regulates global conditions, and these heterogeneous communities emerge from a homogeneous seed population that is subjected to nothing more than competition for resources, reproduction (by splitting) of successful resource gatherers, and genetic operators. This emergence of coordinated group regulation via standard individual selection in a truly large genotype space significantly fortifies Lovelock and Watson's rebuff of the Neo-Darwinians. In addition, our model illustrates the emergence of recycling networks. So both perspectives on Gaian activity, recycling and regulation, are commensurate with Neo-Darwinism, but as our results show, they are not always compatible with one another.

To simulate the evolution of biochemical guilds, we employ a standard GA along with a simple model of chemical interactions. The environment consists of n nutrients/chemicals, $N_1, \ldots, N_n$, with input and output fluxes I_k and O_k, respectively, and internal amount E_k for $k = 1, \ldots, n$. An organism's genome determines both the chemicals that it feeds on and those that it produces during metabolism, with the only chemical constraint being that an organism cannot consume and produce the same chemical. Organisms reproduce by splitting if they manage to double their birth biomass before succumbing to the population-density-dependent mortality rate. The genetic operators are mutation, during splitting, and crossover, via gene swaps between organisms. The growth, reproductive, and genetic dynamics are intended to mirror those of bacteria, which are the basis of Earth's primary biochemical guilds.

In addition, the organisms are assumed to be most active (i.e., have the highest feeding rates) when the relative fractions of the environmental chemicals, E_k, are near a particular user-defined optimum ratio. By producing and consuming chemicals, the organisms can create local ratios that differ from the global values, thus providing a semi-protective buffer against their surroundings. This behavior is borrowed from Daisyworld, where daisies have individual albedos that partially dampen the effects of the global temperature. It also has analogues in nature. For example, by consuming oxygen, nitrogen-fixing microorganisms create the necessary anoxic environments for fixation, that is, the chemical reduction of N_2 to NH_4^+. So individual growth is governed by both the availability of food resources and the degree of satisfaction with the chemical ratios within one's buffer. A single parameter, k_{sat}, determines the degree to which satisfaction affects growth.

As shown in upcoming sections, the general competition for a set of varied resources leads to species diversification and the formation of recycling networks, while the combined effects of the local chemical buffers result in emergent regulation of the global chemical ratios. So in the context of our Guild model, recycling and regulation are both compatible with natural selection, although different settings of k_{sat} can favor one phenomenon over the other.

6.1 The Genome

Each organism's GA chromosome determines the chemicals that it inputs and outputs. The collection of these organisms constitutes a set of biochemical guilds, hereupon refered to as the biota. In addition, each genome contains n enzyme genes, Z_k, where $Z_k = 1$ implies that the organism produces an enzyme capable of freeing N_k from detritus (for its own consumption).

Each of the n chemical genes on the chromosome encodes a real number in the range $[-1, 1]$, where a positive value above Θ_c indicates that the chemical is consumed, while a negative value below $-\Theta_c$ entails production (i.e., release as waste). The length of the neutral region of a chemical gene is $2\Theta_c$, while $2\Theta_e$ is the length of the neutral region of an enzyme gene. Neutral regions indicate no production or consumption of nutrients and no production of enzymes, respectively. For the chemical genes, all non-neutral positive and negative values are grouped and normalized to give the percentages of each nutrient that are input, $F_{k,\text{in}}$, and output $F_{k,\text{out}}$, by each individual. For example, if $n = 4$, $\Theta_c = 0.2$ and the chemical genes are

$$[-0.9 \quad 0.9 \quad 0.55 \quad -0.2]$$

then chemicals 2 and 3 are consumed in a 2:1 ratio: $(0.9 - 0.2)/(0.55 - 0.2) = 2$, so $F_{2,\text{in}} = 0.666$ and $F_{3,\text{in}} = 0.333$. However, only chemical 1 is produced, since gene 4's value falls within the neutral region. Hence, $F_{1,\text{out}} = 1.0$ and $F_{4,\text{out}} = 0$. Positive and negative values in the chromosome vector are called input and output alleles, respectively. In this scheme, a biochemical guild is a set of organisms that input and output the same chemicals, although not necessarily in exactly the same ratios.

6.2 Essential Biological Processes

All organisms share the same values for two parameters: r_f and r_m, the base feeding and metabolism rates, respectively. As shown in Figure 2, these are the main processes for transfering nutrients between the biota and the environment.

6.2.1 Feeding

On each time step, an organism attempts to consume

$$A_{\text{feed}} = (X^{0.75}) r_f S$$

units of nutrients, where X is the organism's biomass, 0.75 is the standard allometric scaling factor, and S is a measure of the organism's satisfaction with the general chemical environment. These nutrients must be consumed in the proportions dictated by the positive, non-neutral alleles on the chromosome. Limiting factor dynamics apply, so the scarcity of one input chemical will reduce uptakes of other chemicals.

For example, given an organism with the chromosome above, $X^{0.75} = 900$, $S = 1$ and $r_f = 0.01$, then 9 units of nutrients will be eaten on the next time step: 6 units of N_2

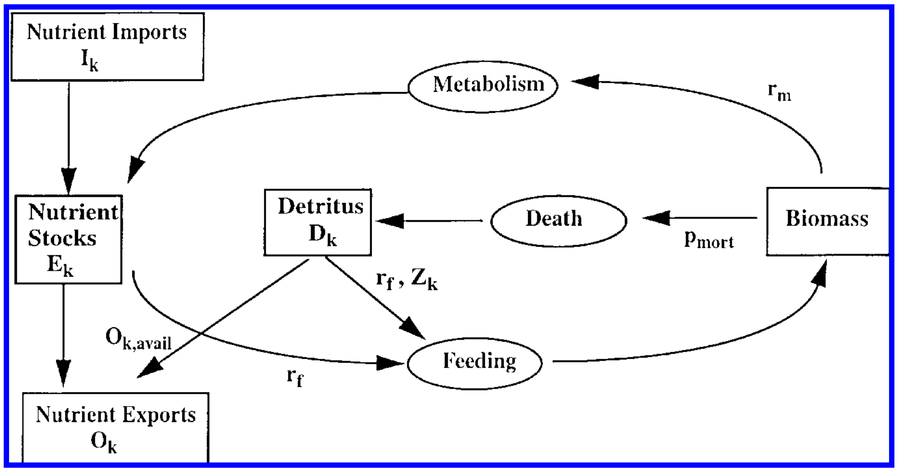


Figure 2. Basic chemical-transforming activities (ovals) and compartments (rectangles) in the guild model, along with the main transfers of nutrients and biomass between them (arrows). Parameters controlling these transfers appear on the arcs.

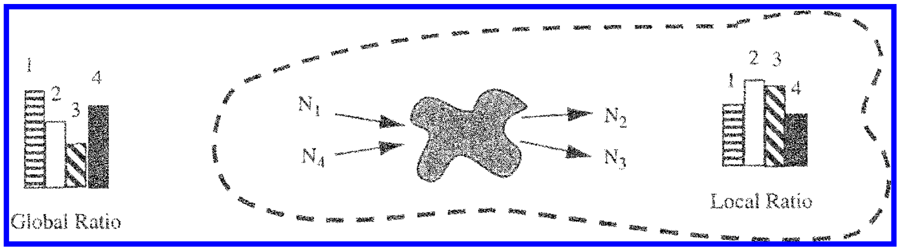


Figure 3. Based on the nutrients that they consume and produce, organisms create local chemical ratios that differ from the global ratios. Here, consumption of N_1 and N_4 and production of N_2 and N_3 result in, respectively, lower and higher local than global fractions. The k_{filter} parameter governs the extent of this local buffering.

and 3 units of N_3. However, if only 2 units of N_2 are available in the environment (i.e., 33.3% of the desired value), then only 1 unit of N_3 (i.e., 33.3% of 3) will be consumed as well. These inputs are then converted directly into biomass such that total chemical mass is conserved.

6.2.2 Satisfaction

The organism's satisfaction is based on the deviation of its local perception of the relative fractions of the environmental chemicals, E_k, from a user-defined optimal ratio (that applies to all organisms). An individual's input and output fractions are taken into account when computing the "effective nutrient fractions" that it experiences. For example, a producer of N_3 will experience a higher local ratio of N_3 than the global ratio, while a consumer will experience a lower value (See Figure 3). Conceptually, the preferred ratio is analogous to an ambient factor such as pH, whose value is dependent upon many different chemical concentrations. Hence, it is not contradictory for an N_1-consuming organism to prefer environments with low N_1 fractions, assuming that reduced N_1 contributes to the equivalent of an optimal pH.

To quantify this satisfaction concept, let E'_k $(k = 1, n)$ be an organism's effective nutrient amounts, with $\tilde{E}'_k$ being their normalized counterparts, the effective nutrient fractions. As a notational convention, if the same symbol is used to represent both a property of an individual and of the entire environment, the individual's version will include a prime mark. Also, let $\tilde{E}^{\circ}{}_k$ be the predefined optimal nutrient fractions. Satisfaction is based on the average deviation error:

$$\varepsilon'_{\text{sat}} = \frac{1}{n} \sum_{k=1}^{n} \left| \frac{\tilde{E}^{\circ}{}_k - \tilde{E}'{}_k}{\tilde{E}^{\circ}{}_k} \right|$$

and a general satisfaction coefficient k_{sat}. High (low) values of k_{sat} make satisfaction an important (irrelevant) factor in computing A_{feed} by severely (mildly) punishing individuals with large deviations from the optimal. Again, this is analogous to individual differences in pH sensitivity.

$$\text{satisfaction} = e^{-k_{\text{sat}} \varepsilon'_{\text{sat}}}$$

To compute the effective nutrient amounts for an individual, we use its input and output fractions to modify the environmental nutrient values:

$$E'_k = E_k(1 + k_{\text{filter}}(F_{k,\text{out}} - F_{k,\text{in}}))$$

where the parameter k_{filter} determines the strength of local consumption and production in smoothing the global values.

6.2.3 Metabolism

To cover its basic energetic needs and to produce enzymes, an organism burns a certain amount of its biomass on each time step:

$$A_{\text{metab}} = (X^{0.75})(r_{\text{m}} + n_{\text{z}} Cost_{\text{z}})$$

where $Cost_{\text{z}}$ is the cost of producing an enzyme and n_{z} is the total number of enzymes produced by the organism. A_{metab} units are thus output to the environmental nutrient stocks in proportions governed by the organism's output fractions. For example, the organism above would produce five units of N_1 when $X^{0.75} = 1000$, $n_{\text{z}} = 0$, and $r_{\text{m}} = 0.005$. Since feeding is meant to be synchronous, the produced chemicals of one time step cannot be consumed until the next time step.

The output flux O_k of each nutrient N_k is $O_{k,\text{avail}} E_k$, where $O_{k,\text{avail}}$ is the export fraction. Exports are drawn at the end of each time step.

6.2.4 Death and Decay

Along with the n nutrients, N_k, the environment contains n detritus compartments, D_k, which represent the amounts of the N_k bound up in dead organic matter. Subject to a density-dependent mortality rate, an organism can die at the beginning of any given time step. Its biomass is then partitioned into the D_k in direct proportion to its input alleles. Hence, an organism that consumes N_1 and N_3 in a 2:1 ratio will return 2/3 of its biomass as D_1 detritus and 1/3 as D_3 detritus. For detritus, the output fluxes, $O^d{}_k$, are computed in the same manner, except that all D_k share the same two export parameters: $O_{n+1,\text{avail}}$ and $O_{n+1,\text{max}}$.

To feed from detritus compartment D_k, an organism must be unable to find enough "free" N_k (i.e., E_k is less than the desired input amount) and must produce enzyme k ($Z_k = 1$). As shown above, enzyme cost is an additive supplement to the basal metabolic rate when computing A_{metab}. This cost is paid on each time step, regardless of whether D_k is actually tapped. Hence, the cost of enzyme production creates a trade-off between exclusive reliance on free nutrients and an investment in machinery for decomposing detritus.

6.2.5 Reproduction

The biota evolves via the replication of individual genotypes. Any organism that doubles its initial biomass can split into two individuals, with both genomes possibly undergoing mutation. An upper bound on population size serves as an explicit carrying capacity and will occasionally prevent replication. But since the mortality rate is directly proportional to the ratio of population density to carrying capacity, the population rarely reaches this maximum size. This scheme is similar to a genetic algorithm with steady-state replacement.

Organisms can also swap genetic material via chromosomal crossover. This is essentially a bidirectional analogue of bacterial conjugation, where organisms inject DNA into one another to dynamically change both genotypes and phenotypes. A fixed percentage of the population is randomly chosen for conjugation. We define a generation as an arbitrary number of time steps and perform statistical summaries and conjugation at the end of each.

6.2.6 Simulation Overview

A simulated time step unfolds as follows:

1. For $k = 1, \ldots, n$: $E_k = E_k + I_k$
2. For each organism, either die, reproduce, or feed and metabolize.
3. For $k = 1, \ldots, n$: $E_k = E_k - O_k$
4. For $k = 1, \ldots, n$: $D_k = D_k - {O^d}_k$

The order in which organisms feed is randomly shuffled on each time step to prevent biases during resource-limited conditions. At the end of each time step, the output fluxes are extracted only if sufficient quantities of the nutrients are available, as given in the equation for O_k.

6.3 Global Measures of System Performance

In an efficiently recycling ecosystem, two types of nutrient transfer can occur: (a) the outputs/wastes of one guild are consumed by another guild, and (b) the detritus of one guild is freed by the enzymes of another guild and immediately consumed. Both processes prevent chemical loss from the environment and increase the total biomass. A high rate of either process will be reflected in elevated cycling ratios for the affected nutrient. Alternatively, if the ecosystem contains consumers but no producers of a nutrient N_k, then as long as E_k at the beginning of each time step is below the total consumption demand of the ecosystem, N_k will not flow out of the system but be sequestered in the biomass. This will not necessarily be reflected in a high cycling ratio, unless a good deal of the consumed N_k comes from detritus.

Cycling ratios are computed for all nutrients at the end of each generation using the following formula:

$$\text{Cycle}_k = \frac{\min(C_k, P_k) + {C_k}^d}{\max(T \times I_k, {O^T}_k)}$$

Here, $C_k(P_k)$ is the total amount of N_k consumed from the environmental stock (produced and added to the stocks) by the biota over the T time steps of the generation, while ${C^d}_k$ is the amount of N_k that was freed from detritus and consumed during the T steps. ${O^T}_k$ is the total amount of N_k flowing out of the ecosystem during the same period. The numerator gives a rough estimate of the amount of N_k that is actually transferred between organisms, whereas the denominator is N_k's external flux.

Another useful statistic, the guild diversity, is the entropy (divided by n) of the distribution of possible input and output patterns across the population of genotypes. This is computed as

$$d = \frac{-1}{n} \sum_{i=1}^{2^n} f_i \log f_i$$

where f_i is the frequency of the ith combination of input (alternatively output) chemicals. Diversity measures are computed for the genomic input and output patterns for each generation.

A third useful metric is the deviation from an ideal free distribution (IFD), denoted as $\varepsilon_{\mathrm{IFD}}$. Ideal free distributions are situations in which consumers distribute themselves in space and/or time in direct proportion to the relative amounts of resource in each temporal or spatial region [3]. In the Guild model, a comparison of the relative amounts of each nutrient (i.e., the $E_k + D_k$ values) to their relative consumption demands across the entire biota indicates the aggregate biota's degree of adaptation to the environment. The differences between normalized sums of environmental nutrients and detritus, ${\tilde{E}^*}_k$, and normalized average input fractions (across the entire biota), $F_{k,\mathrm{in}}$, are the basis for the IFD error:

$$\varepsilon_{\mathrm{IFD}} = \frac{1}{n} \sum_{k=1}^{n} \left| {\tilde{E}^*}_k - \tilde{F}_{k,\mathrm{in}} \right|$$

For example, in a simple two-organism, four-nutrient environment with $E_1^* = 100$ and $E_2^* = 200$, $E_3^* = 300$, and $E_4^* = 400$, an IFD would be attained (i.e., $\varepsilon_{\mathrm{IFD}} = 0$) if the organisms had genomes (0.2 −0.2 −0.3 0.8) and (−0.7 0.4 0.6 −0.8), since $\tilde{E}_1 - \tilde{F}_{1,\mathrm{in}} = 0 \cdot 1$, $\tilde{E}_2 = \tilde{F}_{2,\mathrm{in}} = 0 \cdot 2$, $\tilde{E}_3 = \tilde{F}_{3,\mathrm{in}} = 0 \cdot 3$, and $\tilde{E}_4 = \tilde{F}_{4,\mathrm{in}} = 0 \cdot 4$. Here, Θ_{c}, the zero region of the genome, is 0 for ease of explanation.

In the simulations that follow, rising d and falling $\varepsilon_{\mathrm{IFD}}$ values generally reflect increased coordination among the guilds, but cycling ratios usually remain quite low until the recycling pathways are fully formed.

To assess the ability of the biota to regulate the nutrient ratios of the global environment, the global satisfaction error $\varepsilon_{\mathrm{SAT}}$ is also measured:

$$\varepsilon_{\mathrm{SAT}} = \frac{1}{n} \sum_{k=1}^{n} \left| \frac{\tilde{E}_k - {\tilde{E}^\circ}_k}{{\tilde{E}^\circ}_k} \right|$$

This represents the scaled deviation of each environmental concentration from its optimal value. Detritus-bound chemicals are not used in this calculation, since detritus is presumably localized clumps of particulate matter, while the E_k are assumed to be dissolved chemicals that bathe every organism in the environment.

7 Guild Simulation Results

A series of guild simulations were run to test the ability of the biota to form recycling loops and to regulate environmental chemical concentrations. A handful of these are

Table 1. Parameter settings for Guild runs.

Initial population size	100 individuals
Maximum population size	2000 individuals
Number of generations	800
Timesteps per generation (T)	50
Mutation rate (p_{mut}) per individual	0.5
Conjugation fraction (per generation)	0.2
Number of nutrients (n)	4
Utilities (U_k)	{1, 1, 1, 1}
Initial environmental amounts (E_k)	{0, 0, 0, 0}
Output fractions ($O_{k,\text{avail}}$)	{0.01, 0.01, 0.01, 0.01, 0.01}
Initial individual biomass	20 biomass units
Feeding rate (r_{f})	0.1 biomass units/time step
Metabolic rate (r_{m})	0.05 biomass units/time step
Production cost per enzyme	0.0125 biomass units/time step
Maximum mortality rate (at maximum population size)	0.03 per time step
Gene zero regions (Θ_{c}, O_{e})	0.4, 0.5
Local satisfaction strength (k_{filter})	0.5

presented below. Table 1 provides the parameter settings used for these tests, with exceptions noted in the text for each scenario.

7.1 A Basic Scenario

In the first test case, the goal chemical ratios are (0.4, 0.3, 0.2, 0.1), while the chemical inflows are (20, 20, 20, 20) for the first 400 generations, (5, 10, 25, 5) for generations 401–600, and (50, 25, 10, 5) for the final 200 generations. The environment is initially chemical free: $E_k = 0$ for $k = 1, 4$. All of the initial 100 individuals have the same genotype: They produce N_1, consume N_2, and manufacture no detritus-decomposing enzymes.

As shown in Figure 4c, the population size drops to below 50, where it remains for approximately 100 generations. During this period, the biota is simply too homogeneous, with all individuals competing with one another for the very limited supply of N_2. Consequently, there is a selective advantage to any individuals who consume something other than N_2. As shown in Figure 4g, the input and output diversities gradually increase, but the process is quite slow, despite the high mutation rate. One explanation is that at least two qualitative changes to the initial genome are required to affect a major change in the feeding strategy: (a) a cessation of N_2 consumption, and (b) an initiation of consumption of a different nutrient. Limiting-factor dynamics make both changes necessary, since a dependence upon N_2 and N_3, for example, leaves the organism equally sensitive to N_2 shortages.

Diversity is also charted in Figures 4e and 4f, which show the fractions of producers and consumers of the four nutrients within the population. These reveal a gradual merging of the fractions at near 25% over the first 300 generations. Limiting-factor dynamics creates a slight selective advantage for single-nutrient consumers, whereas production fractions are under no selection pressure of this type. In fact, other simulation runs in which the genome zero region, Θ_{c}, is decreased reveal a persistent convergence to 25% for input fractions but an increase in production fractions to values as high as 75% (an organism cannot produce what it consumes). So the output fractions are clearly under

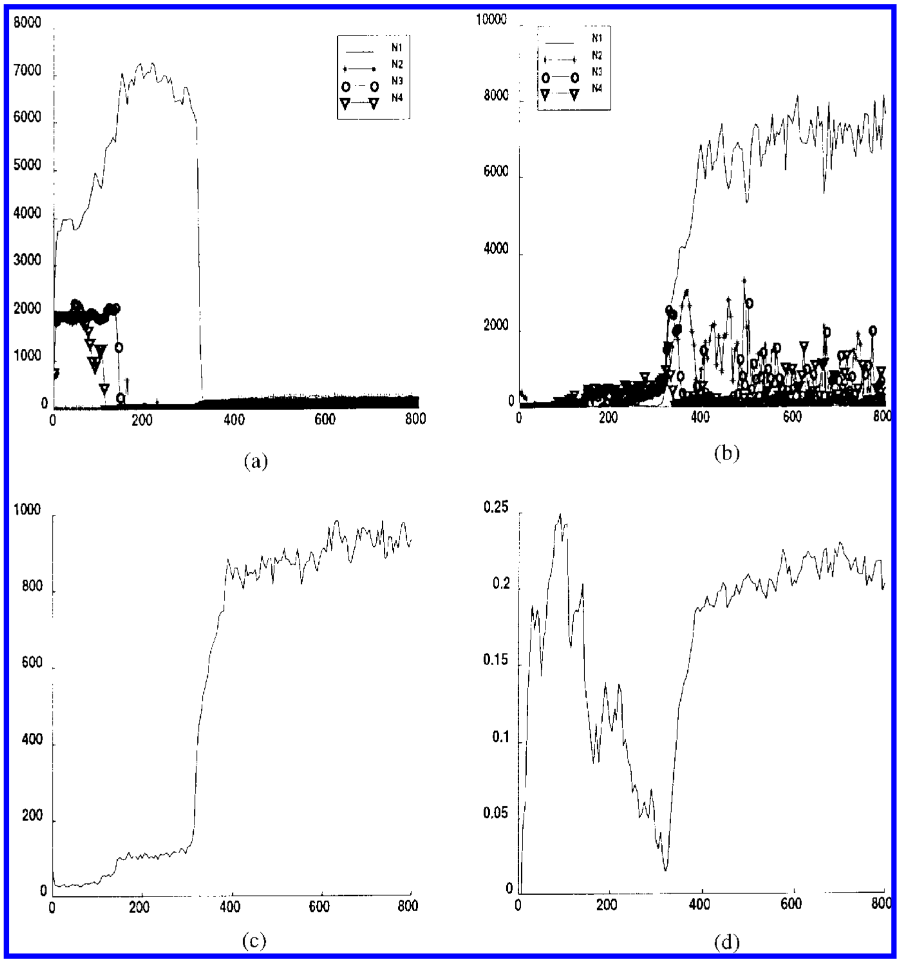
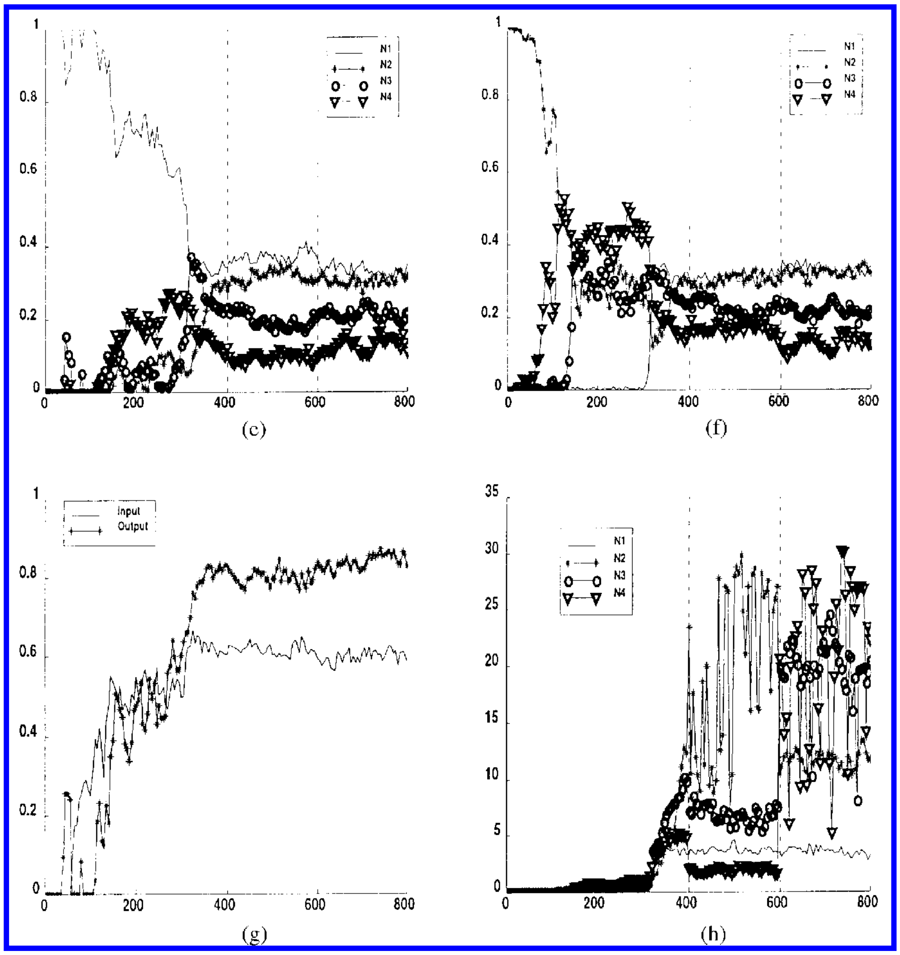


Figure 4. (a) Environmental nutrient amounts for scenario 1. (b) Environmental detritus amounts for scenario 1. (c) Population density for scenario 1. (d) Average enzyme-production cost (expressed as fraction of basal metabolic cost) for scenario 1.

less selective control. However, an organism's need to push effective chemical ratios toward tolerable levels does put selective pressure on both input and output fractions, since consumption and production are equally effective in altering local concentrations.

During the first 300 generations, diversity rises steadily, but population size (i.e., total biomass) and cycling ratios remain low. Hence, many different genoypes exist, but none prospers to any large degree. Cycling ratios are so low that most organisms are simply subsisting on the input fluxes. The investment in enzymes is also high during this period (see Figure 4d) but there is insufficient detritus to support a large decomposer guild, as shown in Figure 4b. As diversity increases over the first 300 generations, competition subsides and enzyme production becomes an unnecessary cost. Consequently, enzyme usage declines between generations 100 and 300.

As shown in Figure 4a, the emergence of an N_1-only consumer requires over 300 generations. Once present, this genotype finds abundant resources and multiplies rapidly, sending the population size from under 100 to over 300 in only a few hundred time steps (i.e., 2–4 generations).



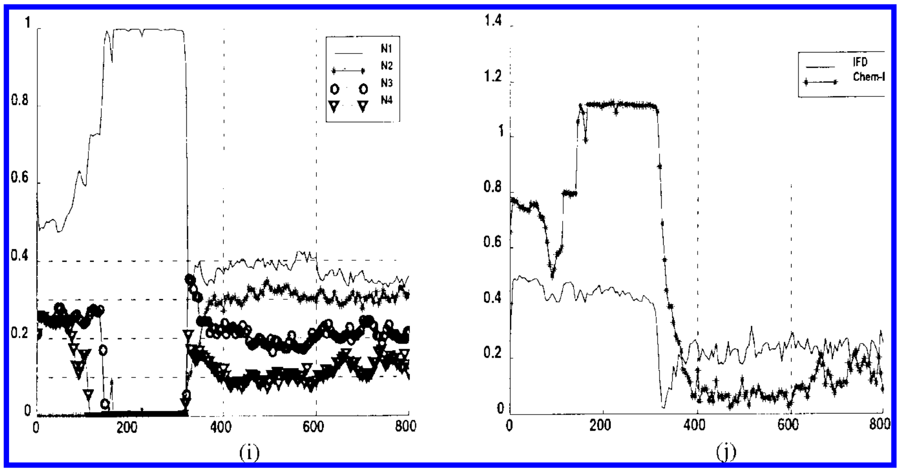
(c) (f)

(g) (h)

Figure 4 cont'd. (e) Fraction of population producing each nutrient in scenario 1. (f) Fraction of population consuming each nutrient in scenario 1. (g) Genotypic input- and output-pattern diversity in scenario 1. (h) Cycling ratios for each nutrient in scenario 1. Dashed vertical lines denote points of dramatic environmental-input change.

The gradual diversity increase during the first 300 generations creates a complex recycling network, but the total biomass (i.e., approximately 30 biomass units multiplied by the population size) is simply too low to circulate large amounts of nutrients. The advent of the N_1-only consumer changes this by converting large amounts of nutrients into biomass. The outputs of these colonizing forms then feed the pre-existing subsistence-level network, which quickly blossoms as all genotypes find ample nutrients and multiply. This pushes the population size over 900 such that the throughput of the recycling loops rises dramatically, as shown by the cycling ratio increases in Figure 4h.

Once the population exceeds 900, the system reaches a new steady-state limit, which can only be increased by changes in the external nutrient fluxes. At this density, competition within the various guilds is high, so enzyme production once again becomes an advantageous trait. The ensuing increase in enzyme production then drives the cycling ratios even higher. These remain elevated for the rest of the simulation, although ratios for individual nutrients vary as the input fluxes change at generations 400 and 600. Remember that an increased external flux will decrease the cycling ratio, assuming that the recycled amount remains relatively constant.



(i) (j)

Figure 4 cont'd. (i) Environmental chemical fractions in scenario 1. (j) Error measures for ideal free distribution (IFD) and environmental chemical fractions for scenario 1. Dashed horizontal lines denote the target ratios of 0.1, 0.2, 0.3, and 0.4. Dashed vertical lines denote points of dramatic environmental-input change.

The emergence of global chemical-ratio control comes shortly after the population and recycling booms. Prior to that period, any chemical-ratio effects that the organisms have are simply dwarfed by the large relative fraction of N_1. Hence, there is no real selective advantage to the chemical-controlling side effects of a genotype. However, after generation 300, the input diversity becomes sufficient to insure the consumption of most available nutrients, thus bringing the E_k into controllable ranges. Recycling loops primed by N_1 consumption then facilitate a biomass increase. With many individual members for each of a diverse array of guilds, the biota becomes a robust distributed controller that is kept in line by natural selection: Too many individuals of any one type will experience negative frequency-dependent selection either as a result of their competition for resources or their overpowering influence upon one or more global nutrient fractions.

In Figure 4i, the biota's controlling effect becomes visible between generations 300 and 400, where the chemical ratios are gradually modified to yield the proper rankings among the four E_k values. Figure 4j then shows the decline in ε_{SAT} as each ratio approaches its optimal value. Full convergence is never achieved, but ε_{SAT} errors near 10% are attained for the 400–600 generation period, and they stay near or below 20% for the final 200 generations. In essence, the high cycling ratios make the population somewhat oblivious to changes in the external fluxes, since the intra-biota transfer amounts are the main determining factors of the environmental nutrient levels. This is evidenced in Figures 4e and 4f, where only very slight changes occur at the 400- and 600-generation boundaries despite major changes in the input fluxes. For instance, N_4 consumption abruptly declines after generation 600, which effectively keeps the global concentration from falling too much in the face of a drastic (10-fold) decrease in the input flux.

Naturally, the biomass has no idea of the control that it is exerting; organisms that consume N_4 are merely at a slight selective disadvantage since their effective (local) N_4 ratios are too low. This disadvantage is density dependent, thus leading to self-regulation: the fewer (greater) N_4 consumers, the less (greater) downward pressure on E_4, and hence the smaller (larger) the disadvantage to any one N_4 consumer. So consumption does not disappear, but merely oscillates around a lower set point. Similarly,

N_4 production increases after generation 600. Conversely, N_1 experiences a minor rise in consumption and a small production decline due to its 10-fold in-flux increase.

Mixed strategists with all the proper control settings may arise, but they will rarely proliferate and dominate the population. For example, if E_1 and E_2 were above optimal, while E_3 and E_4 were below, then an optimal mixed strategist would consume the former two and produce the latter two. If this genotype were to dominate the population completely, then the levels of E_1 and E_2 could easily be driven down to optimal levels or below, while E_3 and E_4 may rise to the optimals or above. Whereas overshoots would open the biota to invasion by the opposite mixed strategists and/or simple strategists such as E_3 or E_4 consumers, optimality would clear the slate and open the environment for all sorts of noncontrolling genotypes. Basically, the only situations in which the mixed strategists could dominate would be those in which their controlling activities gave local selective advantage but failed to affect the global situation. For example, if the inflows of E_1 and E_2 and outflows of E_3 and E_4 were so high that the biota simply could not control the global ratios, then the mixed strategist could achieve stable dominance. In Lenton's [12] terminology, if the mixed strategists realize global chemical-ratio control, then *negative selective environmental feedback* occurs: Their growth reduces their selective advantage via its environmental effects.

7.2 Trade-offs Between Recycling and Control

The degree to which effective chemical ratios, the E'_k, affect satisfaction is determined by the k_{sat} parameter. By raising this, the biota becomes very sensitive to deviations from the optimal chemical ratios. Hence, the selective pressure for controlling genotypes increases. Alternatively, a low value of k_{sat} entails that most organisms will have high satisfaction values (i.e., near 1), regardless of ratio deviations, thus reducing the advantage of controlling genotypes.

Essentially, k_{sat} brokers a trade-off between efficient feeding strategies and environmental control. When k_{sat} is low, environmental chemical ratios will have little effect on satisfaction, so the organism profits most from eating the nutrients that are available. This tends to drive the population toward an ideal free distribution of feeding strategies relative to the resources; but the control of environmental chemical ratios will, in many cases, be weakened.

Conversely, when k_{sat} is high, the heightened sensitivity to chemical ratios will cause the biota to deviate from standard IFD-generating behavior. For example, if a nutrient N_k has a large input flux, then IFD theory would expect many organisms to consume it. However, if organisms require a high N_k ratio for optimal performance, then N_k consumption will be low, despite its abundance. The IFD is therefore traded off for optimal control.

IFD formation supports recycling in the following manner. If the metabolic strategies are properly distributed over the available resources, then majority amounts of each resource type will be consumed and converted into biomass. The diversity of inputs will then lead to a diversity of outputs, since, in the Guild model, organisms cannot produce that which they consume. In general, if the input chemicals span the spectrum of possible chemicals, then so too will the output chemicals. Hence, the wastes of one organism become food for another, and recycling is born. However, if consumption of a nutrient N_k ceases, then not only will input fluxes of N_k be ignored, but so too will all N_k produced by other guilds. This creates a leak in the recycling network that can significantly reduce the cycling ratios of all elements and even drain the entire system if new guilds do not arise to plug the gaps. A similar argument holds for the disappearance of N_k producers, which would then starve the N_k consumers and again reduce the recycling of all or most nutrients. Recycling is clearly very dependent upon stable metabolic diversity.

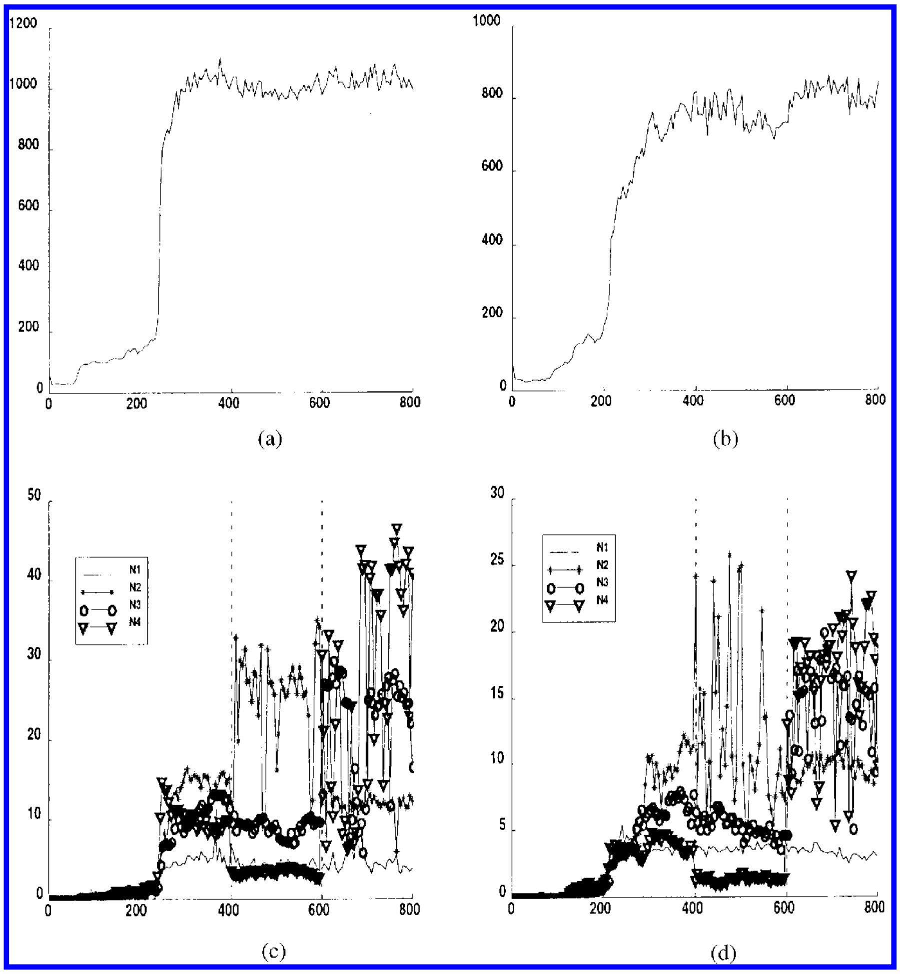
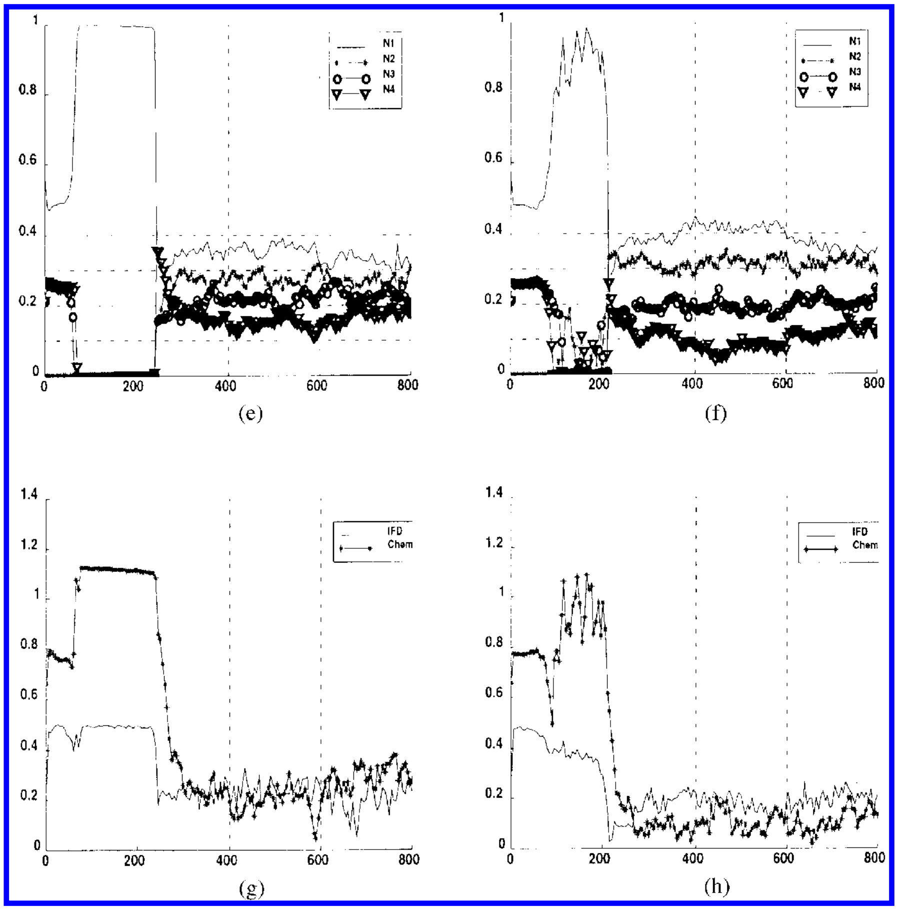


Figure 5. Popoulation density for (a) scenario 2 and (b) scenario 3. (c) Cycling ratios for scenario 2 and (d) scenario 3. (d) Dashed vertical lines denote points of dramatic environmental-input change.

Since IFD formation is the best way to get the most biomass out of the available supply of free nutrients and detritus, we can expect a lower population size and reduced cycling ratios when the IFD is compromised by a high k_{sat} value. To test this, the same scenario as above, where $k_{sat} = 0.25$, is run with a low, 0.1, and a high, 0.4, k_{sat} value.

Figures 5a–d clearly show lower population sizes and cycling ratios in scenario 3 ($k_{sat} = 0.4$) than in scenario 2 ($k_{sat} = 0.1$). However, Figures 5e–h show that scenario 3 achieves better chemical-ratio control. Also note the error graphs for the final 500 generations in Figures 5g and 5h. While the IFD error is generally higher than the chemical-ratio error (ε_{SAT}) in scenario 3, it is normally equal or below that found in scenario 2.

Scenarios 2 and 3 clearly illustrate the trade-off between IFD formation and chemical control. Thus, since the IFD directly affects recycling throughput, cycling ratios and the degree of chemical-ratio control do not always mirror one another. Although scenario 1 shows that recycling promotes stable control by reducing the sensitivity to external flux perturbations, the trade-off between IFD formation and control strains the relationship



(e) (f) (g) (h)

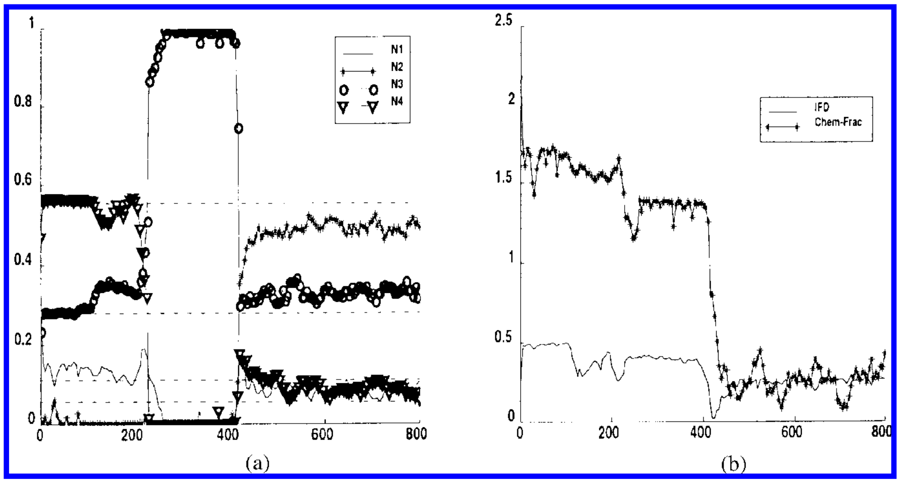
Figure 5 cont'd. Environmental chemical fractions for (e) scenario 2 and (f) scenario 3. (g) Error measures for ideal-free distributions (IFD) and environmental chemical fractions for scenario 2 and (h) scenario 3. Dashed horizontal lines denote the target ratios of 0.1, 0.2, 0.3, and 0.4. Dashed vertical lines denote points of dramatic environmental-input change.

between recycling and control, since only recycling necessarily benefits from the IFD. In short, the two proposed Gaian metrics, recycling and control, are tightly integrated but not always mutually compatible.

7.3 Extreme Control Problems

In scenario 4, the control problem is slightly more difficult: given constant input fluxes (5, 10, 25, 50), achieve the chemical fractions (1/18, 10/18, 5/18, 2/18). Again, the initial environment is nutrient free, and $k_{\text{sat}} = 0.25$, the same intermediate setting as in scenario 1.

Figure 6a shows that the chemical fractions undergo similar transitions to those of the previous scenarios, and control only becomes feasible when biotic diversity reduces the dominance of any one nutrient. After that, the chemicals partition nicely into values close to the desired ratios, although precise ratio matching is not achieved. Figure 6b illustrates no clear dominance of IFD formation or control, as both error values lie near 0.25 (although the control error oscillates a bit). However, the cycling ratios (not shown) reach peak values of only 17, and the population size barely exceeds 800. This



(a) (b)

Figure 6. (a) Environmental chemical fractions for scenario 4. Dashed horizontal lines denote the target ratios of 1/18, 2/18, 5/18, and 10/18. (b) Error measures for ideal-free distribution (IFD) and environmental chemical-fractions for scenario 4.

indicates that the 25% chemical-ratio error (and resulting low satisfaction) and IFD error probably combine to hamper population growth.

Attaining very extreme chemical ratios (i.e., low entropy among the chemical fractions) is difficult. First, a high k_{sat} value is required to insure that the biota are selected for environment-controlling genotypes. However, this also means that if the original ratios deviate considerably from the goal ratios, then the organisms will have very low satisfaction values—so low that they will be unable to grow to reproductive size. Hence, in extreme control cases, the population tends to become extinct. To the extent that it exists in nature, extreme control may involve a gradual evolution of the preferred ratios. Another possibility is that nature's corresponding k_{sat} value is extremely low, but that over millions of years, the global pattern still emerges.

7.4 The Guild Model in Swarm

To investigate Gaian biochemical guilds in two dimensions, we used Swarm [4] to develop the MAG (metabolizing agents) model. In this scheme, agents move around the two-dimensional grid, eating nutrients and producing others as metabolic wastes. Genomes are similar to those of Guild, with the addition of genes for vision radius and maximum metabolic rate. Agents use their vision to detect nutrients and must then burn additional biomass (above the basal metabolic demands) to fuel foraging movements. To more closely mirror true microcosms, mutations occur throughout the lifetime of an agent, although the phenotypic results do not become visible until the next generation, since morphogenesis is only performed once per individual. One important constraint is that no more than one agent can reside within a cell at any given time.

The nutrient inflows are randomly distributed to the grid cells and subjected to diffusion, while each output flux is randomly drawn from the various cells. An organism's chemical satisfaction is based solely on the local chemical ratios of its host grid cell, but since those ratios are affected by the agents' production and consumption, the same basic mechanism for global chemical regulation exists—it is just more implicit in MAG than in the one-dimensional model. Satisfaction in MAG is used to compute an extra metabolic cost, so unsatisfied organisms pay a higher basic metabolic cost but maintain

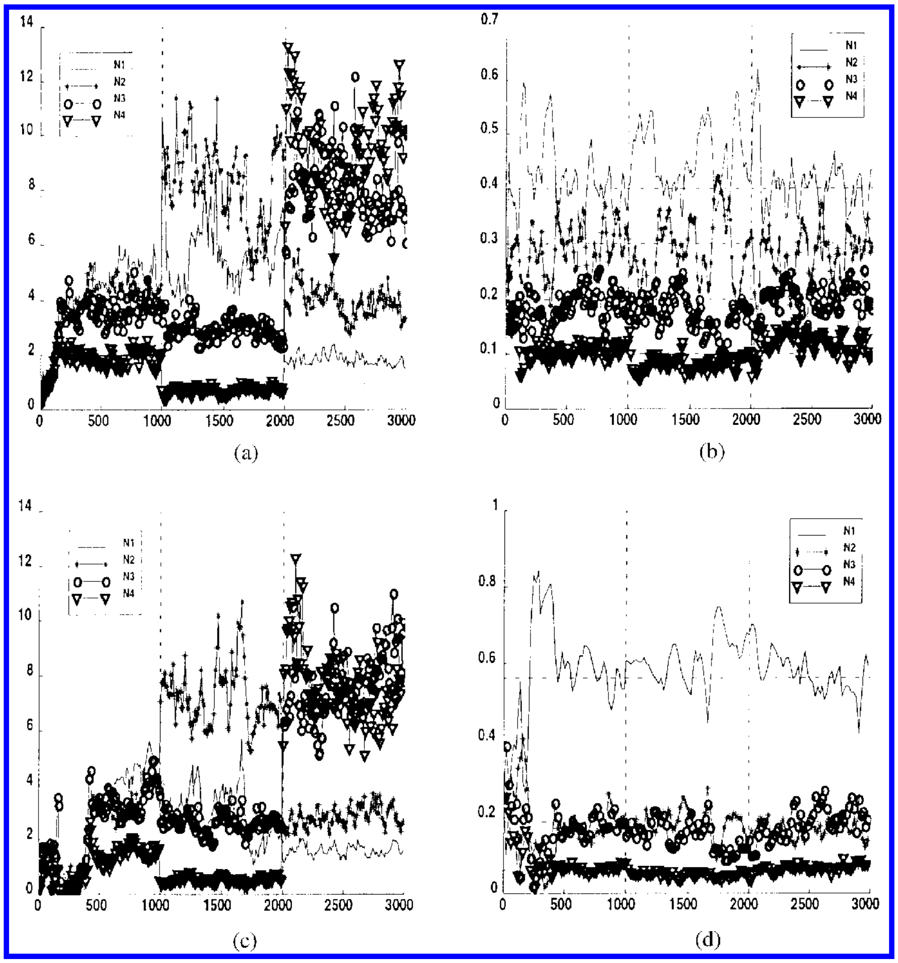


Figure 7. (a) Cycling ratios for scenario 5 (MAG model). (b) Environmental chemical fractions for scenario 5 (MAG model). Dashed horizontal lines denote the target ratios of 0.1, 0.2, 0.3, and 0.4. (c) Cycling ratios for scenario 6 (MAG model). (d) Environmental chemical fractions for scenario 6 (MAG model). Dashed horizontal lines denote the target ratios of 1/16, 3/16, 3/16, and 9/16. All dashed vertical lines denote points of dramatic environmental-input change.

the same feeding rate. Consequently, satisfied individuals can more easily accumulate biomass and grow to reproductive size.

Scenarios 5 and 6 are run on 60×60 and 30×30 MAG grids, respectively, with input fluxes similar to those of scenario 1, except that each of the three input phases lasts for 1000 time steps. The target chemical ratios are (0.4, 0.3, 0.2, 0.1) and (9/16, 3/16, 3/16, 1/16) for scenarios 5 and 6, respectively.

As shown in Figures 7b and 7d, the biota achieve the proper ordinal ranking of nutrient fractions, although the error rates oscillate about 0.5 (not shown). Figures 7a and 7c also reveal lower cycling ratios than in the Guild scenarios. Also note the reduction in cycling-ratio oscillation, as expected, in the larger grid of scenario 5. In general, the two-dimensional environment with random distributions of input and output fluxes over the cells will create a more unstable environment for the biota. To create recycling networks, the biota must not only evolve complementary metabolisms, but must also congregate. Vision aids this process by enabling agents to move toward their desired nutrients, but it cannot compensate for the lack of full biotic and nutrient mixing that occurs in the one-dimensional model. Still, the ability of the biota to regulate chemical ratios to a significant degree in MAG illustrates the clear presence of Gaian activity in a model that more closely mirrors real life than does the one-dimensional world of the basic Guild model. An extensive listing of over 200 MAG runs, along with more details on the SWARM implementation, are available on the internet at http://www.ifi.ntnu.no/~zvirinsk/projects.htm.

7.5 Simulation Summary

Scenarios 1–6 represent a small sampling of our Guild and MAG runs. Similar runs with different random-number seeds give similar results, except for differences in the exact generations in which particular genotypes arise. Otherwise, the emergence of recycling and control are robust phenomena that stem largely from our basic modeling mechanisms and not from merely a select group of parameter settings. For example, simulations involving six and eight nutrients have yielded corresponding results, although emergence takes longer than in the four-nutrient cases, unless the population size is also increased.

To summarize the basic causal mechanisms underlying the emergence of recycling and control in our models, competition drives the initially homogeneous biota toward greater trophic diversity, that is, diversity of input patterns; and since each organism must produce at least one nonconsumed chemical as waste, a diversity of output patterns also emerges. This increasing biotic heterogeneity results in the fortuitous formation of recycling networks. When all of the pieces (i.e., guilds) of these networks fall into place, previously under-consumed nutrients fuel a population explosion and an increase in cycling ratios. The elevated nutrient transfer within the recycling network then facilitates further population growth within each guild. The high transfer fluxes between these large interconnected guilds dwarf the environmental input and output fluxes, thus reducing the biota's sensitivity to external perturbations. Competition within and between this diverse collection of well-populated guilds results in a frequency-dependent selection that enables the guilds to control global chemical ratios effectively via their cumulative production and consumption. In short, competition leads to coordination, with emergence and stability orchestrated by natural selection.

In contrast to those of Daisyworld, the basic constraints of our model inhibit dominance by any one guild. First, since each organism must produce a waste nutrient N_k that it cannot also consume, a niche is created for at least one metabolism that inputs N_k. Also, limiting-factor dynamics in low-resource situations create a selective advantage for single-nutrient consumers over more general feeders and omnivores. Hence, in an n-nutrient environment, niches for at least n different guilds will exist. Since the diversity of input patterns in Figure 4g is 0.6, some mixed-strategist guilds do emerge. The diversity would be at most $0 \cdot 5 = 1/4 \times -4 \times 1/4 \times \log 1/4$, if only four single-nutrient-consumer guilds of exact equal size existed in a four-nutrient scenario; four guilds of differing sizes would yield a diversity value below 0.5.

The simulations show that a variety of connections exist between the two Gaian metrics: recycling and control. First, recycling enhances the robustness of chemical-ratio control by filling the various biochemical guilds, thereby increasing recycling throughput and diminishing sensitivity to external flux perturbations. However, the trade-offs between IFD formation and chemical-ratio control, plus the dependence of efficient recycling on IFD formation can create situations in which cycling ratios and control are inversely related. So both metrics are useful for analyzing Gaian behavior, and both emergent phenomena are consistent with Neo-Darwinian evolution, but the type of correlation between the two factors (if it exists at all) will often be situation dependent.

8 Related Work

As mentioned above, Daisyworld and its many reincarnations [18] support the compatability of Gaia and natural selection, but they exhibit a certain hard-wiredness in that each species is capable of global temperature regulation on its own, and each is a primitive in the model. On the other hand, our model shows that global regulation can also emerge from the aggregate metabolism of a community, with success directly correlated with diversity.

In addition, the Guild model shows that Volk's proposed Gaian metric, the cycling ratio, is also consistent with natural selection and has interesting relationships to regulation. Although the cycling ratios achieved by our simulations are far below those of carbon, nitrogen, and phosphorus in nature, they can be elevated by simple parameter changes. Namely, an increase in maximum population size and a decrease in export fluxes enables much higher recycling throughput. Unfortunately, our limited computing resources did not permit runs with population sizes on the order of 100,000. Of course, nature has had a few billion years to perfect its recycling skills, so we should not necessarily expect to duplicate that effort in a simple simulation.

In artificial life, few researchers have investigated Gaian issues. The EUZONE model [8] of the evolution of aquatic ecosystems is motivated by Gaian phenomena and achieves the emergence of one guild, vertically migrating photosynthesizers, which creates a niche for other guilds (e.g., aerobic bottom-feeders) via its effects upon the chemical environment. However, environmental regulation does not occur in EUZONE. In other work [7], genetic algorithms are used to show that temporal IFDs are the natural consequence of Neo-Darwinian evolution in resource-limited environments.

Our project is related to research into the emergence of autocatalytic sets [10], metabolic-systems [1], and hypercycles [2], except that we focus on (a) interaction pathways involving both organisms and chemicals, and (b) the self-organized regulation of the environment by the evolving biota. In general, a whole host of alife systems involve populations of genotypes that encode for feeding, mating, and other strategies, but questions regarding recycling throughput and whether or how the phenotypes regulate the surroundings are normally not addressed.

9 Discussion

At first glance, the evolution of coordinated behavior among a community of organisms may appear to require group selection, while the emergence of Gaian interaction loops would demand the mystical powers of a natural selection at the levels of ecosystems or higher. However, Gaia experts such as Lovelock, Watson, Volk, and Lenton argue that off-the-shelf Neo-Darwinism offers a convincing explanation. The Guild model bolsters their argument by showing that when a biosphere contains a set of nutrients and a vast number of organisms, resource competition will naturally drive the biota to develop diverse metabolic strategies. Hence, many biochemical guilds will emerge, with one guild's waste products becoming another's resources. These transfers eventually feed back onto one another to form recycling loops, thus enabling the biota to achieve a total biomass well beyond that which the external fluxes alone would support. In short, the emergent integration of a biota into a coordinated ecosystem requires little more than competition for resources, genetic variability of metabolic strategies, and natural selection.

Furthermore, the Guild and MAG models show that the global regulation of environmental substances can result from the emergent biodiversity. This supplements the

Daisyworld results, which essentially show temperature control by alternating dominant species. However, none of these models addresses the issue of evolving biotic preferences [23, 24].

Clearly, models of this simplicity cannot fully explain complex biogeochemical phenomena, but they can often illustrate the sufficiency of particular mechanisms for deriving similar patterns. This work shows that simple local interactions under the scrutiny of natural selection can lead to interesting cooperative arrangements. Since these particular cooperative results, efficient cycling networks and global chemical regulation, are both viewed as fundamental examples of Gaia in action, our simulations lend support to the basic compatibility of Gaia and evolution.

Future extensions to this work will continue our search for abstract models that integrate simple biochemical and physical mechanisms with natural selection in order to evolve Gaian interactions. One possible addition is the potential for couplings between the biota and key physical parameters such as temperature, pH, humidity, and so forth.

One necessary improvement is to the chemistry model, whose current simplicity renders any natural interpretations of these alife simulations extremely speculative. Although a wide array of metabolic pathways exist, real bacteria are not at liberty to transform any input compounds into any other output compounds, since conservation of the basic elements along with energy requirements greatly restrict the possible reactions.

Consequently, the concepts of basic chemical elements and reaction energies should be incorporated, as should some notion of the differences in chemical potential between various compounds. Volk (personal communication) suggests that the relative sizes of molecules should be included, since some organisms (i.e., autotrophs) consume small molecules to build the complex molecules of biomass, while others consume biomass, convert it into other forms of biomass, and expell small molecules; and all of these processes require energy.

Our search for abstract chemistries stems from an alife orientation and the pursuit of bio-logic. The actual chemistry of life is extremely complicated, and although black-box views of bacterial metabolism (i.e., basic inputs and outputs with a disregard for all the intermediate compounds, enzymes, etc.) enable relatively straightforward modeling, the bias of "biochemistry as we know it" could be overly restrictive vis-a-vis our long-term goal of assessing the fundamental mechanisms underlying Gaian phenomena. Our target chemistry is therefore one in which basic fundamental properties such as reaction energies, bond strengths, and so forth, are parameterizable such that different settings will lead to different potential metabolic pathways and varying possibilities for emergent Gaian interactions. Tests over many diverse sets of parameter settings could then give some indication of whether emerging Gaian homeostasis and recycling are inevitable patterns or chance events.

A more restrictive (yet parameterizable) chemistry would also aid investigations of Saunders' [24] evolving-preferences dilemma. Given a set of chemical and energetic primitives, certain preferences of ambient chemicals and physical factors would arise to match the restrictions imposed by the set of metabolic possibilities. Hence, the constraints of chemical principles upon ambient preferences (and their ease or difficulty of change) would shed some light on the actual range of freedom that organisms actually have in "breaking from the regulatory ranks." This agrees with the views of George Williams [29], a prominent biochemist and geophysiologist, who contends that Gaia and the global chemical cycles can be best understood from the level of enzymes and cellular regulation of their production.

Unfortunately, our work sidesteps the evolving-preferences issue, since all guilds are assumed to have the same constant preferred chemical ratios. When included in the Guild genomes, these preferences inhibit regulation, as individuals simply evolve preferences to the current conditions. Although these "regulatory parasites" are clearly a problem, the concept of a "recycling parasite" is more difficult to define. Basically, there is no advantage (but often an indirect disadvantage) to the "greedy" behavior of producing a nutrient that no other organisms can consume. Furthermore, the model permits the consumption of all possible wastes, so none are necessarily useless or harmful. But what is a true parasite in an analogous natural microscopic system? All organisms make chemical contributions to the biosphere, and few (if any) of these are universally toxic. Possibly an organism that consumes resources in one ecosystem and deposits wastes in another would qualify as a true parasite in the first and exemplary altruist in the second.

In general, a critical prerequisite to many Gaian phenomena is a bidirectional causal link between the chemistry and physics of the environment. Organisms then influence the physical environment via chemical consumption and production. When models contain the key physicochemical relationships, or suitable abstractions, then the fortuitous evolution of Gaian feedback loops are possible, assuming that the organisms gain selective advantages via their metabolic strategies and their immediate, local consequences.

In the Daisyworld and Guild models, key mechanisms are (a) the ability of individuals to affect the local conditions for growth, and (b) the ability of the cumulative local conditions to affect global factors. The former provides the selective advantage, while the latter constitutes the actual Gaian link. The Guild model is replete with interesting selective advantages for assorted metabolic choices, but it still lacks a general formalism for linking an abstract chemistry to an abstract physics such that full biogeophysical loops can emerge.

Finally, spatial factors may prove essential to realistic Gaian simulations. Daisyworld itself includes a simple model of competition for space, and MAG includes key multidimensional constraints such as mobility and its energetic demands. Also, Volk's insights draw heavily from the distinctions between three Gaian matrices: air, land, and sea. Transfers between these compartments, and the differences in both physical phases and chemical potentials of matter within them, are important factors in understanding Gaia.

In conclusion, although the details of relationships between Gaia and natural selection are far from resolved, this research takes a first step by showing that two interesting Gaian phenomena, extensive recycling and chemical-ratio regulation, are natural consequences of resource competition and local-buffer formation among evolving populations.

From an artificial life viewpoint, this is one more interesting example of emergent order in yet another possible world. But in general, the "evolution of Gaia" problem seems particularly enticing from the alife perspective, as it requires a fundamental understanding of complex interactions among genetically determined agents, chemical substrates, and physical forces. It is not inconceivable that one of the possible worlds in which alife's bio-logic is being played out and dissected holds clues to the mechanisms underlying the evolution of Gaian networks. Hopefully, this work will motivate other alife researchers to consider more problems from the Gaian perspective.

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