

Gaia and natural selection

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Evidence indicates that the Earth self-regulates at a state that is tolerated by life, but why should the organisms that leave the most descendants be the ones that contribute to regulating their planetary environment? The evolving Gaia theory focuses on the feedback mechanisms, stemming from naturally selected traits of organisms, that could generate such self-regulation.

Organisms alter their material environment and their environment constrains and naturally selects organisms. This connection indicates feedback between life and its environment. The Gaia theory¹ proposes that organisms contribute to self-regulating feedback mechanisms that have kept the Earth's surface environment stable and habitable for life. Gaia theory seeks to explain these mechanisms and how they arise. Natural selection², acting on faithful replication of inherited variation, determines that the organisms that dominate are the ones that leave the most descendants. Together, natural selection and Gaia pose a puzzle: how can self-regulation at the planetary level emerge from natural selection at the individual level³?

Here I attempt to address this question by focusing on the feedbacks to biospheric growth and selective pressures that can arise from environment-altering traits of the biota. This approach helps to bridge the spatial and temporal gaps between the operation of natural selection and the mechanisms of planetary regulation. The arguments are largely restricted to climate regulation, but the principles may be more generally applicable to any environmental variable affecting growth or selective pressures. An example of a feedback on the growth of organisms is the biological amplification of rock weathering, which enhances the uptake of atmospheric carbon dioxide and planetary cooling. Such a feedback tends to stabilize habitable conditions, but can respond only passively to external forcing. To illustrate how biospheric feedbacks affect natural selection, and to explore the impact of random mutation, I extend the Daisyworld model that has underpinned much of the early modelling work on the Gaia hypothesis. In Daisyworld, natural selection can both generate and contribute to environmental regulation. The daisies alter their environment in the same way at the individual and the global level. Therefore, the traits selected at the individual level are ones that change the global environment in a manner favourable to growth.

Moving from models to reality, I discuss how organisms may alter their environment to their benefit, using land ecosystems including rainforest, boreal forest and peat bog as examples. I consider both externally triggered and internally driven vegetation–environment feedbacks. Next, I illustrate the continuing challenge of linking an individual trait to its global consequences by examining the factors affecting dimethyl sulphide production by marine phytoplankton. I discuss the limitations of existing models and make proposals for further testing Gaia theory. At this stage, it seems that natural selection can form an integral part of planetary self-regulation and, where destabilizing effects arise, they may be less likely than stabilizing effects to attain global significance or persist.

Origin of the Gaia hypothesis

In attempting to find a physical basis for detecting the presence of life on a planet, Lovelock⁴ recognized that most organisms shift their physical environment away from equilibrium. In particular, organisms use the atmosphere to supply resources and as a repository for waste products. In contrast, the atmosphere of a planet without life (forced only by solar ultraviolet radiation) should show less disequilibrium (attributable to photochemical processes). Hence, the

presence of abundant life on a planet may be detectable by atmospheric analysis. The atmospheres of Mars and Venus are dominated by carbon dioxide and are only in a mild state of disequilibrium^{5,6}. In contrast, the atmosphere of the Earth is in an extreme state of disequilibrium in which highly reactive gases, such as methane and oxygen, exist together at levels that are different by many orders of magnitude from photochemical steady states⁶ (Fig. 1a). Large, biogenic fluxes of gases are involved in maintaining such disequilibrium (Fig. 1b). This perturbed state is remarkable in that the atmospheric composition is fairly stable over periods of time that are much longer than the residence times of the constituent gases, indicating that life may regulate the composition of the Earth's atmosphere⁷. This concept became the foundation of Gaia theory⁷.

Present conditions at the surface of the Earth are within the relatively narrow boundaries that eukaryotic, multicellular organisms can tolerate⁷. For example, of the major atmospheric gases, nitrogen maintains much of the atmospheric pressure and dilutes

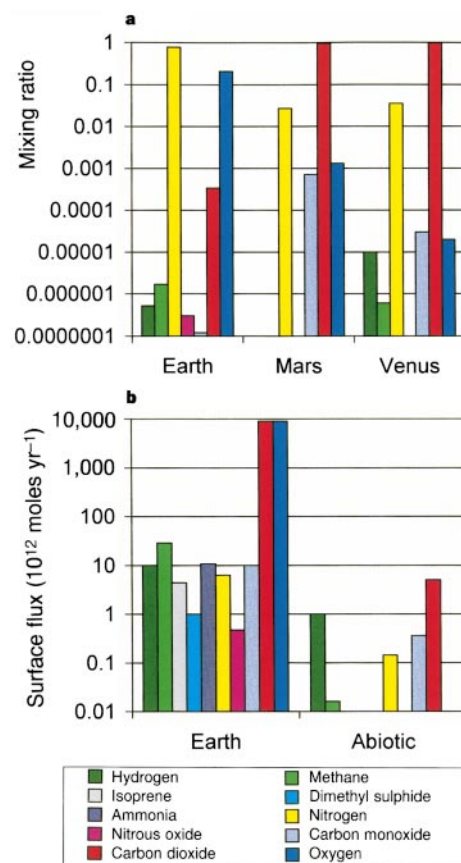


Figure 1 The effect of life on the Earth's atmosphere. **a**, Atmospheric compositions⁹³ of Earth, Mars and Venus (excluding water vapour and noble gases). **b**, Estimated fluxes of gases at the Earth's surface in teramoles (10¹² moles) per year, with (pre-industrial) life^{77,94,95} and without life⁹⁶.

oxygen, which constitutes 21% of the atmosphere, just below the fraction at which fires would disrupt land life⁸. However, oxygen is sufficiently abundant to support the metabolism of large aerobes, and the continuous fossil charcoal record indicates that the oxygen mixing ratio has varied little over Phanerozoic time^{1,8}. The gaseous nitrogen reservoir is largely maintained by the actions of denitrifying organisms, whereas abundant oxygen is the product of past photosynthesis.

Life on Earth has persisted despite major changes in solar forcing⁷. The Sun is thought to have warmed by about 25% (ref. 9) since the origin of life on Earth, over 3.8 billion years ago¹⁰. Assuming a constant radiative response of the Earth to this increased solar input, the Earth's surface temperature would be predicted to have risen by 18 °C, yet the present average temperature is only 15 °C. The continuous habitability of the Earth in the face of a warming Sun indicates that life may have been involved in regulating the climate (although a purely geochemical mechanism is also possible¹¹).

Lovelock and Margulis¹²⁻¹⁴ therefore proposed the Gaia hypothesis of "atmospheric homeostasis by and for the biosphere", adding that both the redox potential and the acidity of the Earth's surface are anomalous, compared with our planetary neighbours, and can be tolerated by life. The hypothesis included regulation of both atmospheric composition and climate, and suggested roles for the major biogenic gases. The Gaia hypothesis was used to make predictions, for example that marine organisms would make volatile compounds that can transfer essential elements from the ocean to the land. The discovery that dimethyl sulphide¹⁵ and methyl iodide¹⁶ are the major atmospheric carriers of the sulphur and iodine cycles, respectively, supported this suggestion. Later, the Gaia hypothesis was extended¹⁷ to include regulation of much of the chemical composition of the ocean¹⁸.

Development of the Gaia theory

Most criticisms of Gaia have focused on the need for evolutionary mechanisms by which regulatory feedback loops could have arisen or be maintained. One criticism was that the hypothesis implies teleology, some conscious foresight or planning by the biota³. Another was that the Earth is not a unit of selection, and therefore Gaian properties cannot be 'adaptations' in a strict neo-Darwinian sense as they cannot be refined by natural selection¹⁹. The challenge is then to explain how Gaian properties could arise from natural selection at lower levels.

The Daisyworld model^{20,21} (Box 1) provided a hypothetical example of planetary regulation emerging from competition and natural selection at the level of individuals, and showed that self-regulation does not necessarily imply teleology. Daisyworld also offered the beginnings of a mathematical framework for understanding self-regulation. The evolved Gaia theory²² recognized that self-regulation is a property of the whole system of life tightly coupled to its environment, and replaced earlier suggestions, which included apparent teleology, that regulation is 'by and for the biota'^{23,24}. Gaia theory aims to be consistent with evolutionary biology and views the evolution of organisms and their material environment as so closely coupled that they form a single, indivisible, process²⁵. Organisms possess environment-altering traits because the benefit that these traits confer (to the fitness of the organisms) outweighs the cost in energy to the individual.

Since the genesis of the Gaia hypothesis, predictions, proposed mechanisms and evidence consistent with self-regulation have accumulated^{1,24,26}. In particular, the continuous habitability of the Earth, despite major, periodic perturbations, is consistent with the existence of a planetary self-regulating system¹. Planetary impacts²⁷ and volcanic outbursts²⁸ (which may be triggered by the impacts²⁹) appear to have caused mass extinctions³⁰ and climate change³¹ and yet, in all cases, diverse, widespread life and a tolerable climate returned within a short period of geological time.

Are there alternative explanations for what appears to be evidence of self-regulation? Perhaps the antithesis of Gaia is that it is random chance that life has persisted on Earth. A long history of life on Earth may not be evidence in itself for self-regulation: it is merely a prerequisite for conscious observers to have evolved³². However, given the large perturbations and changes in forcing of the Earth's surface, being 'just lucky' is a less probable explanation for the persistence of life than the existence of some form of planetary self-regulation.

An intermediate position accepts the existence of regulatory mechanisms on Earth but denies that there is any evolutionary tendency towards planetary self-regulation^{3,33}. In this case, we inhabit a planet that just happened to have stabilizing feedbacks. Where destabilizing feedbacks dominate, life is likely to perish before evolution produces conscious observers. This is consistent with the view that life and climate evolve together^{33,34}, with life adapting to environmental changes, some of which it creates. If an inherent tendency towards self-regulation can be shown it will provide a more probable explanation of the persistence of life on Earth than that of co-evolution.

Some geochemists have asserted that there is no need to invoke life to explain the maintenance of habitable conditions on Earth³⁵. For example, they argue that abiotic, purely geochemical and geophysical feedbacks (Fig. 2) are enough to maintain a favourable climate, offering silicate-weathering negative feedback¹¹ as an

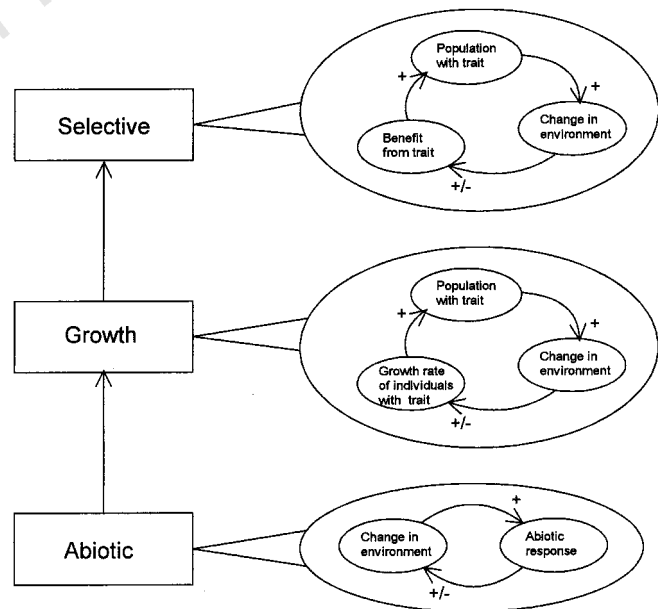


Figure 2 A hierarchy of environmental feedbacks. Three levels are identified, abiotic (purely geochemical and geophysical) feedback, feedback on growth and feedback on natural selection (see text). 'Trait' always refers to an environment-altering trait, and 'growth' includes reproduction. At each level, both positive and negative feedbacks are possible, and these are illustrated in a general form. A plus symbol indicates a direct relationship. For example, an increase in the population with a particular environment-altering trait increases the resulting change in the environment. A plus/minus symbol indicates a relationship that can be either direct or inverse depending on specific conditions. For example, a change in the environment may increase or decrease the growth rate of individuals carrying the responsible trait, depending on the state of the environment and the direction in which it is being altered. When all the links of a complete feedback loop are positive, the feedback is positive; when one link is negative, the feedback is negative. Steps up the hierarchy are often additive. The activities of organisms can alter an underlying geochemical or geophysical feedback, while feedbacks on selection may be superimposed on underlying feedbacks on growth. (The spread of a trait is often subject to a direct positive feedback that is not shown—the larger a population, the larger its rate of growth.)

explanation. The chemical weathering of calcium-silicate rocks by weakly acidic rain liberates calcium ions that may combine with carbon dioxide as solid calcium carbonate. A rise in planetary temperature (for example) would provoke a rise in weathering rate and a counteracting decline in the concentration of carbon dioxide in the atmosphere (until the weathering sink again matched the source flux of carbon dioxide from volcanoes). Negative feedbacks tend to counteract change and thus stabilize a range of conditions. Silicate-weathering should act to maintain liquid water at a planet's surface. However, geochemical negative feedbacks operate slowly and are not very responsive to perturbation.

Positive feedbacks, notably the ice-albedo feedback³⁶, would also be present on an Earth without life. As polar ice-sheets descend in latitude, the resulting increase in planetary albedo (reflectivity) causes cooling, encouraging the ice to spread further. Beyond a certain latitude there is runaway feedback, and the planet becomes completely covered with ice. Such abiotic, positive feedbacks operate over a narrow range and tend to force a system to extreme states. An ice-covered Earth would be uninhabitable for most organisms. The silicate-weathering negative feedback could not prevent runaway of the ice-albedo positive feedback as the latter operates much faster³⁷, indicating that abiotic feedbacks may not be sensitive enough to maintain a habitable climate on Earth for 3.8 billion years.

There are limitations to a purely geochemical view of Earth's climate history. The absence of siderite from palaeosols of over

2.2 Gyr age indicates that levels of atmospheric carbon dioxide in the late Archaean era may have been insufficient to compensate for lower solar luminosity³⁸. Biogenic methane may then have contributed significantly to the atmospheric greenhouse effect^{1,38,39}. Precambrian glaciations appear to have been rare, although glaciation may have occurred at equatorial latitudes at ~0.7 Gyr and ~2.2 Gyr ago⁴⁰. Recovery of a habitable climate from suggested 'snowball Earth' conditions would indicate a remarkable resilience to perturbation⁴⁰. More evidence is needed to test specific hypotheses for the roles of life in maintaining a habitable climate and in recovery from perturbation. However, it is clear that organisms are involved in many environmental feedbacks on Earth (including silicate-weathering; Box 2), and their effects need to be considered.

The basis of environmental regulation

Gaia theory focuses on three intrinsic and one extrinsic property of living organisms¹. First, all organisms alter their environment by taking in free energy and excreting high-entropy waste products in order to maintain a low internal entropy⁴¹. Second, organisms grow and multiply, potentially exponentially, providing an intrinsic positive feedback to life (the more life there is, the more life it can beget). Third, for each environmental variable, there is a level or range at which growth of a particular organism is maximum. Thus, carbon-based chemistry and the structures of cells, with their lipid membranes, limit the tolerable range of climate and chemistry⁴².

Box 1 Daisyworld: self-regulation without teleology

Daisyworld^{20,21} is an imaginary grey world orbiting, at a similar distance to the Earth, a star, like our Sun, which gets warmer with time. The world is seeded with two types of life, black and white daisies. These share the same optimum temperature for growth, 22.5°C, and limits to growth of 5°C and 40°C.

Initial conditions on the planet are so cold that daisy seeds cannot germinate. As solar forcing increases and the temperature reaches 5°C, the first seeds germinate. The paleness of the white daisies means that they are cooler than their surroundings, hindering their own growth. The

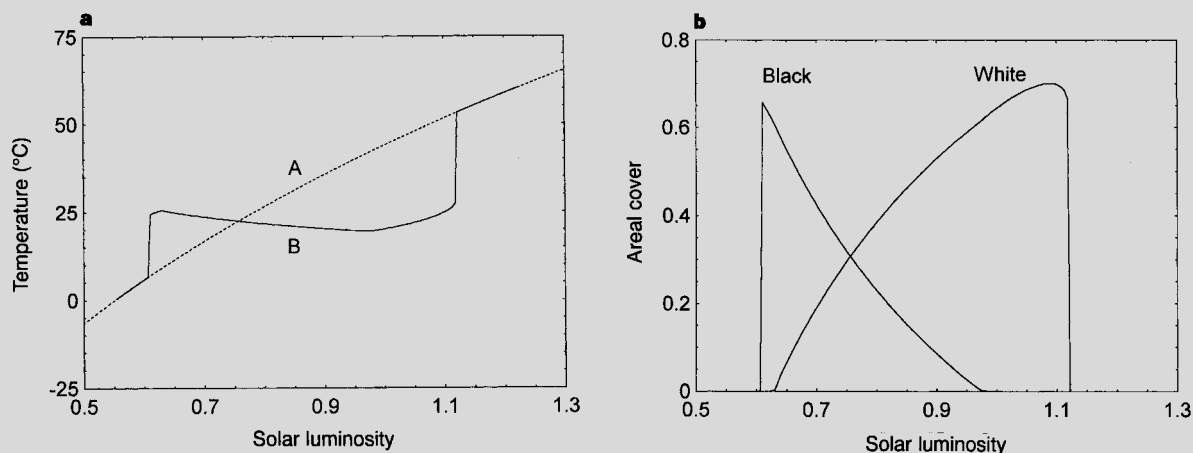
black daisies, in contrast, warm their surroundings, enhancing their growth and reproduction. Hence black daisies come to dominate the initial community (see figure).

As they spread, the black daisies begin to warm the planet. This increases the growth rate of all daisies, an environmental positive feedback that reinforces the spread of life. As the warmer, darker daisies are closer to the optimum temperature than the white daisies, they remain dominant. Soon the limited area of planet surface constrains the expansion of life. When daisies fill the world, the average temperature has risen close to the

optimum for daisy growth.

As the sun warms, the temperature rises to the point at which white daisies begin to appear in the daisy community. As it warms further the white daisies gain the selective advantage over the black daisies and gradually take over. Eventually, only white daisies are left, and when the solar forcing gets too high, self-regulation collapses.

The self-regulation of Daisyworld is impressive: although the solar input changes over a range equivalent to 45°C the surface of the planet is maintained within a few degrees of the optimum temperature for daisy growth.



Box 1 Figure The original Daisyworld model. A thought experiment to show that planetary self-regulation can emerge from natural selection, at the individual level, of types of life with different environment-altering traits^{20,21}. In this case the traits are 'darkness' (albedo 0.15) and 'paleness' (albedo 0.65) of black and white daisies, on a grey planet (albedo 0.4). The equations are

described in ref. 21. **a**, Planetary temperature as solar luminosity increases. The dashed line (A) shows the temperature in the absence of daisies and the solid line (B) shows the temperature in the presence of daisies. **b**, Areal cover of black and white daisies.

Finally, once a planet contains different types of life (phenotypes) with faithfully replicated, heritable variation (different genotypes) growing and competing for resources, natural selection determines that the types of life that leave the most descendants come to dominate their environment².

There is considerable variation in the degree of environmental alteration, rate of growth, environmental constraints and operation of natural selection on different types of life⁴². The argument I develop here focuses on common features of all organisms. Organisms both alter and are constrained by their environment, so feedback is inevitable. Feedback begins at the individual level, but growth implies that feedback has the potential to spread to the global level; the disequilibrium of the Earth's atmosphere indicates that this has occurred.

Gaia theory treats the ways in which organisms alter their environment as (extended¹⁹) phenotypic traits, although, in most cases, the genetic basis of these traits is unknown. From a Gaian perspective, it is the environmental alteration, not which particular organism is responsible for it, that is important. Selection acting on different organisms altering the environment in the same way, to a similar degree, has little environmental consequence.

Some activities that alter the environment are so advantageous (to the organisms carrying out the activities) that they become widespread, fundamental properties of organisms. (An example is photosynthesis, the implications of which have been studied by modelling the Archaean–Proterozoic transition^{25,43}.) Other activities are favourable only under particular environmental conditions and hence are subject to selection. In such cases, it is often changes in one environmental variable that determine whether a trait remains selectively favourable. If the spread of the trait alters this environmental variable, it also alters the forces of selection determining its own value.

A hierarchy of feedbacks. A conceptual hierarchy of feedbacks is used to attempt a synthesis of natural selection and environmental feedback. Abiotic feedbacks, present on a lifeless planet, form the base, added to which are two key steps (Fig. 2). The first step is to add organisms that alter their environment in a manner that affects their growth, without altering the forces of selection on the responsible trait. The resulting ('non-selective') feedbacks on growth rate can be positive (amplifying) or negative (damping). The second step is to consider the spread of traits that alter the forces of selection on themselves. This adds 'selective' feedback (which 'involves selection'). Selective feedback occurs whenever the spread of a trait critically alters the environmental variable that determines the benefit of that trait. The alteration in the variable can maintain, or even promote, conditions in which the trait is advantageous, generating positive selective feedback. Alternatively, the environmental alteration can start to reduce the advantage of the trait, generating negative selective feedback.

Feedbacks on growth. Changes in the environment due to a particular trait can be favourable or unfavourable for growth. However, the spread of a trait that alters the environment in a manner that is favourable to growth tends to be reinforced (positive feedback on growth). In contrast, the spread of a trait that alters the environment away from optimal growth conditions is restrained (through negative feedback on growth). This represents a natural tendency towards environmental self-regulation that can be illustrated by the biological enhancement of silicate weathering^{4,47}. This widespread activity of life on land amplifies the existing geochemical feedback. It is arguably the best established Gaian mechanism and is modelled as a non-selective feedback on growth in Box 2.

To illustrate the first step up the feedback hierarchy (Fig. 2), rock-weathering organisms are introduced to a world in which silicate weathering is the only geochemical feedback (Box 2 Fig.). If the temperature is initially above the optimum for growth (as would be the case for the present Earth without this biological enhancement⁴⁶), the spread of life would increase the rate of rock

weathering and reduce the level of carbon dioxide in the planet's atmosphere, causing cooling. As the temperature decreases and comes closer to the optimum for growth, organisms rapidly fill the world and the temperature drops quickly to below the optimum for growth. Any further spread of life becomes restricted because further cooling reduces growth rate. (If temperatures are initially below the optimum for growth, the spread of rock weathering immediately restricts itself, by reducing growth rates. This is consistent with Gaia theory, because in the real world there are many environment-altering traits. If a warming activity arises under such conditions its spread is reinforced.)

The tendency towards self-regulation is the result of the three intrinsic properties of life. Altering the environment changes existing geochemical and geophysical feedbacks and creates new feedbacks. Growth amplifies any feedback involving organisms. Biological amplification makes geochemical and geophysical feedbacks more sensitive and responsive to perturbation. Environmental constraints determine the form of the function relating growth to each environmental variable. Where there is a range of maximum growth, positive and negative feedback regimes exist on either side of the range. Across a range of external forcing, a system with sufficient biological amplification automatically stabilizes in the negative feedback regime. Hence, in contrast to a dead world, the introduction of organisms brings an inherent tendency to stabilize conditions that are inhabitable by life.

Non-selective feedback on growth provides a basis for environmental self-regulation. However, one such feedback alone can respond only passively to external forcing. As illustrated by the rock-weathering model, the steady state of the system moves in parallel with changes in external forcing, although at a more amenable level.

Feedbacks on selection. The next step up our hierarchy of feedbacks (Fig. 2) is to consider what happens when different types of life with heritable variation arise on a planet and there is competition and natural selection. Daisyworld²¹ (Box 1) provides a simple, albeit hypothetical, example of this situation. The daisy traits of 'darkness' and 'paleness' change the world in a way that alters the forces of selection on them, generating selective feedback.

In Daisyworld, the environmental variable determining selective forces is temperature. In the beginning, when it is cold, being black confers a selective advantage. The spread of the trait of 'darkness' increases the temperature of the world (providing positive feedback on growth). However, this increases the individual temperatures of the daisies, and thus reduces the selective value of 'darkness'. When daisies fill the world the black daisies have brought the planetary temperature to a point where 'darkness' no longer confers much, if any, of a selective advantage. As the sun warms, the white daisies gradually take over.

Daisyworld shows that selective feedback is the result of a trait altering the same environmental variable at the level of selection and at a large scale. In the original Daisyworld, the selective feedbacks are negative. The alteration of the environment resulting from the spread of a trait is one that ultimately reduces the benefit of that trait. This is a consequence of the colour traits altering the environmental conditions in the same direction at the individual and the higher (in this case, global) level.

What happens when the environmental alteration occurs in different directions at the individual and global levels? An example in Daisyworld are black daisies that generate white clouds as a consequence of the convective heat rising from the warm, black daisy clumps²¹. These daisies become warm but, by producing clouds, cool the global environment. As a consequence, the black daisies out-compete the white daisies, driving them to extinction. Thus black cloud-makers maintain the cool conditions in which they are at a selective advantage, an example of positive selective feedback.

Daisyworld shows that natural selection can contribute to envir-

onmental self-regulation. The combination of selective feedbacks shows active regulation: as the solar forcing increases, the surface temperature of the planet is held close to constant.

Evolution on Daisyworld

Evolution by natural selection needs inherited variation on which to act, and in the original Daisyworld such variation is minimal (there are only two shades of daisy). A Daisyworld with a much larger pool of variant daisies of many different colours, has been modelled⁴⁸. The consequence of competition on Daisyworld is exclusion of all but one or two types of daisy at a given solar luminosity⁴⁹. The types of daisy selected give the planetary temperature most closely matching the optimum for daisy growth. This adds to the case that, given variation, selection can help to generate environmental self-regulation.

Evolutionary biologists argue that there is an inherent conflict between the more immediate, local optimization of evolution by

natural selection and the longer term, larger scale process of environmental regulation⁵⁰. To address this issue properly requires a move from 'static' evolutionary models towards those mimicking the generation of new traits⁵¹.

A specific criticism is that 'cheats' will disrupt self-regulation by not contributing to it and thus saving themselves energy. To address this criticism, Lovelock⁴³ introduced into Daisyworld a grey daisy that saved energy by not producing black or white pigment. This cheat did not destroy regulation because it had a selective advantage only when the solar input was close to the level at which regulation was not required. At extremes of solar input, the cost of producing the right pigment is outweighed by the benefit from being at a temperature closer to the optimum for growth. This emphasizes that environmental regulation can only emerge from traits that are more beneficial than costly to the individual.

A different proposal for local optimization has been made⁵². When the average temperature of Daisyworld is at the optimum for

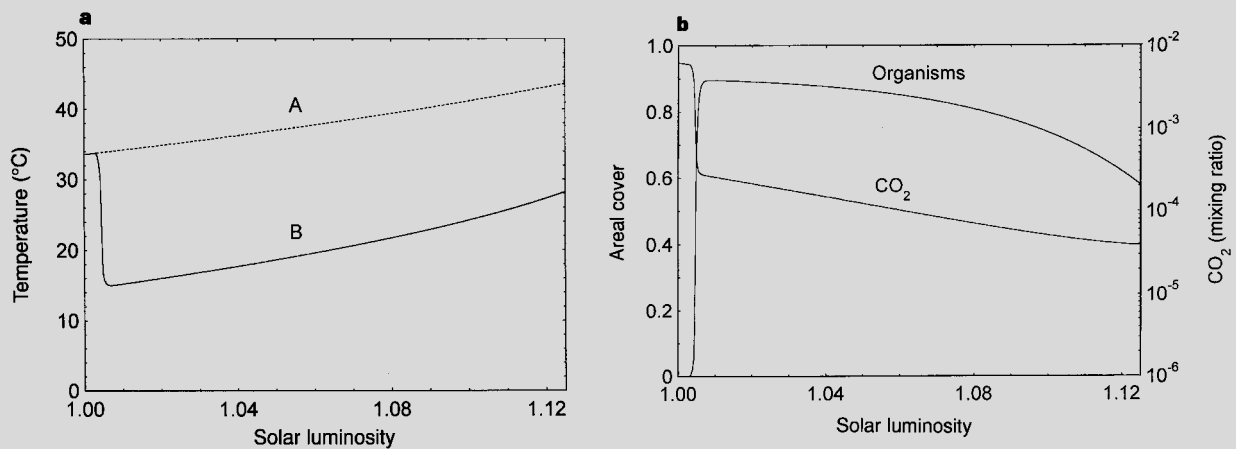
Box 2 Biological amplification of rock weathering

Rock weathering is enhanced by a range of organisms in different ways⁴⁷. There is debate over which effects are most significant. Root respiration and the microbial decay of organic matter enhance soil carbon dioxide levels by 10- to 100-fold over atmospheric levels⁴⁶. The resulting increase in carbonic acid accelerates the weathering reaction. Physical weathering of rocks is enhanced by microbial microfracturing of mineral grains, production of polysaccharides (which swell when wet) by bacteria and fungi and rock splitting by plant roots. These processes create surfaces for chemical weathering. Organic and inorganic acids, actively produced in bacterial

decomposition and by lichen, donate protons which accelerate weathering. The initial formation and subsequent stabilization of soil maintains a high surface area of minerals in contact with acidified water, encouraging further weathering.

From an evolutionary perspective, the biological mechanisms of enhancing rock weathering fall broadly into two categories. Some are the passive result of other processes, whereas others involve an active input of energy. Respiration is part of the fundamental biochemistry of life. The resulting increase in weathering is an inadvertent side effect, which is unlikely to be selected against. In contrast, when microbes and lichens are coloniz-

ing new rock surfaces⁹⁷, several active processes that are subject to selection, such as the production of acids, are used. Where weathering is active, the pursuit of nutrients may be the biological motivation. The global consequence of enhanced rock weathering is a lowering of carbon dioxide levels and hence of temperature. Changes in either of these variables do not alter the selective advantage of seeking nutrients, but they can alter growth rates. Thus, amplification of weathering provides an example of a non-selective feedback on growth (see figure).



Box 2 Figure A simple model of biological amplification of weathering. Rock-weathering land organisms are introduced to a world in which negative feedback on silicate weathering determines the partial pressure of carbon dioxide and the surface temperature. Solar input forces the model, starting at today's value for the Earth and increasing linearly by a total of 12.5%. Carbon dioxide is assumed to be in steady state and the input of carbon dioxide is held constant. Hence, the level of carbon dioxide adjusts so that its removal by weathering matches its input. The radiative relationship between solar luminosity, carbon dioxide level and planetary temperature is a grey atmosphere approximation, fitted to results (L. L. Brown, personal communication) from a one-dimensional, radiative-convective, climate model⁹⁸. The functional dependencies of weathering rate on temperature and carbon dioxide level are those suggested in ref. 11. However, I conservatively⁴⁶

assume that, at present, land organisms amplify weathering rates by a factor of ten. This makes the model world, without life, initially 19°C warmer than today's Earth. Land organisms are introduced after luminosity has increased by 0.2%. The land area covered by organisms is modelled in the same way as in Daisyworld. The weathering rate increases linearly with the area covered by organisms, up to a maximum of ten times the abiotic rate. The optimum temperature for growth is 22.5°C and the relationship between growth rate and temperature is a gaussian curve. Carbon dioxide fertilizes growth. **a**, Planetary temperature evolution, (A) without and (B) with life. **b**, The areal cover of land organisms and the resulting changes in carbon dioxide mixing ratio. (The model is robust to instantaneous perturbations that remove 90% of the organisms. The decline in plant life at the end is due to a lack of carbon dioxide.)

daisy growth, individual black daisies are warmer, and individual white daisies cooler, than their environment. If there is enough heritable variation in optimum temperature among the daisies, we expect the average optimum temperature of the black daisies to evolve upwards, and that of the white daisies to evolve downwards. The gain from this adaptation is a small increase in the area of the planet covered by daisies (at a given solar luminosity in the range of regulation). The loss is a reduction in the range of regulation. In this case, local optimization compromises regulation but does not destroy it.

A problem with all the variations of Daisyworld discussed above is

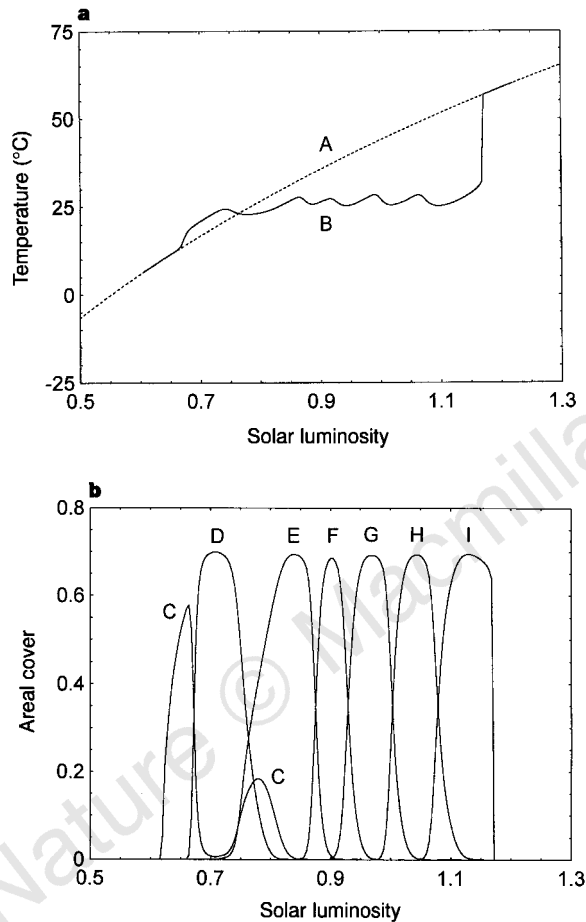


Figure 3 Model for mutating Daisyworld. A model world is seeded with a grey daisy (C) of the same albedo (0.4) as the planet's surface. Daisy albedo can mutate in discrete steps of 0.05 (with limits of 0.2 and 0.65), and the resulting variation is faithfully replicated. The probability of mutation for any individual reproducing daisy is a constant parameter. Thus, the probability of mutation for a particular daisy type is proportional to the population of that type. This means the more abundant types are more likely to beget new types. Mutation is equally probable in either direction of increasing or decreasing albedo. Solar luminosity is increased in steps of 0.004. At each time step there is the possibility of mutation, which is followed by 100 cycles of population dynamics, so the resulting types can approach equilibrium. **a**, Planetary temperature evolution. The dashed line (A) shows the temperature increase without life, and the solid line (B) shows the result of the introduction of daisies (with a mutation probability of one-fifth their areal coverage). **b**, Areal cover of the various daisy types generated. C is the starting type (albedo 0.4) which flourishes initially, when alone, and has a significant population later, when solar luminosity is such that there is no need for regulation. D is a darker mutant of albedo 0.35 that arises and dominates at low solar luminosity. E, F, G, H and I are paler mutants of albedos 0.45, 0.5, 0.55, 0.6 and 0.65, respectively. E–I are favoured in sequence when solar luminosity increases background temperatures above the optimum for daisy growth.

that the types of daisy are determined at the beginning, with no allowance for further evolutionary change⁵³. To address this criticism⁵¹ I introduce a model of mutation in Daisyworld (Fig. 3). The world is seeded with a grey daisy of the same albedo (reflectivity) as the planet's surface; this daisy makes no contribution to regulation. Colour mutation in either direction, increasing or decreasing albedo, is equally likely. At the individual level there is equal probability that 'Gaian' and 'anti-Gaian' behaviour will arise. Under the initial, cold conditions, a paler daisy would be 'anti-Gaian' in the sense that it would alter the environment away from ideal conditions, whereas a darker daisy would be 'Gaian' in that it would make the environment more favourable to growth. If 'Gaian' and 'anti-Gaian' behaviours are equally likely to emerge at the individual level, what grounds are there to expect self-regulation⁵⁴?

Application of the model shows that with sufficient probability of mutation to generate new types, planetary self-regulation emerges (Fig. 3). A trait that brings the resulting organism closer to the optimum growth conditions will spread. Such a trait is, by definition, 'Gaian'. In contrast, a mutation in an 'anti-Gaian' direction will have its spread restricted by putting the organism responsible at an evolutionary disadvantage. This behaviour results from the daisy traits of albedo altering the environment in the same way at the individual and global levels. More complex studies^{55,56} show that mutation of albedo can also extend the range of regulation.

One can imagine situations in which the outcome of natural selection does not contribute to environmental regulation. An example would be mutation of the temperature tolerance of the daisies⁵². Such internal, physiological adaptations to prevailing conditions may reduce the need to alter the environment. However, there are environmental constraints on such adaptation, such as the onset of water-stress. In this case, there may also be energetic reasons to favour albedo change over physiological change⁵⁵. The outcome of the potential for both environmental alteration and internal adaptation to prevailing conditions deserves further testing. However, there are many examples of living plants altering climate to their own benefit (see 'Land ecosystems' section below).

The selective pressures exerted by different types of organism on one another (for example, predators on their prey) are not directly related to the environment. Will they, therefore, undermine environmental regulation? A developing series of Daisyworld models, with increasingly complex ecology^{48,57,58} (Box 3), provides a framework to address this puzzle. Introducing selective herbivory on the daisies slightly impairs regulation but does not destroy it, because selective pressures from the environment dominate. In contrast, when feedback to the environment is arbitrarily removed, regulation of both population dynamics and climate disappear⁵⁷. In addition, when different types of herbivore are present, operating under different feeding strategies⁵⁸, the dominant herbivore is determined by the daisy–environment feedback, rather than the distribution of daisy types being determined by the herbivores (Box 3).

From models to reality

The robust self-regulation of Daisyworld is an outcome of the direct and strong coupling of plant growth to planetary temperature, but the real world is far more complex. The primary value of models is heuristic⁵⁹. The actual mechanisms of climate regulation in Daisyworld were not intended to explicitly represent those on the Earth, although similar feedbacks were later recognized¹ (see below). However, Daisyworld has been usefully adapted to modelling of community ecology^{48,57,58} (Box 3) and of chemical and climatic regulation^{1,25,43,60}.

Daisyworld ignores important levels of the environment between the individual and the global levels. The temperature of an individual daisy is determined only by the difference between its albedo and the albedo of the planet. If the daisies were real, their individual temperatures would depend somewhat on their neighbours and

their region. In a two-dimensional extension of Daisyworld⁵⁶, albedo mutation generates a heterogeneous distribution of daisy colours and the inclusion of spatial heat transport extends the range of climate regulation.

The simple models presented here show a homogeneous world, in which the background conditions are the same everywhere, but the real world has many regions and a range of background conditions. The clearest regional distinction is between land and ocean. Superimposed on this is the varying solar input across the spherical surface of the Earth; this creates a continuum of background temperature and moisture conditions between the Equator and the poles.

Oversimplifying to a one-niche model means that when the system collapses, it does so in one rapid switch. In the two-dimensional Daisyworld⁵⁶, destructive habitat fragmentation impairs temperature regulation once a threshold is reached at which the diminishing areas of daisies become disconnected. This emphasizes the importance of unrestricted competition and natural selection for regulation on Daisyworld. In reality there are many niches, and physical barriers can prevent organisms from competing directly with one another. By modelling separate land and ocean biotas, it can be shown that the demise of regulation in one region may not spell disaster for the entire system, as long as enough organisms in other areas are contributing to regulation⁶⁰.

Land ecosystems

In the real world, coupling between life and its environment occurs at all scales, beginning with localized niche construction⁶¹ and with ecosystems emerging as integrated systems between the individual and the global levels^{62,63}. Gaian feedback concepts may usefully be applied to these levels. Ecosystem-level environmental feedbacks must be understandable in terms of natural selection. Equally, an ecosystem cannot spread and persist indefinitely if it alters regional and global conditions away from those amenable to the constituent organisms²². Ecosystems that have stabilizing feedback will tend to persist and spread, whereas ecosystems that develop destabilizing feedback will tend to collapse and disappear. Thus, we might expect ecosystems with stabilizing internal and environmental feedbacks to predominate (see 'Testing Gaia' section below).

The trees of the Amazon rainforest, through generating a high level of water cycling, maintain the moist environmental conditions in which they can persist⁶⁴ (a positive feedback on growth and selection). Nutrients are also effectively retained and recycled²². If too much forest is removed, the water-regulation system can collapse, the topsoil is washed away and the region reverts to arid semi-desert, a change that may be difficult to reverse⁶⁵.

Boreal forest trees are somewhat analogous to the dark daisies of Daisyworld¹. The individual trees possess the traits of snow-shedding and darkness that give them a low albedo and make them warmer than their surroundings. The presence of forest warms the region and the hemisphere⁶⁶. However, the forest remains well below the optimum temperature for growth for most of the year. Thus, the system shows constrained, positive feedback (on growth). This amplifies any increases in temperature due to regional warming. The winter mean temperature change for 1965–1995 shows a 2.5 °C rise across the band of northern high-latitude forests⁶⁷ and further amplified warming is predicted under global change⁶⁸.

The terrestrial biomes significantly alter climate in different ways^{1,65,66} and compete for space. Thus, their geographical distributions are the result of complex feedbacks involving climate and succession. The resulting dynamic balance can shift in response to both external triggers and internally driven changes.

Shifts in the balance between boreal forest and tundra amplify external forcing: 115,000 years ago, orbital forcing reduced summer temperatures and seems to have triggered the spreading of the arctic tundra southwards to replace boreal forest⁶⁹. The resulting increase in albedo, because of unmasked snow cover, would have added to

regional and planetary cooling and may have generated the onset of glaciation⁶⁹. The positive feedback has probably also operated in the opposite direction: 6,000 years ago, orbital forcing warmed the high latitudes, which would have triggered boreal forests to spread northwards and amplify the initial warming⁷⁰. Indeed, boreal forest may often be involved in maintaining periods of global warmth⁷¹.

Internal changes in ecosystems, involving feedbacks on growth and natural selection, may drive changes in climate^{1,72}. Ecological succession may involve the onset of regulatory feedbacks, including resistance to invasion by damaging outsider species⁵¹. For example, peat bogs have been proposed as a 'climax' ecosystem in many regions⁷². Through promoting soil acidification, iron-capping, water storage and the build up of peat, peat bog plants exclude trees and other plants^{72,73}, generating positive selective feedback.

Marine phytoplankton

The production of dimethyl sulphide (DMS) by marine phytoplankton is an example of an individual trait with global consequences⁷⁴, which illustrates the complex steps linking organisms to their environment^{75–77}. This topical area of research (reviewed in refs 74–77) has been greatly stimulated by Gaian thinking.

Different species of marine phytoplankton produce varying amounts of dimethylsulphoniopropionate (DMSP), the precursor

Box 3 Ecology and biodiversity in Daisyworld

It was proposed⁹⁹ that the mathematics of evolutionary models would be simpler if the evolution of organisms and of their physical environment was considered as a single process. To test this idea, herbivores then carnivores were introduced into a biodiverse Daisyworld model⁴⁸. These predators fed unselectively, eating the same fraction of their prey, regardless of the prey's abundance. The model shows remarkable mathematical stability for many species. Adding the unselective herbivores results in smaller populations of daisies at any given time and, therefore, a small decrease in the range of temperature regulation. Adding the carnivores reduces the herbivore populations, thus increasing the daisy populations and the range of regulation.

The biodiversity model provides a framework in which to explore the implications of interorganism selection for environmental self-regulation. A variation of this model is to compare the effects of an unselective herbivore (type 0) and three different types of selective herbivore (types 1–3) that favour more abundant over less abundant daisies to varying degrees⁵⁷. The frequency-dependent selection leads to exploiter-mediated co-existence of the daisies and differing degrees of daisy biodiversity according to the precise herbivore feeding strategy. One type of selective herbivore (type 3) improves temperature regulation relative to unselective herbivory, whereas the other two (types 1 and 2) slightly impair regulation.

A next step towards modelling a realistic community is to introduce the three types of selective herbivore together⁵⁸ (large types⁵⁷ 1–3). If selection by the herbivores dominates the system, we expect there to be small populations of many daisy colours right up to the extents of regulation, which would therefore be reduced. Instead at extreme solar luminosities there is an innate tendency for a reduction in daisy biodiversity, because only one or two daisy shades (dark ones at the beginning and light ones at the end) are selected by the environment and can provide regulation. The rising populations of these one or two daisy types determine that the dominant herbivore becomes the one that eats the largest proportion of daisies that are at high abundances (type 1). The model thus shows the herbivores being selected by the daisy–environment feedback, rather than the distribution of daisy types being selected by the herbivores. Furthermore, decreasing the number of food-web connections reduces resilience⁵⁸.

of DMS⁷⁶. DMSP is one of a range of compatible solutes, believed to be produced as an osmolyte, that can alleviate salt-stress and prevent freezing^{76,78}. The conversion of DMSP to DMS is catalysed by the enzyme DMSP lyase. This process is enhanced by virus infection and zooplankton grazing^{76,79} and may be adaptive^{79,80}. The main reservoir of DMS is in the ocean, where it is consumed by bacteria and oxidized to dimethylsulphoxide (DMSO)⁷⁶. Air–sea exchange results in a net flux of DMS to the atmosphere⁷⁶ (Fig. 1b). In the atmosphere, DMS is oxidized in a range of oxidation reactions⁸¹. The main pathway generates sulphur dioxide which is further oxidized to sulphate, and which can ultimately contribute to sulphate aerosol formation. (A secondary pathway generates methanesulphonate which can be measured in ice cores and used as a proxy for DMS production in the past^{82,83}.) Sulphate aerosol is a major source of cloud condensation nuclei^{77,84}, which can form cloud droplets that are important scatterers of solar radiation. DMS-derived aerosols can therefore increase cloud albedo⁸⁵ and the consequent return of solar radiation to space, which would be expected to cool the affected region and the planet⁷⁴.

What types of feedback (Fig. 2) are generated by DMS emissions? Any benefits of altering the environment are estimated to be small in comparison to the energy cost of DMSP production⁷⁸; thus, we might expect DMSP production to remain selectively favourable regardless of the environmental alteration. A (non-selective) negative feedback on growth of DMS-emitting phytoplankton and climate was first proposed⁷⁴ whereby a reduction in temperature and light beneath clouds reduces photosynthesis and restricts the spread of DMS producers. Subsequent modelling⁶⁰ elaborated this proposal²⁶, and indicated that the formation of a thermocline at ~10 °C might limit the supply of nutrients to the surface ocean, thus setting an effective optimum for plankton growth. Beneath this temperature lies the originally proposed regime of negative feedback. Above it, however, an increase in temperature may be amplified by a decrease in photosynthetic production⁸⁶, DMS production and cloud reflectivity, generating positive feedback. Evidence that DMS production in the Southern Hemisphere was enhanced during the last ice age^{82,83} indicated that the feedback may then have been negative, but switched to become positive as temperatures rose at glacial termination^{60,75,83}. However, no single relationship between temperature and DMS emissions is consistent with all existing data⁸³. This is not surprising, given the other factors now thought to influence DMS production. For example, it has been proposed⁸⁷ and confirmed^{76,88,89} that when nitrogen is abundant the compatible solute, glycine betaine, is produced instead of DMSP. When nitrogen is limited, organisms switch to making DMSP. Marine organisms are responsible for a sea–air flux of ammonia of similar magnitude to the DMS flux⁹⁰. In the atmosphere, acidic sulphate cloud droplets scavenge the alkaline ammonia, in a process that may be important for particle nucleation⁹¹, and the rain out of these droplets may fuel new photosynthetic production in remote marine areas⁹⁰.

Testing Gaia

The Gaia theory is a valuable hypothesis generator^{1,23–25}. Predictions from Gaia, including ancillary hypotheses of mechanisms, have been tested and corroborated²⁴. However, direct tests of Gaia⁹² are difficult, because of the temporal and spatial scales involved. A challenge for future work will be to develop a range of more realistic and testable models.

One approach would be to test whether adding a realistic environment and random generation of environment-altering traits would enhance the stability of a community ecology model (W. D. Hamilton, personal communication), thus allowing ecosystem-level predictions to be made. For example, the consequences of nitrogen fixation and biological amplification of rock weathering on available nutrient reservoirs and community dynamics could be tested against natural and experimental systems.

Modelling of interacting ecosystems competing for space in a shared planetary environment might test whether those with stabilizing feedbacks come to predominate. A dynamic vegetation component for future global circulation models (GCMs), being developed at present, could be put to this task and offer comparison with the real world (P. M. Cox, personal communication). GCM simulations indicate that vegetation almost always influences climate for its own benefit, by making high latitudes warmer and by increasing continental rainfall everywhere (R. A. Betts, personal communication). However, GCM simulations are restricted to relatively short timescales. A simpler (energy-balance) model of feedbacks between the biosphere and climate would provide a framework with which to explore effects over longer timescales (for example, those involved in glacial–interglacial transitions). In this context, feedbacks that have yet to be incorporated in GCM simulations (such as those involving DMS production) could be quantitatively evaluated and predictions made. In addition, the effects of competition and selection, within the land and ocean realms, could be explored by explicit modelling of different types of terrestrial vegetation and marine phytoplankton with characteristic environment-altering traits.

Conclusions

When asked to explain how planetary self-regulation could have arisen, we are in much the same position as Darwin when asked how the eye could have evolved. We see a complex phenomenon and have only the beginnings of a theory with which to tackle the puzzle. Darwin focused on the exponential growth of organisms, the constraints imposed on them by their environment and the resulting natural selection. The fact that organisms also alter their environment means there is an inevitable feedback connection between the living and non-living. I have tried to describe the forms that such a connection could take. The implications may be far reaching; simple principles suggest that environmental regulation can emerge at levels from the individual to the global. Natural selection is seen as an integral part of Gaia, and Gaia theory also has something to offer evolutionary biology. Gaian models suggest that we must consider the totality of organisms and their material environment to fully understand which traits come to persist and dominate. □

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