



System-dependent Selection, Ecological Feedback and the Emergence of Functional Structure in Ecosystems

J. STEPHEN LANSING,*§ JAMES N. KREMER† AND BARBARA B. SMUTS‡

** Department of Anthropology and School of Natural Resources & Environment, University of Michigan, Ann Arbor, MI 48109-1328, U.S.A., † Department of Marine Sciences, University of Connecticut, Avery Point, CT 06340, U.S.A. and ‡ Department of Psychology, University of Michigan, Ann Arbor, MI 48109-1382, U.S.A.*

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Most models of natural selection assume either that the material environment remains constant or that it fluctuates in ways unrelated to changes in gene frequencies (and therefore changes in the distribution of phenotypes) of the organism undergoing selection. In this paper, we consider what happens when this assumption does not hold, that is, when ecological feedback between organism and environment is included in the evolutionary process. Specifically, we examine the unusual evolutionary dynamics that occur when changes in the distribution of phenotypes (resulting from selection) alter an environmental parameter in ways that, in turn, modify selection pressures. This process, which we term “system-dependent selection”, can produce stable phenotypic diversity which functions to regulate the relevant environmental parameter within a much narrower range than would occur in the absence of ecological feedback. This environmental regulation raises the mean fitness of the population and reduces variance in fitness among different phenotypes. Thus, system-dependent selection produces functional organization at the level of the system as a whole, rather than at the level of the individual organism. We use James Lovelock’s model of the imaginary planet Daisyworld to describe the unusual dynamics of this selective process and then use a similar model to examine the structure of an ancient system of wet-rice farming on the Indonesian island of Bali. This model accurately predicts the actual structure of functional organization along two Balinese rivers. We investigate the stability of such systems by exploring the conditions under which mutant phenotypes can invade Daisyworld. The results suggest that the phenotypic diversity and functional organization produced by system-dependent selection may be maintained when there exists variation, over evolutionary time, in the environmental parameters underlying system-dependent dynamics.

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Introduction

A number of recent studies have debated the significance of self-organization vs. natural selection as the causes of evolutionary change or adaptation (Depew & Weber, 1995; Kauffman, 1993; Maynard Smith, 1995; Saunders, 1994). In this paper we frame these alternatives differently: to do so we describe a selective process we call “system-dependent selection”. In this process, the fitness of individuals, or of phenotypes, is affected by the state of some

environmental parameter which, in turn, is influenced by the frequency distribution of phenotypes in the population as a whole. System-dependent selection operates on individuals, or phenotypes, as predicted by the fundamental theorem of natural selection. However, the process alters the phenotypic distribution in such a way that the environmental parameter is optimized with respect to the system as a whole. Under the action of system-dependent selection, particular phenotypes can either gain or lose absolute fitness, depending on the state of the environment at equilibrium. The mean fitness of the

§Author to whom correspondence should be addressed.

population, however, always increases. System-dependent selection therefore results in a different outcome than conventional natural selection, because it produces functional organization at the level of the system as a whole, rather than at the level of the individual organism. The system may be said to “self-organize” in the sense that the driving force for selection is entirely internal, depending neither on changes in phenotypes (such as those arising from mutation), nor on changes in the environment, except for those induced by changes in phenotypic distribution caused by selection. Our aim is to show how the dynamics of this self-organizing process can be described with reference to frequency-dependent selection and the broader context of conventional evolutionary theory. When framed in this way, the concept of system-dependent selection can provide a link between natural selection and self-organization, and between selection at the level of the individual and selection at higher levels.

The Fundamental Theorem of Natural Selection

The starting-place for our model is the “replicator equation”, recently proposed by Schuster & Sigmund (1983). We begin by describing the replicator equation, and then consider the effects of including system-dependent ecological feed-back in models of dynamical systems of the type specified by the replicator equation.

* Stressing the wide applicability of this type of equation, Schuster & Sigmund (1983, p. 536) “emphasize that this result has not been obtained through a mathematician’s desire to apply a pretty equation to as many fields as possible: the modelling leading to eqns (1)–(4) proceeded independently in genetics, ecology, prebiotic chemistry and sociobiology.”

† Equation (1) defines a dynamical system on the unit simplex

$$S_n = \{ \mathbf{x} = (x_1, \dots, x_n) \in R^n : \sum_i x_i = 1, x_i \geq 0 \text{ for } i = 1, \dots, n \}.$$

Hofbauer & Sigmund (1988) showed that the n -dimensional Lotka–Volterra equation can be mapped onto orbits of eqn (1), as well as the time-continuous version of Fisher’s selection equation, and the hypercycle equation. Such applications introduce frequency dependence to the replicator equation; e.g.

$$f_i(\mathbf{x}) = \sum_j a_{ij} x_j,$$

where a_{ij} is the fitness of E_i in the presence of E_j . However, in the examples to be considered in this paper, fitness is not frequency dependent in this sense (see “Natural Selection on Daisyworld” below, pp. 8–9). Consequently, according to Fisher’s fundamental theorem, the increase in mean fitness is proportional to the variance in fitness, and the highest attainable fitness is the fitness of the fittest individual in the initial population.

In 1930 Fisher published an equation that has come to be known as the “Fundamental Theorem of Natural Selection”, and around the same time Volterra described what is now known as the predator–prey equation (1926, 1931). In 1980, Hofbauer showed that Fisher’s selection equation is a special case of Volterra’s equation, and in 1983 Schuster & Sigmund showed that both equations could be subsumed by another, since “essentially one type of equation models the evolution (1) of allele frequencies in a gene pool, (2) of population densities in a habitat, (3) of concentrations of polynucleotides in a flow reactor, and (4) of probabilities of strategies for conflicts within one species.” They propose the term “replicator equation” for this differential equation, signifying its close relationship to the concept of “replicators” developed by Dawkins (Schuster & Sigmund, 1983).*

The replicator equation describes the behavior of a population divided into n phenotypes E_1 to E_n with relative frequencies x_1 to x_n specified by the vector \mathbf{x} . In a population with more than one phenotype, the fitness of phenotype E_i is conventionally designated as $f_i(\mathbf{x})$. The rate of increase \dot{x}_i/x_i under selection is equal to the difference between the fitness of E_i and the mean fitness of the population,

$$\bar{f}(\mathbf{x}) = \sum_{i=1}^n x_i f_i(\mathbf{x})$$

(Hofbauer & Sigmund, 1988, p. 124). Thus $\dot{x}_i/x_i = (\text{fitness of } E_i - \text{mean fitness})$ and the process of selection can be succinctly described by the “replicator equation”:

$$\dot{x}_i = x_i [f_i(\mathbf{x}) - \bar{f}(\mathbf{x})] \quad i = 1, \dots, n \quad (1)$$

If phenotypes differ in fitness, the replicator equation will cause \mathbf{x} to vary, with changes in \mathbf{x} driven by these differences.† Variance in fitness is implicitly understood to be the result of varying success in adapting to a specific local environment, as Darwin predicted, but the replicator equation does not require us to characterize this environment explicitly. If the environment remains constant and the fitness of each phenotype does not change (“constant selection”: Christiansen, 1988, p. 134; Smouse, 1976, p. 850), then the highest attainable mean fitness $\bar{f}(\mathbf{x})_{\max}$ is the fitness of the most fit phenotype in the initial population, and this phenotype will go to fixation.

Biologists have long recognized, of course, that these simplifying assumptions are often unrealistic, and that both environments and fitnesses vary while populations are undergoing selection (Kojima, 1971). Density-dependent selection and frequency-dependent selection are two well-known examples.* In the case of standard frequency-dependent selection within a single species, the frequency distribution of phenotypes (\mathbf{x}) affects fitnesses [$f_i(\mathbf{x})$], because the fitness of each phenotype depends upon its relative frequency within the population. This can lead to the evolution of stable equilibria involving two or more phenotypes rather than the dominance of one particular phenotype (Smouse, 1976). Under frequency-dependent selection, the mean fitness of the population may or may not increase (Christiansen, 1988, p. 134; Li, 1955). The process of system-dependent selection to be described below also leads to phenotypic diversity but differs from standard intraspecific system-dependent selection in two ways: (1) changes in \mathbf{x} are driven by feedback between \mathbf{x} and some environmental parameter(s) and (2) the mean fitness of the population rises while variance in fitness between phenotypes declines.

We illustrate this process with two examples. The first describes the effects of ecological feedback involving a single environmental parameter (temperature) on James Lovelock's imaginary planet Daisyworld. The second involves the optimization of two opposing parameters (water allocation and pest control) in thousand-year-old Balinese rice terraces.

The Daisyworld Model

In 1983, Watson & Lovelock created a model called Daisyworld as a way to explore relationships between organisms and their physical environments. Here we use a modified version of the Daisyworld model to describe the concept of system-dependent

selection and to distinguish it from other forms of selection.

Daisyworld is an imaginary planet orbiting a star like the Sun and at the same orbital distance as the Earth. The surface of Daisyworld is fertile earth sown uniformly with daisy seeds. The daisies vary in color, and daisies of similar color grow together in patches. As sunshine falls on Daisyworld, the model tracks changes in the growth rate of each variety of daisy, and changes in the amount of the planet's surface covered by different-colored daisies. The simplest version of this model contains only two varieties of daisies, white and black.†

In the Daisyworld model, black daisies have an albedo (or reflectance) of 0.25 and so absorb more heat than bare earth, which has an albedo of 0.5, while white daisies have an albedo of 0.75. The model posits that as a result of these differences in albedo, clumps of same-colored daisies create a local microclimate for themselves, slightly warmer (if they are black) or cooler (if white) than the mean temperature of the planet. The mean temperature of the planet, in turn, is a function of solar luminosity.

Both black and white daisies grow fastest and at the same rate when their local effective temperature (the temperature within their microclimate) is 22.5°C, and they respond identically, with a decline in growth rate, as the temperature deviates from this ideal. For a given average planetary temperature, black and white daisies experience different microclimates and therefore different growth rates. For example, when the Sun's luminance is 1, producing an average planetary temperature of 22.5, black daisies actually experience a slightly higher effective temperature (27.5°C), whereas white daisies experience a lower effective temperature (17.5°C), and both types grow at the same rate, which is a little slower than their maximum possible growth rate. When luminosity drops below 1 and the mean temperature of the planet falls below 22.5°C, black daisies create a warmer microclimate and thus grow faster than white daisies. Thus, following the replicator equation (and in the absence of standard frequency-dependent selection), when luminosity is below 1, we might expect black daisies to go to fixation. In Daisyworld, however, this does not occur, because the daisies themselves influence planetary temperature.

If the daisies cover a sufficiently large area of the surface of Daisyworld, their color affects not only their own microclimate but also the albedo of the planet as a whole. A planet covered by black daisies has a lower albedo and reflects less sunshine than a planet covered by white daisies, or bare earth. Thus, as noted above, when luminosity is below 1, black

* Confusingly, the term frequency-dependent selection has been applied to two distinctive processes: interspecific interactions (e.g. between host and parasite) and intraspecific interactions (e.g. competition among members of the same species) (Seger, 1988). Here we refer to the latter process as "standard" frequency-dependent selection, in which the selective dynamics involve only one species.

† Lovelock (1992) and Saunders (1994) refer to differently colored daisies as different daisy species. In what follows we modify their conceptual model by treating differently colored daisies as different phenotypes of the same species. We do this so that the ecological feedback that drives Daisyworld dynamics can be modeled as an evolutionary process within a single population. We return to the issue of interspecific dynamics toward the end of the paper.

daisies grow faster and begin to warm the planet. Eventually, the spread of black daisies raises planetary temperature above 22.5°C, at which point the white daisies gain an advantage, because they create a colder microclimate for themselves. Now white daisies grow faster than black ones, cooling the planet. As a result of this feedback between the differential growth rate of different-colored daisies and the albedo of the planet, the temperature of Daisyworld is stabilized close to 22.5°C (Fig. 1). This regulation of temperature by the daisies occurs even if solar radiation tends to make the planet much warmer or cooler than the optimum for daisy growth (Watson & Lovelock, 1983; Lovelock, 1992). This process invariably leads to a stable mix of black and white daisies, rather than dominance by one type or the other. The relative frequencies of black and white daisies at equilibrium depends only on luminosity and is not affected by their frequencies in the initial population (see below).

Instead of holding luminosity constant, what if the system is perturbed by a sudden change in luminosity? Figure 2 shows that when luminosity suddenly drops, the growth rates of black and white daisies briefly diverge but then rapidly converge, producing a new stable mixture of phenotypes. As a result, the planetary temperature re-stabilizes after a brief drop. Thus, system-dependent selection allows the daisy population to recover rapidly from a significant environmental perturbation.

The Daisyworld model allows us to define system-dependent selection by contrasting it with three other types of selection: “constant” selection

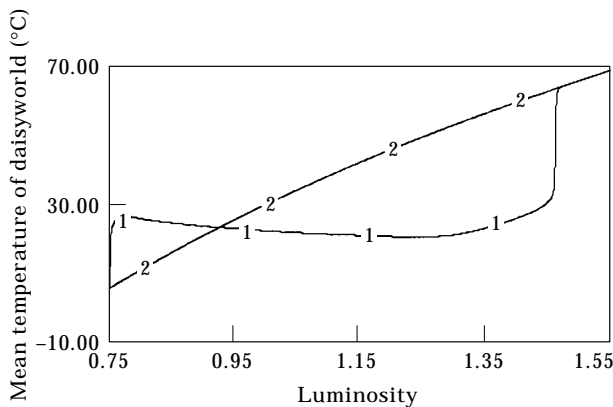


FIG. 1. Results of a simulation of temperature regulation on Daisyworld. As the Sun’s luminosity increases from 0.75 to 1.5 times the present value (1.0), the temperature of a bare planet would steadily rise (2). In contrast, with daisies present, the temperature stabilizes close to 22.5°C (1).

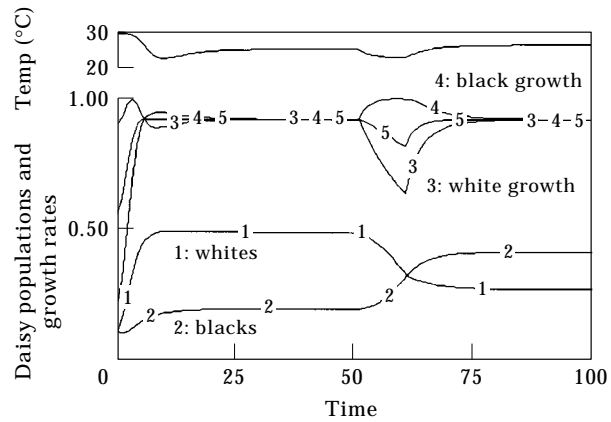


FIG. 2. Solar luminance is 1.1 for $T = 0-50$, and 0.9 for $t = 51-100$. Line 1 is the proportion of Daisyworld covered by white daisies; 2 is the proportion covered by black daisies; 3 is the growth rate of white daisies; 4 is the growth rate for black daisies; and 5 is the mean growth rate for all daisies, $\bar{f}(x)$. Note that as $x \rightarrow x_{opt}$ the mean growth rate also approaches a maximum even though at times $f_i(x)$ is greater than $\bar{f}(x)$.

(Christiansen, 1988, p. 134; Smouse, 1976, p. 850), density-dependent selection, and frequency-dependent selection. To do so, we must consider the equations that define the dynamic behavior of Daisyworld, which are given as follows:

$$T_c = ((SL(1 - A)/s)^{0.25} - 273) \tag{2}$$

$$A = xA_g + (a_1A_1 + a_2A_2 + \dots + a_kA_k) \tag{3}$$

$$T_i = q(A - A_i) + T_c \tag{4}$$

$$b_i = (1 - 0.00326(22.5 - T_i)^2) \tag{5}$$

$$da_i/dt = a_i(xb_i - g_i) \tag{6}$$

$$x = 1 - (a_1 + a_2 + \dots + a_k) \tag{7}$$

where (k) is the number of daisy types, each having constant albedo (A_i), constant death rate (g_i), variable growth rate (b_i), temperature of each microclimate (T_i) in °C, and fractional area coverage of the planet (a_i). The planet has an average albedo (A) and effective temperature (T_c). The fraction of the planet that is bare ground where plants do not grow is (x), and the total planetary surface area is set at unity. The albedo of bare ground is (A_g), (S) is the stellar constant, (s) the Stefan–Boltzmann constant, (L) the relative solar luminosity, and (q) a constant, equal to 20, relating individual daisy temperature to its albedo and the effective temperature of its environment (Lovelock, 1992, p. 384).

Natural Selection on Daisyworld

The replicator equation defines the fitness of each phenotype (i) at time t as a single value, $f_i(\mathbf{x})$. In the real world it is usually impossible to identify all of the selective forces that determine this value. But in the Daisyworld model, we can explicitly define three functions that together determine the rate of increase for each phenotype r_i : the maximum rate of increase under ideal conditions (r_{max}), the effects of density-dependence, and the effects of environmental temperature on r_i . Let

$$g_1 = r_{max} \quad (\text{a constant equal to } 1) \quad (8)$$

$$g_2 = (1 - (a_1 - a_2)) \quad [\text{from eqn (6)}] \quad (9)$$

$$g_3 = f(T_i) \quad (10)$$

Then

$$r_i \propto (g_1, g_2, g_3) \quad (11)$$

Since the daisies do not differ in r_{max} or in their response to changes in density, but only in their response to temperature, only g_3 produces fitness differences subject to selection. Selection based on g_3 involves environmental coupling: phenotypes (E_i) are subject to selection based on the state of \mathbf{x} with respect to temperature. This is a selection process that is based solely on variation in the frequency distribution of phenotypes, \mathbf{x} . Is it therefore an example of frequency-dependent selection?

Most models of frequency-dependent selection involve a rare-genotype (or rare-phenotype) advantage (Levin, 1988). We can introduce an example of this type of frequency-dependent selection to Daisyworld by modifying eqn (5) as follows:

$$b_i = (1 - 0.00326(22.5 - T_i)^2) \times \left[\frac{\sum_{j=1}^n X_j - X_i}{\sum_{j=1}^n X_j} \right] \quad (12)$$

* Here we contrast system-dependent selection with “constant” selection (Christiansen, 1988; Smouse, 1976) as described by the replicator equation. For simplicity, we ignore frequency-dependent selection, which we discussed above.

† Fitness is sometimes defined in relative terms, based on comparisons of growth (in asexual species) or reproductive success (in sexual species) of different phenotypes or genotypes in the same population. Recent mathematical formulations of Fisher’s fundamental theorem of natural selection define “absolute” fitness (Smouse, 1976, p. 850) as a function of the rate of increase of E_i (Hofbauer & Sigmund, 1988, p. 124). Because our purpose is to define system-dependent selection in terms of the replicator equation, we equate fitness with the rate of increase of E_i (growth rate – death rate, or $b_i - g_i$). Because death rate (g_i) is constant in Daisyworld under all conditions, we often substitute growth rate (b_i) as a proxy measure of absolute fitness.

This will cause rare phenotypes to grow faster and so encourage phenotypic diversity. If we were unaware of the environmental coupling on Daisyworld, we might mistakenly conclude that this sort of frequency-dependent selection was occurring, because we observe stable phenotypic diversity. However, if we eliminate the environmental coupling from Daisyworld (the g_3 function), the key feature of the planet—stabilization of temperature—will disappear. Ordinary frequency-dependent selection favoring phenotypes does not lead to temperature regulation.

We propose to call the selection process at work on Daisyworld “system-dependent selection”, to emphasize that the selection process is driven by a feedback relationship between organisms and their environment. We are agnostic as to whether to view it as a kind of frequency-dependent selection, or as a distinct process. Our concern is to identify the rather surprising dynamics that can occur under this type of selection, which clearly distinguish it from standard frequency-dependent (or density-dependent) selection. We summarize these dynamics briefly, and then provide a general description of system-dependent selection.

The Daisyworld model is driven by the Sun. Within the range of values for solar luminosity in which daisies can survive (approximately 0.63 to 1.58), different combinations of daisy phenotypes will produce different values for planetary albedo. For any given luminosity, there exists an optimal value for \mathbf{x} , \mathbf{x}_{opt} , such that any change in \mathbf{x} will move the temperature away from 22.5°C. System-dependent selection favors the growth or reproduction of those phenotypes that shift \mathbf{x} towards \mathbf{x}_{opt} . Note that \mathbf{x}_{opt} is not optimal for either daisy type: at \mathbf{x}_{opt} , the microclimate of both daisy types is equally distant from the ideal temperature, and their growth rates are identical. As $\mathbf{x} \rightarrow \mathbf{x}_{opt}$, mean population fitness increases and variance in growth rates declines. When \mathbf{x} reaches \mathbf{x}_{opt} , mean population fitness is optimized and growth rates are equal.

System-dependent Selection Defined

We conclude this part of our discussion by defining our concept of “system-dependent selection”, using the conceptual framework and variables of the replicator eqn (1):* Suppose that the distribution of phenotypes \mathbf{x} influences some environmental parameter P that in turn influences the rate of increase \dot{x}_i/x_i for all E_i , sometimes called absolute fitness (Smouse, 1976, p. 850)† (In the Daisyworld example

the distribution of daisies influences the temperature of the planet by changing the planet's albedo, so in Daisyworld P is temperature.) Let \mathbf{x}_t and P_t represent the state of \mathbf{x} and P at time $t = 1, \dots, m$. Further let \mathbf{x}_{opt} with respect to P represent \mathbf{x} such that any change in \mathbf{x} will lower the mean fitness $\bar{f}(\mathbf{x})$; i.e. a locally optimal phenotypic distribution with respect to this parameter.* Assume that at time $t = 0$ \mathbf{x} is not at \mathbf{x}_{opt} with respect to P . As time proceeds, \mathbf{x} begins to change, and at any given moment the value of the environmental parameter P_t influences the rate of increase for each phenotype E_i . This causes \mathbf{x} to vary, and as P responds to these changes it acquires a new value. Thus there will be positive feed-back favoring the growth or increase of those E_i that incrementally move \mathbf{x} closer to \mathbf{x}_{opt} . If P has a strong effect on fitness, then selection for \mathbf{x}_{opt} may overwhelm the process of selection due to variance in the inherent fitness advantage of particular phenotypes. On the other hand, when P and \mathbf{x} are uncoupled, or if P has a negligible effect on fitness, then change in \mathbf{x} is once again driven by variance among phenotypes in individual characteristics that give some an inherent advantage. Thus, fitness may include several components, one or more of which is system-dependent.

This simple model shifts our attention from changes in the rate of increase of phenotypes based on their individual characteristics to the behavior of the dynamic system of \mathbf{x} interacting with P . The model has several interesting implications. First, as $\mathbf{x} \rightarrow \mathbf{x}_{opt}$ with respect to P_t , the absolute fitness of the fittest phenotype will rise, and so will the mean fitness of the

population. Second, the outcome of this process is phenotypic diversity. In contrast, if we remove the effects of environmental coupling, only the frequency of phenotypes changes, not their absolute fitness, and the fittest phenotype in the initial population goes to fixation. The main conclusion is that under the conditions described in the model, in which there is a well-defined process of ecological feedback, selection can drive a dynamical system to solve an optimization problem resulting in higher mean fitness and suppressing the effects of selection driven by phenotypic differences.†

A Real-World Example: the Water Temple Networks of Bali

Daisyworld provides an intriguing example of a selective process that operates very differently from the way evolutionary biologists normally conceptualize natural selection. But the Daisyworld model requires such an intricate set of assumptions that one is led to wonder whether it is simply a mathematical curiosity. Here we introduce a second example based on our studies of the role of an ancient system of "water temples" in managing irrigated rice production on the island of Bali. We suggest that the structure and ecological functions of the temple networks can be predicted as the outcome of a process of system-dependent selection driven by two environmental parameters: the control of pests and the management of irrigation flows. Here selection is modeled as a process of trial and error by communities of farmers over a period of centuries, in which it is assumed that they prefer cropping patterns that increase their rice harvests.

Bali is a rugged volcanic island in the Indonesian archipelago, located in a region of monsoon rains. Rice is grown in paddy fields fed by irrigation systems dependent on rainfall. Rainfall varies by season and elevation, and in combination with groundwater inflow determines river flow. Depending on irrigation demand, water is diverted by a series of weirs into a maze of ancient tunnels, canals and aqueducts supplying 97337 hectares of rice paddies in Bali (Kantor Statistik Bali, 1986, p. 4). Availability of irrigation water determines whether farmers grow up to three crops of rice or vegetables annually. Farmers plant both high-yielding "Green Revolution" rice and slower-maturing native varieties. Harvest yields may be reduced by water stress or pest infestations. Pest population density in each field depends on dispersal from neighboring fields, as well as growth *in situ* on locally available food. All of these processes were formulated into a simulation model based on

* We emphasize that in this context, \mathbf{x}_{opt} does not refer to optimal conditions for any particular phenotype but rather to the optimal value of this parameter for maximizing mean population fitness.

† Several colleagues have speculated that it might be necessary for the daisies to grow in homogeneous patches, for temperature regulation to occur. This, however, is not the case: it is not necessary for each patch to be all white or all black, for the temperature feedback loop to function. The equation governing the relationship between the albedo of each patch of daisies and the aggregate planetary albedo is

$$A = xA_g + (a_1A_1 + a_2A_2 + \dots + a_kA_k);$$

clearly A_k need not be 0.25 (all black daisies) or 0.75 (all whites), but can assume an intermediate value without affecting the model's feedback dynamics. If there is *any* variation in the net albedo of each patch, system-dependent selection will occur. Only a perfect and complete admixture of species in all patches such that the albedo of each patch is identical to all the others ($A = A_1 = A_2 = \dots = A_k$) will prevent system-dependent selection (and temperature regulation by feedback) from occurring. This is an unstable equilibrium, however, since a single mutation changing the net albedo of a single patch is enough to restart the feedback process. We have modeled this by creating multiple "patches" on Daisyworld, identical except for variation in their initial species composition. Regardless of the number of patches, or the admixture of species in each patch, system-dependent selection will occur as long as there is any variation in patch albedo.

empirical data for the watersheds of two adjacent rivers in Bali, the Oos and the Petanu (Fig. 3).

The watershed of the Oos and Petanu rivers includes 6136 hectares of irrigated rice terraces. Balinese farmers manage their fields and irrigation systems in organizations called *subaks*: local

associations of farmers which set cropping patterns for units with an average size of 42 hectares and 92 farmers. The 172 subaks that obtain water from the Oos and Petanu rivers are indicated by small squares in Fig. 3. The amount of water flowing at any point in the river at any given moment is determined by

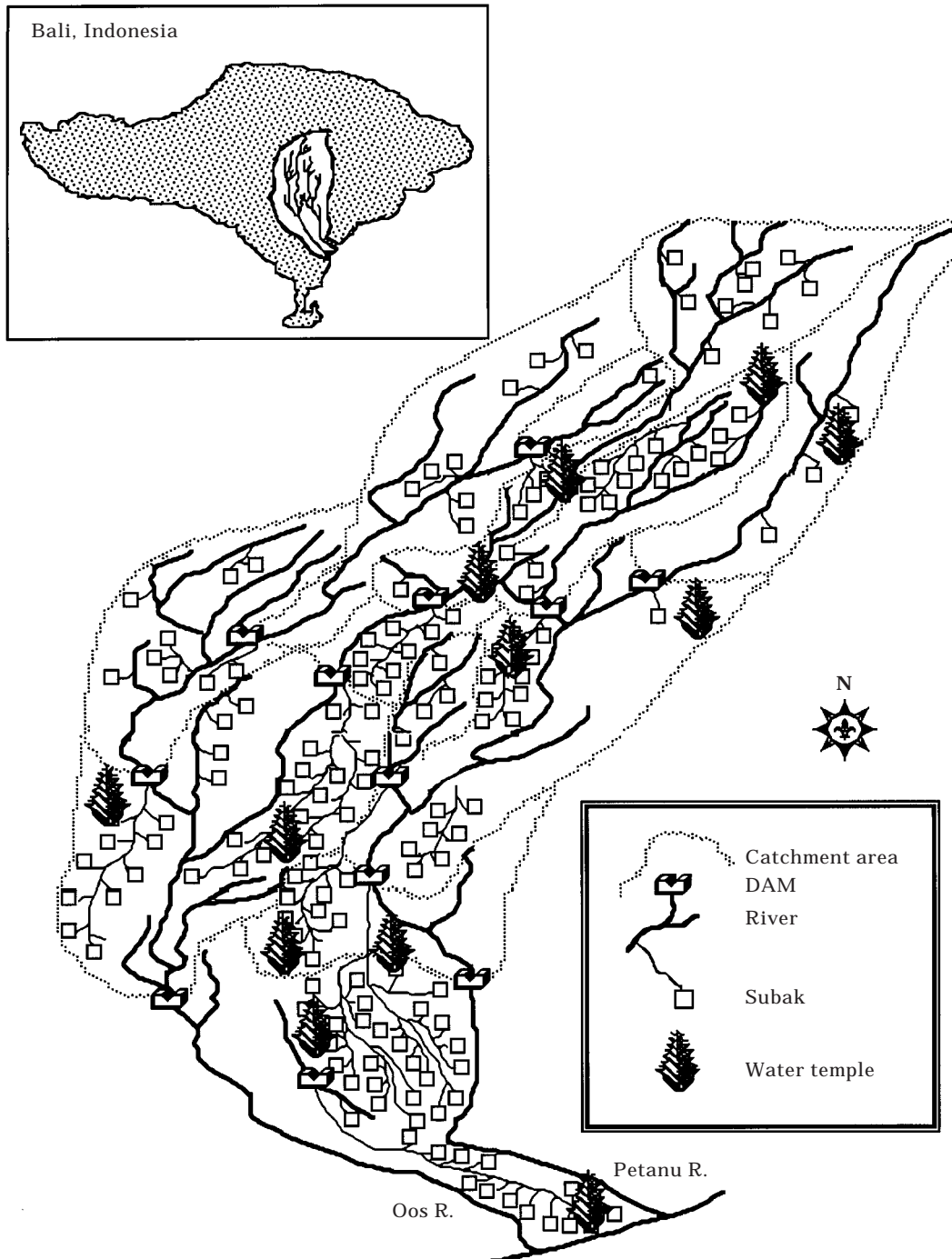


FIG. 3. Location of subaks and irrigation systems along the Oos and Petanu rivers included in the Bali model.

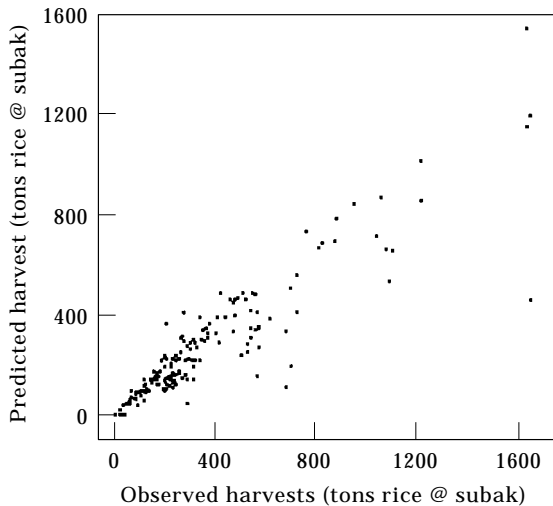


FIG. 4. Comparison of model predictions with actual rice harvests by subak in 1988–1989 for 72 (of 172) subaks for which data were acquired. The accuracy of the model improved from the first crop of the year ($r = 0.85$) to subsequent harvests ($r = 0.96$), because as time proceeds the accuracy of the pest submodel increased (when the simulation starts, pests are at background levels, and it takes time for the effects of synchronized cropping to affect population levels). Considering the simplicity of the model, *yields per hectare* were also well correlated with $r = 0.5$. To eliminate the possibility that the model results were simply not responsive to variations in cropping plans, we ran additional simulations in which we disrupted the local coordination implicit in the planting schedules followed by the subaks in 1989. When the cropping patterns were randomized but the actual crops planted remained the same, the correlation for the second crop in 1989 dropped from 0.50 to 0.01 (Lansing & Kremer, 1993).

both the seasonal pattern of rainfall and groundwater flow, and irrigation diversions upstream. Since the amount of irrigation water available for each subak is influenced by the irrigation schedules of its upstream neighbors, by staggering their planting cycles (the dates they begin to plant) the subaks can act to avoid water shortages.

The planting and irrigation schedules followed by the subaks also influence the growth and dispersal of rice pests (including rats, insects and insect-borne diseases). In the traditional farming system, groups of subaks try to adjust cropping patterns cooperatively to achieve fallow periods over sufficiently large areas to minimize dispersal of pests. If one or more subaks plant the same variety of rice at the same time, they will also harvest at the same time, and the fields can be burned and flooded to remove pest habitat. Recent

* Testing the model on the 1988 data showed that it was insensitive to uncertainty in the coefficients for evapotranspiration and pest damage, but sensitive to groundwater flow. Subsequently, using only 1989 data on rainfall and planting schedules, the unchanged model was used to predict a range of variables for 1989 including harvest yields for each crop planted by each subak, the effects of water stress and pest damage, and monthly average flows for each of 12 weirs (Lansing & Kremer, 1993).

studies have confirmed that this is an effective method for pest control (Aryawan *et al.*, 1993). However, synchronization of rice planting over too large a scale would create inefficient peaks of water demand. Choosing the best cropping pattern involves finding the scale of spatial synchronization that optimizes the trade-off between water shortages (caused by too many synchronized subaks experiencing peak irrigation demand at the same time) vs. pest damage (caused by too little synchronization of cropping patterns).

We built a model to test this hypothesis, with the simplifying assumption that most of the variation in rice yields is caused by water stress and pest damage. We undertook a field survey and obtained 2 years of data on hydrology, actual planting schedules and harvest yields. We calibrated the model with these data from August to December 1988 for 43% of the 172 subaks included in the model.* Figure 4 shows the correlations between simulated and reported rice harvests for two harvests for 72 subaks in Bali in 1989. The high correlation provides strong support for the underlying assumption that water stress and pest damage are the critical environmental variables influencing rice yields.

Comparing Bali and Daisyworld

In what sense does the Bali rice simulation model resemble the Daisyworld model? In Daisyworld, a single environmental parameter (temperature) influences the growth or “fitness” of the daisies: for any given temperature, there is an optimal frequency distribution of daisy phenotypes (\mathbf{x}_{opt}). In the Bali model, not one but two environmental parameters affect the growth of the plants. For each of these two parameters (irrigation water and rice pests), there is an optimal frequency distribution of cropping patterns. But they are not identical. Let P_w be the water stress parameter; P_p be the pest damage parameter, and E_i be the cropping patterns (the schedule that specifies what crops will be growing in each field from month to month). Analytically, finding the \mathbf{x}_{opt} (pests) is quite simple: the smaller the variance in cropping schedules, the larger the fallow period, and the fewer the pests. Analysing \mathbf{x}_{opt} (water) is more complicated, since it depends on seasonal variation in rainfall and river flow as well as irrigation demand, but in general the greater the variance in cropping patterns, the more the available water can be shared. The combined \mathbf{x}_{opt} (pests and water) may be viewed as the best compromise between these two parameters for the entire system of subaks. There is no simple analytic solution for \mathbf{x}_{opt} since it depends on

the complex local interaction of water flows and pest diffusion: each subak's cropping pattern affects its neighbors.

Can all of the subaks in an entire watershed, such as that modeled above, find x_{opt} (pests and water)? We created a second simulation model, in retrospect quite similar to Daisyworld, in which each subak behaves as an adaptive agent that seeks to improve its harvest by imitating the cropping pattern of more successful neighbors (Lansing & Kremer, 1993, p. 212):

As a new year begins, each of the 172 subaks in the model begins to plant rice or vegetables. At the end of the year, harvest yields are calculated for each subak. Subsequently, each subak checks to see whether any of its closest neighbors got higher yields. If so, the target subak copies the cropping pattern of its (best) neighbor. The model then simulates another year of growth, tabulates yields, and continues to run until each subak has reached its local optimum.

The simulation begins with a random distribution of cropping patterns (Fig. 5). After a year the subaks in the model begin to aggregate into patches following identical cropping patterns, which helps to reduce

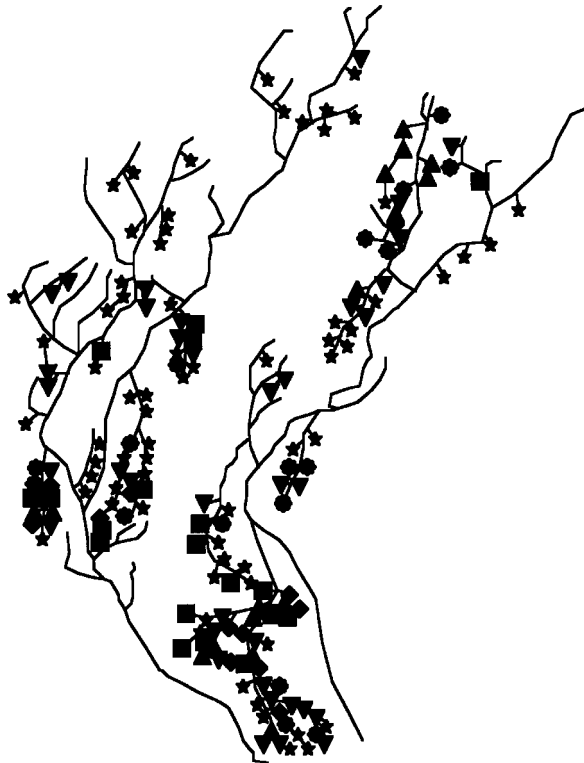


FIG. 5. Initial conditions for a simulation model of irrigation flows and rice and pest growth for 172 subaks. Differences in cropping patterns are indicated by different symbols (subaks with the same symbols have identical cropping patterns). For a complete description, see Lansing & Kremer (1993).

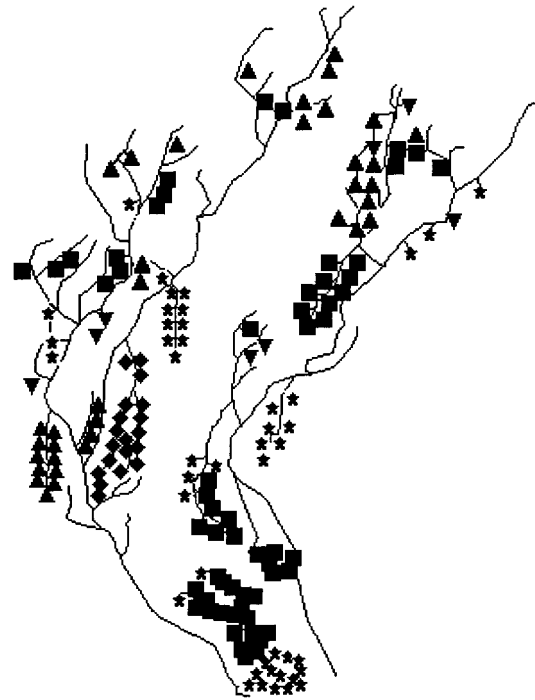


FIG. 6. Model cropping patterns after 11 years.

pest losses. As time goes on these patches grow until they overshoot and cause water stress. Yields fluctuate but gradually rise. The program ends when the model generates a distribution of cropping

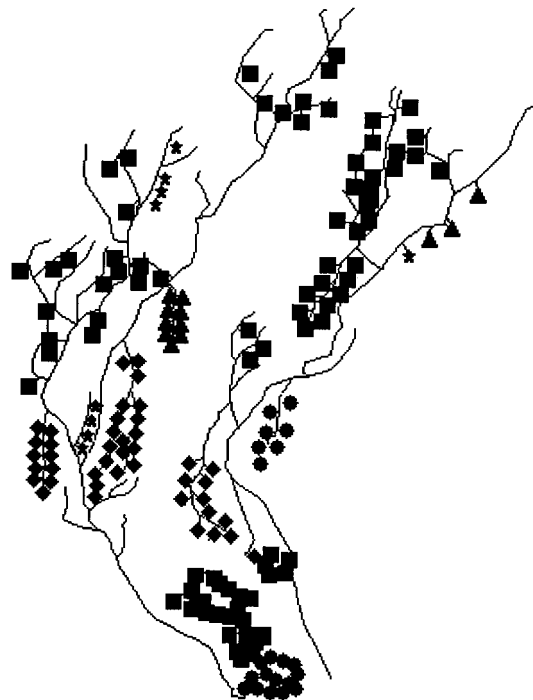


FIG. 7. Cropping patterns in the real water temple system.

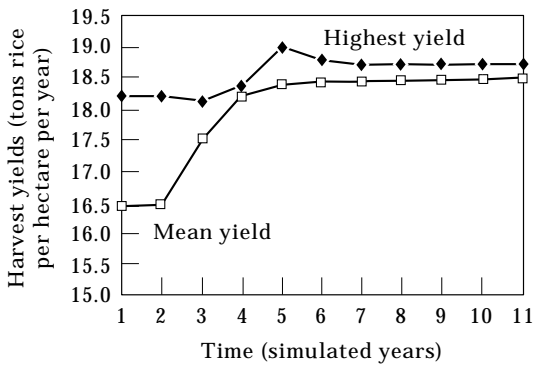


FIG. 8. Increase in $\bar{f}(x)$ and $f_{i(max)}$ as $x \rightarrow x_{opt}$ in the Bali model. Variance in yields also declines, as yields converge on the mean.

patterns that optimizes both pest control and water sharing (Fig. 6). The close relationship between x_{opt} (pests and water) as calculated in the model (Fig. 6), and the actual water temple networks of synchronized planting units (Fig. 7) is apparent. In the model, as patterns of coordination resembling the water temple networks emerge, both the mean harvest yield and the highest yield increase, and variance in yield across subaks declines (Fig. 8). Quite often, the subak with the highest yield changes from year to year (Fig. 9). Subsequent runs showed that if the environment was perturbed dramatically by decreasing rainfall or increasing the virulence of pests, a few subaks change their cropping patterns, and within a few years a new

equilibrium is achieved (Lansing & Kremer, 1993, pp. 215–216).

The similarities between the Bali and Daisyworld models can be clarified by formulating the Bali model in terms of the functions influencing rice growth. Recall that in Daisyworld, g_1 referred to the intrinsic growth rates for each daisy type (which are identical). In the Balinese model, g_1 can be defined analogously as the intrinsic yields for different cropping patterns, which are also identical. The Daisyworld model also included g_2 , growth modified as a function of density-dependence, and g_3 , growth modified as a function of temperature. In the Bali model, by analogy g_2 describes growth as a function of water stress, and g_3 means growth as a function of pest damage. Then eqn (11) will also apply to the growth of rice in the Bali model: $r_i \propto (g_1, g_2, g_3)$. As in Daisyworld, x indicates the frequency distribution of different phenotypes; in this case different cropping patterns.

Our main conclusion is that similar dynamics occur in both models. In both, the distribution of phenotypes influences environmental conditions, which in turn affects fitness. Similarly, in both models this environmental coupling drives the system toward a stable equilibrium characterized by phenotypic diversity. Moreover, in both models as $x \rightarrow x_{opt}$, mean fitness (yield) goes up, and variance in fitness declines.

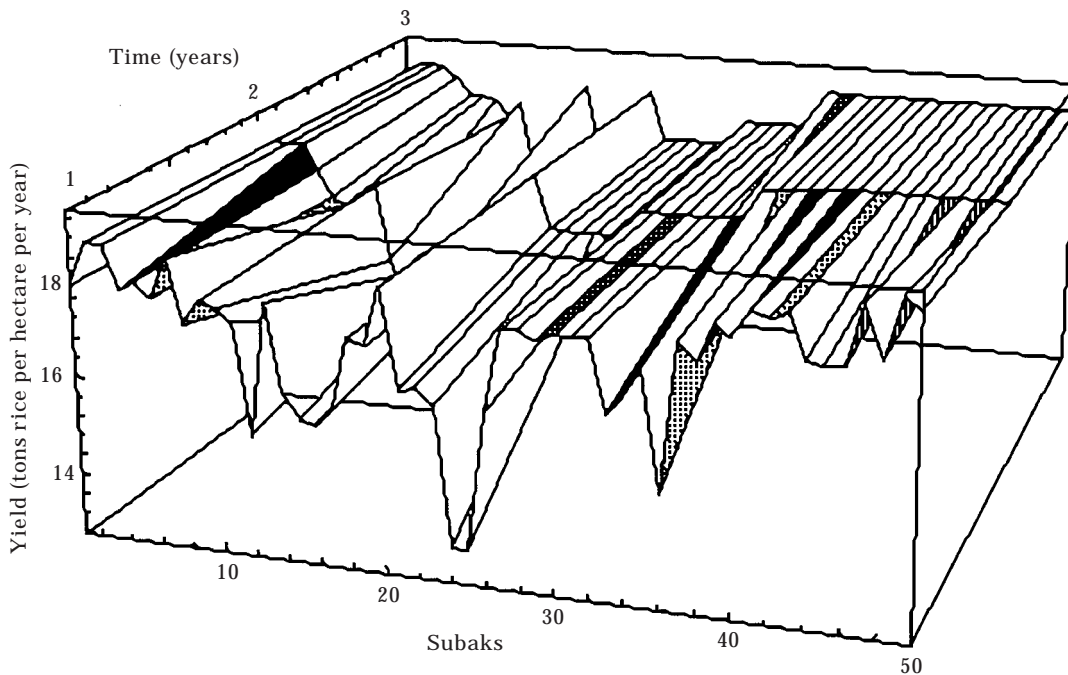


FIG. 9. Changes in harvest yields caused by changes in x , the distribution of cropping patterns. The x axis shows 50 (of 172) subaks; y is tons of rice harvested per year; z is time (3 years are shown here). Average yields increase as $x \rightarrow x_{opt}$, but some subaks experience temporary declines in yields.

Finally, in both models, when the environment is dramatically perturbed, the system quickly adapts by achieving a new, stable phenotypic distribution.

Discussion

“Ἦτοι μὲν πρότιστα Χάος γένετ’· ἀτὰρ ἔπειτα/Γαί’
(First Chaos came into being, but next Gaia)
Hesiod, *Theogony*, 116–117.

Strictly speaking, the replicator equation describes a process of selection based on a one-way influence between organism and environment. This assumption simplifies the analysis of selective processes, because it avoids consideration of feedback loops that could produce highly complex, or even chaotic, dynamics (Ferriere & Fox, 1995). However, empirical evidence increasingly implicates organisms as important contributors to environmental change (Jones *et al.*, 1994; Lovelock, 1988), and, as our models show, interesting and highly predictable (rather than chaotic) dynamics can occur when organisms and environment are treated as a coupled system. In particular, system-dependent selection produces the following effects:

- (1) regulation (i.e. stabilization) of an environmental parameter (or parameters) within a much narrower range than would occur in the absence of the organisms;
- (2) a stable pattern of a mixture of phenotypes;
- (3) a response to environmental perturbation that buffers the system as a whole (measured by effects on mean fitness) against the negative impact of such changes;
- (4) an increase in mean fitness, which may exceed the fitness of the most fit phenotype expressed in the initial population;
- (5) reduced variance in fitness among phenotypes, which converges toward the mean fitness.

The last two effects of system-dependent selection are intriguing because they are identical to the effects obtained in models of intra-demic group selection (Wilson, 1977, 1979; Wilson & Sober, 1994). These models show that when gene frequencies differ between groups or between populations, and when these differences lead to large differences in the mean fitness of different groups, selection can (but does not always) favor genes that contribute to group fitness; the result is a better adapted group. Such models require a metapopulation structure involving reproductive competition among different groups (or populations) with varying phenotypic distributions.

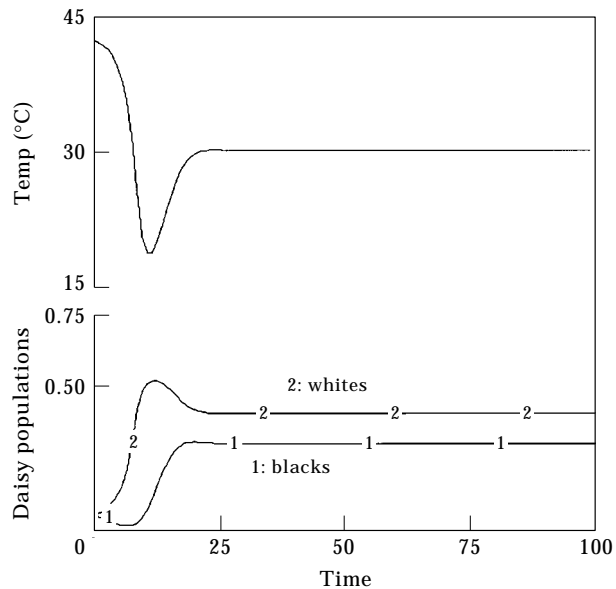


FIG. 10. Growth of white and black daisies on Daisyworld when black's intrinsic growth rate is twice as fast as white's, and solar luminosity is 1.05, favoring whites. In further experiments, we found that giving blacks a tenfold advantage in growth leads to equal populations of blacks and whites, a smaller coverage of the planet by daisies, and a higher average planetary temperature.

System-dependent selection differs from group selection because the optimization or adaptation obtained in our models does not depend on a meta-population structure. Rather, the ideal phenotypic distribution for solving the environmental optimization problem was achieved through the internal dynamics of the system. In this sense, system-dependent selection represents a “self-organizing” system that “maintains order through internal interactions . . . [that] . . . channel different initial conditions into the same final state” (Perry, 1995, p. 241). Evolutionary biologists on both sides of the group selection debate have long agreed that group selection is the only process that can produce adaptation at the level of the group (or population or other higher level) (Williams, 1966; Wilson & Sober, 1994). Our results raise the interesting possibility that system-dependent selection, as a self-organizing process, can also produce group-level functional organization, or adaptation.

If we provisionally assume that system-dependent selection can produce group-level adaptations, it is still critical to consider whether this same process can maintain such adaptations over time. In other words, is the functional organization produced by system-dependent selection evolutionarily stable? To answer this question, we need to determine whether the phenotypic distributions resulting from

system-dependent selection can be invaded by alternative feasible phenotypes.

We have used the Daisyworld model to explore this question, by introducing two types of mutants as potential invaders:

Mutant 1

Suppose a mutant daisy appears that is identical to either the black or white phenotype except that it grows faster, for example, twice as fast. We found that even when black daisies had such a large advantage, white daisies were maintained in the population within a wide range of luminosity values, albeit at lower frequencies than when blacks had equal growth rates to whites. In addition, whenever the luminosity value favored whites (i.e. was >1), whites stabilized at a higher frequency than blacks, despite black's two-fold growth advantage (Fig. 10). This occurs because the black's faster growth rapidly shifts their microclimate further from the optimum, canceling the effects of its intrinsic growth advantage. For this reason, a faster-growing mutant cannot go to fixation, both phenotypic variants will be maintained, and temperature regulation will persist. Thus, the dynamics of system-dependent selection suppress the fitness advantage of any mutation that simply increases r_{max} (the g_1 component).

Mutant 2

Consider grey daisies that grow a little faster than blacks or whites (under the same temperature) because they gain a small energy advantage from not producing pigment. This mutant was first suggested by Dawkins (1982, pp. 235–236) who argued that natural selection would favor such “cheaters”. Lovelock (1988, pp. 46–47) responded by introducing a species of grey cheaters to his model: black and white daisies were both subjected to a 1% “growth tax” to represent the cost of making pigments, while grey daisies were not taxed. Lovelock claimed that, despite their slight growth advantage, grey daisies did not out-compete the colored daisies except when the luminosity produced a surface temperature near the optimum. We repeated Lovelock's experiment but modeled the grey daisies as mutant invaders of the same species. Our results indicate that, for any constant luminosity value, grey daisies *do* out-compete either whites (if luminosity is below 1) or blacks (if luminosity is above 1). This happens because, although grey daisies do not produce pigment, they still have an albedo (equal to that of bare earth) and therefore create a microclimate for themselves with a temperature in between the effective temperatures for blacks and whites. When the planet is cold, blacks do

best, because their microclimate is warmest, but greys do better than whites, because their microclimate is warmer than that of whites and thus closer to optimum. Thus, the grey mutants replace the whites. Contrary to Dawkins' suggestion, however, the critical factor favoring greys is not their slight growth advantage; virtually identical results are obtained if greys have the same growth rate as blacks and whites. Rather, greys do better than one or the other pigmented variant at any given luminosity because their microclimate effects are more moderate, and therefore put them closer to the optimum than whites (if it's cold) or blacks (if it's warm). More generally, whenever a mutant arises with an albedo intermediate between the existing phenotypes, its growth rate at any constant luminosity will be higher than that of one or the other existing phenotype, and it will therefore replace that phenotype.

Thus, Dawkins' hunch that grey daisies can invade Daisyworld was correct, but for the wrong reasons. Greys invade not because they do not pay the cost of creating pigment, but because their intermediate albedo moves their effective temperature closer to the optimum. Alternatively, one could imagine mutants that, instead of shifting their effective temperature, shift their growth-response curves such that their optimum growth temperatures are identical to the temperatures of their microclimates. Saunders (1994) showed that, like greys, such mutants will gain an advantage. Saunders also showed that when such mutants replace blacks and whites, the range of luminosity values over which daisies can achieve temperature regulation declines (the same thing occurs if greys replace blacks or whites). Saunders then pointed out that such a change would significantly reduce the daisies' long-term chances of survival (under the assumption that luminosity values will eventually change). He referred to this as “the central theoretical problem of Daisyworld” and argued that “If we do not insist on accounting for everything in terms of natural selection, the paradoxes evaporate” (Saunders, 1994, p. 372).

Saunders, however, fails to explain what could prevent the appearance and spread of these mutants; he implicitly assumes that such mutants will not spread because of their long-term costs to the system as a whole. However, natural selection within populations is blind to such long-term costs; in this sense, Dawkins was right. There is a clear mechanism by which grey daisies (or similar mutants) could spread and overwhelm the effects of system-dependent selection: if luminosity remains constant for long enough (on an evolutionary time scale), any phenotype with an intermediate albedo can invade the

population, and this can occur iteratively until the mutant phenotype converges on the optimum for that particular luminosity value, at which point all phenotypic variance is eliminated. Thus, when luminosity remains constant over sufficiently long periods of time, the dynamics of system-dependent selection disappear. (This is not surprising, because in the absence of any variation in luminosity values, there is no “need” for temperature regulation and thus no selection for phenotypic diversity.) Thus, in Daisyworld, phenotypic diversity is not an evolutionarily stable strategy when the environmental parameter (luminosity) remains constant. Sasaki & Ellner (1995) reached a similar conclusion in their models relating environmental variation to phenotypic diversity in the absence of environmental feedback.*

Details of the relationship between the pattern of environmental fluctuation and the maintenance of either phenotypic diversity or biodiversity require much more attention. However, whatever the precise nature of these relationships, under at least some regimes of environmental fluctuation, system-dependent selection can maintain diversity. Typically, biologists explain stable diversity as the result of standard frequency-dependent selection. But we suggest that such diversity may sometimes involve system-dependent selection. An experimental population of bacteria studied by Levin (1988) provides a possible example.

Levin introduced two strains of bacteria to a toxic medium: a resistant strain able to detoxify the medium and a sensitive strain unable to do so. Because of its detoxifying ability, the resistant strain initially has an advantage. Once a population of resistant bacteria is established, the sensitive strain can invade. The sensitive strain has a higher intrinsic growth rate and so increases in frequency relative to the resistant strain. As this occurs, the concentration

of toxin increases, and the population eventually reaches a stable equilibrium with both strains present. Levin’s description of this equilibrium is reminiscent of the dynamics of Daisyworld: “At this equilibrium, the intrinsic disadvantage of the resistant bacterial population . . . is exactly overcome by its resistance to toxin, and the intrinsic advantage of the sensitive cells is exactly offset by loss due to the action of toxin” (p. 463). Levin considers this an example of frequency-dependent selection, but we suggest that it is better characterized as system-dependent selection, since the frequency of one of the phenotypes (the resistant strain) influences the environment in ways that affect the fitness of both phenotypes. In this instance, the system is regulated by a single phenotype and the other phenotype is a “free rider”. Similarly, Saunders (1994) shows that even in the presence of only one type of daisy, some temperature regulation occurs on Daisyworld.

As Lovelock’s (1992) paper on biodiversity indicates, the intraspecific dynamics modeled here should also be applicable to interactions between different species.† A possible example involves interactions between mosses and black spruce trees in the boreal forests of interior Alaska (Bonan & Korzhuhin, 1989). Field data indicated that on cold, wet north-facing slopes, the presence of moss makes the ground colder, inhibiting sexual reproduction by spruce. This keeps the forest canopy from becoming too thick, which allows sufficient light for mosses to continue to grow. The presence of the mosses, in turn, promotes asexual reproduction (“layering”) by the spruces, resulting in enough canopy to prevent too much light, which protects the mosses from desiccation. Bonan & Korzhuhin’s (1989) simulations of these complex interactions showed that, regardless of initial conditions (biomass of mosses and spruces), moss–tree dynamics always converged on a single stable equilibrium characterized by a large biomass of moss and a lesser biomass of spruce. This interspecific process resembles intraspecific system-dependent selection in its dynamics, and both processes result in stable diversity (species diversity in the former case and phenotypic diversity in the latter). However, Bonan & Korzhuhin’s results (1989, p. 37, Fig. 4) indicate that interspecific system-dependent dynamics do not necessarily maximize biomass in the way that system-dependent selection maximizes mean fitness. This is to be expected because within species, different phenotypes respond similarly but not identically to the value of the environmental parameter P . As a result, as the frequency of a given phenotype increases, P will eventually reach a state where the alternative phenotype gains an advantage, reversing

* These results converge in interesting ways with Lovelock’s recent (1992) utilization of the Daisyworld model to analyse the effects of environmental change on biodiversity. Lovelock introduces more complex ecosystems, including up to 100 daisy species and examines their fate as luminosity slowly increases. He concludes that “biodiversity is least when there has been a prolonged period of steady state” (p. 390). In contrast, “biodiversity . . . is greatest when . . . a rapid change of the material environment, well within the limits of toleration, has just taken place” (p. 390). Thus, whether daisies are modeled as different phenotypes or as different species, environmental variation over evolutionary time appears to be critical to the maintenance of diversity.

† This conclusion follows from the mathematical equivalence of Fisher’s selection equation (which models natural selection within populations) and Volterra’s equation, which models the rate of increase of interacting species in a given habitat (Schuster & Sigmund, 1983, p. 536).

the feedback relationship until a stable equilibrium is reached. This stable equilibrium point corresponds to maximum mean population fitness with respect to P . In contrast, in the interspecific case, different species utilize different resources, and so may be affected by P in different ways. These dynamics can move the system toward an equilibrium point that is considerably more advantageous for one species than for another; as a result, the payoff to the "system" as a whole (measured in terms of biomass) will not be optimized.

Conclusion

In a recent commentary, Brown (1995) emphasized the need for new theoretical tools to analyse the coupling between organisms and environments that has long been observed by ecologists. Here we offer such a tool: we have shown that a simple extension of the replicator equation to include a process of ecological feedback in a dynamical system can lead to environmental regulation, stable phenotypic diversity, and an increase in mean fitness. We suggest the term "system-dependent selection" for this process, to signal that in such cases selection is driven not only by the frequency distribution of phenotypes, but by the interaction of phenotypes and one or more environmental parameters that they collectively influence. Put another way, we have shown that environmental feedback can influence selection dynamics in predictable ways and generate functional structure in a population through a process that is, quite literally, self-organizing. Thus, rather than viewing self-organization as an alternative to natural selection (Depew & Weber, 1994; Kauffman, 1992; Saunders, 1992), we conclude that in the presence of environmental feedback, natural selection provides a mechanism by which functional self-organization can arise.

The ecology of Daisyworld is, of course, both simple and imaginary. But we have also shown that the concept of system-dependent selection provides a simple explanation for the complex patterns of cooperation among Balinese rice farmers. Unlike Daisyworld, the Bali model involves multiple (and varying) environmental parameters, and initial conditions that are both complex and arbitrary: dozens of irrigation systems, hundreds of subaks and arbitrary numbers of alternative cropping patterns ("phenotypes"). Yet modeling the selection of cropping patterns as a process of system-dependent selection quickly generates a solution that predicts with remarkable accuracy the actual patterns of

synchronized cropping patterns. And, just as in Daisyworld, this self-organizing process optimizes environmental parameters, raises mean "fitness", and reduces fitness variance. Thus, both the basic dynamics and the consequences of system-dependent selection remain identical when we shift from the simplest possible imaginary model to a formidably complicated real-world example.

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