

# The value of death in evolution: A lesson from Daisyworld

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## Abstract

The first Daisyworld model showed how simple interactions and varying growth rates of daisies could lead to a type of global homeostasis. This idea has been extended to include variable mortality rates as a form of natural selection. This paper shows that this extension can increase the temperature regulation and persistence of Daisyworld systems, even with higher overall mortality rates.

## Introduction

Death is the natural endpoint of all living things, and while it is tempting to think of death as an inherently random process, this is not always the case. Environmental factors, such as lack of food and temperature variations, increase the chance of death in many organisms. This idea is one of the central tenants of Darwin's theory of natural selection. Organisms which are less fit for their environment are replaced by those which are more fit.

Standard theory is that the fitness of an organism is determined by how many breeding offspring it bears and how many of those live to breeding maturity. This fitness is really a combination of two factors – fecundity and survival. For example, Leatherback sea turtles lay many hundreds of eggs per season but only about 1 to 3 individuals per 100 eggs survive to breed. Compare this with Asian elephants, which give birth to one calf every 3 to 4 years with about 80% of the calves surviving to a breeding age. However, there is another force, environmental modification, hidden within the survival factor. It has been known for some time that organisms modify their environment during their lifetimes and these modifications often result in a more favorable environment for their offspring.

In 1978 Andrew Watson and James Lovelock introduced the Daisyworld model as a way of lending credence to the Gaia hypothesis (Watson and Lovelock, 1983). This hypothesis suggests that organisms can not only change their local environment, but the global environment as well. Daisyworld is a toy-world, intended as a proof of concept, rather than a model of a real physical system. The idea is simple –

localized interactions can affect global dynamics and generate homeostatic behavior. The model consists of a “planet”, heated by the sun and populated by black and white daisies. The black daisies have a lower albedo (reflectiveness) than the white daisies, thus they absorb a greater amount of solar radiation and raise the local temperature. White and black daisies have albedos of 0.75 and 0.25 respectively, and the surface of the planet has a neutral albedo of 0.5. The growth rate of the daisies is linked to the local temperature, which is directly influenced by albedo. This difference in growth rate causes the area covered by black and white daisies area to vary, thus warming and cooling parts of the planet. This creates a homeostatic response to external forces, such as increasing incoming solar radiation (insolation), and keeps the temperature of the planet relatively constant.

One major criticism of the Daisyworld model when it was introduced was that it did not model natural selection. Since this time the model has undergone been numerous extensions and reformulations that have addressed this concern to some extent (Saunders, 1994; Stöcker, 1995; Lenton and Oijen, 2002; Harding, 1999; Weber, 2001; Lenton, 1998; von Bloh et al., 1997). However, all of these subsequent models have concerned themselves only with varying the fecundity of the daisies and not varying their survival rates, assuming a constant mortality rate. For natural selection to work efficiently in this context, there must be some differential selection pressure on organisms – a point which will be addressed in more detail later in the paper. For now, the relevance of a few of the Daisyworld models to natural selection will be reviewed.

Saunders suggests a scenario where evolution happens without natural selection – organisms mold their environment to their own needs, rather than being molded to the environment (Saunders, 1994). He shows if the daisies adapt their birth rate to local conditions, they cover slightly more area, at the cost of a decreased range in planetary temperature regulation.

As a counterpoint, Stöcker takes the stance that the daisy's growth rate is more a matter of physics than genetics, and assumes that the mutations affect daisy albedos rather than

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birth rates. Based on this he shows that the mutation of albedos increases the temperature regulation range as well as the stability of the system (Stöcker, 1995). Other studies of mutation in the Daisyworld model confirm these findings (Lenton and Oijen, 2002; von Bloh et al., 1997). In particular, von Bloh attributes this increase to the fact that mutation allows higher albedos than the original “white” daisies.

Of particular interest is von Bloh’s formulation and analysis of a 2D cellular automata version of the Daisyworld, which will be used as the basis for these simulations (von Bloh et al., 1997). In this paper, his model is extended with temperature-dependent mortality rates. The next section describes the original model and the extension in detail. This extended model is then compared to von Bloh’s original model to determine the effect of variable mortality rates on the homeostatic response of the system. The results are analyzed and related back to the concepts in the introduction.

### Model Description

As mentioned previously, this paper extends von Bloh’s 2D Daisyworld model (henceforth referred to as the VB model) (von Bloh et al., 1997). While the implementation differs from the original Watson-Lovelock (WL) model, the salient features remain the same. There are white and black daisies on a “planetary sheet” that have slightly different growth rates and thus exhibit the same homeostatic response as the WL model.

The basic equations governing the effective temperature of the original WL model are

$$\sigma_B(T_e)^4 = S(1 - A), \quad (1)$$

$$d\alpha_b/dt = \alpha_b(x\beta(T) - \gamma), \quad (2)$$

$$d\alpha_w/dt = \alpha_w(x\beta(T) - \gamma), \quad (3)$$

where  $\sigma_B$  is the Stefan-Boltzmann constant,  $S$  is the luminosity of Daisyworld’s sun, and  $A$  is the albedo of the planet. The fraction of total planetary area covered by the black and white daisies is  $\alpha_b$  and  $\alpha_w$  is respectively. The fractional area of the uncovered ground is  $x$ ,  $\beta(T)$  is the birth rate of the daisies with respect to local temperature, and  $\gamma$  is a constant mortality rate.

Interestingly, if we set the growth rate of the daisies to a constant rate and vary the mortality rate with temperature, the system still exhibits homeostasis. Reformulating the general growth rate equation by swapping the terms for the mortality and growth rates yields

$$d\alpha/dt = \alpha(x\gamma - (1 - \beta(T))). \quad (4)$$

This is functionally equivalent to the original equation and, with the correct values, exhibits a similar homeostatic response. Restating the equations in this provides very

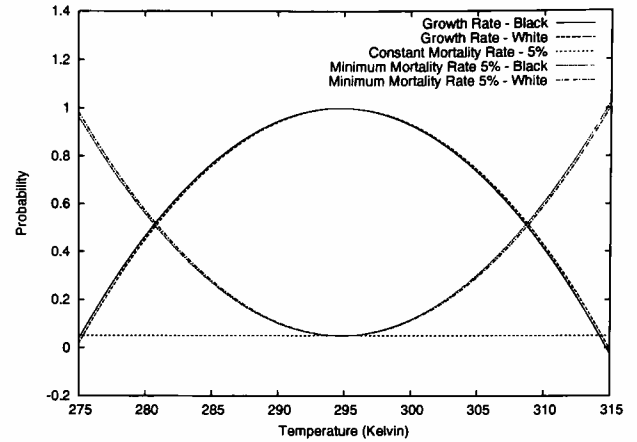


Figure 1: Growth and mortality rates for the Daisyworld model. The parabola represents the growth rates of the daisies and the inverted parabola represents the temperature-dependent mortality rate with a minimum mortality rate of 5%. The straight line along the bottom of the graph represents a constant mortality rate of 5%.

model the idea of survival in a Daisyworld context. This paper will build on this premise and link both mortality and growth rates to the temperature such that

$$d\alpha/dt = \alpha(x\beta(T) - \gamma(T)). \quad (5)$$

Returning to the von Bloh’s model, this 2D version of the Daisyworld model includes heat diffusion between cells as well as the effect of the daisies on the local temperature. The equation used is

$$C \frac{\partial T(x, y, t)}{\partial t} = D_T w \left( \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \right) T(x, y, t) - \sigma_B T(x, y, t)^4 + S(1 - A(x, y, t)), \quad (6)$$

where  $D_T$  is the heat diffusion constant and  $A(x, y)$  is the space/time distribution of albedo.

Growth patterns for the daisies are generated using a cellular automata (CA) model (von Bloh et al., 1997). If a cell is empty, then there is a chance that a daisy in a neighboring cell will produce offspring in the empty cell. This chance is based upon the temperature of that cell and is shown graphically in Figure 1 and given by

$$\beta(T) = \frac{4}{(T_{max} - T_{min})^2} (T - T_{min})(T_{max} - T) \quad (7)$$

where  $T_{max}$  and  $T_{min}$  are the maximum and minimum temperatures at which the daisies can grow and  $T$  is the current temperature of the cell. Heat diffusion between the cells allows the temperature of uncovered cells to be affected by neighboring covered cells, making the probability of colonization higher than otherwise possible. The daisy albedos

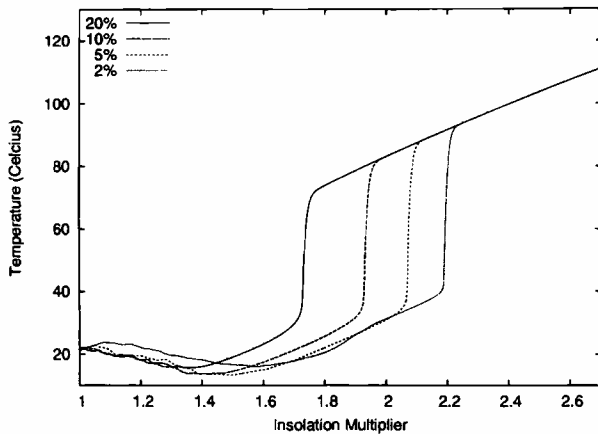


Figure 2: Average temperature of the constant mortality rate model with no mutation ( $r = 0$ ) and mortality rates of 2%, 5%, 10%, and 20%.

vary from 0 to 1 inclusive and are evolved at birth with mutation rate  $r$  by adding a random value  $\mathcal{R} \in [-r, r]$ ,  $\mathcal{R} = 0$  to the parent albedo.

If a cell is covered by a daisy, then the probability that it dies is  $\lambda$ . The model was tested using two different methods of determining the mortality rate of the daisies. In the first method, denoted as CMR (constant mortality rate),  $\lambda$  is held constant regardless of temperature. This was the method used in von Bloh's formulation. With the second, denoted as VMR (variable mortality rate),  $\lambda$  was varied with respect to temperature. The curves used (Figure 1) were obtained by

$$\gamma(T) = 1 - \frac{4\rho}{(T_{max} - T_{min})^2} (T - T_{min})(T_{max} - T) \quad (8)$$

where  $\rho \in [0, 1]$  and serves set the minimum mortality rate. If  $\rho$  is large, then the minimum mortality rate will be low. This is just a reformulation of the birth rate equation and serves as a means of introducing a temperature-dependent mortality rate to the system.

## Results

All of the experiments were performed on a 50 by 50 square lattice and consisted of 50 simulation runs for any given parameter value. In each, 10% of the the planet surface area was populated randomly by approximately equal numbers of black and white daisies. The temperature of the planet was uniformly set to 26° C. Each simulation was allowed to reach an equilibrium temperature and then the solar output was increased linearly. The transition from a cold dead planet to an equilibrium state is not considered, only the transition from this equilibrium state to planetary "death" from increasing temperatures.

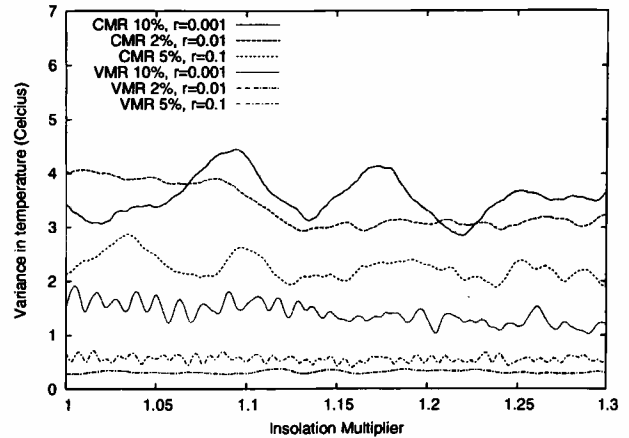


Figure 3: Variance in average temperature over a range of parameter values, detail from insolation multiplier 1 to 1.3.

Figure 2 shows the model response with no mutation and a variety of different mortality rates after averaging the 50 runs. The system performs the best when mortality rates are low, as is expected, maintaining a temperature of 40° C when the insolation is 2.2 times the initial values. The runs with a mortality rate of 20% fare the worst – only regulating temperature to 1.7 times the initial insolation.

Figures 4 and 5 show the results of the model with a mutation rate  $r$  of 0.01. With minimum mortality rates less than 5% the VMR model persists for significantly longer than the CMR model, even though the mortality rates are higher (Figure 1). At minimum mortality rates higher than 5% the CMR models persist for longer.

However, this does not tell the whole story. Looking at the variance of the simulation runs (Figure 3) shows that the temperatures in the VMR models are much less variable than that of the CMR models across all mortality and mutation rates. This means the VMR models remain closer to the optimum growth temperature over a wide variety of daisy configurations.

To determine the effects of mutation on these models, the simulations were run with varying mutation rates. As can be seen by Figure 6, without mutation the VMR models are less persistent than the corresponding CMR models. At higher mutation rates, the situation is reversed. All the VMR models perform far better than the corresponding CMR models, as shown by Figure 7. The VMR models with a 10% minimum mortality rate regulate far better than the CMR models with only a 2% mortality rate.

## Discussion and Conclusion

These results are rather surprising. How could a higher mortality rate yield increased persistence, and why does this effect not hold true all the time?

To answer the first question, consider the CMR model

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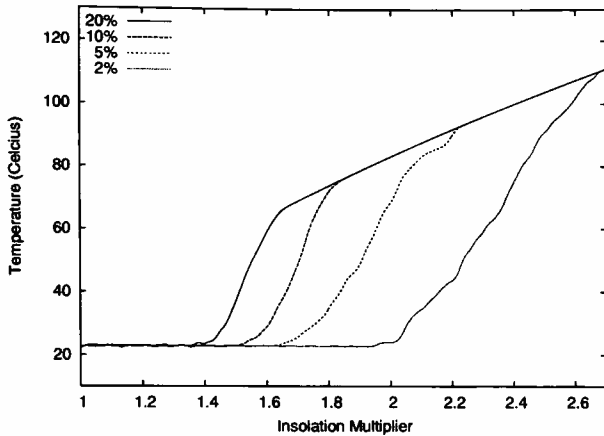


Figure 4: Average temperature of the VMR model with mutation rate 0.01 and minimum mortality rates of 2%, 5%, 10%, and 20%.

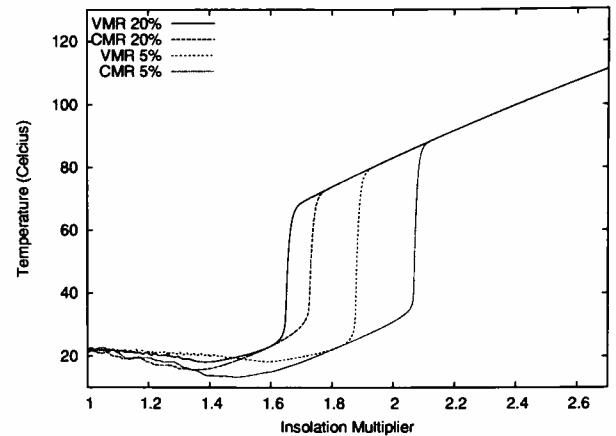


Figure 6: Comparison of average temperatures between the VMR and CMR models with no mutation.

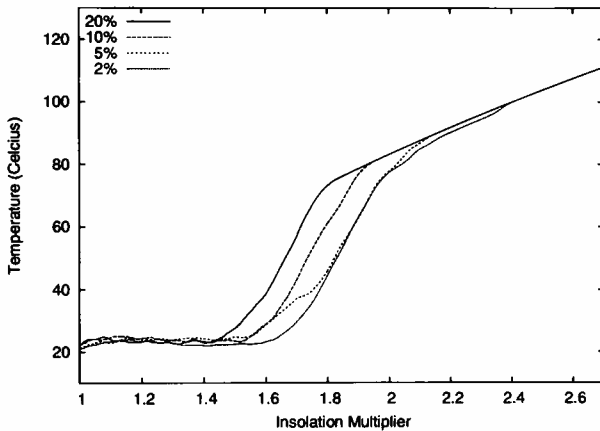


Figure 5: Average temperature of the CMR model with mutation rate 0.01 and minimum mortality rates of 2%, 5%, 10%, and 20%.

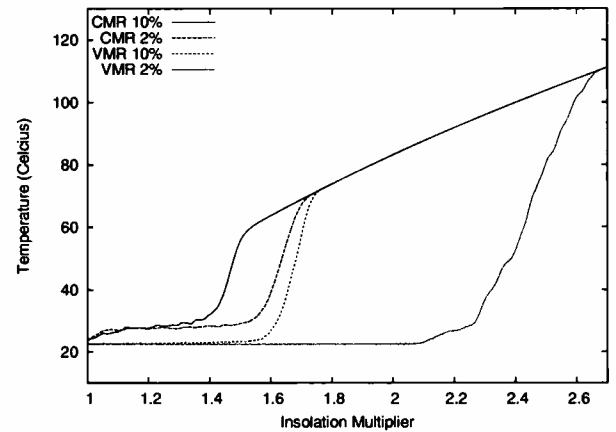


Figure 7: Comparison of average temperatures between the VMR and CMR models with a mutation rate of 0.1.

where daisies are killed randomly. Daisies well suited to their local environments could be killed while those that are not are allowed to persist. This could create local instabilities in temperature and cause the global system to be less stable. However with the variable mortality rate, those daisies that are unsuitable for their local environment are more likely to die while those that are suited remain. This effect is most noticeable when mutation rates are high. As the potential difference between parent and offspring increases, the chance for a unsuitable offspring being born also increases. Under the VMR model, these offspring die off fairly quickly and open up the cells that they inhabited for regrowth, while under the CMR model they could persist and serve to destabilize the neighborhood.

ature under the VMR model yields a higher selection pressure. This provides important feedback to daisy patches and allows a patch to tune albedos to the optimum values for a given local temperature. However, it also means less variation in the albedos – a fact that helps in some case and hinders in others. In an unperturbed system, this high selection pressure means that the variance in daisy albedo across the planet will tend to some minimum value, determined mainly by the albedo mutation rate. While fine for unchanging systems, a low variance in albedos means that the daisies must mutate in order to persist when faced with increasing insolation. With a high variance in albedos, it is far more likely that there could be a daisy suitable for the increasing temperature. Systems with high mutation rates have a double advantage – a greater rate of change in response to the environment and more inherent variation.

The higher rate of mortality outside the optimum temperature under the CMR model due to the lower selective pressure, this allows the

systems to persist for longer at low mutation rates. With higher high mutation rates, the higher selective pressure of the VMR model weeds out the unsuitable daisies quicker and leads to those systems persisting for longer.

To see how this works, imagine a patch of light daisies surrounded by uncovered land. As the temperature increases in the VMR model, the daisies on the outside of the patch die more often than those in the middle. With low mutation rates, they stand to be replaced by daisies very similar to themselves – thus the replacement daisies stand a similar chance of dying. Eventually the combined effect of lower birth rates and higher death rates becomes too much and, unable to replace daisies fast enough, the patch dies from the outside-in. With high mutation rates, there is more variation in albedos and a higher chance of a daisy being born which is capable of surviving the increasing temperatures. This creates a small scale feedback loop where the daisy patch can replenish its borders at a higher rate.

Local interactions of these types play a large part in the dynamics of any system – especially in small systems. The model world used in this paper is incredibly small. For comparison, von Bloh used a CA lattice of 1600 cells a side in his simulations (von Bloh et al., 1997). Larger worlds result in less variation in global temperature, especially in the CMR models, and they tend to persist for longer, though more work needs to be done to fully detail this relationship.

Natural selection and the environment provides pressure on organisms. Gaia theory suggests organisms provide pressure on their environment. Combining the two gives surprising results – even with much higher overall mortality rates, natural selection can increase temperature regulation and persistence within Daisyworld. Whether this effect extends to real world systems remains to be seen.

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