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On Daisyworlds

The Reconstruction of a Model on the Gaia Hypothesis

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On Daisyworlds

A personal account on the reconstruction of a model to test the Gaia hypothesis

by

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Zürich, March 1990

Abstract

Lovelock (1988) states the so-called Gaia hypothesis, which postulates that the surface of the globe forms an ecosystem which can be considered to be a living super-organism. To demonstrate that this argument is neither teleological nor mystical, he has constructed a simple mathematical model. It simulates the competition of two daisy species, each with a different colour and hence a different albedo. The global albedo varies in function of the current species composition and thus the daisies become capable of regulating homoeostatically the global temperature of this Daisyworld. This text describes in more or less chronological order an attempt to reconstruct the mathematical equations of a Daisyworld model, since in his book Lovelock gives no precise description of such a model, nor a proper reference to a more detailed article. The purpose of this exercise was to test the robustness of Lovelock's conclusions, by reconstructing a Daisyworld model independently and from scratch, solely in accordance with the basic assumptions Lovelock has sketched in his book. After an initial, but minor parameter fitting, the behaviour of the newly derived model matches the results Lovelock describes. Thus, the homeostatic property of a Daisyworld as postulated by the Gaia hypothesis appears to be fairly robust and independent of a particular mathematical formulation, for instance that chosen by WATSON and LOVELOCK (1983).

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Introduction

In his new book LOVELOCK (1988) postulates once more the so-called Gaia hypothesis (LOVELOCK, 1972; LOVELOCK & MARGULIS, 1974; MARGULIS & LOVELOCK, 1974). It amounts to the idea that the biosphere of the globe together with the biota form a homeostatic system which controls its environment and which can be considered to be a living super-organism. His idea got from enthusiastic appraisal and complete condemnation (e.g. POSTGATE, 1988) an impressively vast range of responses, at least a lot of attention (SCHNEIDER, 1989; LOVELOCK, 1990). However, it seems to me to be obvious that the Gaia hypothesis as formulated by LOVELOCK (1988), actually encompasses several, distinct issues. Each issue can be investigated independently from the other, thus allowing to give Lovelock merit where he deserves it and to challenge him where he might really fail to make a convincing and scientifically sound argument. The three issues are: The biosphere forms a super-ecosystem on a global scale; the biosphere is alive; the biosphere has the capability to regulate homoeostatically its environment to its own profit.

Concerning the first issue, Lovelock adopts a terminology, which requires some clarification. Unfortunately he contributes once more to the already big enough confusion in regard to the term biosphere: He uses it as the topic entity (SCHWERDTFEGER, 1975), that is the space which life occupies; but he does not clearly separate it from the biota, i.e. all living organisms together, which form the biotic entity (SCHWERDTFEGER, 1975). According to the meaning Lovelock attaches to the term Gaia, it is the ecological entity, i.e. the global system formed by the topic and biotic entities together. On a smaller spatial scale the term ecosystem is well established and almost unanimously considered to be the ecological entity, i.e. it encompasses first the habitat as the topic entity and second the biocoenosis as the biotic entity. Ecologists prefer to adopt a similar terminology on the global scale. Accordingly, in contrast to Lovelock, I will call Gaia the ecosphere, it encompasses a topic and a biotic entity: the topic entity is called toposphere and the biotic biosphere. GILLARD (1969) and SCHWERDTFEGER (1975) have proposed this scheme and it seems to offer many advantages. For instance, analogies between synecological theory and global ecology are much easier to postulate, than this would be possible otherwise, and arguments made on a global scale are easier to understand clearly. E.g., if Lovelock refers in an argument to the oceanic biosphere, one often does not know what he really means; is it now the whole surface layer of the oceans, i.e. the photic zone, which is a distinctly structured water layer of about 100 m depth, or the biomass composed of algae and zooplankton living in this layer?

Of course, more importantly than terminology is the meaning of the term Gaia. Note, the same basic functions which are attributed to an ecosystem, such as a lake or a forest, can be found again in the ecosphere: The structuring into several trophic levels like plants, consumers, and destruents; the essential functions like primary production and the subsequent flow of energy through the trophic structure; an, at least to some degree, autonomous metabolism such as nutrient cycling, e.g. the global carbon cycle². Hence, nothing seems to be wrong with the statement: "the biosphere forms a super-ecosystem on a global scale". By the way, Lovelock uses a nice metaphor to describe these relationships: Gaia resembles a snail, which consists of a shell (abiotic, topic entity like the lithosphere, atmosphere, and hydrosphere) and a body (biota or biosphere).

²On the contrary, the ecosphere is even better bounded than this is the case for many classical ecosystems; the latter have usually fuzzy borders only, the so-called ecotones and as a consequence it is often difficult to define precisely where the ecosystems starts and ends. E.g. consider the gradual differences between forests with a closed canopy, open forests (crowns of trees don't touch each other any more), savannah, bush- and grasslands.

Lovelock claims that the global ecosystem Gaia is alive. He fails to give a clear definition of alive. Biology is the science of life, and it might provide us with better clues about its meaning: For biologists to be alive is a property, which is typically attributed to particular beings such as animals or trees only, not to just any conceivable system. Applied to such easily recognizable entities as organisms, to be alive represents a rather well defined property which requires that at least the following three characteristics hold: A living system ought to be capable of self-replication, a metabolism, and a modifiable inheritance (@KAPLAN, 19xx). Some authors (CZIHAK *et al.*, 1976) assert the additional criterion of a cellular structure. In any case, alive can be defined in a way which has some specific meaning in biology and which matches the intuitive, every-day understanding, and it appears to be a term, which has to be and has been defined almost axiomatically³. However, Lovelock seems to equate the state of a system to be alive with its homeostasis. Now, the latter might be a property of some living systems, yet it is neither an obvious nor an unanimously understood property of living systems. Thus Lovelock's claim that the ecosphere Gaia is alive, seems to be based on shaky grounds, i.e. it is merely based on a personal redefinition of the term, which ignores the usual meaning.

Yet, less questionable is the statement, that the ecosphere is actually capable to regulate homoeostatically its environment to its own profit, i.e. the homeostasis of the ecosphere. This statement appears to be the most interesting and the least trivial part of the Gaia hypothesis. Lovelock himself follows a viable procedure to test and corroborate it: He claims to have constructed a simple mathematical model, called Daisyworld, built from simple, testable elements, and that the hypothesized homeostasis only emerges from the overall system behaviour. According to Lovelock this demonstrates that the Gaia hypothesis is neither teleological nor mystical. As described in the book, Lovelock's model is funded on the following basic assumptions:

Daisyworld consists of a sole continent with a surface which can be populated by several daisy species. Each daisy species has a different colour and hence a different albedo⁴. Bare ground is described to have an albedo in-between the lightest and darkest daisy species. Depending on the current species composition of the daisies, the global albedo differs and thus the daisies can influence the global earth temperature⁵. The solar luminosity increases as the sun ages, and leads to a relatively rapid change in the global temperature regimes.

Lovelock presents several graphs (Fig. 2.1, p.38; Fig. 3.2, p.47; Fig. 3.3, p.49; Fig. 3.4, p.53; and Fig. 3.5, p.55) showing that the daisies are capable to regulate the earth's temperature in a relatively narrow range of 20-30 °C during a long period of time. Without this mechanism of temperature regulation, the period with a viable temperature range allowing the daisies to live would be much shorter. In the course of billions of years, Daisyworld is therefore capable of a homeostatic temperature regulation by adapting its species composition such that the community of daisies can live in a more favourable temperature regime. However, it is not obvious that homeostasis follows necessarily from just the assumptions stated above. Further assumptions, in particular on the specific mathematical formulation of the here described relationships ought be needed, in order to conclusively derive or associate the homeostatic property with the basic assumptions of the Gaia hypothesis.

³For an excellent essay on the definition of life read MONOD (1970).

⁴The albedo α of a surface is defined as the reflected fraction of an incident radiation s expressed as the ratio between the reflected and the incoming radiation measured in Wm^{-2} .

⁵Between temperature T in °K of a surface, its albedo α , and the radiation incidence hold certain physical relationships, i.e. at equilibrium between absorbed and emitted radiation holds Kirchhoff's law: $S(1 - \alpha) = \epsilon \tau s T^4$, where for our world S is the solar constant, ϵ is the infrared emissivity of the atmosphere, τ is the transmissivity of the atmosphere, and s is the Stefan-Boltzmann constant.

Unfortunately, Lovelock does not describe the mathematics behind the daisy model; he only mentions a paper he has written, but fails to give a proper reference and it took me several weeks before I finally succeeded to locate that work (WATSON & LOVELOCK, 1983). In the meantime I was so frustrated, I decided to try it on my own. Moreover, I felt even more challenged to construct my own daisy model, because of the following reasons: First, Lovelock light-heartedly expresses his jubilation about the robustness of his daisy model, a property he claims to be in sharp contrast with all other results of modern ecological theory (see e.g. GARDNER & ASHBY, 1970; MAY, 1972, 1974; PIMM, 1984). Second, Lovelock tries to impress the reader with the claim that he is the first author considering abiotic factors to play an important role in ecosystems. He mentions a single exception, i.e. E.P. Odum (ODUM, 1970), but at least to me, it appears rather difficult to actually ignore the vast ecological literature which addresses this issue properly (e.g. WEBSTER *et al.*, 1974; the many references cited in ODUM, 1970; KREBS, 1972; SCHWERTDFEGER, 1975).

Finally, the exercise appeared to be worth-wile, in particular because I wanted also to find out whether the robustness of Lovelock's daisy model was due to the assumptions of the Gaia hypothesis or rather due to the particular structure of the equations WATSON and LOVELOCK (1983) employed. Lovelock's basic assumptions offer still much freedom in the mathematical formulation of the systems particular properties and the essential relationships between the daisy populations and the temperature of the planet Gaia⁶. The latter question seems to me to be of much greater importance than Lovelock admits, who favours the idea that all what matters is the basic assumptions of the Gaia hypothesis as described above. He claims, that they are fully and sufficiently responsible for all this nice robustness of the ecosphere Gaia, in particular if the species diversity becomes bigger than this is the case on Daisyworld. The latter is certainly true on our globe, but, Lovelock's expectation is another, among ecologists highly debated topic and therefore simply another questionable assertion⁷, I prefer not to discuss here.

Thus the main question addressed in this paper is whether the homeostasis postulated by the Gaia hypothesis is really as robust as Lovelock claims. In a first step to test this I attempted to falsify it, by constructing a daisyworld model which is based on the same basic assumptions but otherwise derived independently. On the other hand, the more daisyworld models, which are mathematically formulated differently, exhibit the postulated homeostatic behaviour, the more likely it becomes that the Gaia hypothesis is correct. If homeostasis should emerge from this first model, Lovelock's Gaia hypothesis could at least be interpreted as being so robust as not to depend on the idiosyncrasies and specialities of the particular mathematical formulation WATSON and LOVELOCK (1983) employed.

Model derivation

It seemed to me to be appropriate to choose a model as simple as possible⁸ to follow a top-down approach with step-wise refinement along the way. I started with the

⁶For instance, as it is well known in systems theory, the existence of a negative feed-back loop is necessary but not sufficient to warrant the stability of a system if it contains additional feed-back loops or if it is non-linear; additional system properties such as specific parameter values or the exact mathematical structure are required to determine the stability of a steady-state. Note, the existence of a non-trivial, stable steady-state is a necessary prerequisite of homoeostasis.

⁷The issue of diversity and stability has been debated strongly within ecology; see e.g. @PIMENTEL, MAY, MAYNARD-SMITH, ELLENBERG, HOLLING.

⁸ You see that I sympathize with Occam's razor (For an informative as well as amusing explanation of Occam's razor I recommend HUTCHINSON, 1978)

assumption that population densities ought to be the same for all species and constant throughout time. From this follows that daisies cover a certain portion of the globe's continent on daisy world, which are given solely by the current population sizes. Bare ground is populated as the population grow, till there is no more space available any more. This situation matches exactly the notion of the carrying capacity as used in the equation of logistic growth. Normally logistic growth is for a single species only; but it was easy to derive a variant allowing for competition between species and still following a growth process with saturation once the carrying capacity is reached:

$$\dot{x}_i = r_i \left(\frac{K - \sum_{j=1}^n x_j}{K} \right) x_i \quad \forall i \text{ species} \quad (1)$$

where x_i denotes the population size of the i -th species, K the carrying capacity given by the size of the continent's surface and r_i the species specific per capita growth rate of the i -th daisy species.

However, in contrast to the classical logistic equation, the growth rate r is not a constant model parameter, but an auxiliary variable: In accordance with the Gaia hypothesis I assumed that species do grow in function of the temperature regime, i.e. r is a function of the current temperature T . In reality all poikilothermic species show a growth rate r_i which depends on temperature in a species specific manner, similar to the function shown in Fig. 1. Below $T_{\min/i}$, the minimum development threshold temperature, plants don't grow. Beyond $T_{\max/i}$, the maximum development threshold temperature, all growth ceases again⁹. I used the following equations to describe the relationship between growth rate r_i and temperature T (s.a. Fig. 1):

$$r_i = \begin{cases} r_{\max} \frac{T - T_{\min/i}}{T_{\text{opt}/i} - T_{\min/i}} & T_{\min/i} \leq T \leq T_{\text{opt}/i} \quad \forall i \text{ species} \\ r_{\max} \frac{T_{\text{opt}} - T}{T_{\max/i} - T_{\text{opt}/i}} & T_{\text{opt}/i} \leq T \leq T_{\max/i} \quad \forall i \text{ species} \\ 0 & T < T_{\min/i} \quad T_{\max/i} < T \quad \forall i \text{ species} \end{cases} \quad (2)$$

where

- r_{\max} maximum growth rate of daisies
- $T_{\min/i}$ minimum threshold temperature of development for species i
- $T_{\max/i}$ maximum threshold temperature of development for species i
- $T_{\text{opt}/i}$ optimum growth temperature for species i

The maximum growth rate any daisy population can reach is given by parameter r_{\max} . This is because the term within parentheses in equation (2) never becomes larger than 1 which it reaches exactly when $T=T_{\text{opt}/i}$ and becomes exactly zero when $T=T_{\min/i}$ respectively $T=T_{\max/i}$ (Fig. 1).

⁹Although extreme temperatures are not necessarily lethally cold respectively lethally hot, they won't allow daisies to exist permanently. The permanent survival of any plant species requires at least during a minimum life-span some growth. Therefore, we may interpret any mean global temperature T smaller than $T_{\min/i}$ respectively bigger than $T_{\max/i}$ to disallow for the existence of daisies.

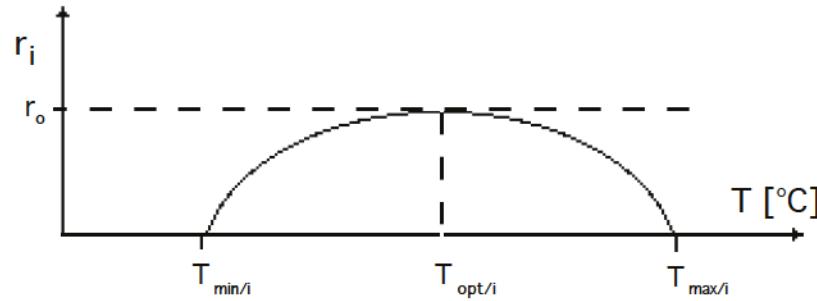


Fig. 1: Temperature dependence of the per capita growth rate r_i of a particular daisy species i . r_{\max} ; T - global temperature on daisy world; $T_{\text{opt}/i}$, $T_{\min/i}$, $T_{\max/i}$ are the species specific growth parameters defining within which range daisies grow and which temperature corresponds to optimal growth conditions.

The lighter a daisy, the better heat adapted it is, hence the higher the parameters $T_{\min/i}$, $T_{\text{opt}/i}$, and $T_{\max/i}$ and vice versa. Since these parameters are species specific, it results for each species a specific, temperature T dependent growth rate $r_i(T)$. This gives the high albedo daisies a chance to cool and the low albedo dark ones to warm the daisy world.

However, the equation (1) has a significant flaw: Once a particular species composition has been established, proportions remain the same forever. This is because no changes take place in population sizes once the population total of all species has reached the carrying capacity; in this case the equation

$$K = \sum_{j=1}^n x_j \quad (3)$$

holds and hence

$$\dot{x}_i = 0 \quad \forall i \quad (4)$$

a state which corresponds to a true equilibrium state. In order to allow for changes in species composition even when there is no more free space available, I have modified equation (1) in this way:

$$\dot{x}_i = r_i(T) \left(\frac{K - \sum_{j=1}^n x_j}{K} \right) x_i - m_i x_i \quad \forall i \text{ species} \quad (5)$$

where m_i denotes a mortality rate of the i -th species and all other parameters and variables have the same meaning as in (1). This can be interpreted as a continuous, interspecific competition among the daisies. At equilibrium now not equation (3) but the following species specific condition holds

$$K \left(1 - \frac{m_i}{r_i} \right) = \sum_{j=1}^n x_j \quad (3')$$

Equation (3') can be interpreted such, that the carrying capacity is reduced for each species by the proportion $p_i = m_i/r_i$. If there is at least one p_i , which has a value smaller and different from all other p_i 's, this particular species is still allowed to grow, while all other have already reached zero growth condition, i.e. except for species i , condition (3') is satisfied. According to equation (1) or (5) growth rates become negative if the right-hand parts of equation (3) respectively (3') become larger than the left-hand parts. This means

that a still growing species with a low p_i can take away space from another species by reducing its population, given that this species has already ceased to grow because of its bigger p_i . The important characteristic of the whole model (5) resulting from this behaviour is that even once equilibrium has been reached, changes in the environment can alter the equilibrium condition and thus shift the equilibrium state away from its current position. The latter would not be possible for model (1).

Concerning the daisy behaviour the model is now complete. What still remains is a relationship between the global albedo a_g as given by

$$a_g = \frac{1}{K} \left(\sum_{i=1}^n a_i x_i + a_b (K - \sum_{i=1}^n x_i) \right) \quad (6)$$

where

- a_i albedo of i -th species
- a_b albedo of bare ground.

and the mean global temperature T . This relationship must be negatively correlated, and again following parsimony, I used a linear relationship of the form:

$$T = (T^*_{\max} - T^*_{\min}) (1 - a_g) \quad (7)$$

where a_g is given by equation (6) and T is the associated global temperature (Fig. 2). The parameters T^*_{\min} and T^*_{\max} are the temperatures at which the albedo is maximal respectively minimal.

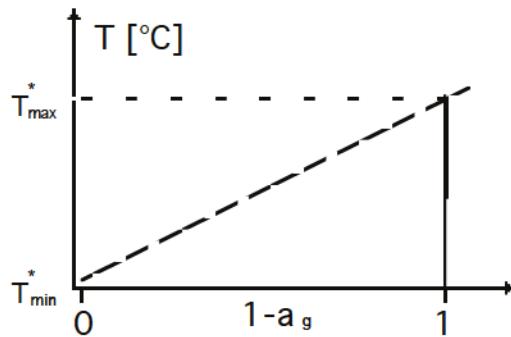


Fig. 2: Linearized relationship between the means of global temperature and the global albedo a_g on daisy world. At any moment a_g is calculated from equation (6) which depends on the current sizes of daisy populations and the proportion of unpopulated, bare ground. The albedo then determines the global temperature T varying within range T^*_{\min} and T^*_{\max} .

According to the basic assumption the model should also allow to gradually change the temperature regime by increasing the solar luminosity through its ageing process. To obtain this behaviour I have introduced an additional state variable s , a strictly positive anomaly which accounts for the temperature increase due to the changing solar luminosity. I assumed that the temporal behaviour of this effect is given by this differential equation

$$\dot{s} = \sigma \quad (8)$$

where σ is a constant. Equation (7) then also to be modified to

$$T = (T^*_{\max} - T^*_{\min}) (1 - a_g) + (s - s_0) \quad (7)$$

The model is now complete, and the equations (2), (5), (6), (7'), and (8) describe all dynamics on daisyworld. In addition the parameter equations (2a), (2b) must be satisfied and a non-trivial equilibrium state for a particular solar luminosity is determined by equation (3'). The model describes in particular the changes in daisy populations given by the drifting equilibrium state as it is determined by the ageing of the sun. It adheres in all aspects to the basic assumptions of the Gaia hypothesis.

Parameter estimates

Only a few model parameters have been given by LOVELOCK (1988), the majority had to be estimated from known physical properties, such as current temperature regimes etc.

Since the model equations (2), (5), (6), (7'), and (8) form a continuous time system of ordinary, non-linear differential equations, the basic time unit must be defined before any other parameters can be determined. The solar luminosity increases from 0.6 to 1.4 relative to what it is today in about $8 \cdot 10^9$ years. Accordingly, the period of interest for which the equations ought to be solved lies in-between the time points $t_0 = 0$ and $t_{\text{end}} = 8 \cdot 10^9$ years.

Parameter	symbol	unit	value
Rate of increase of temperature due to the increase of solar luminosity	σ	${}^\circ\text{C } 4 \cdot 10^{-9}$	6
Initial solar luminosity in % of solar constant	s_0	%	60.0
Global carrying capacity for daisies	K	#	1.0
Maximum per capita daisy growth rate	r_{\max}	$4 \cdot 10^{-9}$	60.0
Global temperature at albedo = 1	T^*_{\min}	${}^\circ\text{C}$	0.0
Global temperature at albedo = 0	T^*_{\max}	${}^\circ\text{C}$	30.0
Mortality of light daisies	$m[\text{light}]$	$4 \cdot 10^{-9}$	40.0
Mortality of dark daisies	$m[\text{dark}]$	$4 \cdot 10^{-9}$	80.0
Minimum temperature for growth of light daisies	$T_{\min}[\text{light}]$	${}^\circ\text{C}$	15.0
Minimum temperature for growth of dark daisies	$T_{\min}[\text{dark}]$	${}^\circ\text{C}$	5.0
Temperature for optimum growth of light daisies	$T_{\text{opt}}[\text{light}]$	${}^\circ\text{C}$	32.5
Temperature for optimum growth of dark daisies	$T_{\text{opt}}[\text{dark}]$	${}^\circ\text{C}$	22.5
Albedo of light daisies	$a[\text{light}]$	-	0.7
Albedo of dark daisies	$a[\text{dark}]$	-	0.2
Albedo of bare ground	a_b	-	0.4

Tab. 1: Parameters used to numerically solve the daisyworld model given by the equations (2), (5), (6), (7'), and (8).

The initial state vector used was: $\underline{x}_0' = [0.01, 0.01]$ and $s_0 = 60$. The integration method was a variable step length Runge-Kutta 5th order algorithm.

The following parameters have been given by LOVELOCK (1988) for a two species model: light daisies have an albedo of 0.7, dark daisies one of 0.2. Bare ground is described to have an albedo of 0.4.

The remaining parameters have been derived theoretically or slightly adjusted to operate in the same range of system behaviour as described by LOVELOCK (1988). No true parameter identification procedure has been applied.

Simulation results

To solve them numerically, the system of differential equations defined by Eq. (2), (5), (6), (7'), and (8) have been implemented as a ModelWorks model definition program (FISCHLIN *et al.*, 1993; see Appendix). Using the parameter values given in Tab. 1 I obtained for just two daisy species, a light and a dark one, the results shown in Fig. 3.

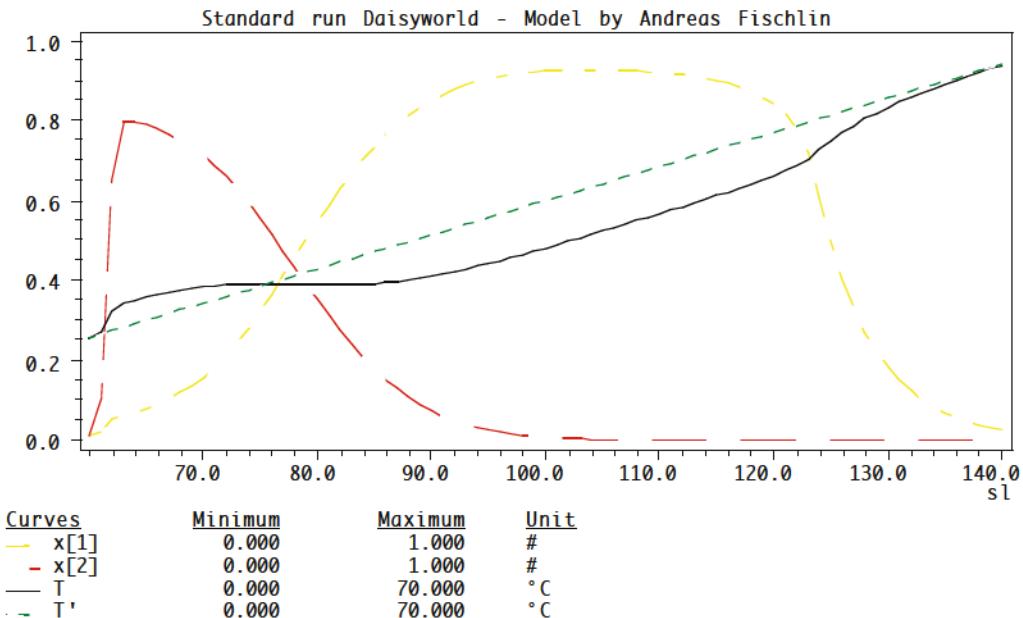


Fig. 3: Simulation results of the derived daisy world model (Eq. (2), (5), (6), (7'), and (8)). It resembles qualitatively the results depicted in Fig. 2.1 in Lovelock's book «The Ages of Gaia» (LOVELOCK, 1988), i.e. two daisy species, a dark and a light one, are populating daisy world and are capable of regulating homoeostatically the globe's temperature T . The graph shows also what the mean global temperature T' would have been without any daisies on a life-less planet. Legend: $x[1]$, $x[2]$ - sizes of light respectively dark daisy populations; T , T' - mean global temperatures in presence respectively absence of daisies; \square - range of temperature $[T_{\text{opt}/1..T_{\text{opt}}/2]$ encompassing optimal growth conditions for all daisy species; sl - solar luminosity in percents of today's solar luminosity.

In this model it is easy to have a life-less planet by simply setting the initial state vector $\underline{x}_0' = [0.0, 0.0]$, the trivial steady state of all life (Fig. 3, curve T'). If one compares the temperature T with T' , i.e. the temperature on the globe with respectively without daisies, the homeostasis property clearly emerges, since the daisies on the planet are capable to regulate temperature close to their optimum growth conditions (Fig. 3, curve T). On a life-less planet that regulation would be missing and would show just a ramp, i.e. according to Eq. (8) the constant increase of temperature T' as daisyworld's sun becomes older.

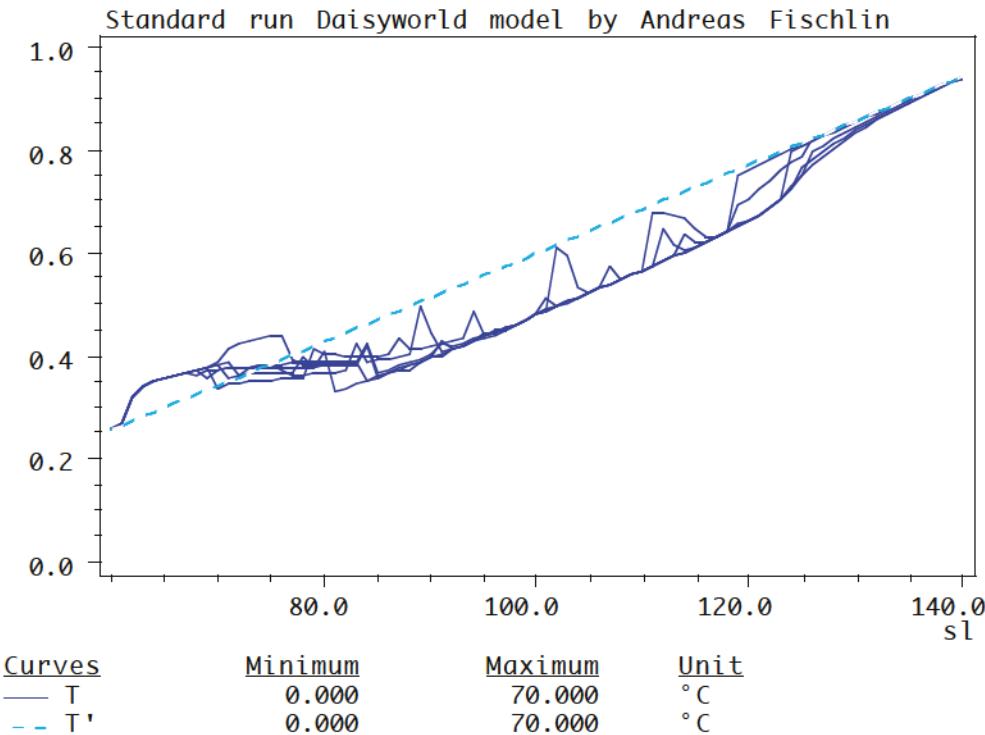


Fig. 4: Empirical investigation of the stability of the daisy world model (Eq. (2), (5), (6), (7), and (8)) under randomly impacting meteorites. Depending on the size of the meteorite, a varying fraction of the daisies are destroyed and the temperature on daisy world is disturbed. Unless all daisies are completely wiped out, the systems capability to regulate the globe's temperature T remains. The graph shows also what the mean global temperature T' would have been without any daisies on a life-less planet. Legend: T , T' - mean global temperatures in presence respectively absence of daisies.

First the behaviour of the model is qualitatively similar to that shown in Lovelock's book (LOVELOCK, 1988; e.g. Fig. 2.1). The daisies are capable first to increase the temperature T above what it would be without the daisies. This condition is closer to the temperature for optimum growth of the daisies ($T > T'$, see left part of Fig. 3). The planet is dominated by dark daisies, which will give up this position only if the solar luminosity has increased so much, that the temperature becomes much too hot for the dark daisies, giving place to the light daisies' cooling capability. The latter succeed in cooling the temperature now below what it would have been on a life-less planet, thus postponing the collapse of all life ($T < T'$, see middle part of Fig. 3). If the solar luminosity has reached such great values as to causing the temperature to be too hot even for the light daisies, daisy populations disappear and any temperature regulation by life collapses, indicated by the merging of the two curves T and T' ($T \approx T'$, see right part of Fig. 3).

Discussion and conclusions

Second this investigation shows that the main point of Lovelock's Gaia hypothesis, i.e. the homeostatic capability of life to regulate global temperature within a range favourable for living organisms, can be reproduced by using models which are different and derived independently from that formulated by WATSON and LOVELOCK (1983). Hence Lovelock's conclusion appears not to depend solely on the more or less arbitrary chosen equations which model the competition of the daisy populations (CARTER & PRINCE, 1981), but to be robust enough for a wide number of competition models. However, the latter ought still to be explored further.

I failed to falsify the most interesting part of the Gaia hypothesis, i.e. life's capability of homeostasis, nevertheless, its other parts can either be shown to be almost trivial, i.e. the analogy between an ecosystem and the ecosphere, or to be merely the result of a subjective redefinition of the term life. At least to me it appears, that his hypothesis would deserve more attention by serious scientists, than it is likely to receive because of Lovelock's way to reason without persistent rigor throughout all his arguments. Maybe that's the price to pay for thought provoking ideas...

References

- CONNELL, J.H. & SOUSA, W.P., 1983. *On the evidence needed to judge ecological stability or persistence.* Amer. Nat., **121**: 789-824.
- CONNELL, J.H., 1978. *Diversity in tropical rain forests and coral reefs.* Science, **199**: 1302-1310.
- CZIHAK, G., LANGER, H., & ZIEGLER, H., 1976. Biologie - Ein Lehrbuch für Studenten der Biologie. Springer, Berlin a.o., 837pp.
- DEMETRIUS, L., 1969. *On community stability.* Math. biosci., **5**: 321-325.
- FISCHLIN *et al.*, 1993. ModelWorks.@
- GARDNER, M.R. & ASHBY, W.R., 1970. *Connectance of large dynamic, cybernetic, systems: critical values for stability.* Nature, **228**: 708.
- GARFINKEL, D., 1967. *Effect on stability of Lotka-volterra ecological systems of imposing strict territorial limits on populations.* J. Theor. Biol., **14**: 325-27.
- GILLARD, A., 1969. *On the terminology of biosphere and ecosphere.* Nature, **223**: 500-501.
- HAIRSTON, N.G., ALLEN, J.D., COLWELL, R.K., FUTUYAMA, D.J., HOWELL, J., LUBIN, M.D., MATHIAS, J. & VANDERMEER, J.H., 1968. *The relationship between species diversity and stability: An experimental approach with protozoa and bacteria.* Ecology, **49**: 1091-1101.
- HOLLING, C.S., 1973. *Resilience and stability of ecological systems.* Ann. Rev. Ecol. and Systemat., **4**: 1-23.
- HUBBEL, S.P., 1973. *Populations and simple food webs as energy filters: I, One-species systems.* Amer. Nat., **107**: 94-121.
- HUBBEL, S.P., 1973. *Populations and simple food webs as energy filters: II, Two-species systems.* Amer. Nat., **107**: 122-51.
- HURD, L.E., MELLINGER, M.V., WOLF, L.L. & MCNAUGHTON, S.J., 1971. *Stability and diversity at three trophic levels in terrestrial successional ecosystems.* Science, **173**: 1134-36.
- HUTCHINSON, G.E., 1978. *An introduction to population ecology.* Yale University Press, New Haven and London 5th ed.(1980), 260pp.
- KAPLAN,@
- LOVELOCK, J.E., 1972. @. Atmos. Environ., **6**: 579-80.
- LOVELOCK, J.E., 1983. *The ages of Gaia - a biography of our living earth.* Oxford a.o.: Oxford University Press, 252pp.
- LOVELOCK, J.E. & Margulis, L., 1974. @. Tellus, **26**: 1-10.
- LOVELOCK, J.E., 1990. *Hands up for the Gaia hypothesis.* Nature, **344**: 100-2.
- MARGALEF, R., 1969. *Diversity and stability: A practical proposal and a model of interdependence.* In: Woodwell, G.N. & Smith, H.H. (eds.), *Diversity and stability in ecological systems*, Brookhaven Symp. Biol 22, Upton, N.Y., 264pp., 25-37pp.
- Margulis, L. & LOVELOCK, J.E., 1974. @. Icarus, **21**: 471-89.
- MAY, R.M., 1972. *Will a large complex system be stable?* Nature, **238**: 413-14.
- MAY, R.M., 1974. *Stability and complexity in model ecosystems.* Princeton University Press: Princeton, New Jersey (Monographs in population biology (edited by May, R.M.); Vol. 6), 265pp.
- MONOD, 1970. Zufall und Notwendigkeit. Philosophische Fragen der modernen Biologie. Piper, München, 238pp.
- PIMM, S.L., 1984. *The complexity and stability of ecosystems.* Nature, **307**: 321-26.
- POSTGATE, J., 1988. New Scientist 60: @.
- REJMÁNEK, M. & STARY, P., 1980. *Bounds on food web connectance.* Nature, **285**: 591-592.

- SCHNEIDER, S.H., 1989. *Global warming*. San Francisco, Sierra Club Books.
- SCHWERDTFEGER, F., 197. *Ökologie der Tiere. III Synökologie*. Paul Parey, Hamburg.
- TALBOT, F.H., RUSSELL, B.C. & ANDERSON, F.R.V., 1978. *Coral reef fish communities: Unstable, high-diversity systems*. Ecol. Monogr., **48**: 425-440.
- WATSON, A.J. & LOVELOCK, J.E., 1983. *Biological homeostasis of the global environment: the parable of Daisyworld*. Tellus, **35B**: 284-9.
- WEBSTER, J.R., WAIDE, J.B. & PATTEN, B.C., 1974. *Nutrient recycling and the stability of ecosystems*. In: Howell, F.G., Gentry, J.B. & Smith, M.H. (eds.), *Mineral cycling in Southeastern ecosystems*, ERDA Symp. Series (CONF-740513), Springfield, Va.: TIC and ERDA, 1-27pp.
- WIRTH, 1985. @
- YODZIS, P., 1976. *Species richness and stability of space-limited communities*. Nature, **264**: 540-541.

Appendix

The here described model has been implemented, numerically solved, and its behavior studied by the following simulation model. It represents a ModelWorks model definition program (FISCHLIN *et al.*, 1993) written in Modula-2 (WIRTH, 1985).

```

MODULE Daisyworld;
(* **** *)
ModelWorks model: Daisyworld
Copyright ©1989 by Andreas Fischlin and Swiss
Federal Institute of Technology Zurich ETHZ
Department of Environmental Sciences
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ETH-Zentrum
CH-8092 Zurich
Switzerland

Purpose Models the daisyworld, which demondescrStrates, according
to its author Lovelock the essence of the
Gaia-hypothesis: The temperature regime on a globe
covered by a single continent is regulated by daisy
species differing in their color from dark to light and
thus influencing the albedo of the globe.

References
Lovelock, J. 1988. The ages of gaia. New York and London:
W.W. Norton & Co., Inc. 252pp. ISBN 0-393-02583-7.

Implementation and Revisions:
=====
Author Date Description
----- -----
af 07/03/90 First implementation (MacMETH 2.6+, DM 2.0, MW 1.3a)
(* **** *)
FROM DMStrings IMPORT
Concatenate;
FROM DMConversions IMPORT
IntToString;
FROM DMMenus IMPORT
Menu, Command, AccessStatus, Marking, InstallMenu,
InstallCommand, InstallAliasChar;

FROM SimBase IMPORT
Model, DeclM, NoOutput, IntegrationMethod, DeclSV, RTCType,
DeclP, NoTerminate, StashFiling, DeclMV, Tabulation, NoAbout,
Graphing, SetDefltCurveAttrForMV, Stain, LineStyle,
SetIntegrationStep, SetMonInterval, SetSimTime,
SetDefltProjDescr;
FROM SimMaster IMPORT
RunSimEnvironment, CurrentTime;

FROM RandGen IMPORT U;

TYPE
Color = (light,dark);

VAR
m: Model;
daisy: ARRAY [MIN(Color)..MAX(Color)] OF
RECORD
x,xDot,
albedo,mu,optTemp,minTemp, r,m
: REAL;
END (*RECORD*);
r0,K,

```

```

albedoGlob,sumOfx,albedoB,
Temp,TempDash, TempMaxStar,TempMinStar,
solLum,solLumDeltaT,solLumDeltaTDot,sigma,
meteorDeltaT,
clipGrowthR: REAL;
clipGrowth: BOOLEAN;

PROCEDURE Input;
  VAR c: Color;
BEGIN
  sumOfx := 0.0;
  FOR c:= MIN(Color) TO MAX(Color) DO
    sumOfx := sumOfx+daisy[c].x;
  END(*FOR*);
  albedoGlob := 0.0;
  FOR c:= MIN(Color) TO MAX(Color) DO
    albedoGlob := albedoGlob + daisy[c].albedo*daisy[c].x/K;
  END(*FOR*);
  albedoGlob := albedoGlob + (K-sumOfx)/K*albedoB;
  Temp := TempMaxStar-(TempMaxStar-TempMinStar)*albedoGlob+solLumDeltaT;
  TempDash := TempMaxStar-(TempMaxStar-TempMinStar)*albedoB+solLumDeltaT;
  FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
      r := r0*(mu*(Temp-optTemp)*(Temp-optTemp)+1.0);
      IF (r<=0.0) AND clipGrowth THEN r := 0.0 END;
    END(*WITH*);
  END(*FOR*);
  solLum := CurrentTime();
END Input;

PROCEDURE Initialize;
  VAR c: Color;
BEGIN
  FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
      mu := -1.0/((minTemp-optTemp)*(minTemp-optTemp));
    END(*WITH*);
  END(*FOR*);
  clipGrowth := clipGrowthR<>0.0;
END Initialize;

PROCEDURE Dynamic;
  VAR c: Color;
BEGIN
  FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
      xDot := r*((K-sumOfx)/K)*x - m*x;
    END(*WITH*);
  END(*FOR*);
  solLumDeltaTDot := sigma;
END Dynamic;

PROCEDURE DeclModelObjects;
  VAR descrStr,symStr,istr: ARRAY [0..127] OF CHAR; c: Color;
  nrSpecies,nrIntervals: REAL;
BEGIN
  nrSpecies := FLOAT(ORD(MAX(Color))+1); nrIntervals := nrSpecies-1.0;
  DeclSV(solLumDeltaT,solLumDeltaTDot,0.0,MIN(REAL),MAX(REAL),"Solar luminosity","s","");
  DeclP(sigma,0.6,MIN(REAL),MAX(REAL),rtc,
  "Rate of increase of solar luminosity", "sigma","/time");
  DeclP(K, 1.0, 0.0, MAX(REAL), rtc,
  "Global carrying capacity of globe", 'K', '#');
  DeclP(r0, 3.0, MIN(REAL), MAX(REAL), rtc,
  "Daisy growth rate", "r0", '/time');
  DeclP(clipGrowthR, 1.0, 0.0, 1.0, rtc,
  "Flag to clip growth outside Tmin and Tmax", "clipGrowth", '0 or 1');
  DeclP(albedoB, 0.4, 0.0,1.0, rtc,
  "Albedo of bare, unpopulated ground", "ab", '');
  DeclP(TempMinStar, 0.0, MIN(REAL), MAX(REAL), rtc,
  "Temperature at albedo minimum", "T*min", "°C");
  DeclP(TempMaxStar, 30.0, MIN(REAL), MAX(REAL), rtc,
  "Temperature at albedo maximum", "T*max", "°C");
  DeclP(meteorDeltaT, 20.0, MIN(REAL), MAX(REAL), rtc,
  "Meteorite impact temperature jump", "ΔTm", "°C");

  DeclMV(albedoGlob,0.0,1.0,'Global albedo','ag','');
  notOnFile,writeInTable,notInGraph);
  DeclMV(daisy[light].r,-1.0,1.0,'Growth rate','r[1]','/time',
  notOnFile,notInTable,notInGraph);
  DeclMV(daisy[dark].r,-1.0,1.0,'Growth rate','r[2]','/time',
  notOnFile,notInTable,notInGraph);
  DeclMV(sumOfx,0.0,K,'Global daisy population','Σx','#',
  notOnFile,notInTable,notInGraph);
  DeclMV(Temp,0.0,70.0,'Global temperature','T','°C',
  notOnFile,writeInTable,isY);
  SetDefltCurveAttrForMV(m,Temp,sapphire,unbroken,0C);
  DeclMV(TempDash,0.0,70.0,'Global temperature without life','T','°C',
  notOnFile,writeInTable,isY);
  SetDefltCurveAttrForMV(m,TempDash,turquoise,spotted,0C);
  DeclMV(solLum,60.0,140.0,'Solar luminosity','sl','');
  notOnFile,writeInTable,isX);

  FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
      descrStr := 'Population of ';
      IF c=MIN(Color) THEN
        Concatenate(descrStr,"light ",descrStr);
      ELSIF c=MAX(Color) THEN
        Concatenate(descrStr,"dark ",descrStr);
      ELSE
        Concatenate(descrStr,"intermediate ",descrStr);
      END(*IF*);
      Concatenate(descrStr,"daisies",descrStr);
      symStr := "x["+
      IntToString(1+ORD(c),istr,0);
      Concatenate(symStr,istr,symStr);
      Concatenate(symStr,"]" ,symStr);
      DeclSV(x, xDot,0.01, 0.0, K, descrStr, symStr, '#');
      DeclMV(x,0.0,K, descrStr,symStr,'#',
      notOnFile,writeInTable,isY);
    END(*WITH*);

```

```

    IF c=MIN(Color) THEN
        SetDefltCurveAttrForMV(m,daisy[c].x,gold,dashSpotted,0C);
    ELSIF c=MAX(Color) THEN
        SetDefltCurveAttrForMV(m,daisy[c].x,coal,broken,0C);
    ELSE
        SetDefltCurveAttrForMV(m,daisy[c].x,emerald,autoDefStyle,0C);
    END(*IF*);
END(*FOR*);

FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
        descrStr := "Mortality of ";
        IF c=MIN(Color) THEN
            Concatenate(descrStr,"light ",descrStr);
        ELSIF c=MAX(Color) THEN
            Concatenate(descrStr,"dark ",descrStr);
        ELSE
            Concatenate(descrStr,"intermediate ",descrStr);
        END(*IF*);
        Concatenate(descrStr,"daisies",descrStr);
    symStr := "m[";
    IntToString(1+ORD(c),istr,0);
    Concatenate(symStr,istr,symStr);
    Concatenate(symStr,"]",symStr);
    DeclP(m, 0.2+0.2/nrIntervals*FLOAT(ORD(c)), MIN(REAL),MAX(REAL), rtc,
          descrStr, symStr, '/time');
    END(*WITH*);
END(*FOR*);

FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
        descrStr := "Temperature minimum for growth of ";
        IF c=MIN(Color) THEN
            Concatenate(descrStr,"light ",descrStr);
        ELSIF c=MAX(Color) THEN
            Concatenate(descrStr,"dark ",descrStr);
        ELSE
            Concatenate(descrStr,"intermediate ",descrStr);
        END(*IF*);
        Concatenate(descrStr,"daisies",descrStr);
    symStr := "Tmin[";
    IntToString(1+ORD(c),istr,0);
    Concatenate(symStr,istr,symStr);
    Concatenate(symStr,"]",symStr);
    DeclP(minTemp, 15.0-10.0/nrIntervals*FLOAT(ORD(c)), MIN(REAL), MAX(REAL), rtc,
          descrStr, symStr, 'C');
    END(*WITH*);
END(*FOR*);

FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
        descrStr := "Temperature optimum for growth of ";
        IF c=MIN(Color) THEN
            Concatenate(descrStr,"light ",descrStr);
        ELSIF c=MAX(Color) THEN
            Concatenate(descrStr,"dark ",descrStr);
        ELSE
            Concatenate(descrStr,"intermediate ",descrStr);
        END(*IF*);
        Concatenate(descrStr,"daisies",descrStr);
    symStr := "Topt[";
    IntToString(1+ORD(c),istr,0);
    Concatenate(symStr,istr,symStr);
    Concatenate(symStr,"]",symStr);
    DeclP(optTemp, 32.5-10.0/nrIntervals*FLOAT(ORD(c)), MIN(REAL), MAX(REAL), rtc,
          descrStr, symStr, 'C');
    END(*WITH*);
END(*FOR*);

FOR c:= MIN(Color) TO MAX(Color) DO
    WITH daisy[c] DO
        descrStr := 'Albedo of ';
        IF c=MIN(Color) THEN
            Concatenate(descrStr,"light ",descrStr);
        ELSIF c=MAX(Color) THEN
            Concatenate(descrStr,"dark ",descrStr);
        ELSE
            Concatenate(descrStr,"intermediate ",descrStr);
        END(*IF*);
        Concatenate(descrStr,"daisies",descrStr);
    symStr := "al[";
    IntToString(1+ORD(c),istr,0);
    Concatenate(symStr,istr,symStr);
    Concatenate(symStr,"]",symStr);
    (* albedos range from 0.2 (dark daisy) to 0.7 (light daisy) *)
    DeclP(albedo, 0.7-0.5/nrIntervals*FLOAT(ORD(c)),
          0.0, 1.0, rtc, descrStr, symStr, '');
    END(*WITH*);
END(*FOR*);

END DeclModelObjects;

VAR
    myMenu: Menu; impactCmd: Command;

PROCEDURE MeteorImpact;
    VAR c: Color;
    PROCEDURE Sign(x: REAL): REAL;
    BEGIN
        IF x<0.0 THEN RETURN -1.0 ELSE RETURN 1.0 END
    END Sign;
    BEGIN
        Temp := Temp - Sign(U()-0.5)*meteorDeltaT + (U()-0.5);
        FOR c:= MIN(Color) TO MAX(Color) DO
            WITH daisy[c] DO
                x := U()*x
            END(*WITH*);
        END(*FOR*);
    END MeteorImpact;

PROCEDURE AddCommands;
BEGIN
    InstallMenu(myMenu,'Events',enabled);
    InstallCommand(myMenu, impactCmd,"Meteorite impact", MeteorImpact,
                  enabled, unchecked);

```

```
    InstallAliasChar(myMenu,impactCmd,"z");
END AddCommands;

PROCEDURE DeclModel;
BEGIN
    DeclM(m, RungeKutta4, Initialize, Input, NoOutput, Dynamic,
          NoTerminate, DeclModelObjects,
          'Daisyworld model and the Gaia hypothesis','m', NoAbout);
    SetSimTime(60.0,140.0);
    SetMonInterval(1.0); SetIntegrationStep(0.5);
    SetDefltProjDescrs(
        "Standard run Daisyworld - Model version by Andreas Fischlin","","",
        TRUE, FALSE, TRUE, TRUE, TRUE, TRUE, TRUE);
    AddCommands;
END DeclModel;

BEGIN
    RunSimEnvironment(DeclModel);
END Daisyworld .
```

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- 1 FISCHLIN, A., BLANKE, T., GYALISTRAS, D., BALTENSWEILER, M., NEMECEK, T., ROTH, O. & ULRICH, M. (1993, 2. korrigierte und erweiterte Aufl.): Unterrichtsprogramm "Weltmodell 2". 34pp. doi: [10.3929/ethz-a-004271259](https://doi.org/10.3929/ethz-a-004271259)
- 1 FISCHLIN, A., BLANKE, T., GYALISTRAS, D., BALTENSWEILER, M., NEMECEK, T., ROTH, O. & ULRICH, M. (2010, 3. korrigierte Aufl.): Unterrichtsprogramm "Weltmodell 2". 36pp. doi: [10.3929/ethz-b-000729485](https://doi.org/10.3929/ethz-b-000729485)
- 2 FISCHLIN, A. & ULRICH, M. (1990): Unterrichtsprogramm "Stabilität". 20pp. doi: [10.3929/ethz-a-004271266](https://doi.org/10.3929/ethz-a-004271266)
- 2 FISCHLIN, A. & ULRICH, M. (2010, 2. korrigierte Aufl.): Unterrichtsprogramm "Stabilität". 20pp. doi: [10.3929/ethz-b-000729486](https://doi.org/10.3929/ethz-b-000729486)
- 3 FISCHLIN, A. & ULRICH, M. (1990): Unterrichtsprogramm "Drosophila". 13pp. doi: [10.3929/ethz-a-004271268](https://doi.org/10.3929/ethz-a-004271268)
- 3 FISCHLIN, A. & ULRICH, M. (2010, 2. korrigierte Aufl.): Unterrichtsprogramm "Drosophila". 16pp. doi: [10.3929/ethz-b-000729487](https://doi.org/10.3929/ethz-b-000729487)
- 4 ROTH, O. (1990): Maisreife - das Konzept der physiologischen Zeit. 5pp. doi: [10.3929/ethz-b-000728532](https://doi.org/10.3929/ethz-b-000728532)
- 5 FISCHLIN, A., ROTH, O., BLANKE, T., BUGMANN, H., GYALISTRAS, D. & THOMMEN, F. (1990): Fallstudie interdisziplinäre Modellierung eines terrestrischen Ökosystems unter Einfluss des Treibhauseffektes. 35pp. doi: [10.3929/ethz-b-000728533](https://doi.org/10.3929/ethz-b-000728533)
- 6 FISCHLIN, A. (1990): On Daisyworlds: The Reconstruction of a Model on the Gaia Hypothesis. 19pp. doi: [10.3929/ethz-b-000728534](https://doi.org/10.3929/ethz-b-000728534)
- 7^{1*} GYALISTRAS, D. (1990): Implementing a One-Dimensional Energy Balance Climatic Model on a Microcomputer (*out of print*)
- 8 FISCHLIN, A., & ROTH, O., GYALISTRAS, D., ULRICH, M. UND NEMECEK, T. (1990): ModelWorks - An Interactive Simulation Environment for Personal Computers and Workstations (*for new edition see Systems Ecology Report 14*). 174pp. doi: [10.3929/ethz-b-000728535](https://doi.org/10.3929/ethz-b-000728535)
- 9 FISCHLIN, A. (1990): Interactive Modeling and Simulation of Environmental Systems on Workstations. 16pp. doi: [10.3929/ethz-b-000728536](https://doi.org/10.3929/ethz-b-000728536)
- 10 ROTH, O., DERRON, J., FISCHLIN, A., NEMECEK, T. & ULRICH, M. (1992): Implementation and Parameter Adaptation of a Potato Crop Simulation Model Combined with a Soil Water Subsystem. 30pp. doi: [10.3929/ethz-b-000728537](https://doi.org/10.3929/ethz-b-000728537)
- 11^{*} NEMECEK, T., FISCHLIN, A., ROTH, O. & DERRON, J. (1993): Quantifying Behaviour Sequences of Winged Aphids on Potato Plants for Virus Epidemic Models. 16pp. doi: [10.3929/ethz-b-000728538](https://doi.org/10.3929/ethz-b-000728538)

* Out of print

- 12 FISCHLIN, A. (1991): Modellierung und Computersimulationen in den Umweltnaturwissenschaften. 13pp. doi: [10.3929/ethz-b-000728539](https://doi.org/10.3929/ethz-b-000728539)
- 13 FISCHLIN, A. & BUGMANN, H. (1992): Think Globally, Act Locally! A Small Country Case Study in Reducing Net CO₂ Emissions by Carbon Fixation Policies. 9pp. doi: [10.3929/ethz-b-000728540](https://doi.org/10.3929/ethz-b-000728540)
- 14 FISCHLIN, A., GYALISTRAS, D., ROTH, O., ULRICH, M., THÖNY, J., NEMECEK, T., BUGMANN, H. & THOMMEN, F. (1994): ModelWorks 2.2 – An Interactive Simulation Environment for Personal Computers and Workstations. 324pp. doi: [10.3929/ethz-b-000728541](https://doi.org/10.3929/ethz-b-000728541)
- 15 FISCHLIN, A., BUGMANN, H. & GYALISTRAS, D. (1992): Sensitivity of a Forest Ecosystem Model to Climate Parametrization Schemes. 27pp. doi: [10.3929/ethz-b-000728542](https://doi.org/10.3929/ethz-b-000728542)
- 16 FISCHLIN, A. & BUGMANN, H. (1993): Comparing the Behaviour of Mountainous Forest Succession Models in a Changing Climate. 14pp. doi: [10.3929/ethz-b-000728543](https://doi.org/10.3929/ethz-b-000728543)
- 17 GYALISTRAS, D., STORCH, H. v., FISCHLIN, A., BENISTON, M. (1994): Linking GCM-Simulated Climatic Changes to Ecosystem Models: Case Studies of Statistical Downscaling in the Alps. 33pp. doi: [10.3929/ethz-b-000728544](https://doi.org/10.3929/ethz-b-000728544)
- 18 NEMECEK, T., FISCHLIN, A., DERRON, J. & ROTH, O. (1993): Distance and Direction of Trivial Flights of Aphids in a Potato Field. 13pp. doi: [10.3929/ethz-b-000728545](https://doi.org/10.3929/ethz-b-000728545)
- 19 PERRUCHAUD, D. & FISCHLIN, A. (1994): The Response of the Carbon Cycle in Undisturbed Forest Ecosystems to Climate Change: A Review of Plant–Soil Models. 29pp. doi: [10.3929/ethz-b-000728546](https://doi.org/10.3929/ethz-b-000728546)
- 20 THÖNY, J. (1994): Practical considerations on portable Modula 2 code. 6pp. doi: [10.3929/ethz-b-000728547](https://doi.org/10.3929/ethz-b-000728547)
- 21 THÖNY, J., FISCHLIN, A. & GYALISTRAS, D. (1994): Introducing RASS - The RAMSES Simulation Server. 32pp. doi: [10.3929/ethz-b-000728548](https://doi.org/10.3929/ethz-b-000728548)
- 22 GYALISTRAS, D. & FISCHLIN, A. (1996): Derivation of climate change scenarios for mountainous ecosystems: A GCM-based method and the case study of Valais, Switzerland. 23pp. doi: [10.3929/ethz-b-000728549](https://doi.org/10.3929/ethz-b-000728549)
- 23 LÖFFLER, T.J. (1996): How To Write Fast Programs. 20pp. doi: [10.3929/ethz-b-000728550](https://doi.org/10.3929/ethz-b-000728550)
- 24 LÖFFLER, T.J., FISCHLIN, A., & ULRICH, M. (1996): Benchmark Experiments on Workstations. 40pp. doi: [10.3929/ethz-b-000728551](https://doi.org/10.3929/ethz-b-000728551)
- 25 FISCHLIN, A., LISCHKE, H. & BUGMANN, H. (1995): The Fate of Forests In a Changing Climate: Model Validation and Simulation Results From the Alps. 18pp. doi: [10.3929/ethz-b-000728552](https://doi.org/10.3929/ethz-b-000728552)
- 26 LISCHKE, H., LÖFFLER, T.J., FISCHLIN, A. (1996): Calculating temperature dependence over long time periods: Derivation of methods. 19pp. doi: [10.3929/ethz-b-000728553](https://doi.org/10.3929/ethz-b-000728553)
- 27 LISCHKE, H., LÖFFLER, T.J., FISCHLIN, A. (1996): Calculating temperature dependence over long time periods: A comparison of methods. 14pp. doi: [10.3929/ethz-b-000728554](https://doi.org/10.3929/ethz-b-000728554)
- 28 LISCHKE, H., LÖFFLER, T.J., FISCHLIN, A. (1996): Aggregation of Individual Trees and Patches in Forest Succession Models: Capturing Variability with Height Structured Random Dispersions. 16pp. doi: [10.3929/ethz-b-000728555](https://doi.org/10.3929/ethz-b-000728555)
- 29 FISCHLIN, A., BUCHTER, B., MATILE, L., AMMON, K., HEPPERLE, E., LEIFELD, J. & FUHRER, J. (2003): Bestandesaufnahme zum Thema Senken in der Schweiz. Verfasst im Auftrag des BUWAL. 86pp. doi: [10.3929/ethz-b-000728556](https://doi.org/10.3929/ethz-b-000728556)
- 30 KELLER, D. (2003): Introduction to the Dialog Machine, 2nd ed. Price,B (editor of 2nd ed). 35pp. doi: [10.3929/ethz-b-000728557](https://doi.org/10.3929/ethz-b-000728557)
- 31 FISCHLIN, A. (2011, ed.2): IPCC estimates for emissions from land-use change, notably deforestation. 3pp. doi: [10.3929/ethz-b-000728558](https://doi.org/10.3929/ethz-b-000728558)

- 32 FISCHLIN, A. (2010): Leben im und mit dem Klimawandel – Lebensgrundlagen in Gefahr?. 17pp. doi: [10.3929/ethz-b-000728559](https://doi.org/10.3929/ethz-b-000728559)
- 33 FISCHLIN, A. (2010): Andreas Fischlin nimmt Stellung zu Fragen rund um die Klimaproblematik - unter Mitwirkung von Markus Hofmann, Christian Speicher, Betty Zucker, Martin Läubli und Jürg Fuhrer. 49pp. doi: [10.3929/ethz-b-000728560](https://doi.org/10.3929/ethz-b-000728560)
- 34 FISCHLIN, A. & FISCHLIN-KISSLING, M.M. (2011): Limits to Growth and Courseware «World Model 2». Update and translation of “Unterrichtsprogramm «Weltmodell 2»” by Fischlin, A., T. Blanke, D. Gyalistras, M. Baltensweiler & M. Ulrich, 1993 (Systems Ecology Report No. 1). 41pp. doi: [10.3929/ethz-b-000728561](https://doi.org/10.3929/ethz-b-000728561)
- 35 FISCHLIN, A. & ULRICH, M. (2025): Courseware «Stability». Revision and translation of “Unterrichtsprogramm «Stabilität»” by Fischlin, A. & M. Ulrich, 2010 (Systems Ecology Report No. 2). 20pp. doi: [10.3929/ethz-b-000728562](https://doi.org/10.3929/ethz-b-000728562)

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