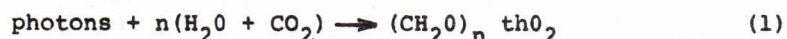


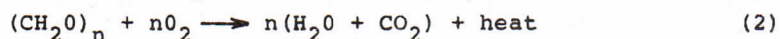
11 Ecosystems

R. Harmsen

In my previous lecture in "Nature, Science and Man", we have seen one hypothetical model for the origin of life on earth. Living matter arose in an environment where there was much "inorganic" matter suspended in the ocean, but the total mass of such "inorganic" matter on Earth at the time of the origin of life was much lower than now. Organic molecules are not chemically stable in an oxygen containing environment, they can only maintain themselves when protected by the life process, and that is how nowadays most of our organic matter is protected. We must therefore postulate that even if life had not arisen, the concentration of archaic organic matter would have levelled off at a point where its synthesis:



would have been balanced by its oxidation:



Reaction (1) in the primitive hydrosphere must have been a constant, or decelerating reaction in that the supply of photo energy is constant, water is overly abundant, and CO_2 can become a limiting factor when its concentration falls. Reaction (2) on the other hand must have been an accelerating one, in that its rate is highly dependent on the concentration of O_2 . At first some O_2 may have gone towards oxidizing hydrogen, but soon it would have started to accumulate, leaving the atmosphere far too reactive for further accumulation of organic matter. We can even see how this semi-reactive environment would provide a strong natural-selective force in favour of the more "stable" molecules and in favour of those molecular complexes capable of self maintenance and eventually self replication. In other words, pre-biotic evolution may have selected for "life" properties!

One life arose, the concentration of organic matter fell, and at the new equilibrium level, the living portion of all organic matter must have comprised a very low biomass. The main limiting factor for life on earth

was the constant, but low, rate of inorganic photosynthesis (Reaction 1) which was balanced by a combined effect of the new very low inorganic breakdown (Reaction 2) and life centred oxidation (respiration). Only two possible mechanisms existed which could lead to an increase in biomass. Since natural selection would obviously favour any increase in biomass one would expect both these mechanisms to become part of life sooner or later. The first mechanism was a more efficient respiration based on several alternative pathways and utilizing as many electron transfer steps as possible, so as to optimize the "usefulness" of each bit of low-entropy energy before discarding it in the form of heat or unuseable chemical energy. The second mechanism would be a truly revolutionary advance: concentrate the photosynthetic process into the living organism, and improve its efficiency by providing in abundance photoreceptive chemicals and catalysts.

Both these mechanisms did occur. It is even possible that life controlled photosynthesis was already present in the original living organisms. Whether it was present from the onset or started somewhat later is rather immaterial to our argument. Let us, however, consider the impact this new development had on the biosphere.

We now have three ways in which a living organism can obtain energy, one is through photosynthesis, another through consuming non-living organic matter. Since each of these sources of energy represents a totally different methods of exploitation, one would expect natural selection to favour the evolution of specialists. This indeed happened, and we find three or four main categories of organisms each deriving their energy supply in a totally different way. They are called trophic categories. The first kind are photosynthesizers, producers, energy converters, or autotrophs. In our present day world they include plants, algae, and some bacteria. They convert photo-energy into potential chemical energy (Reaction 1) and use the thus synthesized organic materials to structure their own bodies, and as reserve food (to be used at night, for instance).

The second, third and fourth kind all use low entropy chemical energy as their energy source. They are all called heterotrophs, but are further divided on the basis of the kind of "food" they take in. The primary consumers specialize in consuming the photosynthesizers. The secondary consumers consume consumers; they are therefore predators, parasites or cannibals. Finally, the decomposers consume non-living organic matter.

The subdiscipline of biology called "Ecology" studies the relationships of these various categories to one another, and to the non-living world. Ecology is often defined in a narrower sense, and also quite often in a broader sense. Personally, I prefer to play a bit of a semantic game, and define ecology as the study of ecosystems. I do, however, follow this statement with a definition of ecosystem.

An ecosystem is a system in which the constituent parts are whole organisms, populations of organisms, or trophic categories, and their non-living environment. Ecosystems are, of course, open systems. In broad, general lines all ecosystems can be represented by the energy and matter flow chart represented in Figure 1.

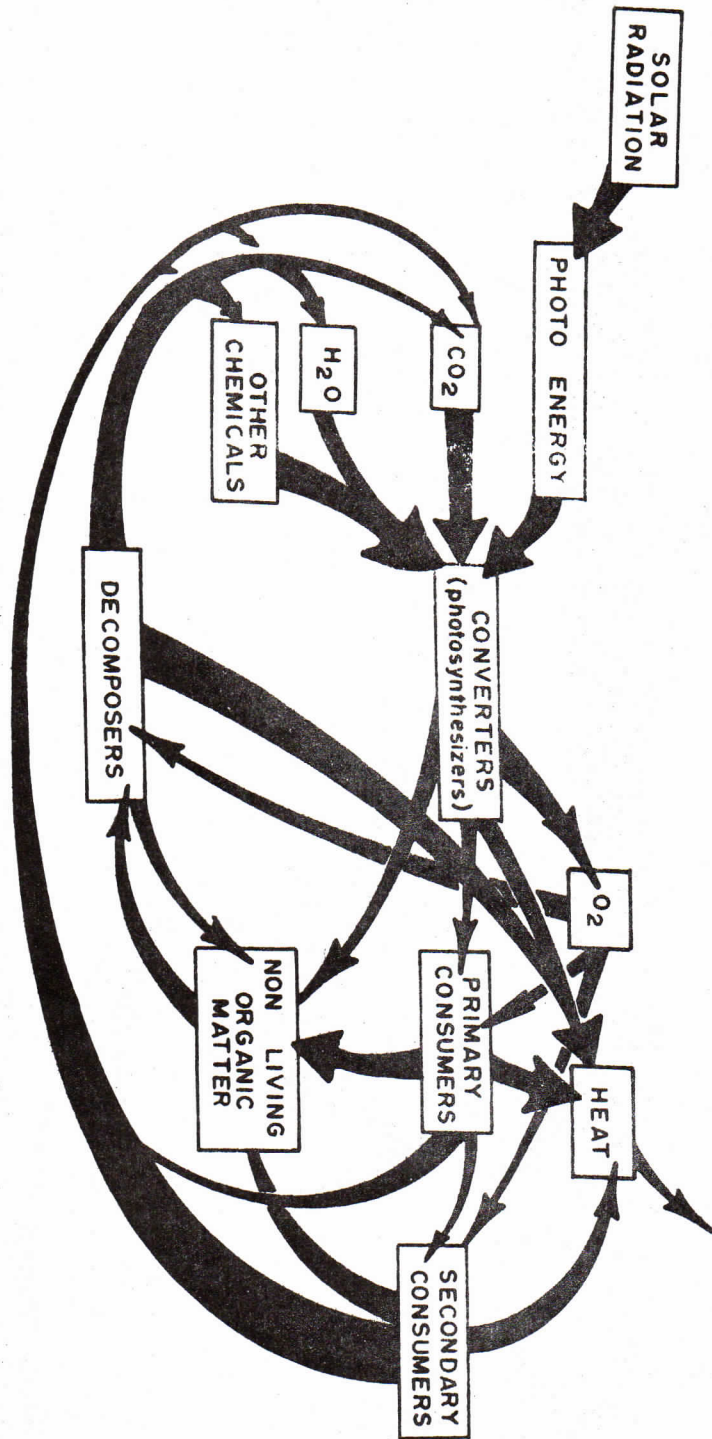


Figure 1. A general ecosystem energy and matter flow chart.

There are, of course, often more complexities and more constituents. For instance, non-living organic matter can under certain circumstances be "fossilized" into stable organic compounds such as peat, humus, coal, oil and gas, so that the earth has accumulated large quantities of that type of material. Also, many organisms are not quite as specialized as to fit neatly into one trophic category. Man, himself, can be primary consumer, secondary consumer and decomposer.

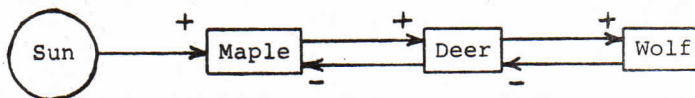
Before we look at some of the pronounced general qualities of ecosystems, let us look at one specific ecosystem, the typical Northern forest of, for instance, Algonquin Park.

We can begin with an energy balance sheet with an input and an output, as well as a more or less analyzed storage and decay delay, while the energy is part of the biosphere. The input consists for 99+% of radiant energy emitted from the sun, and the output consists of heat. Of course, only a small fraction of all incident radiation is trapped in the bioconversion system, the rest is biologically transferred directly into heat or re-emitted back into space. Also, much unuseable energy, in the form of heat, is brought into the ecosystem via warm air masses, and heat is lost that way too. The most important observation to make, however, is that no energy is permanently stored, that there is no accumulation of energy (except for very localized peat bogs). The implication of this observation is, of course, that the input equals the output -- that we are dealing with a dynamic equilibrium, a steady-state system.

The richness of the Algonquin Park forest ecosystem depends on many factors. The evolutionary trend towards ever increasing complexity and diversity is counteracted constantly by changes in the environment leading to localized extinctions of certain life forms. Also, certain factors limit the potential level of overall biological activity, for instance low temperatures in winter time virtually arrest all photosynthesis, lack of essential chemicals such as phosphate or nitrate slow down plant growth, on shallow soils a shortage of water may be an important limiting factor, etc. etc.

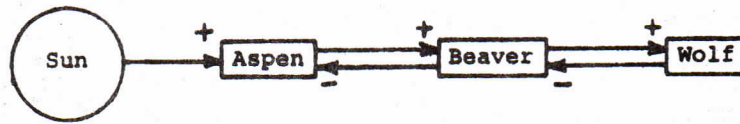
Obviously, in the Algonquin Park ecosystem all the different limiting factors working together do not prevent the presence of a rich and varied assemblage of interacting life forms to maintain a distinct ecosystem. It is clearly a mammoth job to study each and every one of the multitude of interactions that exist between all the different constituents of this system, a job which is totally beyond the scope of this lecture.

Yet, a knowledge of these interactions is essential in that the basic steady state nature of the system is maintained by all these reactions. If we look at one of the sequences of trophic units in our system, we will immediately sense the importance of the interactive reactions. For instance the sequence:

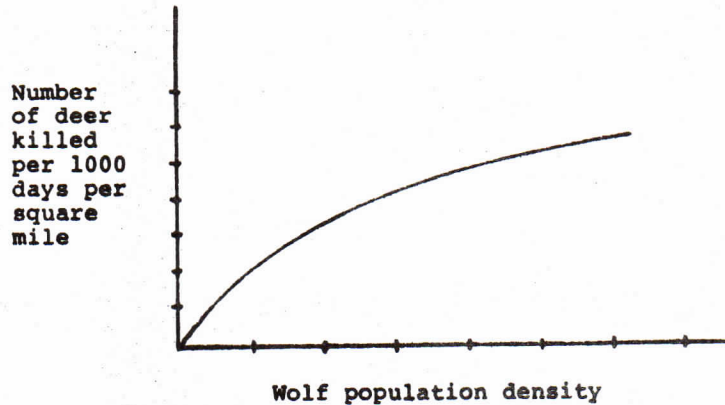


shows five basic interactions, the effect of sun light on the growth of maple trees, the effect of maple foliage on the growth of the deer population, the effect of deer on the growth of the wolf population, the effect of wolves on the demise of the deer population, and finally, the effect of the deer on the defoliation of the maple forest.

Similarly, the complexity of the system is immediately apparent, when we realize the partial overlap, and therefore interaction between the maple-deer-wolf sequence and another such trophic sequence:



For each reaction, we can usually add a positive or negative indication, and sometimes we can even do better. We can graphically represent the functional relationship. For instance, the effect of the number of wolves on the rate at which deer are being killed can be represented as follows:



It is, however, obvious that in reality such a relationship is affected by a large number of other factors, and that actual units on the ordinate and abscissa, as well as an actual shape for the curve can only be established on the basis of carefully gathered "hard" data.

If, however, we merely want to understand the nature of the dynamics of an ecosystem, we may proceed without the encumbrance of hard data collecting. We can effectively construct a model, which includes the essential state variables of a simple ecosystem and is dynamically isomorphic with such a system.

Let us, therefore, forget about Algonquin Park, and in our mind create an ecosystem consisting of only two state variables: a utilizer (U) and its resource (R). In Fig. 2, we see a phase plane diagramme of potential interactions of U and R. Along the ordinate we have an ascending plot of the density of U, and along the abscissa we have a plot of R. Both plots use arbitrary scale units. If we make a number of assumptions, we can predict the dynamic behaviour of the model for each (U,R) starting point. These assumptions are the following:

1. Below a certain density of R, the average U individual cannot maintain himself, above that density he can. This means that all (U,R) coordinates with an R value less than a certain value (3.6 in Fig. 2), will display a dynamic behaviour that will reduce the density of U.
2. That a curve can be plotted below which R can increase, and above which R will inevitably decrease. The complex nature of this curve is the

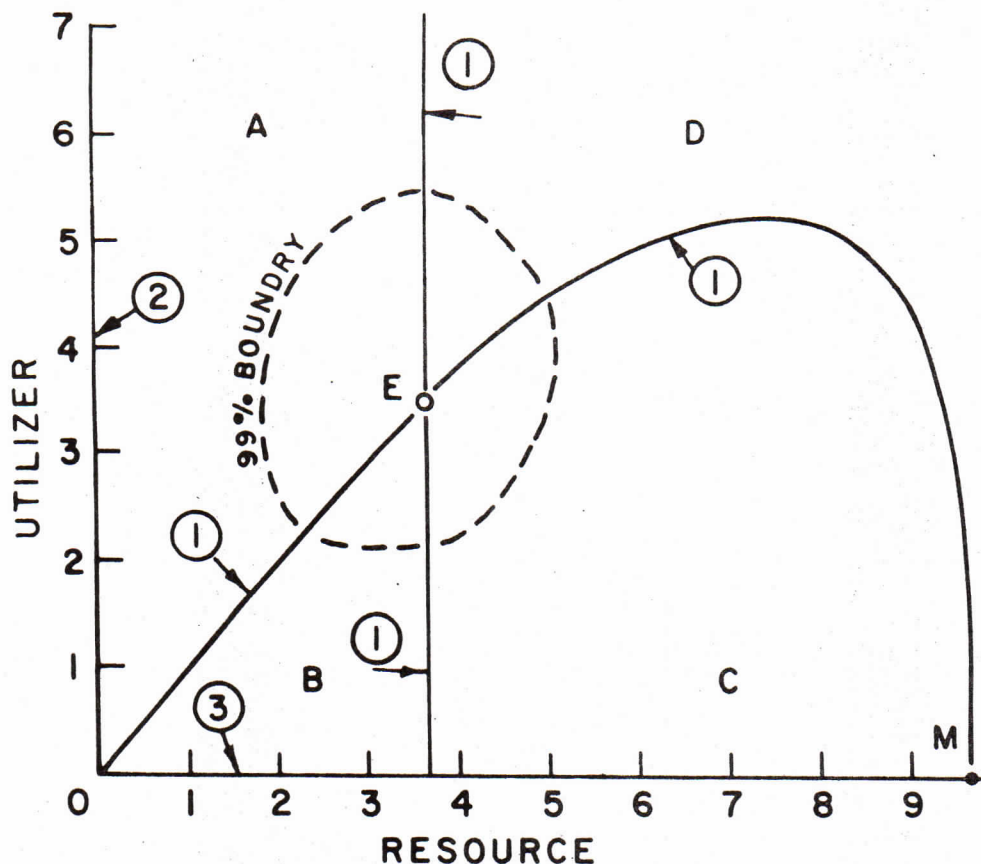


Figure 2. Phase-plane diagramme of dynamic relationship of a utilizer and its resource. (see text for detailed explanation)

result of increased U effectiveness at higher U densities, of increased R reproductive output at higher R densities, and of some intrinsic maximum R can not exceed.

We can now see that our field is partitioned into four sections, A, B, C and D, and for each section we recognize one or more dynamic possibilities. Within section A any (U,R) point can develop over time into one of two pathways: (1) it proceeds towards section B, or (2) it proceeds towards the ordinate (zero resource) and from there to the $(0,0)$ coordinate. In section B it also has two potential pathways: (1) it proceeds towards section C, or (3) it proceeds towards the abscissa (zero utilizer), and along there to point M, coordinate $(0, 9.5)$. In section C only one possible pathway exists, all points will proceed towards section D. In section D, again, only one thing can happen; all trajectories will cross into section A. Basically, therefore, we only have three possible dynamic trajectories: an outward spiralling one leading to the destruction of the system, a stable cycling one, and an inward spiralling one, which leads to stability around point E.

In existing, undisturbed ecosystems one would not expect to find outward spiralling trophic relationships -- such relationships, if present, would at best be transitory, certainly not very observable. In stable ecosystems cycling trophic relationships occur, but must be considered exceptional, perhaps because only minor changes in the system could so easily lead to an outward spiral and destruction of the system. Most stable systems are of the inward spiralling type, with superimposed on it a certain amount of random noise, so that both point E and the (U,R) coordinate oscillate randomly around some average E point. One can imagine that it would be possible to draw for any particular (U,R) system a boundary line denoting the location area for 99% (or 95%, or whatever) of all randomly chosen real (U,R) pairs. All along, of course, we assume, that all external factors remain constant.

The most fascinating property of a simple utilizer-resource system appears to be its self-regulatory property. This behavioural trait of trophic systems is called ecological homeostasis. There is theoretical evidence which indicates that the evolution of the constituent parts of an ecosystem is likely to proceed so as to increase the strength of this homeostasis for the entire ecosystem (in other words, evolution leads to changes in both U and R, so that under prevailing circumstances (U,R) systems will strongly spiral inwards).

In the past couple of pages I have made two important qualifying statements, I have mentioned that outward spiralling systems are not likely to be found in undisturbed conditions, and that inward spiralling will develop under prevailing conditions. Clearly, if conditions are drastically changed, or if ecosystems are suddenly disturbed, one could witness normally inward spiralling systems either to change to outward spiralling, or merely oscillate randomly to a point of no return. Such phenomena are called "exceeding the homeostatic limits of the system", and it is the theoretical basis of the more commonly used, less scientific term "pollution".

Let me conclude with a rather well documented case of human interference leading to the destruction of an ecosystem because of our stressing this ecosystems beyond its homeostatic limits.

In the late 19th century the Kaibab plateau in Arizona was typified by a vegetation of sparsely distributed massive, fire resistant pine trees and a lush undergrowth of shrubbery. The shrubbery burned locally and frequently, but there was always an abundant growth which provided a sizeable mule deer population with browse. The deer, in turn, were the main resource of a population of cougar. This was a simple ecosystem, and all indications are that a dynamic equilibrium was maintained between the cougar (U) and the deer (R), as indicated in the left half of Fig. 3.

The right half of Fig. 3 indicates the relationship of deer and browse. Clearly, browse density was limited not by deer, but by an intrinsic limitation, or by a combination of space, moisture, fire, nutrients, etc. Whereas in the cougar-deer system all (U,R) points are close to E_1 , in the deer-browse system all the (U',R') points are in a cloud centering on a point of much higher browse and much higher deer density than E_2 . One could

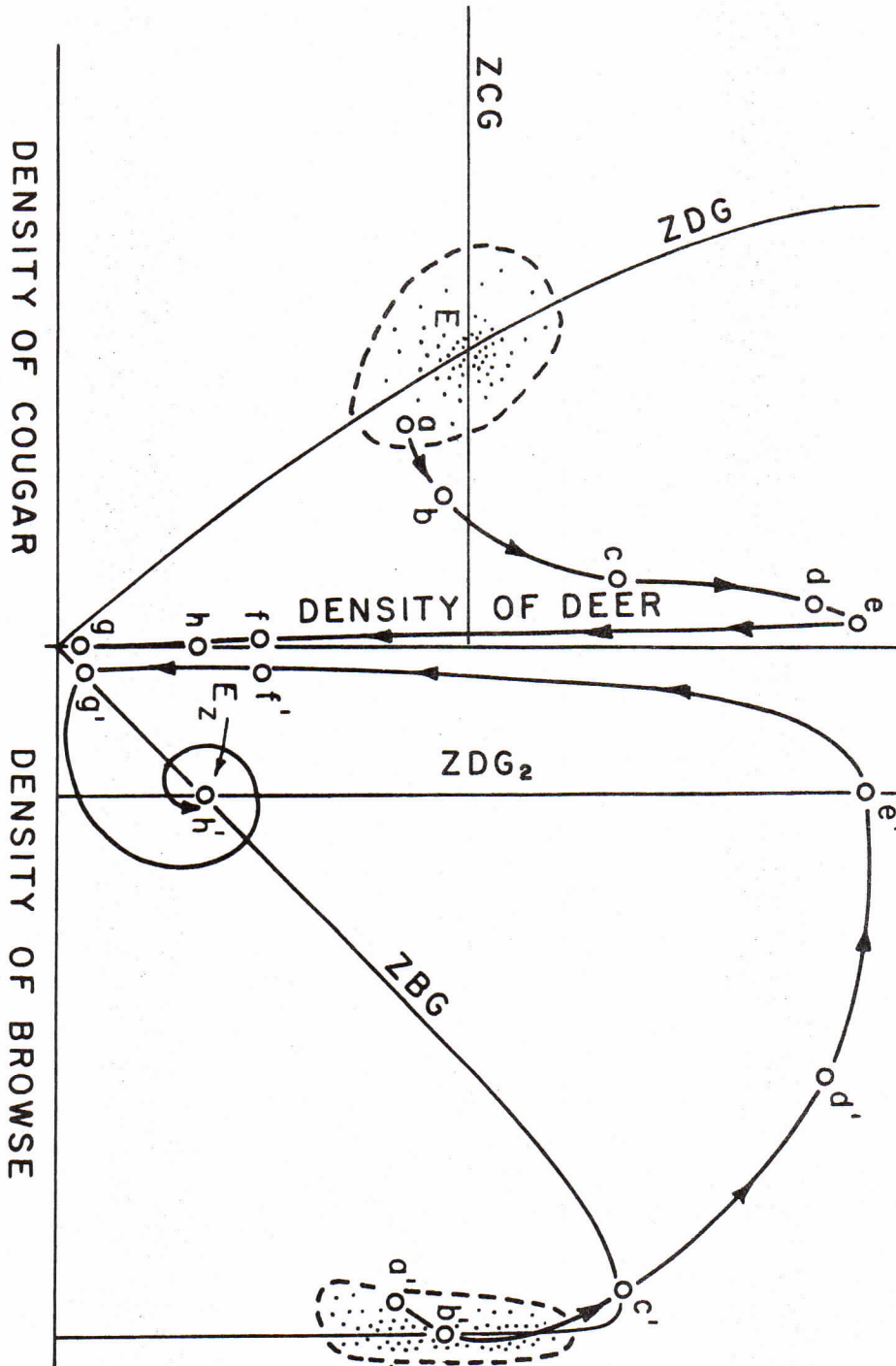


Figure 3. Dual phase-plane diagram of a tri-state variable trophic sequence. This particular diagram is a rough model for the Kaibab plateau and its populations of deer and cougar. (see text for details)

describe this ecosystem as being maintained at a high biomass level, or at a high level of "richness", through the activities of the predator (the cougar).

Unfortunately, the local settlers and their government did not understand the intricacies of ecological homeostasis, and they decided to try to exterminate the varmints.

Exact records are not available and those that are, are not terribly reliable. Documentation, however, is sufficiently clear, that the following more or less speculative scenario can be presented. At a certain point in time, the cougar, deer and browse populations were at points "a" (Fig. 3), and let us assume that severe, organized, Teddy Roosevelt type cougar hunting was initiated at that time. Both sets of points a - h represent a series of cougar-deer-browse population levels over approximately a 20 year time sequence. From a to e, we witness a virtually complete elimination of the cougar from the region. Simultaneously, the deer population explodes. Up to time c, nothing irreversible has happened, but once beyond c we realize that nothing can prevent our trajectory from crossing line ZDG₂, which in fact happens at e'. Once beyond e, the deer population begins to collapse, but only when we reach g' is the deer/browse ratio so low that the browse can recover. In the absence of cougars, however, the deer also start to recover soon after, and the growth rate of the deer population is high enough to bring the deer/browse ratio back above ZBG. The inevitable result is the establishment of a new, less diverse, and less "rich" ecosystem equilibrium. Notice that complete local extinction may in fact have occurred, but reinvasion has brought the deer back. The cougar, on the other hand, cannot come back, at least not until the deer population will increase so as to exceed line ZCG, which will not happen naturally as long as the new equilibrium is maintained. Perhaps consciously planned management can lead to a reinstatement of the old system, but perhaps that is not the case, since the very low vegetation level of the past 50 years has resulted in high degrees of erosion. Soil conditions may by now be too poor for the re-establishment of a sufficiently high vegetation density to allow a sufficiently high deer density to allow the return of the cougar.

In summary, we recognize that ecosystems are maintained in some equilibrium state by homeostatic mechanisms inherent in the structure of the ecosystem itself. These mechanisms can absorb a considerable amount of external stress. Too much external input, however, will exceed the homeostatic limits of the system, and it will collapse. The nature of the internal interactions between system constituents and their inherent homeostasis form the essence of the study of ecology, the manipulation of these interactions can lead to a "good" management, but can also lead to a destruction of ecosystem equilibrium, or pollution.

References:

1. Boughey, A.S. 1973. Ecology of Populations. Collier-MacMillan, Toronto (180 page paperback).
2. Caughley, G. 1970. Eruption of Ungulate Populations. In Ecology, Vol. 51, pp. 53-72.