

Applications of the Survival Theory to Ecology

(steady-state theory of mutations/population and community dynamics)

D. CARL FREEMAN*, LIONEL G. KLIKOFF*, AND HENRY EYRING†

*Department of Biology, †Department of Chemistry, University of Utah, Salt Lake City, Utah 84112

Contributed by Henry Eyring, July 1, 1974

ABSTRACT The Eyring-Stover theory of survival developed in earlier papers can be readily applied to a wide diversity of ecological phenomena, with implications for identifying basic responses of organisms to their environment. We report several examples to demonstrate the generality of the theory.

Over the last two decades ecology has begun to develop a theoretical basis. The works of Holling (1), Hutchinson (2), Levins (3), MacArthur (4, 5), Wilson (4), and others have contributed to that framework, permitting the prediction of some ecological phenomena. The model that follows is an attempt to analyze many ecological questions with a more concise theory, enhancing the ability to predict ecological events with general confidence.

In 1970, Eyring and Stover (6-10) developed their survival theory. Their theory was based on a 20-year study of the effects of aging, cancer, and various forms of internal irradiation in beagles. The irradiation was administered in a manner such that various types of irradiation could act simultaneously on the same site through the same mechanism, through independent mechanisms on the same site, and on independent sites through independent mechanisms. They were able to show that the probability of an individual surviving in a homogeneous population is given by

$$S = (1 + e^{-(a-bt)})^{-1} \quad [1]$$

where S is survival, a is the organisms reserves that it can use in resisting those forces leading to nonsurvival, and b is the difference between the rates of damage and repair, with t representing time. By using the absolute rate theory, they were able to show that

$$(a - bt) \equiv [(\Delta G^{\neq}_{oi} - \Delta G^{\neq}_{oj}) / (RT - \sum_i \ln C_{oi} + \sum_j \ln C_{oj}) + (\sum_i k_i - \sum_j k_j)t] \quad [2]$$

ΔG^{\neq}_{oi} represents the free energy of activation of the damaging process, with C_{oi} being the concentration of i th molecule entering into the damaging reaction; ΔG^{\neq}_{oj} is the free energy of activation of the repair process, with C_{oj} being the initial concentration of the j th molecule used in the repair process. R is a constant, T is temperature, and the k terms are rate constants for destruction of the genes manufacturing the j th molecule.

The Eyring-Stover equation [$S = (1 + e^{-(a-bt)})^{-1}$] can be derived from other considerations: (a) Let r be the number of sites available. We suppose further that (b) n sites are occupied, and (c) the rate at which a site becomes occupied is proportional to the product of the number of organisms seek-

ing to fill that site and the number ($r - n$) of empty sites. This yields the equation

$$\frac{dn}{dt} = k(r - n)n \text{ or } \frac{dn/r}{dt} = (k'r) \left(\frac{r-n}{r} \right) \frac{n}{r} \quad [3]$$

Now if we let $n/r = N$, the fraction of sites that are filled, we have

$$\frac{dN}{dt} = k N(1 - N) \quad [4]$$

The solution to this equation is readily found to be

$$N = (1 + e^{-k(\tau-t)})^{-1} \quad [5]$$

k is a rate constant, and is equal to the algebraic sum, b , of the processes promoting or hindering occupation (see Eq. [1]). τ represents the time of half survival, and $k\tau$ is equal to a , the reserve strength of our system. If the time of the initial observation does not correspond to $t = 0$, then the equation is

$$S = (1 + e^{-(a-b(t+\tau))})^{-1} \equiv (1 + e^{-(a'-bt)})^{-1}$$

where a' may be positive or negative depending on whether t starts before or after the time (τ) of half survival. Note that $S = (1 + e^{a-bt})^{-1}$ corresponds to growth, while $S = (1 + e^{-(a-bt)})^{-1}$ corresponds to decline.

The equation $N = (1 + e^{a-bt})^{-1}$ was derived by Verhulst (11) from somewhat different assumptions. We do not maintain, as Verhulst did, that this is the equation for population growth unless there is only one cause affecting the growth of the population and the population is homogeneous, in which case the equation would be of the form described below in Case A, otherwise it will follow a more complex form, Case B or C, below.

Considering the generality of the Eyring-Stover theory, we hypothesized that their mathematical formalization could be applied to a diversity of ecological phenomena, including population growth; growth of an individual; the number of species colonizing an island as a function of time, distance or area; and the dynamics of seral communities and ecosystems.

Eyring and Stover described five cases of the theory, each of which can be applied to ecological events. Those cases and examples are described below:

Case A. "Nonsurvival of a homogeneous population from a single cause."

Using Eq. [1] we see that

$$dS/dt = -bS(1 - S). \quad [6]$$

TABLE 1. Decline in density of a population of *Ranunculus acris* in Wales. Sarukhan's population G_2

Time (in weeks)	Observed	Predicted
0	26	24
4	23	23
5	23	23
8	23	22
10	23	22
13	23	22
15	21	22
23	20	20
26	17	20
28	17	19
32	16	18
42	15	16
50	15	14
54	15	13
56	13	13
58	12	12
59	11	12
62	11	11
66	8	10
77	5	8
81	5	7
107	4	3

$a = 2.18, b = 0.04.$

TABLE 2. Decline in density of a population of *Ranunculus bulbosus* in Wales. Sarukhan's population F_1 .

Time (in weeks)	Observed	Predicted
0	28	26
5	28	25
6	27	25
8	23	25
11	23	24
18	22	23
27	20	21
28	20	21
30	19	20
31	17	20
57	11	12
58	11	11
60	11	11
62	11	10
66	11	9
77	11	6
78	11	6
82	11	5
107	10	2

$a = 2.44, b = 0.0489.$

We have used Case A to describe decline of populations due to aging in two species of *Ranunculus* (12). We assumed that aging was the principle cause for the decline and that it was effected principally through one mechanism. Tables 1 and 2, based on data from Sarukhan and Harper (12), show the success of the model based on these assumptions.

The growth of a tree under ideal conditions, i.e., no competition or minerals limiting, can be treated as the result of a single cause, the addition of cells. The high correlation

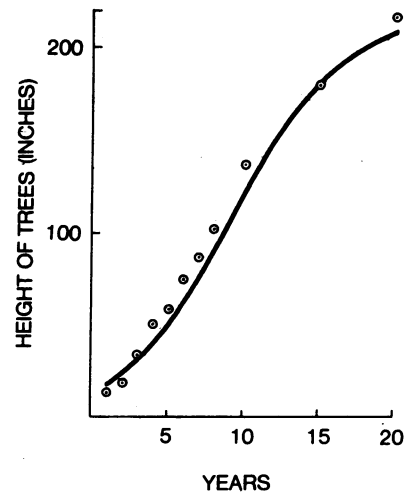


FIG. 1. Growth of an individual tree, American elm, with time. ($a = 2.63, b = 0.28359.$)

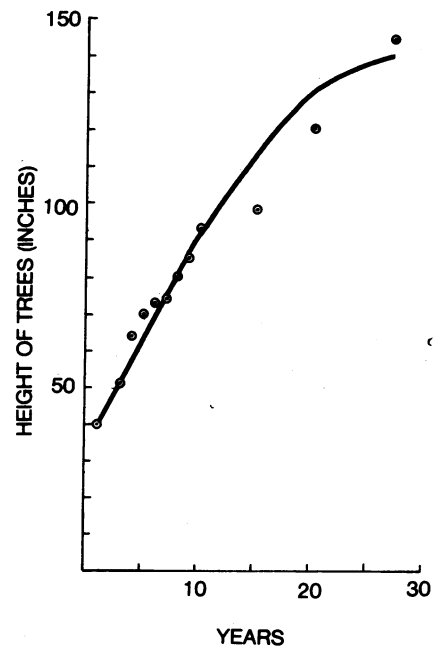


FIG. 2. Growth of an individual tree, hawthorn, with time. ($a = 1.0619, b = 0.159.$)

between DenUyl's (13) data and the predicted values lend confidence to the theory (Figs. 1 and 2).

If there is more than one cause contributing to survival or nonsurvival, then the survival S would follow either Case B or Case C as described below.

Case B. "Survival with several simultaneous independent mechanisms contributing to nonsurvival."

$$S = \prod S_i; \text{ where } S_i = (1 + e^{-bt_i})^{-1}$$

$$\frac{dS}{dt} = \sum_j \frac{dS_j}{dt} \prod_{i \neq j} S_i \tag{7}$$

$$\frac{d \ln S}{dt} = \sum_j \frac{d \ln S_j}{dt} \tag{8}$$

Note that the individual rates of nonsurvival are multiplied by the probability that the organism or population has not become extinct from the other causes.

TABLE 3. Decline in density of *Pinus taeda* in a North Carolina forest

Time (in years)	Observed	Predicted
11	26.8	25.2
22	18.2	20.2
31	15.1	15.8
34	12.2	14.3
42	12.5	10.7
75+	3.4	2.3

$$a = 1.46, b = 0.055.$$

This form of the equation would be applicable where one species was in competition with several other species, and competing through different mechanisms with each species. Competition with and/or predation of a species would follow this form. The only requirement is the independence of the mechanisms.

Case C. "More than one cause acting through the same mechanism." The only difference between the formalization of Case A and Case C is that the b term in Case A is replaced by $\sum_i b_i$.

$$\text{So the equation is } S = (1 + e^{-(a - (\sum_i b_i)t)})^{-1}.$$

Case C would be applicable where several species are in competition for the same resource and competing through the same mechanism. This case would also apply where several species of predators are preying on the same species.

Oosting's data (14) on *Pinus taeda* (Table 3) and oak-hickory (Fig. 3) in North Carolina illustrate the theory for this case. The number of species colonizing an island as a function of time is also an example of this case; the rates of immigration and extinction are summed to equal b . The data in Fig. 4 are after MacArthur and Wilson (15) and demonstrate the vigor of the model in this island biogeographical question.

Case B and Case C are compounded frequently in ecology: one can have several species competing for the same resource through the same mechanism and competing for different resources through another mechanism, both forms taking place at the same time. Eyring and Stover point out (16) that "it will be important in each case to establish whether a new cause acts through the same mechanism as in Case C or through an independent mechanism as in Case B or in both ways. In the

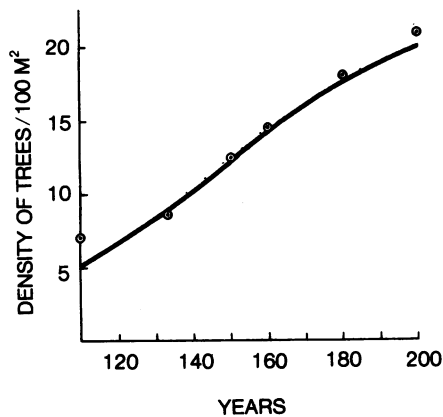


FIG. 3. Increase in density of oak-hickory in North Carolina. ($a = 5, b = 0.034$).

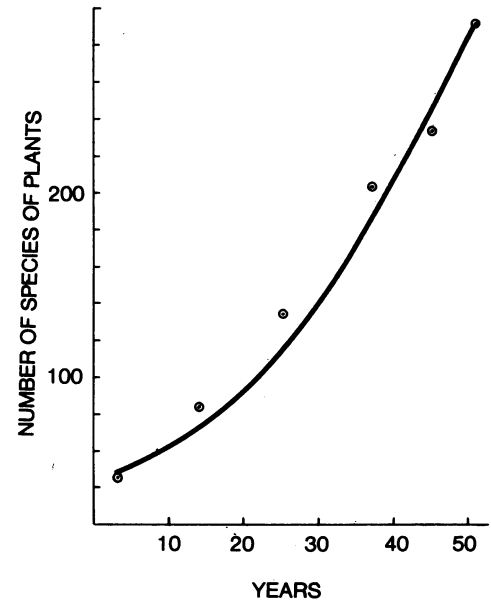


FIG. 4. Increase in number of species of higher plants on the three islands of the Krakatua group. ($a = 3.08, b = 0.0606$).

latter circumstance, we would have Case C with possible changes in the cell's reserves, the a_i values, and also in the rates of change, the b_i values." The last circumstance is the case in population growth and some island biogeographical questions. To handle this case, the cause that is acting in both ways should be treated as a product of causes. Fig. 5 shows the increase in numbers of species of higher plants on islands as a function of area rather than time (17).

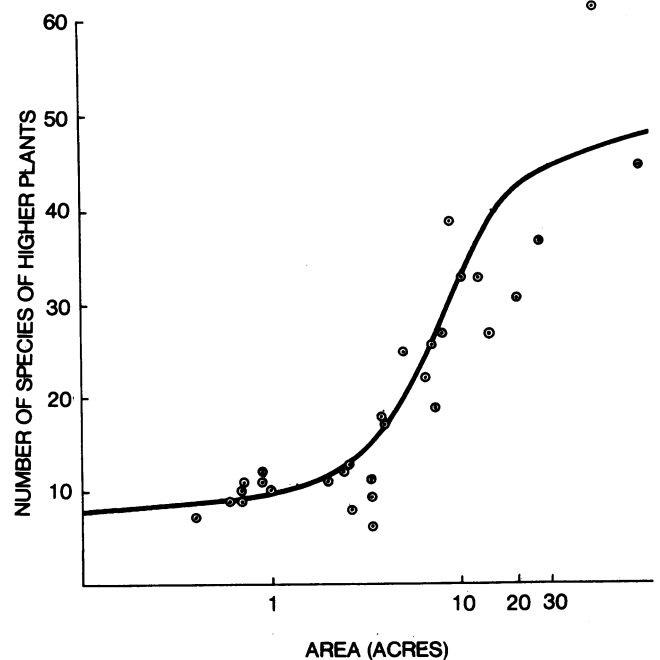


FIG. 5. Relationship between number of higher plant species and area of islands in the South Pacific. (Note that area has replaced time in the equation and the calculated value was based on a running average, and assuming 88 acres to be the maximum allowable area.) ($a = 1.40, b = 0.23$).

Case D. "A single mechanism of nonsurvival requiring m like unchanged sites and n changed sites." Each site in the Eyring-Stover theory can be considered to be the population of a single species in a seral community. The survival (S) of the community is given by:

$$S = \prod_{r=0}^{n-1} \frac{(m+r)}{(n-1)!} \sum_{r=0}^{n-1} \frac{(-1)^r (n-1)! P^{m+r}}{(n-1-r)! r! (m+r)} \quad [9]$$

where $P = (1 + e^{-(a-b)})^{-1}$.

Case E. "Nonsurvival due to independent action on separate systems of sites."

$$S = \prod_i S_i \quad [10]$$

The Eyring-Stover model has far-reaching possibilities in ecology, as demonstrated above. The single formalization is being used to explore predation, competition, aging, community dynamics, and ecosystems.

We thank the National Science Foundation and the United States Forest Service.

1. Holling, C. S. (1973) *Annu. Rev. Ecol. Syst.* 4, 1-25.
2. Hutchinson, G. E. (1965) *The Ecological Theater and the Evolutionary Play* (Yale University Press, New Haven and London).

3. Levins, R. (1968) *Evolution in Changing Environments* (Princeton University Press, Princeton, N.J.).
4. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton University Press, Princeton, N.J.).
5. MacArthur, R. H. (1972) *Geographical Ecology* (Harper and Row, New York, Evanston, San Francisco, London).
6. Stover, B. J. & Eyring, H. (1970) *Proc. Nat. Acad. Sci. USA* 66, 132-139.
7. Eyring, H. & Stover, B. J. (1970) *Proc. Nat. Acad. Sci. USA* 66, 441-444.
8. Stover, B. J. & Eyring, H. (1970) *Proc. Nat. Acad. Sci. USA* 66, 672-676.
9. Eyring, H. & Stover, B. J. & Brown, R. A. (1971) *Proc. Nat. Acad. Sci. USA* 68, 1670-1672.
10. Johnson, F. H. & Eyring, H. & Stover, B. J. (1974) in *The Theory of Rate Processes in Biology and Medicine* (John Wiley and Sons, Inc., New York), pp. 549-598.
11. Pearl, R. (1925) in *The Biology of Population Growth* (Alfred A. Knopf Inc., New York), pp. 4; 242.
12. Sarukhan, J. & Harper, J. (1973) *J. Ecol.* 61, pp. 690-691.
13. DenUyl, D. (1962) in *Regional Silviculture of the United States*, ed. Barrett, J. W. (The Ronald Press Co., New York), p. 169.
14. Oosting, H. J. (1942) *Amer. Midl. Natur.* 28, 22; 55.
15. MacArthur, R. H. & Wilson, E. O. (1967) in *The Theory of Island Biogeography* (Princeton University Press, Princeton, N.J.), p. 49.
16. Stover, B. J. & Eyring, H. (1970) *Proc. Nat. Acad. Sci. USA* 66, 679.
17. Niering, W. A. (1963) "Terrestrial ecology of Kapingamarangi Atoll, Carolina Islands," *Ecol. Monogr.* 33, 131-160.