1999

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Amitrajeet A. Batabyal

Utah State University

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ON SPECIES SUBSTITUTABILITY, RESILIENCE, AND THE OPTIMAL MANAGEMENT OF ECOLOGICAL-ECONOMIC SYSTEMS

by

AMITRAJEET A. BATABYAL

Department of Economics
Utah State University
3530 Old Main Hill
Logan, UT 84322-3530

March 1999
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Amitrajeet A. Batabyal, Associate Professor

Department of Economics
Utah State University
3530 Old Main Hill
Logan, UT 84322-3530

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ABSTRACT

The significance of the concept of resilience in determining the static and the dynamic behavior of jointly determined ecological-economic systems has been recognized by ecologists at least since Holling (1973). This notwithstanding, there are very few formal studies of such systems that analyze the ecological and the economic aspects of the problem. Consequently, this paper has two objectives. First, a new renewal theoretic measure of resilience is proposed. This measure explicitly accounts for the role of species substitutability in determining ecological resilience. Next, this measure is used to study some aspects of the optimal management of ecological-economic systems.

Key words: Ecological-economic system, optimal management, renewal theory, resilience

JEL classification: Q30, D80
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1. Introduction

In recent times, a consensus has emerged among ecologists and economists that the optimal management of jointly determined ecological-economic systems (hereafter ecosystems) calls for the prudent use—and possibly the conservation of at least some—of the resources provided by such ecosystems. The question as to how ecosystems are best managed is closely related to the notion of substitutability; in particular, to two kinds of substitutability. The first kind concerns the substitutability between natural and produced capital and the second kind concerns the substitutability between different kinds of natural capital. As far as this second kind of substitutability is concerned, economists now generally agree that it is not reasonable to assume that environmental resources that are substitutes in terms of consumption are also substitutes in the performance of ecological functions. Nevertheless, as Perrings (1996, p. 232) has noted, "...the complementarity between species in many ecosystems is still very imperfectly understood."

This inter-species complementarity is significant because the resilience of ecological functions in most terrestrial ecosystems is an increasing function of the number of substitute species that can perform those functions. (Schindler, 1990; Holling, 1992). Increasingly, this concept of ecological resilience has come to represent an integral part of the academic debate about the optimal

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1This paper has benefitted from the comments of (i) participants at the 1998 Annual Meeting of SRIEG 70, (ii) participants at a seminar at Utah State University, and (iii) an anonymous referee. We acknowledge financial support from (i) the Faculty Research Grant program at Utah State University, and (ii) the Utah Agricultural Experiment Station, Utah State University, Logan, UT 84322-4810, by way of grant UTA 024. Approved as journal paper #5095. The usual disclaimer applies.
management of ecosystems. In this context, resilience—or resilience of the second kind—refers to “...the amount of disturbance that can be sustained [by an ecosystem] before a change in system control or structure occurs.” (Holling et al., 1995, p. 50). This definition tells us that the resilience of an ecosystem is intimately connected to its stability. Consequently, prudent ecosystem management involves taking those steps which optimize the flow of services provided to society by such ecosystems and which enhance ecosystem stability. From the standpoint of biodiversity conservation, this means that in designing optimal conservation rules, policy makers should not focus on the loss of genetic information, but instead, on the loss of ecosystem resilience.

Despite the significance of the concept of resilience, there are very few quantitative studies of resilience. In particular, there do not appear to be any formal characterizations of resilience that account for the important fact that resilience is generally a function of the number of substitute species that can perform a given set of ecological functions. For instance, consider the work of Common and Perrings (1992) and that of Perrings (1996). Although these authors do provide formal definitions of resilience, these definitions make no mention of the substitutability between species that we have just referred to. Instead, these definitions essentially say that an ecosystem is resilient as long as the maximum perturbation that can be sustained by the state variables of this system lies in a certain neighborhood of an equilibrium.

Recently, Batabyal (1998a, 1998b) has provided probabilistic definitions of resilience. While these definitions do link resilience to the number of species in an ecosystem, they do not specifically account for species substitutability. In fact, one of Batabyal’s definitions equates resilience with the expected value of $S$, where $S$ denotes “...the number of shocks that are required for all the

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2 For a more detailed corroboration of this claim, see Dasgupta and Maler (1997a), and the papers in Perrings et al. (1995).
ecosystem species to perish."") (Batabyal, 1998a, p. 5, emphasis added). This suggests that either inter-species substitutability in the performance of ecological functions is zero, or that this kind of substitutability, to the extent that it is present, is not germane to the determination of ecosystem resilience. The work of Schindler (1990), Holling (1992), and Perrings (1996) has clearly demonstrated that the resilience of ecological functions is intimately connected to the number of substitute species in an ecosystem that can perform those same functions. Consequently, it would appear to be important to link definitions of ecosystem resilience to the number of substitute species that can perform a specific set of ecological functions.

Given the limited attention that has been accorded to the quantitative dimension of the concept of resilience, and the undeniable significance of this concept for the design of prudent ecosystem management policies, this paper has two objectives. The first objective is to use renewal theory to provide a characterization of resilience as a stationary probability. Inter alia, this characterization proposes that in thinking about resilience, we explicitly account for the inter-species substitutability in the performance of ecological functions. The second objective is to use this renewal theoretic characterization of resilience to study some aspects of the optimal management of ecosystem services.

2. A Renewal Theoretic Characterization of Resilience

2a. The basics of renewal theory

A stochastic process \( \{Z(t): t \geq 0\} \) is said to be a counting process if \( Z(t) \) denotes the total number of events that have taken place by time \( t \). Since \( Z(t-1), Z(t), Z(t+1), \) etc. are stochastic, the

---

3 This discussion is taken from Batabyal and Yoo (1994) and Ross (1997). For additional details on renewal theory, the reader should consult Karlin and Taylor (1975), Wolff (1989), and Ross (1996).
time between any two counts is also stochastic. This time between any two counts is called the interarrival time. A counting process for which the interarrival times have an arbitrary distribution is a renewal process. Renewal theory is concerned with the study of renewal processes and their properties.

In this paper, we shall focus on alternating renewal processes. Here we are interested in stochastic systems that can be in one of two possible states. Let us call these two states up and down. Now suppose that initially our system is up and that it remains up for a time $X_1$. The system then is down, and it stays down for a time $Y_1$. The system then is up again for a time $X_2$, and then down again for a time $Y_2$, and so on. We suppose that the random vectors $\{X_t, Y_t\}$, $t \geq 1$ are independent and identically distributed (i.i.d.). In other words, the sequences of random variables $\{X_t\}$ and $\{Y_t\}$ are i.i.d. Note well that we are permitting $X_t$ and $Y_t$ to be dependent. What this means is that each time our stochastic system goes up, in a probabilistic sense, everything begins anew. However—and this will be important in the subsequent discussion in section 2b—when the system is down, we allow the length of the down period to depend on the previous up period. Given this conceptual framework, a key task in the study of alternating renewal processes involves the determination of the long run proportion of time that the system is up. Now it turns out that under a fairly general set of conditions⁴, this long run proportion of time is equal to the stationary or limiting probability that the stochastic system is up.

This renewal theoretic framework is useful for determining the resilience of an ecosystem because of two reasons. First, as Wolff (1989, p. 55) has noted, “[r]enewal theory is primarily concerned with limiting behavior...” as time approaches infinity. This is particularly useful for us

⁴See Ross (1997, p. 374).
because resilience has widely been considered to be an asymptotic property of ecosystems. (see Neubert and Caswell, 1997, and the citations therein). Second, as indicated in the previous paragraph, a key task in the study of alternating renewal processes is the determination of the stationary probability that a stochastic system is up. This again is useful for us because as Krebs (1985, p. 587) has noted, resilience can be thought of as a particular kind of probability. Let us now use the conceptual framework of this section to determine the resilience of a stylized ecosystem.

2b. The determination of ecosystem resilience

We have been unable to solve the problem of determining the resilience of an ecosystem with an arbitrary, i.e., a finite number of species. Consequently, in what follows, we analyze a stylized version of the problem. Consider an ecosystem which consists of \( n=4 \) species. Economic activities such as agriculture, fishing, and grazing affect the four species of this ecosystem. In particular, excessive economic activity of the above kind can result in the death of these species. With regard to the death of a species, we have two cases in mind. In the first case, species numbers have dwindled to such an extent that preventive policy measures such as moratoriums on grazing and regulations on the nature of fishing equipment are put in place to ensure that literal death (extinction) does not occur. In this case, we say that a species is endangered.

In the second case, some species may die literally, i.e., become extinct. Here we suppose that an ecosystem manager can introduce this species to our ecosystem from some other ecosystem. What this means is that the ecosystem manager physically introduces the (now) locally extinct species into our ecosystem from some other ecosystem.

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5 See section 2c for a discussion of how the general case might be analyzed.

6 The growth curve for one or more species in our ecosystem may exhibit critical depensation. In this case, the species would be endangered when the population size is at or near what Clark (1990, p. 17) calls the “minimum viable population level.” For such species, an ecosystem manager would have to take actions to ensure that the minimum viable population level is not reached.
ecosystem. If a particular species is not unique, then this can be done. Indeed, as Pimm (1991, p. 334) has noted, "[p]eople have moved species around the world for millenia, sometimes by accident but often with considerable enthusiasm." In our modeling framework, unique species can be endangered, but the ecosystem manager ensures that they never become extinct. The reader should note that all subsequent references to death include both the cases that we have just discussed.

As noted in section 1, there will generally be some inter-species substitutability in the performance of ecological functions. To this end, we shall say that our ecosystem is functional whenever at least one of species 1 and 2 is alive and at least one of species 3 and 4 is alive. From an ecological standpoint, this means that species 1 and 2 and species 3 and 4 are substitutes in the performance of ecological functions. Now suppose that as a result of the continuance of economic activities, the \textit{ith} species, \( i=1,2,3,4 \), alternates between life and death in accordance with a nonlattice alternating renewal process, and that the stochastic processes governing the life and the death times are independent. Let us be clear about the meaning of this independence assumption. What we are saying is that for the \textit{ith} species, the sequences of the random variables denoting the life and the death times are i.i.d. We are not requiring that the random variables denoting the life and the death times at the beginning of a particular cycle be independent. Using the notation of section

\footnote{For more on the species introduction literature, see chapter 15 in Pimm (1991). This book also contains a comprehensive list of references.}

\footnote{If we allow unique species to become extinct, then the mathematical problem of determining ecosystem resilience becomes intractable. In the terminology of section 2a, we would now have a situation in which our stochastic system is down for an infinite period of time. Consequently, in this case, it is not possible to compute the stationary probability that our system is up or down.}

\footnote{In the sense that this ecosystem is able to provide a flow of services to society over time.}

\footnote{A random variable \( X \) is lattice if it takes on integral multiples of some positive number \( d \). If \( X \) is lattice and \( H \) is the distribution function of \( X \), then \( H \) is lattice. If this condition is not met, then a random variable and its distribution function are nonlattice. For more details, see Wolff (1989, pp. 115-116).}
2a, suppose that for the \textit{ith} species, the sequences of the life and the death times are denoted by \( \{X_i\} \) and \( \{Y_i\} \). Then we are requiring these two sequences to be i.i.d. However, we permit \( X_t \) and \( Y_t \) to be dependent. In other words, when a particular species is dead, we are allowing the length of this death period to depend on the length of time during which this species is alive.

To comprehend the meaning of this dependence, consider the following example. Recall that in our framework, a species is dead either when it is endangered or when it becomes extinct. Suppose that the ecosystem under consideration is a rangeland, and that a particular kind of grass on this rangeland is endangered. As indicated previously, when this rangeland grass is endangered, an ecosystem manager takes actions to ensure that this species does not become extinct. One such action would be to put a moratorium on grazing. Now the length of time during which this moratorium applies (also the length of time during which the rangeland grass is dead) clearly depends on the degree to which this species is endangered. In turn, this degree of endangerment is directly related to the severity with which economic activities like grazing were being carried out when this grass was alive. Thus we see that the length of a death period can easily depend on the length of time during which a species is alive. This is why we have allowed the length of a death period to depend on the length of time during which a species is alive. To the best of our knowledge, without the requirement that the sequences of the random variables denoting the life and the death times be i.i.d., the problem of determining the resilience of an ecosystem is intractable.

We shall say that the \textit{ith} species, \( i=1,2,3,4 \), is alive for a time with distribution function \( F_i(\cdot) \), and that it is dead for a time with distribution function \( G_i(\cdot) \). Let \( \alpha_i \) and \( \beta_i \) denote the means of these two distribution functions. The death times of the various species are stochastic because the rate at which species regenerate or recuperate is generally a stochastic function of environmental variables and the preventive policy measures that have been put in place by an ecosystem manager.
Our task now is to determine the resilience of this stylized ecosystem. As indicated in section 2a, resilience is an asymptotic property of ecosystems and it can be thought of as a probability. Putting these two facts together, we shall define the resilience of our stochastic ecosystem to be the stationary probability that this ecosystem is functional. Mathematically, we are interested in computing \( \lim_{t \to \infty} \text{Prob\{ecosystem functional at time } t \} \). Because the process of being alive and then dying constitutes an alternating renewal process for each of the four species, the probability that species \( i \) is alive at time \( t \) is

\[
p_i = \frac{a_i}{a_i + \beta_i}, \quad i=1,...,4.
\]  

From equation (1), and from our independence assumption, we can compute the desired stationary probability. We get

\[
\lim_{t \to \infty} \text{Prob\{ecosystem functional at time } t \} = \{p_1 + p_2 - p_1 p_2\} \{p_3 + p_4 - p_3 p_4\}.
\]  

Upon further simplification, equation (2) becomes

\[
\lim_{t \to \infty} \text{Prob\{ecosystem functional at time } t \} = \frac{\alpha_1}{(a_1 + \beta_1)(a_2 + \beta_2)} \left(\frac{\alpha_3(a_4 + \beta_4) + \alpha_4 \beta_3}{(a_3 + \beta_3)(a_4 + \beta_4)}\right).
\]  

The expression in equation (3) is our probabilistic characterization of ecological resilience. The reader will note that we have equated the resilience of our ecosystem with the long run probability that in the face of continued economic activity, this ecosystem is functional. Elementary calculus tells us that (i) an increase in the mean life times \( (a_i) \) of the various species increases ecosystem resilience, and that (ii) an increase in the mean death times \( (\beta_i) \) decreases ecosystem resilience.
Our measure of ecosystem resilience depends on the means of the survival and the death time distribution functions. Consequently, in order to operationalize this measure of resilience, it will be necessary to compute the probabilities given in equation (1). To do this, it will first be necessary to obtain estimates of the $\alpha_s$'s and the $\beta_s$'s. Krebs (1985, pp. 164-165) discusses how survival and death rates can be calculated. In addition to this, techniques used in the computation of ecological life tables—see Krebs (1985, pp. 180-181)—are also likely to be useful in obtaining estimates of the $\alpha_s$'s and the $\beta_s$'s.

In this paper, we used the theory of alternating renewal processes to model the species of our ecosystem. In this connection, it should be noted that we have not used specific functional forms to model the life and the death time distribution functions. The reader will recall that these life and death times were modeled using general functional forms ($F_i(\cdot)$ and $G_i(\cdot)$). Consequently, as far as the use of functional forms is concerned, our analysis is general. To fix ideas, we now provide two examples that illustrate the use of equation (3). We then discuss a way in which the analysis of this section might be generalized.

2c. Examples and a possible generalization

Suppose that $\alpha_i = 10, \forall i$, and that $\beta_i = 3, \forall i$. If we measure time in years, then this means that each of the four species is alive for a mean time of 10 years and then dead for a mean time of 3 years. Substituting these values in equation (3), we get 0.8963 as our numerical value of resilience. As a second example, suppose that $\alpha_1 = 10, \alpha_2 = 20, \alpha_3 = 15, \alpha_4 = 25$, and that $\beta_1 = 1, \beta_2 = 3, \beta_3 = 4, \beta_4 = 1.5$. Now the means of the survival and the death time distribution functions are different for all the four species. Once again, substituting these numbers in equation (3), we get 0.9764 as the numerical value for the resilience of our ecosystem. This completes the two examples.
We indicated in section 2b that we have been unable to solve the general problem of determining the resilience of a \( n \in \mathbb{N} \) species ecosystem with inter-species substitutability. Our purpose now is to outline a procedure that appears likely to yield a general solution to the problem at hand. This procedure uses some of the properties of associated random variables.\(^{11}\) Suppose that each of the \( n \) species of an ecosystem is either alive or dead for a time with specific distribution functions. To account for inter-species substitutability, group the \( n \) species into subsets \( S_1, \ldots, S_p \), so that all the species in any subset are substitutes in terms of their ability to perform a given set of ecological functions. We can then say that our ecosystem is functional if and only if at least one of the species in each of the subsets is alive. The task of determining the resilience of this ecosystem now involves computing the stationary probability that this ecosystem is functional. If this probability can be computed, then we will have a general measure of resilience which accounts for inter-species substitutability in the performance of ecological functions, and which—at least in principle—can be operationalized.

We now use our measure of resilience, i.e., \( \lim_{t \to \infty} \text{Prob}\{\text{ecosystem functional at time } t\} \), to study some aspects of the optimal management of ecosystems in a framework in which an ecosystem manager takes the ecological and the economic aspects of the problem into account.

3. The Optimal Management of Ecosystems

In recent times, the question of how best to utilize ecosystem services has attracted a considerable amount of attention from ecologists and economists.\(^{12}\) While this research has certainly

\(^{11}\)For more on associated random variables, see Shaked and Shanthikumar (1994).

\(^{12}\)For instance, see the papers in Swanson (1995), in Perrings et al. (1995), and in Dasgupta and Maler (1997b).
advanced our understanding of the many and varied intricacies of the optimal management question, this same research has not explicitly considered the nexus between ecological resilience and ecosystem management. Consequently, in what follows, we study a simple model that incorporates the ecological and the economic dimensions of the problem into the analysis.

Suppose that our ecosystem provides economic and ecological benefits to society. The economic benefits include the flow of services provided by activities such as biodiversity prospecting, fishing, grazing, and hunting. Clearly, the continuance of these benefits depends on the resilience of the underlying ecosystem. As well, we suppose that society derives benefits from a resilient ecosystem. To this end, let $B[\bar{x}, \lim_{t \to \infty} \text{Prob}\{\text{ecosystem functional at time } t\}]$ denote society's benefit function. The vector $\bar{x}=(x_1, \ldots, x_r)$ denotes the $r$ possible economic activities that society may engage in and $\lim_{t \to \infty} \text{Prob}\{\text{ecosystem functional at time } t\}$ is the resilience of our ecosystem. We suppose that $B[\cdot]$ is concave and increasing in both its arguments. In other words, increasing the level of economic activities and/or the resilience of the ecosystem enhances social benefits, but at a decreasing rate.

Economic activities result in two kinds of social costs that are relevant for our analysis. The first kind of cost stems from the deleterious effects of such activities on the ecosystem itself. The effects of excessive fishing, grazing, etc. readily come to mind. Let $C_1[\bar{x}]$ denote this cost. The second kind of cost results from the preventive measures—such as temporary bans on grazing and the introduction of species from other ecosystems—that are undertaken by the ecosystem manager when species die. We suppose that these policy measures allow the ecosystem manager to control the means of the death time distribution functions, i.e., the $\beta_i$s. To this end, let $\bar{\beta}=(\beta_1, \ldots, \beta_4)$. Then $C_2[\bar{\beta}]$

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13This kind of benefit function has been used by Li and Lofgren (1998),
denotes this second kind of cost. We assume that $C_1[\cdot]$ is an increasing function, that $C_2[\cdot]$ is a decreasing function, and that both these functions are convex. This means that an increase in the level of economic activity or a decrease in the means of the death time distribution functions will lead to higher costs, at an increasing rate.

Our ecosystem manager's problem can now be stated. This manager solves

$$\max_{\tilde{s}} \beta B[\tilde{x}, \lim_{t \to \infty} \text{Prob}\{\text{ecosystem functional at time } t\}] - C_1[\tilde{x}] - C_2[\tilde{s}].$$

Before we write down the first order necessary conditions to this problem, let us discuss three aspects of the approach that we have used to model the ecosystem manager's problem. First, this manager's control variables are the $\tilde{s}$'s. This means that the manager is directly able to choose the length of time during which a species is dead. To see why this is a reasonable approach, recall the section 2b example of an endangered species of grass on a rangeland. In this case, an example of a preventive policy measure is a moratorium on grazing. By setting the length of the moratorium, our manager is able to directly control the length of time during which this species of grass is dead. A similar line of reasoning applies to other kinds of preventive policy measures such as a temporary ban on fishing and/or hunting. Further, note that in our modeling approach, the $\tilde{s}$'s are indirectly conditioned on the economic activities that have an impact on the ecosystem. As indicated in section 2b, this is because we have allowed the length of the death period for any particular species to depend on the length of time during which this species is alive. Having said this, it should be noted that this is not the only reasonable way of modeling the activities of an ecosystem manager. As a referee has noted, one can think of the means of the death time distribution functions themselves being functions of the set of preventive policy measures that an ecosystem manager might take. In this case, the impact of a manager's actions on society's benefits and costs would be indirect; the
actions would affect the $\beta_i$s, and in turn this would affect the level of social benefits and costs. Note that this second modeling approach would involve the introduction of additional variables into the analysis. Second, in our approach we have not let the $\beta_i$s be time dependent. This is because the objective of this section of the paper is to study the nexus between ecological resilience and ecosystem management. As indicated in section 2a, resilience is an asymptotic property of ecosystems. Consequently, even if we had modeled the $\beta_i$s as being time dependent, in the limit as $t \to \infty$, this time dependence would disappear. Third, it should be noted that we have not allowed for the presence of time lags in our modeling approach. However, as a referee has noted, in reality one can expect there to be a lag between the time at which a particular policy is put in place and the time at which its ecological impacts are felt.

Returning to problem (4), the first order necessary conditions to this problem are\(^{14}\)

$$\frac{\partial B[\cdot,;]}{\partial x_q} = \frac{\partial C_1[\cdot]}{\partial x_q}, \quad q=1,\ldots,r, \quad (5)$$

and

$$\frac{\partial B[\cdot,;]}{\partial \{\lim_{t \to \infty} \text{Prob}\{\cdot\} \}} = \frac{\partial C_2[\cdot]}{\partial \beta_i}, \quad i=1,\ldots,4. \quad (6)$$

Equation (5), the economic first order condition, tells us that optimal ecosystem management involves pursuing each of the $r$ activities up until the point at which the marginal social benefit from this activity equals its marginal social cost. Equation (6), the ecological first order condition, has somewhat different implications for the management of our ecosystem. This equation says that the ecosystem manager should take ameliorative policies so that the marginal social cost of these

\(^{14}\)We assume that the second order conditions are satisfied.
policies equals the marginal social benefit. The reader should note the tradeoff that the manager faces. Social benefits can be enhanced by increasing the resilience of the ecosystem. In turn, resilience can be increased by decreasing the $\beta^\prime$. So the benefits side of things calls for diminishing the $\beta^\prime$s. In contrast to this, because $C_2[\cdot]$ is a decreasing function, costs can only be lowered by increasing the $\beta^\prime$s. In other words, the cost side of things calls for raising the $\beta^\prime$s. Our ecosystem manager accounts for this tradeoff optimally by choosing the $\beta^\prime$s so that they satisfy equation (6). This analysis tells us that the economic and the ecological aspects of the management problem are inseparable. Consequently, prudent ecosystem management involves balancing these two aspects of the problem appropriately.

4. Conclusions

In this paper we provided a new renewal theoretic characterization of the concept of ecological resilience. This characterization depends on the exogenously given number of species in the ecosystem, and on the means of the survival and the death time distribution functions. We then used this characterization to study the optimal management of an ecosystem. We noted that given the number of ecosystem species, in order to operationalize this paper’s measure of resilience, it will be necessary to fit distributions to the life and the death times of the species and then determine the means of these distribution functions.

The analysis of this paper can be extended in a number of different directions. In what follows, we suggest two possible extensions. First, the characterization of resilience provided in this paper depends on the exogenously given number of ecosystem species. As discussed in section 2c, an important generalization will involve the analysis of an ecosystem with $n \in \mathbb{N}$ species and an arbitrary level of inter-species substitutability in the performance of ecological functions. Second,
we studied the case of unique species only indirectly by assuming that when they are endangered, appropriate policy measures to resuscitate them are put in place. A useful extension will be to provide a measure of resilience when unique species are allowed to die in the literal sense of the word.

Formal studies of resilience which incorporate these aspects of the problem into the analysis will provide richer and more realistic characterizations of resilience, and permit more elaborate analyses of the connections between ecological resilience and the optimal management of our ecosystems.
References


