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**AN ANALYSIS OF PERSISTENCE, RESILIENCE, AND
THE CONSERVATION OF KEYSTONE SPECIES**

by

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**AN ANALYSIS OF PERSISTENCE, RESILIENCE, AND
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Amitrajeet A. Batabyal

ABSTRACT

Ecologists and economists are increasingly in agreement that ecological and economic systems are linked and that these systems should be viewed as one system. However, because this recognition has been recent, there are very few formal studies of jointly determined ecological-economic systems (ecosystems). Consequently, this paper has two objectives. First, the ecological concepts of persistence and resilience are characterized in the context of a stylized ecosystem. Next, these concepts are used to study a conservation problem with two noteworthy features. In this problem, the objects of interest are keystone species, and society is assumed to derive benefits from the ecological *and* the economic aspects of conservation.

Key words: Conservation, keystone species, persistence, resilience

AN ANALYSIS OF PERSISTENCE, RESILIENCE, AND THE CONSERVATION OF KEYSTONE SPECIES¹

1. Introduction

Ecologists and economists are increasingly in agreement that ecological and economic systems are linked and that these systems should be viewed as one system (hereafter ecosystem). A consensus is also emerging among ecologists and economists that if the general process of economic development is to be sustainable, then it will be necessary to conserve at least some environmental resources. The decision as to how many and which species to conserve 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 unreasonable to assume that environmental resources which are substitutes in terms of consumption are also substitutes in terms of their ecological functions. Despite this agreement, as Perrings (1996, p. 232) has noted, “the complementarity between species in many ecosystems is still very imperfectly understood.”

This is important because the *persistence* of ecosystems, and the *resilience* of ecological functions in most ecosystems is a function of this inter-species complementarity. Persistence refers to “how long a variable lasts before it is changed to a new value...” (Pimm, 1991, p. 14), and resilience 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). The reader should note

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that the concepts of persistence, and particularly resilience, have come to dominate much of the present center stage of academic debate about conservation related issues.² The above definition of resilience tells us that ecosystem resilience and ecosystem stability are linked. Consequently, the aim of conservation policy should be to take those steps which enhance ecosystem stability. Put differently, prudent conservation policy should *not* focus on the loss of genetic information, but instead, on the loss of ecosystem resilience.

Despite the significance of these two concepts, there are virtually no studies of either persistence or resilience in the economics literature. Common and Perrings (1992) and Perrings (1996) have studied resilience, and these authors have provided formal definitions of resilience. These definitions say that an ecosystem is resilient as long as the maximum perturbation that can be sustained by the state variables of this system lie in a certain neighborhood of an equilibrium. While these definitions do provide a link between resilience and ecosystem stability, they do not provide any link between resilience and either the number of ecosystem species, or the number of keystone species in an ecosystem.³ Consequently, if one is interested in questions such as the number of species that should be conserved, then one cannot use the Common and Perrings (1992) definition or the Perrings (1996) definition, to incorporate either persistence or resilience considerations into an appropriate conservation framework.

In the ecology literature, there are a number of studies—see Steinman et al. (1991), Cottingham and Carpenter (1994), and Neubert and Caswell (1997)—of resilience and related

²For a more detailed corroboration of this claim, see Batabyal (1998a), Levin et al. (1998), and Perrings *et al.* (1995).

³The structure and the dynamics of an ecosystem often depend on the existence of certain key species. Hence, these “keystone species” are very important to the functioning of the ecosystem. Consequently, we shall focus most of our subsequent analysis on these species. The term “keystone species” is due to Paine (1966).

concepts, but most of these studies have analyzed the resilience of *deterministic* systems. Commenting on this state of affairs, Ives (1995, p. 217, emphasis added) has noted that in order “to apply generally to ecological communities, stability [concepts such as resilience need] to be defined for *stochastic* systems in which environmental perturbations are continuous and equilibrium [population] densities are never achieved.” Further, even in this literature, there do not appear to be any formal characterizations of either persistence or resilience which link these concepts to the number of species, or to the number of keystone species in an ecosystem.

This review of the literature yields three conclusions. First, the economics literature has paid scant attention to the concepts of persistence and resilience. Second, while the ecology literature has analyzed resilience and related concepts at some depth, most of this analysis has focused on deterministic systems. Third, neither the economics nor the ecology literatures have explored the links between persistence, resilience, and the keystone species of an ecosystem. In a recent theoretical paper, Batabyal and Beladi (1999) have provided rigorous definitions of persistence and resilience. These definitions apply to stochastic systems; moreover, they connect the notions of persistence and resilience to the keystone species of an ecosystem. Given this situation, our paper has two objectives. First, we use renewal theory (see Wolff, 1989, particularly pp. 89-92, and Ross, 1996, particularly pp. 123-132) to intuitively discuss the Batabyal and Beladi (1999) definitions of persistence and resilience. Second, we use these renewal theoretic definitions to study the optimal number of keystone species that should be conserved.

2. Persistence and Resilience: An Intuitive Approach

2.1. Preliminaries

Consider a stylized ecosystem which consists of n species. Of these n species, m ($m < n$) are

independent keystone species. As indicated in footnote 3, it is these species that are essential for the functioning of an ecosystem. Consequently, in the rest of this paper, we abstract from the remaining $(n-m)$ species and we focus on these m keystone species. The reader should note that all subsequent references to species are to these m keystone species.

Economic activities such as fishing, grazing, and hunting affect the species of this ecosystem. In particular, excessive economic activity will result in the death of one or more of these species. We are referring to death literally and figuratively. In particular, we have two cases in mind. In the first case, species numbers have dwindled to such an extent that preventive policy measures such as regulations on the nature of fishing equipment and moratoriums on grazing are put in place to ensure that literal death does not occur. This is the case of figurative death. In the second case, some species may die literally. Here, we suppose that an ecosystem manager can introduce this or a closely related species to our ecosystem from some other ecosystem.⁴ Unique species fall into the first case. The reader should note that all subsequent references to death include both these cases.

As discussed in section 1, there will generally be some substitutability between species in the performance of key ecological functions. Hence, we will need to make an assumption about the degree of this substitutability. The cases of zero substitutability and partial substitutability between species have been analyzed in Batabyal (1998b, 1999). Consequently, in this paper we study the case of perfect substitutability. In particular, we shall say that our ecosystem is functional⁵ at time t if at least one of the m species is alive. From an ecological standpoint, this means that our ecosystem's vitality essentially depends on the survival of one keystone species.

⁴For more on the introduction of species, see Pimm (1991).

⁵In the sense that this ecosystem is able to provide a flow of services to society over time.

Suppose that as a result of the continuance of economic activities, the *ith* species, $i=1,\dots,m$, alternates between life and death in accordance with an exponential alternating renewal process. Specifically, we say that the *ith* species, $i=1,\dots,m$, 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 α_i and β_i denote the means of these two distribution functions. The death times of the various species are stochastic because the rate at which species recuperate is generally a stochastic function of environmental variables and the preventive policy measures that have been put in place.⁶ Let us now determine the persistence of this stylized ecosystem.

2.2. Persistence

Recall that persistence refers to “how long a variable lasts before it is changed to a new value...” (Pimm, 1991, p. 14). This tells us that persistence is measured in time units. In the context of our stylized ecosystem, this translates into the time between ecosystem breakdowns. Because this time is a random variable, we are interested in computing the expected length of time during which our ecosystem is functional. Formally, we can express this as $E[\textit{time ecosystem functional}]$, where $E[\cdot]$ is the expectation operator. To compute this expectation, let us first note that the probability of an ecosystem breakdown in a small time interval $(t, t+\Delta t)$ for large t and a small time increment Δt , depends only on the event in which a single keystone species is alive, all others are dead, and then this surviving species dies.⁷ Now applying Blackwell’s Theorem⁸ to this probability, we get an expression for the expected length of time between ecosystem breakdowns. Let us denote this

⁶For more on this in the context of one keystone species, see Paine (1974).

⁷All other events are irrelevant because they have negligible probabilities. For more details, see the proof of Theorem 1 in Batabyal and Beladi (1999).

⁸See Theorem 3.4.1 on p. 110 of Ross (1996).

expression by

$$E[\textit{ecosystem breakdown time}] = \frac{1}{\prod_{j=1}^m \frac{\beta_j}{\alpha_j + \beta_j} \sum_{i=1}^m \frac{1}{\beta_i}}. \quad (1)$$

Our next task is to compute the expected length of time during which our ecosystem is down.

This expectation is given by

$$E[\textit{length breakdown period}] = \frac{1}{\sum_{i=1}^m \frac{1}{\beta_i}}. \quad (2)$$

We are now in a position to compute the persistence of our ecosystem. As shown in Figure 1, persistence, i.e., $E[\textit{time ecosystem functional}]$, can be determined by subtracting the expected length of time of a breakdown period (the right hand side of equation (2)) from the expected length of time between ecosystem breakdowns (the right hand side of equation (1)). We get

$$\textit{Persistence} \equiv E[\textit{time ecosystem functional}] = \frac{1 - \prod_{j=1}^m \frac{\beta_j}{\alpha_j + \beta_j}}{\prod_{j=1}^m \frac{\beta_j}{\alpha_j + \beta_j} \sum_{i=1}^m \frac{1}{\beta_i}}. \quad (3)$$

Equation (3) is our probabilistic characterization of persistence. There are two things to note about this equation. First, the assumption of perfect substitutability between species in the performance of ecological functions notwithstanding, persistence depends on *all* the keystone species. Second, persistence depends on the means of the life and the death time distribution functions of the species in the ecosystem. This tells us that if we are able to estimate these parameters, then we will be able to operationalize this measure of ecosystem persistence.

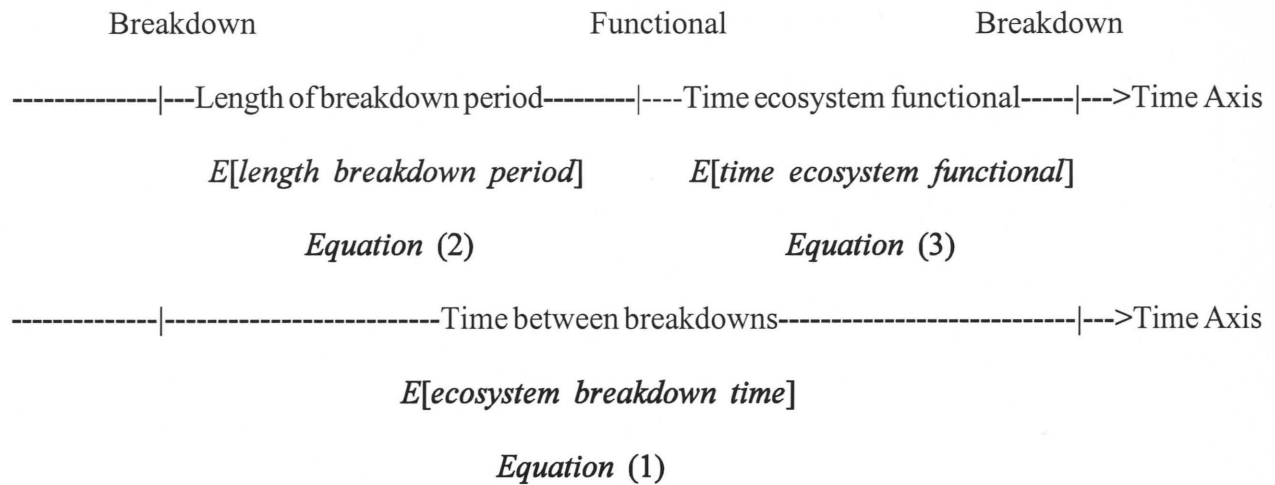


Figure 1. Time Line of Events in the Ecosystem

Despite the significance of persistence, it is the notion of ecosystem resilience that has come to dominate much of the present center stage of academic debate about conservation related issues. Consequently, we now use the framework of section 2.1 to provide an intuitive characterization of resilience.

2.3. Resilience

Resilience is (i) a particular kind of probability, and (ii) an asymptotic property of ecosystems (see Krebs, 1985, p. 587, and Neubert and Caswell, 1997, p. 654). Unlike most of the literature on this subject, we shall think of resilience as a *stochastic*—and not as a deterministic—asymptotic property. In particular, we shall characterize resilience by exploiting the mathematical links between persistence and resilience.

Recall that resilience refers to the amount of disturbance that can be withstood by an ecosystem before a change in this ecosystem's control or structure occurs. In our modeling framework, the disturbances are captured by the death time distribution functions of the different

species. Further, a change in an ecosystem's control or structure occurs when it breaks down. Putting these two observations together, we conclude that resilience can be conceptualized as the stationary probability that an ecosystem is functional. Mathematically, this means that we want to compute $\lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\}$. This probability can be computed by noting that

$$\lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\} = \frac{E[\text{time ecosystem functional}]}{E[\text{ecosystem breakdown time}]} \quad (4)$$

We have already computed the two expectations on the right hand sides of equation (4), in section 2.2. These expectations are given by equations (3) and (1), respectively. Now dividing equation (3) by equation (1), the expression for ecosystem resilience simplifies to

$$\text{Resilience} \equiv \lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\} = 1 - \prod_{j=1}^m \frac{\beta_j}{\alpha_j + \beta_j} \quad (5)$$

Equation (5) says that like persistence, resilience also depends on *all* the species in the ecosystem. Specifically, resilience depends on the means of the survival and the death time distribution functions.

Equations (4) and (5) tell us two important things about the connections between persistence, resilience, and ecosystem management. First, note that the numerator of the right hand side of equation (4) is the persistence of our ecosystem. This means that ecosystem resilience is proportional to ecosystem persistence. Put differently, ecosystems that are very persistent are also those that are likely to be very resilient. From the perspective of ecosystem management, this tells us that managers whose goal is to make ecosystems resilient will want to focus on those factors that make ecosystems persistent. Some of these factors are described in the right hand side of equation (3).

Second, resilience is inversely proportional to the expected length of time between ecosystem breakdowns. This points to the role of management in promoting ecosystem resilience because the time between breakdowns corresponds in part to periods in which an ecosystem manager has taken preventive actions to protect species from the adverse effects of continued economic activity.⁹ As discussed in section 2.1, these actions include things like regulations on the nature of fishing equipment, moratoriums on grazing, and the introduction of species. If all economic activities are terminated, then the expected length of a breakdown period—which will now depend exclusively on natural factors—will presumably have been made as short as possible. However, in most practical situations, such termination will not be a feasible course of action. In these situations, this analysis tells us that if ecosystem resilience is to be enhanced, then managers will need to implement those policies which ensure that the expected length of a breakdown period is kept as short as possible.

We now use our measure of ecosystem resilience (equation (5)) to study the question of the optimal conservation of keystone species. We use a framework in which an ecosystem manager/social planner takes the ecological *and* the economic aspects of conservation into account.

3. Resilience and the Conservation of Keystone Species

In recent times, the question of what to conserve has received a considerable amount of attention from ecologists and economists.¹⁰ While these studies have increased our understanding of the many intricacies of the conservation question, the studies themselves have *not* considered the nexus between resilience and conservation. Consequently, we now analyze a simple model of

⁹As shown in Figure 1, the expected length of time between breakdowns is equal to the sum of the expected time during which our ecosystem is functional (equation (3)) and the expected length of a breakdown period (equation (2)).

¹⁰For instance, see Balick and Mendelsohn (1992), Weitzman (1993), and Spash and Hanley (1995).

optimal species conservation which incorporates the ecological and the economic dimensions of the question.

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, and grazing. The continuance of these benefits depends on the resilience of the ecosystem. Consequently, we suppose that society derives benefits from the resilience of this ecosystem. To this end, let $B[\vec{x}, \lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\}]$ denote society's benefit function.¹¹ The vector $\vec{x}=(x_1, \dots, x_r)$ denotes the r possible economic activities that society may engage in, and $\lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\}$ is the resilience of the ecosystem. We suppose that $B[\cdot, \cdot]$ 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 are costly to undertake and these activities have varied effects on the m keystone species of the ecosystem. Consequently, there is a cost involved in conserving these species. Let $C_1[\vec{x}]$ denote the cost of engaging in economic activities, and let $C_2[m]$ denote the cost of species conservation. We assume that these two cost functions are convex and increasing in their arguments. This means that an increase in either the level of economic activity or the number of species will lead to higher costs, at an increasing rate. Our ecosystem manager's problem can now be stated. This manager solves

$$\max_{\vec{x}, m} B[\vec{x}, \lim_{t \rightarrow \infty} \text{Prob}\{\text{ecosystem functional at time } t\}] - C_1[\vec{x}] - C_2[m]. \quad (6)$$

This is a mixed integer programming problem because \vec{x} is a continuous control variable (by

¹¹This kind of benefit function has been used by Batabyal (1998b) and by Li and Lofgren (1997).

assumption) and m is an integer control variable. In order to apply the calculus to this problem, we shall interpret m as a rate of species conservation. With this interpretation of m , the first order necessary conditions to problem (6) are¹²

$$\frac{\partial B[\cdot, \cdot]}{\partial x_q} = \frac{\partial C_1[\cdot]}{\partial x_q}, \quad q=1, \dots, r, \quad (7)$$

and

$$\frac{\partial B[\cdot, \cdot]}{\partial \lim_{t \rightarrow \infty} Prob\{\cdot\}} \frac{\partial \lim_{t \rightarrow \infty} Prob\{\cdot\}}{\partial m} = \frac{dC_2[\cdot]}{dm}. \quad (8)$$

Equation (7), the economic first order condition, says that each of the r economic activities should be pursued to the point where the marginal social benefit from this activity equals its marginal social cost. Of greater interest is equation (8), the ecological first order condition. The reader should note that although this first order condition clearly has implications for species conservation, it is this kind of optimality condition that is *absent* in standard economic analyses of conservation questions.

Equation (8) tells us that our ecosystem manager should conserve keystone species at a rate so that the marginal social cost of conservation equals the marginal social benefit. The marginal social benefit is the product of two terms. The first term captures the effect of a marginal increase in resilience on social benefit, and the second term captures the effect of an incremental increase in the rate of conservation on ecological resilience. Note that because we have characterized resilience

¹²We assume that the second order conditions are satisfied.

as a function of the number of keystone species in an ecosystem, we have been able to study the question of optimal species conservation in a way that jointly considers the ecological and the economic aspects of the problem.

4. Conclusions

In this paper we studied three important questions in ecological economics that have largely been ignored by the economics literature. First, we provided intuitive characterizations of the ecological concepts of persistence and resilience in a dynamic and stochastic framework. Second, we demonstrated the links between persistence and resilience, and we then discussed the implications of these links for the management of ecosystems. Third, we used our characterization of resilience to study the optimal conservation of keystone species in an ecological-economic framework.

Our analysis shows that in order to operationalize the measures of persistence and resilience, it will be necessary to estimate two parameters for each species. These two parameters are the means of the life and the death time distribution functions for the different keystone species. We also showed that the notions of persistence and resilience have definite implications for ecosystem management and the conservation of species. In particular, an ecosystem manager who chooses to make conservation decisions on the basis of economic criteria alone will adopt practices that are quite different relative to a manager who recognizes the ecological and the economic aspects of the problem.

The analysis of this paper can be extended in a number of different directions. In what follows, we suggest two possible extensions. The characterizations of persistence and resilience depend on the distributional assumption about the life and the death time distribution functions, and

on the assumption of independence between species. Although these assumptions are strong, they are necessary for the analysis. Our ongoing research on this subject leads us to conjecture that without some distributional assumption and without the independence assumption, the task of characterizing persistence and resilience is intractable. However, additional research is needed to determine whether this conjecture is true, and more generally to determine the kinds of interaction effects between species that can be studied in an analytically manageable manner.

Second, as Neubert and Caswell (1997) have noted, we are often interested in the short term behavior of an ecosystem following a perturbation. The asymptotic notion of resilience that we have studied in this paper focuses only on the long term behavior of an ecosystem; short term, transient behavior is ignored. A useful extension of this paper would be to construct measures of persistence and resilience in a stochastic framework which capture the short term response of an ecosystem to perturbations.

Formal studies of ecosystems which incorporate these aspects of the problem into the analysis will provide richer and more realistic characterizations of ecosystem properties such as persistence and resilience. Further, such studies will also provide useful guidance about how to manage ecosystems whose behavior is governed by a great deal of unpredictability.

References

- Balick, M., and Mendelsohn, R. O. 1992. Assessing the Economic Value of Traditional Medicines From Tropical Rain Forests, *Conservation Biology*, 6, 128-130.
- Batabyal, A. A. 1998a. The Concept of Resilience: Retrospect and Prospect, *Environment and Development Economics*, 3, 235-239.
- Batabyal, A. A. 1998b. An Ecological Economic Perspective on Resilience and the Conservation of Species. *Mimeo*, Department of Economics, Utah State University.
- Batabyal, A. A. 1999. Species Substitutability, Resilience, and the Optimal Management of Ecological-Economic Systems, *Mathematical and Computer Modelling*, 29, 35-43.
- Batabyal, A. A., and Beladi, H. 1999. The Stability of Stochastic Systems: The Case of Persistence and Resilience. Forthcoming, *Mathematical and Computer Modelling*.
- Common, M., and Perrings, C. 1992. Towards an Ecological Economics of Sustainability, *Ecological Economics*, 6, 7-34.
- Cottingham, K. L., and Carpenter, S. R. 1994. Predictive Indices of Ecosystem Resilience in Models of North Temperate Lakes, *Ecology*, Vol. 75, pp. 2127-2138.
- Holling, C. S., Schindler, D., Walker, B. W., and Roughgarden, J. 1995. Biodiversity in the Functioning of Ecosystems: An Ecological Synthesis," in C. Perrings, K. Maler, C. Folke, C. S. Holling, and B. Jansson, (Eds.), *Biodiversity Loss*. Cambridge University Press, Cambridge, UK.
- Ives, A. R. 1995. Measuring Resilience in Stochastic Systems, *Ecological Monographs*, 65, 217-233.
- Krebs, C. J. 1978. *Ecology*, 2nd edition. Harper and Row, New York, USA.

- Levin, S., Barrett, S., Aniyar, S., Baumol, W., Bliss, C., Bolin, B., Dasgupta, P., Ehrlich, P., Folke, C., Gren, I., Holling, C. S., Jansson, A., Jansson, B., Martin, D., Maler, K., Perrings, C., and Sheshinsky, E. 1998. Resilience in Natural and Socioeconomic Systems, *Environment and Development Economics*, 3, 229-235.
- Li, C., and Lofgren, K. 1997. The Optimal Preservation of Biodiversity. *Mimeo*, University of Umea.
- Neubert, M. G., and Caswell, H. 1997. Alternatives to Resilience for Measuring the Responses of Ecological Systems to Perturbations, *Ecology*, 78, 653-665.
- Paine, R. T. 1966. Food Web Complexity and Species Diversity, *The American Naturalist*, 100, 65-75.
- Paine, R. T. 1974. Intertidal Community Structure: Experimental Studies on the Relationship Between a Dominant Competitor and its Principal Predator, *Oecologia*, 15, 93-120.
- Perrings, C. 1996. Ecological Resilience in the Sustainability of Economic Development, in S. Faucheux, D. Pearce, and J. Proops, (Eds.), *Models of Sustainable Development*. Edward Elgar, Cheltenham, UK.
- Perrings, C., Maler, K. G., Folke, C., Holling, C. S., and Jansson, B., (Eds.). 1995. *Biodiversity Loss*. Cambridge University Press, Cambridge, UK.
- Pimm, S. L. 1991. *The Balance of Nature?* University of Chicago Press, Chicago, USA.
- Ross, S. M. 1996. *Stochastic Processes*, 2nd edition. Wiley, New York, USA.
- Spash, C. L., and Hanley, N. 1995. Preferences, Information and Biodiversity Preservation, *Ecological Economics*, Vol. 12, pp. 191-208.
- Steinman, A. R., Mulholland, P. J., Palumbo, A. V., Flum, T. F., and DeAngelis, D. L. 1991. Resilience of Lotic Ecosystems to a Light-Elimination Disturbance, *Ecology*, 72, 1299-1313.

Weitzman, M. L. 1993. What to Preserve? An Application of Diversity Theory to Crane Conservation, *Quarterly Journal of Economics*, 108, 157-183.

Wolff, R. W. 1989. *Stochastic Modeling and the Theory of Queues*. Prentice-Hall, Englewood Cliffs, USA.