

# A discrete optimization model for preserving biological diversity

Fred Glover

*Graduate School of Business Administration, University of Colorado at Boulder, Boulder, CO, USA*

Ching-Chung Kuo and Krishna S. Dhir

*School of Business Administration, Penn State University at Harrisburg, Middletown, PA, USA*

*In this paper we propose an operational framework within which the concept of diversity is measurable. Based on an interspecies dissimilarity index, we develop a series of progressively more efficient integer programming formulations with the objective of maximizing biological diversity under resource constraints. To illustrate the solution procedure, the model is applied to the preservation of the crane family. We also show how additional modelling considerations can be incorporated in a simple and direct fashion. Finally, an alternative approach to measuring biodiversity is presented to exemplify that different measures of diversity can lead to differing ecological conservation policies.*

**Keywords:** biological diversity, mathematical modelling, integer programming, dynamic programming, data analysis

## 1. Introduction

Human activities are destroying the natural world at an ever increasing rate. As a result of environmental degradation, the global biological system is in crisis. Although efforts have been made to protect endangered species, resources available for preserving biological diversity, or biodiversity, are limited. It is therefore important that conservation expenditures be allocated in the most efficient manner possible.

To ensure the optimal allocation of resources for the preservation of biological diversity, it is necessary to define the term diversity. As one of the central themes in ecology, diversity appears to be a simple, straightforward concept of which people have an intuitive grasp. However, there has been considerable debate on its definition. The problem is further complicated by the fact that a bewildering number of indices have been devised for measuring biodiversity.

According to Magurran,<sup>1</sup> diversity measures take into account two factors: species richness, i.e., number of species and evenness, i.e., how equally abundant the species

are. However, as pointed out by Norton,<sup>2</sup> conservationists almost invariably view diversity as species richness. Biological diversity is desirable since many species have actual or potential economic benefits to man.<sup>3</sup> Moreover maximizing biodiversity will lead to a natural portfolio diversification of future options for finding new sources of food and/or medicine.<sup>4,5</sup> Finally, the preservation of genetic diversity is a frequent concern to geneticists and biochemists.<sup>6,7</sup>

In the existing literature, a significant amount of discussion has been devoted to the economic aspect of diversity conservation. For example, economists have conducted extensive analyses to estimate the value, direct or indirect, of saving species that will ultimately become extinct.<sup>8</sup> Another issue of growing concern is how to allocate limited funding among various conservation activities to optimize some diversity-related goal.<sup>9</sup>

The remainder of the paper is organized as follows. In Section 2 the current literature on biological diversity is reviewed. In Section 3 we propose an operational framework within which the concept of diversity is quantifiable as well as measurable. Basing the computation of diversity on an interspecies dissimilarity measure, in Section 4 we develop a quadratic zero-one integer programming model with the objective of maximizing biodiversity subject to resource constraints, which is subsequently converted into an equivalent linear model in Section 5. In Section 6 we present a simple application of the model to the preservation of diversity in the crane family. Following the intro-

---

Address reprint requests to Dr. Krishna S. Dhir at the School of Business Administration, Penn State University at Harrisburg, Middletown, PA 17057-4898, USA.

Received 21 June 1994; revised 10 May 1995; accepted 6 June 1995

duction of an alternative measurement of biodiversity in Section 7, a comparison is made between the two approaches examined in this paper using a real example on DNA divergence in hominoid species. Finally in Section 8 we conclude that mathematical modelling of biological diversity is an important area where significant progress can be made both in theoretical development and in real-world applications.

## 2. Literature survey

Biological diversity refers to the richness and equal abundance of species. The study of biodiversity intrigued many of the early investigators of the natural world, and it continues to stimulate the minds of biologists today.<sup>10,11</sup> Magurran<sup>1</sup> provides a succinct summary of the relevant work on ecological diversity, including a practical guide to the measurement of ecological diversity. Solow et al.<sup>12</sup> give a critique of some simple proposals for measuring biodiversity. They also suggest a new approach for analyzing a number of conservation issues. In his recent study, Weitzman<sup>5</sup> develops a diversity function that satisfies a basic dynamic programming equation. Moreover, a novel index of taxic diversity has been introduced by Vane-Wright et al.<sup>13</sup> and applied to the evaluation of wildlife conservation.

During the recent efforts in preserving biological diversity, researchers have drawn upon the tools of mainstream resource economics to assess the benefits of individual species.<sup>14</sup> Ray,<sup>15</sup> on the other hand, emphasizes the importance of higher-taxon diversity. Along the same line, Eiswerth and Haney<sup>9</sup> have shown how the consideration of interspecies genetic difference might affect the allocation of limited budget among habitats for preserving ecological diversity.

Given the volume of relevant research on biological diversity, few previous studies have employed the tools in mathematical programming to address the issue of diversity maximization. This paper aims at the formulation of the maximum biodiversity problem as an integer program as well as the solution of such an optimization model. A comparative study will also be performed to show how different approaches to diversity measurement can lead to different conclusions.

## 3. Measurement of diversity

From our perspective, a sensible approach to biological diversity involves two steps: first selecting a measure of dissimilarity and then calculating diversity. Let  $N = \{1, 2, \dots, n\}$  be an index set and let  $S = \{s_i: i \in N\}$  be a set of operational taxonomic units (OTUs) in biological taxonomy.<sup>16</sup> Further let  $d: S \times S \rightarrow R^+$  be a distance function which satisfies the following conditions:

$$\begin{aligned} d(s_i, s_j) &\geq 0, & i, j \in N \\ d(s_i, s_i) &= 0, & i \in N \\ d(s_i, s_j) &= d(s_j, s_i), & i, j \in N \end{aligned}$$

The quantity  $d(s_i, s_j)$  represents the dissimilarity, or distance, between  $s_i$  and  $s_j$ . It is a function of the differences between the two OTUs with respect to some attributes of interest, such as petal color,<sup>16</sup> unison call,<sup>17</sup> the number of gene substitutions per locus,<sup>18</sup> and so on. According to these conventions, we define  $Z$ , the diversity of the elements over any subset  $I$  of  $N$ , as the sum of the distances between each distinct pair of OTUs in this subset. In particular, let  $P(I) = \{(i, j): i, j \in I \text{ and } i < j\}$ . Then we may express  $Z$  as

$$Z = \sum [d(s_i, s_j): (i, j) \in P(I)]$$

Such a quantitative definition of diversity will be used in the sequel, except in Section 7 where an alternative approach to the measurement of biodiversity is utilized. Our goal in general will be to identify a best (maximally diverse) subset  $I$  of elements in  $N$ .

## 4. Mathematical formulations for preserving biological diversity

Consider the situation in which a conservation planner is to allocate resources to preserve the biological diversity in a habitat. Given a limited endowment for conservation, he is confronted with the problem of determining which species to protect so that the biological diversity in the region is maximized.

Suppose there are  $n$  species in the habitat designated by  $s_1, s_2, \dots,$  and  $s_n$ . It is assumed that, due to limitations of resources available, only a total amount of  $b > 0$  is available and  $c_i > 0$  is the amount of the resource required to preserve species  $s_i, i \in N$ . We define a binary variable  $x_i$  for each species, where  $x_i = 1$  indicates that species  $s_i$  will be preserved and  $x_i = 0$  otherwise,  $i \in N$ . Finally, for  $P(I)$  as previously defined, let  $P = P(N)$ . A quadratic zero-one programming model for maximizing biodiversity is then

(M1)

$$\text{Maximize } Z = \sum [d(s_i, s_j)x_i x_j: (i, j) \in P]$$

subject to

$$\sum [c_i x_i: i \in N] \leq b$$

$$x_i \in \{0, 1\}, \quad i \in N$$

Apparently, the foregoing problem is trivial if only two species are to be preserved. We simply rank all the interspecies distances in descending order. Then, beginning with the top of the list, the first pair of species should be selected for which the preservation requirement does not exceed the total amount of resource available. In other words, we should choose to preserve the first pair of species  $s_p$  and  $s_q$  so that  $c_p + c_q \leq b$ . However it can be shown by scaling that the general maximum biodiversity problem is reducible to the maximum diversity problem examined by Kuo et al.<sup>19</sup> which has been shown to be NP-hard.<sup>20</sup> Consequently the maximum biodiversity problem is NP-hard as well; namely (M1) is so intractable that

no existing algorithms can be applied to obtain (and verify) the optimal solution within a reasonable amount of time as a polynomial function of the problem size.

**5. Linearization of nonlinear zero-one programs**

Although several algorithms are available for solving quadratic integer programs such as (M1),<sup>21-24</sup> they are relatively inefficient even for medium-sized problems and have not found widespread use in real-life applications. In order for nonlinear models to be solved effectively, it is desirable that they be transformed into equivalent linear models. Toward this end it can be established that, based on the results of Glover and Woolsey,<sup>25</sup> (M1) can be converted into the following linear integer program:

(M2)

$$\text{Maximize } Z = \sum [d(s_i, s_j) y_{ij} : (i, j) \in P]$$

subject to

$$\begin{aligned} \sum [c_i x_i : i \in N] &\leq b \\ x_i + x_j - y_{ij} &\leq 1, \quad (i, j) \in P \\ -x_i + y_{ij} &\leq 0, \quad (i, j) \in P \\ -x_j + y_{ij} &\leq 0, \quad (i, j) \in P \\ y_{ij} &\geq 0, \quad (i, j) \in P \\ x_i &\in \{0, 1\}, \quad i \in N \end{aligned} \tag{1}$$

We note that since  $d(s_i, s_j) \geq 0$  for all  $(i, j) \in P$ , constraint (1) will be nonbinding at an optimal solution and hence can be disregarded. Thus (M2) reduces to (M3) presented below:

(M3)

$$\text{Maximize } Z = \sum [d(s_i, s_j) y_{ij} : (i, j) \in P]$$

subject to

$$\begin{aligned} \sum [c_i x_i : i \in N] &\leq b \\ -x_i + y_{ij} &\leq 0, \quad (i, j) \in P \\ -x_j + y_{ij} &\leq 0, \quad (i, j) \in P \\ y_{ij} &\geq 0, \quad (i, j) \in P \\ x_i &\in \{0, 1\}, \quad i \in N \end{aligned}$$

(M3) can be further refined using the observations of Glover,<sup>26,27</sup> but its present form gives a useful formulation for treating the maximum biodiversity problem.

**6. An application**

In this section, we will describe an application of the maximum biodiversity model to the conservation of the crane family under resource constraints. We will use (M3), the simplest linearized form of the model, and show how particular concerns can be addressed by incorporating additional constraints into the formulation.

According to Peters,<sup>28</sup> most researchers agree that there are 14 existing species of crane, though Walkinshaw<sup>29</sup> has considered the African crowned cranes as the 15th species. These have been listed in *Table 1*.<sup>12,30</sup>

Suppose a new wildlife preservation program is initiated to protect cranes. The total funding is \$1 million and it costs \$150,000 to conserve any of the 14 existing crane species. The problem is to determine which species should be preserved so that the biological diversity is maximized.

To begin, we need information about the extent to which a crane species differs from the others. While in literature no single approach to diversity measurement captures all the dimensions of interspecies dissimilarity, geneticists have used a number of methods to measure the distinctiveness between taxa.<sup>18</sup> We will employ data on the differences between the DNA sequences of different species resulting from the DNA-DNA hybridization method.<sup>31</sup> The genetic distances, which are calculated as the delta median melting points between homologous and heterologous hybrids, between each pair of the 14 crane species have been summarized in *Table 2*,<sup>12,30</sup> where average melting points have been used to establish the symmetry of the distance matrix.

In light of the maximum biodiversity model (M3), the problem of determining which species of crane to conserve can be formulated as the following mixed linear integer program:

(M4)

$$\text{Maximize } Z = 3.75 y_{1,2} + 3.85 y_{1,3} + \dots + 0.65 y_{13,14} \tag{2}$$

subject to

$$\begin{aligned} 150,000 x_1 + 150,000 x_2 + \dots + 150,000 x_{14} &\leq 1,000,000 \\ -x_1 + y_{1,2} &\leq 0 \\ -x_1 + y_{1,3} &\leq 0 \end{aligned}$$

**Table 1.** Species list of the crane family.

No.	Common name	Latin name
1	South African	<i>Balearica regulorum</i>
2	Demoiselle	<i>Anthropoides virgo</i>
3	Blue	<i>Anthropoides paradisea</i>
4	Wattled	<i>Bugeranus carunculatus</i>
5	Siberian	<i>Grus carunculatus</i>
6	Sandhill	<i>Grus leucogeranus</i>
7	Sarus	<i>Grus antigone</i>
8	Australian	<i>Grus rubicunda</i>
9	White-naped	<i>Grus vipio</i>
10	Eurasian	<i>Grus grus</i>
11	Hooded	<i>Grus monachus</i>
12	Whooping	<i>Grus americana</i>
13	Black-necked	<i>Grus nigricollis</i>
14	Japanese	<i>Grus japonensis</i>

$$\begin{aligned} & \vdots \\ & -x_{13} + y_{13,14} \leq 0 \\ & -x_2 + y_{1,2} \leq 0 \\ & -x_3 + y_{1,3} \leq 0 \\ & \vdots \\ & -x_{14} + y_{13,14} \leq 0 \\ & y_{1,2}, y_{1,3}, \dots, y_{13,14} \geq 0 \\ & x_1, x_2, \dots, x_{14} \in \{0, 1\} \end{aligned}$$

Using LINDO<sup>32</sup> to solve the problem, we obtain an optimal solution of  $(x_1^*, x_2^*, x_3^*, x_4^*, x_5^*, x_6^*, x_7^*, x_8^*, x_9^*, x_{10}^*, x_{11}^*, x_{12}^*, x_{13}^*, x_{14}^*) = (1, 0, 1, 1, 1, 0, 1, 0, 0, 0, 1, 0, 0, 0, 0)$  with a total diversity of  $Z^* = 34.5$ . The result indicates that the subset of cranes exhibiting the highest degree of biodiversity consists of South African, blue, wattled, Siberian, sarus, and hooded.

According to Johnsgard,<sup>33</sup> among the 14 existing species of crane, the Siberian crane (#5) and the whooping crane (#12) are considered endangered. While the current optimal choice includes the former, it omits the latter. It might be desirable that all the members of a given subset of species, indexed by  $J \subset N$ , be preserved. More generally, we may seek to assure that at least a certain minimum number  $L(J)$  of the species from this subset be conserved. This can be handled by adding the constraint  $\sum [x_i; i \in J] \geq L(J)$  to the model. If we do this for  $J = \{5, 12\}$  and  $L(J) = 2$  to ensure the preservation of Siberian and whooping cranes, the optimal solution of  $(x_1^*, x_2^*, x_3^*, x_4^*, x_5^*, x_6^*, x_7^*, x_8^*, x_9^*, x_{10}^*, x_{11}^*, x_{12}^*, x_{13}^*, x_{14}^*) = (1, 0, 1, 1, 1, 0, 1, 0, 0, 0, 1, 0, 0, 0)$  shows that the following six species should be protected: South African, blue, wattled, Siberian, sarus, and whooping. The total biological diversity for this collection of cranes is  $Z^* = 33.65$ . Upper bounds on numbers of species from a given subset can be accommodated in a similar way, thus making certain that particular subsets are not "over-represented" in the optimal solution.

It is sometimes important to impose a minimum inter-species genetic distance in the conservation of wildlife when polymorphism is a major concern or when there is a

danger of inbreeding in populations isolated in nature reserves. We can meet this additional requirement by replacing each of the objective function coefficients in the maximum biodiversity model that lie below a chosen value  $t$  with  $-M$ , where  $t$  represents the threshold value of genetic distance and  $M$  is an extremely large positive number. For instance, suppose that in the previous illustration the genetic distance between each distinct pair of the crane species to be preserved must be at least  $t = 1.18$ . To maximize the biological diversity and yet satisfy the additional constraint, we make the following replacements in equation (2) of (M4):  $d(s_2, s_3) = -9,999$ ,  $d(s_2, s_4) = -9,999$ ,  $d(s_2, s_8) = -9,999$ , ...,  $d(s_{13}, s_{14}) = -9,999$ . It can be shown that the optimal solution to the new problem calls for the preservation of the following six species of crane with a total diversity of 34.2: South African, blue, wattled, Siberian, sandhill, and Japanese.

If, however, the conservation planner wishes to maximize the minimum genetic distance between each pair of the cranes to be preserved, the following "maximin" biodiversity model can be utilized to achieve the goal:

$$\begin{aligned} & \text{(M5)} \\ & \text{Maximize } Z = w \\ & \text{subject to} \\ & 150,000x_1 + 150,000x_2 + \dots + 150,000x_{14} \\ & \leq 1,000,000 \\ & (M - 3.75)y_{1,2} + w \leq M \\ & (M - 3.85)y_{1,3} + w \leq M \\ & \vdots \\ & (M - 0.65)y_{13,14} + w \leq M \\ & -x_1 + y_{1,2} \leq 0 \\ & -x_1 + y_{1,3} \leq 0 \\ & \vdots \\ & -x_{13} + y_{13,14} \leq 0 \\ & -x_2 + y_{1,2} \leq 0 \\ & -x_3 + y_{1,3} \leq 0 \\ & \vdots \\ & \vdots \end{aligned}$$

Table 2. Genetic distances among crane species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.00	3.75	3.85	4.10	3.55	3.90	3.70	3.60	3.60	3.55	4.05	3.65	3.55	3.80
2	3.75	0.00	0.50	1.10	1.80	1.35	1.50	1.15	1.05	1.00	1.05	1.25	1.50	1.55
3	3.85	0.50	0.00	1.25	1.90	1.30	1.75	1.00	1.15	1.05	1.20	1.30	1.15	1.75
4	4.10	1.10	1.25	0.00	1.55	1.20	1.50	1.40	1.35	1.10	1.60	1.30	1.25	1.40
5	3.55	1.80	1.90	1.55	0.00	1.45	1.15	1.50	1.60	1.25	1.55	1.65	1.50	1.65
6	3.90	1.35	1.30	1.20	1.45	0.00	1.40	1.20	1.10	1.10	1.45	1.40	1.75	1.55
7	3.70	1.50	1.75	1.50	1.15	1.40	0.00	0.60	0.50	1.15	1.80	1.45	1.50	1.40
8	3.60	1.15	1.00	1.40	1.50	1.20	0.60	0.00	0.65	1.10	1.40	1.50	1.75	1.35
9	3.60	1.05	1.15	1.35	1.60	1.10	0.50	0.65	0.00	1.10	1.15	1.35	1.30	1.05
10	3.55	1.00	1.05	1.10	1.25	1.10	1.15	1.10	1.10	0.00	0.20	0.15	0.60	0.35
11	4.05	1.05	1.20	1.60	1.55	1.45	1.80	1.40	1.15	0.20	0.00	0.35	0.60	0.55
12	3.65	1.25	1.30	1.30	1.65	1.40	1.45	1.50	1.35	0.15	0.35	0.00	0.65	0.65
13	3.55	1.50	1.15	1.25	1.50	1.75	1.50	1.75	1.30	0.60	0.60	0.65	0.00	0.65
14	3.80	1.55	1.75	1.40	1.65	1.55	1.40	1.35	1.05	0.35	0.55	0.65	0.65	0.00

**Table 3.** Species list of six higher primates.

No.	Common name	Latin name
1	Human	<i>Homo sapiens</i>
2	Common chimpanzee	<i>Pan troglodytes</i>
3	Gorilla	<i>Gorilla gorilla</i>
4	Orangutan	<i>Pongo pygmaeus</i>
5	Common gibbon	<i>Hylobates lar</i>
6	Siamang gibbon	<i>Hylobates syndactylus</i>

$$\begin{aligned}
 & -x_{14} + y_{13,14} \leq 0 \\
 & y_{1,2}, y_{1,3}, \dots, y_{13,14} \geq 0 \\
 & x_1, x_2, \dots, x_{14} \in \{0, 1\}
 \end{aligned}$$

The LINDO solution turns out to be  $(x_1^*, x_2^*, x_3^*, x_4^*, x_5^*, x_6^*, x_7^*, x_8^*, x_9^*, x_{10}^*, x_{11}^*, x_{12}^*, x_{13}^*, x_{14}^*) = (1, 0, 1, 1, 1, 0, 1, 0, 0, 0, 1, 0, 0, 0)$  with a total biodiversity of  $Z^* = 1.20$ .

Finally, we observe that resource constraints of a much more general form can be introduced into the maximum biodiversity model. Specifically, if  $c_{ki}$  represents the amount of resource  $k \in M = \{1, 2, \dots, m\}$  required to ensure the preservation of species  $i$  and  $b_k$  represents the total amount of resource  $k$  available (such as available land area of a particular type of habitat, available quantity of a particular type of food supply, or available budget for obtaining additional necessary forms of sanctuary or food, etc.), then we may incorporate the following constraints in the model:

$$\sum [c_{ki}x_i; i \in N] \leq b_k, \quad k \in M$$

Constraints of this form make it possible to model a wide variety of considerations in a straightforward way when examining the maximum biodiversity problem and other related issues.

### 7. An alternative measurement of biological diversity

In contrast to the framework proposed in the present study, Weitzman<sup>5</sup> considers the measurement of ecological diversity from a different perspective and suggests an alternative approach which is based on the concept of dynamic programming.<sup>34</sup> As before, let  $N = \{1, 2, \dots, n\}$  be an index set and let  $S = \{s_i; i \in N\}$  be a set of OTUs. Let  $I \subseteq N$  be the index set for  $Q \subseteq S$ . According to Weitzman,<sup>5</sup> the distance between any element  $s_i \in S$  and  $Q$  is defined as the distance between  $s_i$  and its nearest neighbor in  $Q$ ; namely,

$$d(s_i, Q) = \min_{j \in I} d(s_i, s_j)$$

**Table 4.** Genetic distances among hominoid species.

	1	2	3	4	5	6
1	0	159	250	349	495	513
2	159	0	234	328	448	448
3	250	234	0	357	532	498
4	349	328	357	0	477	488
5	495	448	532	477	0	126
6	513	448	498	488	126	0

Furthermore, the formula for computing the diversity over the elements in  $Q$ ,  $D(Q)$ , is as follows:

$$D(Q) = \max_{i \in I} \{d(s_i, Q \setminus \{s_i\}) + D(Q \setminus \{s_i\})\}$$

Now, let  $f(Q, y)$  be the maximum diversity over the elements in  $Q$  subject to the total resource availability of  $y$ . A dynamic programming formulation for the constrained maximum biodiversity problem is presented below:

(M6)

Recursive function:

$$\begin{aligned}
 f(Q, y) = \max_{i \in I} \{ & d(s_i, Q \setminus \{s_i\}) \\
 & + f(Q \setminus \{s_i\}, y - c_i), \quad 0 \leq y \leq \sum_{i \in I} c_i
 \end{aligned} \tag{3}$$

Boundary conditions:

$$f(\{s_i\}, y) = 0 \text{ for all } y \geq 0, i \in N \tag{4}$$

Objective function:  $f(S, b)$

$$\tag{5}$$

The dynamic program (M6) consisting of equations (3), (4), and (5) can be solved through the recursive fixing process.<sup>34</sup>

In what follows, we will compare the integer programming-based model (M1) with the dynamic programming-based model (M6) by considering a real example in which the objective is to maximize the genetic variety. Pertinent information on six major species of higher primates has been shown in Table 3 and Table 4.<sup>5,35</sup> The goal is to determine the subset of species with the largest genetic variability with respect to DNA divergence.

Given the fictitious cost of \$240,000 for preserving any of the six hominoid species, we have obtained the optimal solutions to both (M1) and (M6) under different budgetary constraints. These have been displayed in Table 5.

It is seen that while the optimal solutions to both models are the same when  $b = \$500,000$  and  $b =$

**Table 5.** Optimal solutions based on two models.

$b$	(M1)		(M6)	
	Optimal solution	Maximum diversity	Optimal solution	Maximum diversity
\$500,000	(0, 0, 1, 0, 1, 0)	532	(0, 0, 1, 0, 1, 0)	532
\$750,000	(0, 0, 1, 1, 1, 0)	1,366	(0, 0, 1, 1, 1, 0)	889
\$1,000,000	(0, 0, 1, 1, 1, 1)	2,478	(1, 0, 1, 1, 1, 0)	1,139
\$1,250,000	(1, 0, 1, 1, 1, 1)	4,085	(1, 1, 1, 1, 1, 0)	1,298

\$750,000, they differ in the cases of  $b = \$1,000,000$  and  $b = \$1,250,000$ . Moreover, given the same optimal solutions, the maximum total diversities resulting from both models differ.

## 8. Conclusion

We have proposed a new framework for measuring and computing biological diversity of a habitat. Our maximum biodiversity model is based on introducing and exploiting measures of genetic distinctiveness for selecting the optimal subset of OTUs to conserve when resource limitations prevent the preservation of all the species. An application of the model in a rudimentary form is illustrated for the preservation of endangered crane species with the maximum genetic diversity. We also demonstrate the various ways to expand the model to handle additional relevant concerns. Furthermore, the results from a comparative study demonstrate how different approaches to the measurement of biodiversity may lead to different conservation policies.

We note that there are many ecological systems in which the extinction of some species may threaten the survival of others. In such cases, the interspecies interaction can be accounted for by incorporating the joint probability distribution into the maximum biodiversity model.<sup>5,12</sup> Throughout this paper, we have focused exclusively on the biological diversity among species. It should be pointed out, however, that maximum diversity alone can be highly misleading as a yardstick in making conservation decisions. Economic values accruing from individual species<sup>9</sup> or the value of saving species<sup>8</sup> should also be explored.

The development of what May<sup>11</sup> has called the calculus of biological diversity is still very much in its infancy. The methodology suggested here represents only one approach to this calculus. It is hoped that the present work will stimulate further interest in the measurement and computation issues of this important research area.

## References

- Magurran, A. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ, 1988
- Norton, B. G. *The Preservation of Species*. Princeton University Press, Princeton, NJ, 1986
- Helliwell, D. R. Assessment of conservation values of large and small organisms. *J. Environ. Management* 1982, **15**, 273–277
- Oldfield, M. L. *The Value of Conserving Genetic Resources*. U.S. Department of the Interior, Washington, DC, 1984
- Weitzman, M. L. On diversity. *Q. J. Econ.* 1992, **107**(2), 363–406
- Harris, L. D., McGlothlen, M. E. and Manlove, M. N. Genetic resources and biotic diversity. *The Fragmented Forest*, ed. L. D. Harris, University of Chicago Press, Chicago, IL, 1984, 93–107
- Vida, G. Genetic diversity and environmental future. *Environ. Conserv.* 1978, **5**, 127–132
- Brown, G., Jr. and Goldstein, J. H. A model for valuing endangered species. *J. Environ. Econ. Management* 1984, **11**, 303–309
- Eiswerth, M. E. and Haney, J. C. Allocating conservation expenditures: Accounting for inter-species genetic distinctiveness. *Ecological Econ.* 1992, **5**, 235–249
- Currie, D. J. and Paquin, V. Large-scale biogeographical patterns of species richness of trees. *Nature* 1987, **329**, 326–327
- May, R. M. Taxonomy as destiny. *Nature* 1990, **347**, 129–130
- Solow, A., Polasky, S. and Broadus, J. On the measurement of biological diversity. *J. Environ. Econ. Management* 1993, **24**, 60–68
- Vane-Wright, R. I., Humphries, C. J. and Williams, P. H. What to protect?—Systematics and the agony of choice. *Biol. Conserv.* 1991, **55**, 235–254
- Fisher, A. C. and Hanemann, W. M. Option value and the extinction of species. *Advances in Applied Microeconomics: A Research Annual*, ed. V. K. Smith, JAI Press, Greenwich, CT, 1986, 169–190
- Ray, G. C. Ecological diversity in coastal zones and oceans. *Biodiversity*, ed. E. O. Wilson, National Academy Press, Washington, DC, 1988, 36–50
- Jardine, N. and Sibson, R. *Mathematical Taxonomy*. John Wiley & Sons, New York, 1971
- Archibald, G. W. Crane taxonomy as revealed by the unison cell. *Crane Research Around the World*, eds. J. C. Lewis and H. Masatomi, International Crane Foundation, Baraboo, WI, 1976
- Nei, M. *Molecular Evolutionary Genetics*. Columbia University Press, New York, 1987
- Kuo, C.-C., Glover, F. and Dhir, K. S. Analyzing and modeling the maximum diversity problem by zero-one programming. *Decision Sci.* 1993, **24**(6), 1171–1185
- Garey, M. R. and Johnson, D. S. *Computers and Intractability: A Guide to the Theory of NP-Completeness*. Freeman, New York, 1979
- Laughunn, D. J. Quadratic binary programming with application to capital-budgeting problems. *Operations Res.* 1970, **18**(3), 454–461
- Lawler, E. L. and Bell, M. D. A method for solving discrete optimization problems. *Operations Res.* 1966, **14**(6), 1098–1112
- Taha, H. A. A Balasian-based algorithm for zero-one polynomial programming. *Management Sci.* 1972, **18**(6), B328–B343
- Taha, H. A. Further improvements in the polynomial zero-one algorithm. *Management Sci.* 1972, **19**, B226–B227
- Glover, F. and Woolsey, R. E. Converting the 0-1 polynomial programming program into a 0-1 linear program. *Operations Res.* 1974, **22**(1), 180–182
- Glover, F. Improved linear integer programming formulations of nonlinear integer problems. *Management Sci.* 1975, **22**(4), 455–460
- Glover, F. An improved MIP formulation for products of discrete and continuous variables. *J. Info. Optimization Sci.* 1984, **5**(1), 69–71
- Peters, J. L. *Check-List of Birds of the World*, Vol. 2. Harvard University Press, Cambridge, MA, 1934
- Walkinshaw, L. H. The African crowned cranes. *Wilson Bull.* 1964, **76**, 355–377
- Krajewski, C. Phylogenetic relationships among cranes (gruiformes: gruidae) based on DNA hybridization. *Auk* 1989, **106**, 603–618
- Ahlquist, J. E., Bledsoe, A. H., Sheldon, F. H. and Sibley, C. G. DNA hybridization and avian systematics. *Auk* 1987, **104**, 556–563
- Schrage, L. *Linear, Integer, and Quadratic Programming with LINDO*. Scientific Press, Palo Alto, CA, 1984
- Johnsgard, P. A. *Cranes of the World*. Indiana University Press, Bloomington, IN, 1983
- Denardo, E. *Dynamic Programming*. Prentice-Hall, Englewood Cliffs, NJ, 1982
- Caccone, A. and Powell, J. R. DNA divergence among hominoids. *Evolution* 1989, **43**, 925–942