

ANALYSIS

Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter

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Abstract

Accounting for biodiversity is important in several different types of constrained choice problems, including public and private decisions for habitat and species conservation, the establishment of recreational parks and natural areas, mitigation banking, and natural resource damage assessment (particularly primary and/or compensatory restoration planning and scaling). In such applications it is important to give careful consideration to (1) the choice of biodiversity indicator(s) to be used, and (2) the role of discontinuous, nonlinear ecological processes in light of the decisionmaker's chosen time horizon. The former is important because the choice of indicator(s) can substantially influence decisions about conservation priority-setting and planning. The latter is critical for the same reason, notwithstanding that dynamic ecosystem processes have rarely been considered sufficiently, if at all, in such applications (in part because the processes usually are poorly understood or measured). In this manuscript we use avian diversity data, collected by one of the authors, from hardwood forest ecosystems in the eastern United States. We couple these data with estimates of species prevalence factors to construct a case study of how indicator choice and consideration of ecological thresholds influence the outcomes of biodiversity preservation problems. We show that (1) the choice of indicator(s) is critical, (2) failure to account for nonlinear, threshold effects in an ecosystem's future progression alters preservation decisions and ignores important information, (3) the effect of choosing different time horizons depends on the indicator used, and (4) for any given biodiversity indicator, dynamic solutions can depend on the time horizon chosen but not necessarily in monotonic or simple fashion. Our case study highlights the importance of further system-specific research on dynamic ecological progressions as well as uncertainty regarding future supply and demand for ecosystem service flows. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Despite the existence of accepted general definitions of biodiversity, debate continues over just

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what biodiversity is, how it should be measured, and why it is important. Ecologists have defined a number of different types, or levels, of biodiversity, with an increasing consensus that no one indicator can or should be relied upon to characterize it. Different measures provide different indications of the variety and integrity of ecosystems, however, and the choice of measures to use in a given context depends on the research or policy objectives at hand.

In previous research, we compared the outcomes from applying different biodiversity indicators to constrained choice problems of ecosystem/habitat preservation (Eiserwerth and Haney, 1992; Haney and Eiserwerth, 1992). In more recent research, one of the authors collected a substantial amount of plant and animal data from hardwood forest ecosystems in the eastern United States. The data collection project was designed to investigate the ecological importance of old growth via comparisons to younger seral (successional) stages of hemlock-northern hardwood forest (Haney, 1994, 1995; Haney and Schaadt, 1995). In this manuscript we use a portion of these data to construct a case study of how the choice of biodiversity indicators may affect constrained choice problems, for example, public decisions related to habitat conservation, restoration, or mitigation activities. In addition, this case study illustrates the dynamic considerations that are important to such decisions. The forest ecosystem we focus on is characterized by nonlinear changes over time in structure and function, with discontinuities occurring as the ecosystem moves from one developmental stage to the next. As a result, biodiversity in this system is a discontinuous function of time. This has implications for problems in which the desired outcome is to maximize the flow of future services provided by biodiversity. We show how the dynamic solution to a biodiversity preservation problem may depend significantly on the time horizon considered and the biodiversity indicator used.

2. Background

2.1. Relevant literature

Biodiversity has long been recognized to be a multidimensional attribute of natural systems, with scientists referring to different levels of biodiversity including ecosystem, species, and genetic diversity (Office of Technology Assessment, 1988; McNeely et al., 1990; National Research Council, 1992). Several years ago, Ray (1988) observed that an “accounting of species alone can be highly misleading as a yardstick of diversity”, which led him to emphasize the importance of higher-order taxonomic diversity. Atkinson (1989) placed this consideration in clear perspective by stating that “given two threatened taxa, one a species not closely related to other living species and the other a subspecies of an otherwise widespread and common species, it seems reasonable to give priority to the taxonomically distinct form.”

Observations such as these have encouraged the development of measures that use taxonomic information (May, 1990; Altschul and Lipman, 1990; Vane-Wright et al., 1991) or information from limited molecular sequences (Crozier, 1992; Faith, 1992). Researchers have also used genetic distinctiveness data to indicate biodiversity, by incorporating genome-wide data and linking composite information about an organism’s entire genetic makeup to data on species richness (Eiserwerth and Haney, 1992). This is the kind of information that can be useful in many contexts, including (but not limited to) the search for species that have pharmaceutical and other values (e.g. Reid et al., 1993a; Simpson et al., 1994).

In setting priorities for conservation, relevant metrics may include combinations of indicators that reflect both diversity and the amount of diversity at risk. For example, species risk factors can be combined with taxonomic distinctiveness indicators to yield a layered proxy (e.g. Haney and Eiserwerth, 1992). Such layered indicators illustrate how decisions comparing diversity among regions can change as more (and better) information is considered in addition to simply species richness. Reid et al. (1993b) provided an

informative summary of a wide range of indicators useful for policymakers, including ones that embody risk. Such indicators are important in applied decision-making because direct measures of ecosystem value are in most cases unavailable, insufficient, or too expensive to develop using standard valuation methods (King, 1997). Indicators that are easy to use, are applicable to large areas, and have a close linkage with specific elements, processes, or qualities of ecosystem integrity are likely to be the most useful (Bradford et al., 1998; Miller et al., 1998/1999).

To model ecological attributes of ecosystems realistically, it is necessary to consider dynamic thresholds and other nonlinear processes in system structure and function. Such dynamic processes are rarely considered sufficiently, if at all, in exercises such as habitat protection, restoration, or conservation planning. Nonlinear, threshold processes are considered even less frequently, in part because they usually are poorly understood or measured. The importance of such processes is sometimes at least recognized in the literature (e.g. King, 1997), but to date their incorporation in decision-making is woefully inadequate.

2.2. *Pertinent concepts and applications*

Concepts about biodiversity that we explore in this manuscript include: (1) the choice of biodiversity indicator does matter, and can drive conservation decisions, (2) it is important to account for dynamic ecosystem processes, and decision rules that do so may yield quite different results from those that do not, (3) for any given indicator of biodiversity, investments in conservation may depend on the time horizon considered, but not necessarily in monotonic fashion, and (4) the effect on the dynamic solution of changes in the time horizon may depend upon the biodiversity indicator used.

These concepts have relevance for a number of different activities and decisions. Examples include: (1) decisions related to the purchase of land for conservation easements, (2) the establishment of new recreational parks or natural areas, (3) agency priority-setting for habitat and/or species conservation expenditures, (4) decisions involved in mitiga-

tion banking, and (5) natural resource damage assessment (NRDA), particularly primary and/or compensatory restoration planning and scaling.

Forest biodiversity receives wide attention because of the multiple ecological, social, and economic values associated with forest ecosystems (National Research Council, 1998). Our case study involving eastern forests is particularly relevant given that decision-makers are currently attempting to determine the optimal mix of management regimes for sustainable forests. For example, individuals in Maine recently expressed an interest in purchasing lands from timber companies to create a large reserve in which forests would stand undisturbed (Northern Forest Alliance, 2000). In this and related situations, one of the relevant choice problems is, or at least ought to be: ‘Given a set of forest tracts and a budget constraint for preservation, what is the optimal mix of conservation efforts (or more broadly, management regimes) that maximizes the preservation of biodiversity?’ The answer depends on the way in which the problem is formulated and the characteristics of the candidate conservation areas. While this manuscript deals solely with indicators of biodiversity rather than the broader (and more complex) set of potential indicators of all ecosystem functions and services, we recognize that in many decision contexts such broader indicators are generally of interest. We focus on biodiversity per se as one characteristic of natural systems, and show that consideration of even one such characteristic is in itself a complex step.

3. *Case study forest areas: characteristics and data*

This case study is based on avian data collected from over 20 study plots in hemlock-northern hardwood forest. Numerical values for avian populations and communities were obtained from field studies conducted in Clearfield, Potter, and McKean counties on the Allegheny Plateau, Pennsylvania (unpubl. data, J.C. Haney, collected 1992–1994; Dessecker and Yahner, 1984). Censuses were conducted in each of five forest age classes: 4, 9, 50, 120, and 300+ years. Forest age

was computed as the time elapsed since the last stand-replacing disturbance (either catastrophic windthrow or even-aged timber harvest). These five classes are termed early, transitional, mid-successional, late successional, and old growth, respectively. Hemlock-northern hardwood forest displays temporal discontinuities in vegetation structure, threshold effects, and other nonlinear patterns in successional development (see, e.g. Tyrrell and Crow, 1994).

Taxonomic groups can be used as indicators in two fundamentally different ways: as proxies for biodiversity and as proxies for environmental conditions. For a variety of reasons, focusing on a diverse taxon such as birds is useful since a number of structural and functional elements of the environment are automatically integrated. As a group, birds require very diverse microhabitats arising from structural attributes related to stand and floristic composition, snag availability, foliage height diversity, horizontal complexity, core area, and local moisture conditions (Wiens, 1989). Bird communities also exhibit marked, well-documented differences in assemblage structure associated with forest developmental sequences (Lanyon, 1981; Smith and MacMahon, 1981; May, 1982; Glowackinski and Weiner, 1983; Helle, 1984). Compared to other taxonomic groups, birds perform quite well as indicators of specific environmental conditions (Morrison, 1986; Croonquist and Brooks, 1991). However, because a few species do not always serve as accurate substitutes for many others (Niemi et al., 1997), we make no assumption that this single taxon serves as a suitable proxy for other species groupings or biodiversity in general (but see Pharo et al., 1999).

We used bird species richness derived from breeding bird census methodology (Lowe, 1995) as the initial proxy for forest biodiversity. A number of approaches have been proposed to estimate total species richness, C , within an area (Bunge and Fitzpatrick, 1993). For comparisons across forest development (seral) stages, however, we required only a bias-free estimate of relative species richness, c . This approach is equivalent to the data-analytic class of methods reviewed by Bunge and Fitzpatrick. Point estimates of c were

first derived from random subsampling of study plots available from this forest type ($N = 21$). Because there are other potential biases to c , estimates also conformed to the following criteria: visiting or wandering bird species were eliminated; data collection was standardized by sampling frequency (eight visits) and area (each plot was of equal size — 6 hectares (James and Rathbun, 1981); sampling was conducted wholly within a single habitat type; and study plots were located within large tracts of consolidated forest that were not in close proximity to other habitats (Remsen, 1994).

Following application of the criteria above, the resulting data were combined with other information sources to develop multiple indicators of biodiversity as well as biodiversity at risk. First, numbers of bird species (S) and higher taxa (genera [G], families [F]) were computed for each of the five forest age classes. Next, we calculated a layered proxy (S_a) that combined species richness with local (physiographic province) population species prevalences derived from Breeding Bird Atlas programs in nine contiguous states in the northeastern United States (Laughlin and Kibbe, 1985; Andrie and Carroll, 1988; Brauning, 1992; Bevier, 1994; Buckelew and Hall, 1994; Foss, 1994; Palmer-Ball, 1996; Robbins and Blom, 1996; Nicholson, 1997). This layered proxy S_a was computed as:

$$S_a = \sum_{i=1}^{S_i} [1 - LP_i] \quad (1)$$

where LP_i denotes the prevalence factor for species i at the local (physiographic province) scale. The prevalence factor from the Breeding Bird Atlas data can assume any value between 0 and 1, inclusive. For example, a value of 0.50 for local species prevalence means that the species is found on 50% of the land area at the level of the physiographic province studied (in this case, the Appalachian Plateau of Pennsylvania). As the average prevalence of a collection of species rises, the value of S_a for the collection falls. Weighting species richness in this manner thus provides us with an indication of not only (1) the number of species present in our study area, but also (2) the subset of those species present that are not preva-

lent at a larger geographic scale. This metric provides information somewhat similar to that offered by specificity indicators reflecting the occurrence (abundance) of species within a given geographic space or ‘cluster’ of sites (Dufrene and Legendre, 1997; Legendre and Legendre, 1998).

Finally, we computed a similar indicator (S_b) by weighting species richness again, this time by regional population prevalence as calculated from the Breeding Bird Atlas programs. S_b was computed as:

$$S_b = \sum_{i=1}^{S_i} [1 - RP_i] \quad (2)$$

where RP_i denotes the prevalence factor for species i at the regional scale. This indicator weights species richness to reflect those species present in our study area that are not common at the regional level (in this case, across the northeastern United States). As the number of species in a forest age class that are not prevalent regionally goes up, S_b rises as well.

The work described above yields multiple indicators of diversity or diversity/prevalence for each

of the five different forest age classes (seral stages). The values for each of these indicators, by forest stage, are shown in Table 1. Table 1 also indicates the percentage of species that were uniquely detected within each seral stage. This illustrates that each forest seral stage displays its own particular set of species.

Of course there are additional indicators that one could develop and use. For example, one of the factors that a conservation planner may wish to consider might involve the relative scarcity of different forest types, in combination with the number of species unique to each type. Such a metric would provide somewhat different information when compared to indicators S_a and S_b . However, note that S_a and S_b do explicitly incorporate the underlying relative scarcity of habitat types that play host to each particular species considered. These indicators do this by weighting each species by the percentage of land (on either a local or regional basis) on which the species is estimated to occur (and hence the percentage of land that currently provides habitat suitable to each particular species). To the extent that a

Table 1
Indicators of biodiversity in Pennsylvania hemlock-northern hardwood forest plots of different seral stages^a

Indicators	Forest seral stage ^{b,c}				
	Early (15.2%)	Transitional (31.2%)	Mid-successional (41.2%)	Late successional (12.0%)	Old growth (0.4%)
Total number of bird species	9	17	20	34	20
% Bird species uniquely detected in seral stage	22	24	10	29	40
Total number of bird genera	9	17	16	25	15
Total number of bird families	2	9	8	11	10
Species richness weighted by physiographic province (local) population prevalence (S_a)	2.5	4.3	5.9	12.9	10.1
Species richness weighted by regional population prevalence (S_b)	2.6	5.0	7.2	15.9	11.5

^a Sources of data: J.C. Haney, unpubl. data collected 1992–1994; Dessecker and Yahner, 1984; Laughlin and Kibbe, 1985; Andrie and Carroll, 1988; Brauning, 1992; Bevier, 1994; Buckelew and Hall, 1994; Foss, 1994; Palmer-Ball, 1996; Robbins and Blom, 1996; Nicholson, 1997.

^b Early seral stage = stand age of 4 years; transitional = 9 years; mid-successional = approx. 50 years; late successional = approx. 120 years; old growth = 300+ years.

^c The relative prevalence of each seral stage forest type found in Pennsylvania (as a percentage of total forestland) is given in parentheses under the seral stage names. These relative prevalence values are derived from Alerich (1993).

particular species is associated with (unique to) only one forest type, S_a and S_b embody the relative scarcity of that forest type.

As a second example, a relative measure such as S_a/S , where S denotes number of species, may be of value in certain situations with particular conservation management objectives. Such a relative measure could provide a higher indicator value for a region that has very few species (e.g. 10) but where a high percentage of those species are rare, as compared to a region with many more species (e.g. 100) but relatively few rare ones. Some conservation decision contexts may call for placing a premium on rarity (and ignoring the absolute number of species) and in such cases a measure such as S_a/S may be useful. At the same time, the attraction of S_a by itself is that it does combine two different kinds of information: species richness and species rarity.

We do not attempt in this manuscript to identify any one best indicator; indeed, indicators need to be matched carefully to management objectives since the choice of indicator will influence the decision outcome. Various alternative indicators, including but not limited to those in Table 1, have different meanings with respect to conservation objectives and social/economic values. As an example, a skilled birdwatcher may attach a great deal of importance to the sheer number of species that he or she is able to see, on average, upon visiting the forest. In contrast, an avid hiker or angler untrained in birdwatching may derive pleasure from the incidental viewing of a wide variety of birds while recreating, but may be unable to discern (or uninterested in noticing) differences among species that are closely related. Such an individual may attach more importance to the indicators in Table 1 that relate to the total number of bird genera or families, rather than species richness.

Similarly, the importance of indicators such as S_a and S_b in comparison with the others depends largely on the extent to which the conservation planner's objectives are tied to a broader spatial (e.g. regional) context. If none of the species under consideration is rare in terms of prevalence within a larger spatial area, then the meaning of S_a and S_b would be minimal. If,

however, at least one of the forest types contained species not commonly found elsewhere, then S_a and S_b would hold great meaning for objectives such as preserving population sources, preventing further habitat fragmentation, increasing wildlife corridors, and providing recreational services (i.e. viewing rare species) even to visitors from far away.

4. Static approach and results

4.1. Static illustration 1: choice of biodiversity indicator can drive habitat rankings and thus discrete choices regarding habitat conservation

The simplest problem involves a discrete choice problem of conservation. In such cases a decision-maker may be interested in choosing a subset of all geographic areas (one, in the simplest case) in which to devote habitat conservation efforts. This situation may occur when available funding for conservation is sufficiently constrained. It also may occur in processes that involve mitigation banking or compensatory restoration for lost natural resource service flows.

Table 1 reveals several points relevant to ranking our case study forest types. Perhaps the most apparent feature is that regardless of the indicator chosen, the decision-maker would rank the late successional forest first in terms of biodiversity as well as biodiversity weighted by prevalence. This forest stage dominates the others in species richness (34 species), higher taxa diversity (25 genera), species richness weighted by physiographic province (local) prevalence, and species richness weighted by regional prevalence.

Rankings of forest stages below the late successional are more problematic. If number of species is used as a biodiversity indicator, the decision-maker's second choice for conservation efforts could be either the mid-successional or old-growth seral stage. If, however, the number of genera were used as an indicator of higher taxonomic diversity, the decision-maker would pick the transitional age class over both the mid-successional and old growth as the second priority for conservation efforts.

Consideration of species prevalence factors yields even more interesting results. First, on average, species found in the early, transitional, and mid-successional forest types have high prevalence values (relative to older forests) and correspondingly lower species rarity factors. In contrast, on average, species found in older forests are less prevalent at broader spatial scales. If the indicator is defined as species richness weighted by prevalence at either the physiographic province (S_a) or regional (S_b) levels, then the old growth forest age class becomes the clear second choice for conservation efforts.

The usefulness of S_a and S_b as indicators is now clear, in that they attach a premium to forest age classes containing species that are not common. Such forest areas are potential population ‘sources’ (Pulliam, 1988) of species not prevalent at broader scales. In Section 3 we also mentioned other possible indicators, including relative measures such as S_a/S that attach complete importance to relative species rarity with no weight attached to the number of species. Such indicators would give a higher priority to old growth forests.

4.2. Static illustration 2: choice of biodiversity indicator can significantly influence the allocation of conservation expenditures among multiple geographic areas

In some instances a decision-maker may need to make decisions regarding the allocation of habitat conservation efforts in multiple geographic areas, rather than a discrete choice of which area(s) to conserve. Such decision-making requirements provide a richer context for analysis.

We assume that characteristics of one geographic area are not substitutes for the same characteristics found in another geographic area. In our case study this means, for example, that the presence of a species in a forest of a given seral stage is not a substitute for its presence in another forest area of a different stage. This is not a restrictive assumption, but rather is consistent with a number of real-world contexts. For example, it is consistent with a situation in which a decision-maker is interested in devoting efforts to natural or recreation areas some distance apart

from one another, or with differences in visitor profiles across the areas. Public preferences may also be of a type such that it is important that natural attributes (such as species) can be enjoyed in multiple areas, even when the areas are not that far apart. If demand for natural areas and the service flows (e.g. birdwatching) that they offer is high relative to supply (this is the case in many wildlife refuges today), then congestion comes into play to make the presence of a species in one area a poor substitute for its presence in another. Consideration of risk and uncertainty provides an additional basis for this assumption. As discussed in King (1997), uncertainty exists regarding the effects on ecosystems of future natural and anthropogenic changes. Since we do not know how future natural changes or human activities close to natural areas may affect their structure and function, a motivation exists to expend conservation efforts in multiple areas, even if they offer similar ecosystem services today.

Given this assumption, a decision-maker that is concerned with habitat conservation in multiple areas may wish to maximize the sum of biodiversity across the areas, subject to a budget constraint for conservation efforts. Consider the following relationship between conservation expenditures and an indicator of biodiversity:

$$b_i = \gamma_i + f_i(M_i) \quad (3)$$

where b_i is the expected value of a biodiversity indicator in area i , $\gamma_i \geq 0$ is the expected value of a biodiversity indicator in area i given no conservation expenditures in area i , M_i denotes conservation expenditures in area i , and where $f'_i(M_i) > 0$, $f''_i(M_i) < 0$. The function $f_i(M_i)$ denotes the addition to the level of the biodiversity indicator expected to result from conservation expenditures M_i .

Eq. (3) and the equations that follow are written in the standard economic format of maximizing a variable subject to a constraint on expenditures (M). However, the term M can also be interpreted more broadly as a money metric equivalent of efforts devoted to conserving biodiversity. Similarly, it is possible to interpret the term b in (1) as a function of conservation efforts rather than expenditures. One reviewer of this

article has wisely pointed out that some important conservation management steps may require less out-of-pocket expenditure and more good (and timely) planning, relative to alternative management efforts. However, the standard economic view is that such good and timely planning would come at an opportunity cost, for example, hiring a well-trained (and presumably well paid) ecologist or wildlife biologist to spend part of his or her time on the conservation planning process. For this reason as well as ease of exposition, we refer to M as conservation expenditure while realizing that a more complex indicator of conservation effort is also possible.

Consider a case in which a decision-maker is interested in two different geographic areas in different forest age classes. If the decision-maker is interested in allocating conservation expenditures between these areas, a relevant constrained maximization problem is:

$$\begin{aligned} &\text{Max}[\gamma_1 + f_1(M_1) + \gamma_2 + f_2(M_2)] \\ &\text{s.t.: } M_1 + M_2 = M \end{aligned} \quad (4)$$

where M denotes the total resources available to the decision-maker.

As an illustration of the way in which the choice of biodiversity indicators affects the solution, we consider a specific case of the generalized problem. First, assume for simplicity that $\gamma_1 = \gamma_2 = 0$; that is, in both areas, the indicator of biodiversity is expected to be zero if conservation efforts are zero. This is a special case of the more general case $\gamma_i \geq 0$ and corresponds to a situation where a decision-maker is interested in protecting all or a portion of a land area from complete development, e.g. total conversion of land into housing subdivisions, a relevant scenario in many parts of the United States. That is, the special case is that if the decision-maker makes no conservation expenditures, then complete habitat destruction will occur. We certainly recognize that in reality biodiversity does not necessarily equal zero even when land is completely developed. However, we have not collected data on biodiversity for our case study bird species in a formerly comparable area (e.g. close to our study sites) that has been deforested and developed. Therefore we

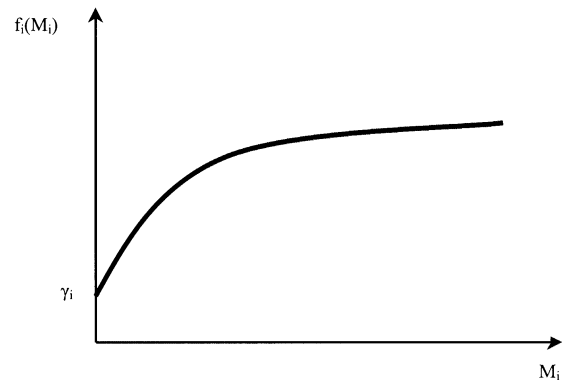


Fig. 1. General shape of illustrative function linking expected biodiversity to conservation expenditure.

make the simplifying assumption that $\gamma_1 = \gamma_2 = 0$. Relaxation of this assumption could change the numerical solution to the problem, but would not change the flavor of the concepts and results upon which we focus in this manuscript.

Second, we assume for illustration that the conservation expenditures necessary to set the expected level of the biodiversity indicator equal to the baseline (existing) level of biodiversity are equal across the two geographic areas. For example, if conservation expenditures involve purchasing land, this assumption would denote that land costs are equal for the two areas. For our illustrations, we use a specification that is consistent with these assumptions as well as the standard economic assumption of diminishing returns to expenditures:

$$f_i(M_i) = (b_i^0)(M)^{-1/2}(M_i)^{1/2} \quad (5)$$

where i denotes forest area i and b^0 the baseline (current) level of biodiversity there. The general shape of this function is shown graphically in Fig. 1, which illustrates that additional conservation efforts purchase a higher level of expected biodiversity but at a diminishing rate. Though we assume for simplicity in our numerical analyses that $\gamma_i = 0$, Fig. 1 depicts the more general case in which $\gamma_i > 0$ (some biodiversity will remain if no conservation efforts are undertaken).

The first-order condition, which gives the solution to the constrained maximization problem (noneconomists may see Chiang (1974) for an

introduction to constrained maximization) shown in Eq. (4), is:

$$(b_1^0)(M_1)^{-1/2} = (b_2^0)(M_2)^{-1/2}. \quad (6)$$

To show the implications of using alternative indicators of biodiversity as input to the constrained maximization problem, we consider the case in which forest areas 1 and 2 are currently in transitional and mid-successional stages, respectively. The comparison between these two stages is interesting because neither one dominates in terms of biodiversity.

The results from using alternative indicators are summarized in Fig. 2. Clearly the choice of indicator can influence decisions on how to allocate efforts. In our illustration, the difference between using species richness and a higher taxa diversity indicator is significant (33% more expenditures devoted to the transitional forest area using a higher-taxa indicator rather than species richness). For the subclass of problems where a decision-maker is interested in purchasing land or preventing development so as to preserve biodiversity, even the differential found in our illustration would lead to a difference in the portfolio of forest areas that the planner chooses to buy/protect. In some cases, the choice between these two indicators can have a substantial influence on

conservation planning. Some natural systems have a very large number of species but relatively low diversity at higher taxonomic levels. In contrast, some systems, for example, some marine and coastal ecosystems, are strikingly rich in their endowment of diverse families with relatively few species representing each of those families (Ray, 1988).

When species richness is weighted by regional population prevalence (to form the indicator S_b), the allocation of expenditures shifts substantially toward the older (mid-successional) forest. Using this indicator, 68% of total conservation expenditures will be targeted toward the mid-successional forest class. This outcome reflects the area's ability to act as a source for species that are not highly prevalent on a wider regional basis. As shown in Fig. 2, for the three indicators examined, the outcome may range from a low of 44% to a high of 68% of total available conservation expenditures being devoted to the older forest area. The sensitivity of the solution to the choice of indicator illustrates the potential volatility of decision-making processes to the types of information considered.

5. Dynamic approach and results

The relatively small subset of structural attributes that exhibit temporal linearity, and the threshold changes that occur in forests during succession, create distinct stages in forest ecosystems. To adequately characterize such ecosystems, time-varying stages and threshold effects must be taken into account. As in other ecosystems, diversity in our case study system is time-scale dependent, that is, dependent upon time from the most recent disturbance.

As a result, it is important to consider not only the current levels of diversity in particular areas, but also the diversity levels that the areas can potentially offer society in the future. The general problem may be viewed as choosing management options to maximize the expected 'flow' of diversity from the present to some point in the future, subject to a budget constraint.

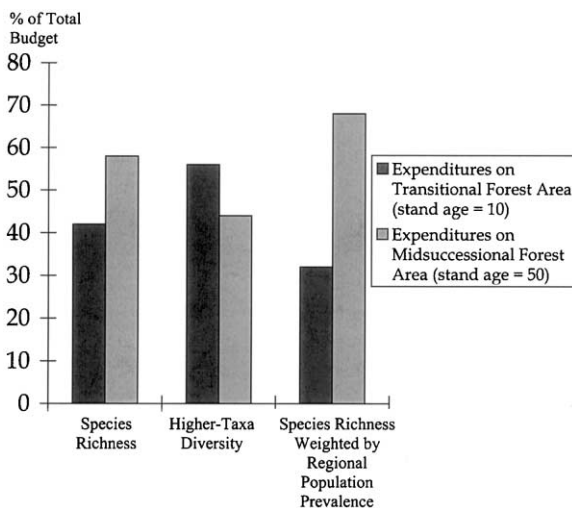


Fig. 2. Allocation of conservation expenditures: static framework.

Forests can experience abrupt structural changes in either of two directions. Successional changes occur as the forest moves through growth phases (seres), each consisting of varying intervals when structure is relatively constant but where rapid transition occurs between seres. Succession can also be reversed, and the entire set of ecological processes renewed, when catastrophic disturbance (either man-made or natural) shifts forest structure back to an earlier sere. In the forests used in our analysis, natural disturbances that completely remove canopy trees occur very rarely, about every 1200 years (Canham and Loucks, 1984; Frelich and Lorimer, 1991). At large landscape scales all successional stages can be maintained in perpetuity, although not always in the same amount or location (Shugart, 1984). In other words, by protecting relatively large areas of forest, it is possible to ‘purchase’ increased levels of certainty that a forest area will progress as anticipated through its natural growth phases.

In this section we provide illustrations of the relevance of natural dynamic processes. Section 5.1 illustrates the importance of recognizing that change may not be linear, and highlights the need for better data on how and when ecosystems encounter thresholds. Section 5.2 shows that choice of time horizon and biodiversity indicator may affect the dynamic solution to preservation, but not necessarily in the expected ways. Section 5.3 illustrates how a dynamic approach may differentiate natural areas that look equivalent from a static viewpoint.

5.1. Dynamic illustration 1: the importance of accounting for nonlinear, discontinuous ecological processes

Consider the case in which a decision-maker wishes to maximize the sum of a biodiversity indicator across two different forest areas, the first stand of 30 years and the second stand of 90 years. We assume that, for each of the seral stages we examine, diversity is characterized by the observations shown in Table 1. Suppose that the decision-maker’s time horizon, T , is 100 years. It is expected that, by time T , both of these forest areas will have evolved to the late successional

seral stage. If the decision-maker is interested in maximizing biodiversity over this period, then the relevant maximization problem is:

$$\begin{aligned} \text{Max } & \sum_{t=1}^T [f_t^1(M^1) + f_t^2(M^2)] \\ \text{s.t.: } & M^1 + M^2 = M \end{aligned} \quad (7)$$

where M^1 , M^2 , and M may be thought of as the discounted present values of the opportunity costs of conservation that are incurred between now and period T (expressed in this way to simplify the exposition). As with the static case, M is the total amount of resources available for conservation, and M^1 and M^2 are the amounts to be allocated to forest areas 1 and 2, respectively.

For most natural systems, scientists have not collected continuous data on the ways in which various indicators of biodiversity change over time. At best, a limited set of observations may exist for particular stand ages in forests, for example. In other cases, very little direct information is available. For our case study, we have the benefit of possessing standardized observations of bird diversity in forests that are very similar (in terms of climate, geographic zone, etc.) except that they are of different ages.

To illustrate the importance of knowing how natural systems evolve, suppose for a moment that all that we knew about the problem was the current number of species and higher taxa for both areas, as well as the same information for the late successional stage that both areas are expected to evolve into over the next 100 years. Assume further that diversity is expected to increase in linear fashion over time in either forest area. In this case, the choice problem would involve choosing M^1 and M^2 to maximize the sum of the areas under the (linear) biodiversity time paths in the two forests. Solution of this problem, using species as a biodiversity indicator and the same diversity–expenditure functional forms shown in Eq. (5), would provide the answer that 42% of the available resources (opportunity costs) for conservation would be devoted to forest area 1 (transitional), and 58% to forest area 2 (mid-successional).

Table 2

Allocation of conservation expenditures among transitional and mid-successional forest areas, under alternative time horizons and indicators of biodiversity^{a,b}

Time horizon	Number of species indicator (S)	Number of families indicator (F)	Species richness indicator weighted by regional population prevalence (S_b)
Time horizon = 50	Area 1: 44%	Area 1: 55%	Area 1: 36%
	Area 2: 56%	Area 2: 45%	Area 2: 64%
Time horizon = 100	Area 1: 37%	Area 1: 47%	Area 1: 29%
	Area 2: 63%	Area 2: 53%	Area 2: 71%
Time horizon = 150	Area 1: 41%	Area 1: 47%	Area 1: 36%
	Area 2: 59%	Area 2: 53%	Area 2: 64%

^a Forest area 1 is currently in the transitional seral stage with a stand age of 10 years. Forest area 2 is currently in the mid-successional seral stage with a stand age of 50 years.

^b Each percentage in the table denotes the percentage of total conservation expenditures that will be devoted to a forest area, according to the solution of the dynamic constrained maximization problem defined in the text.

Now consider the problem given our knowledge that the biodiversity time path more closely resembles a step function than a linear function. It is intuitively clear that forest area 2, currently at stand age 90, will enter the late successional seral stage significantly sooner than forest area 1. Once the late successional stage is reached, the forest area will exhibit higher levels of biodiversity as measured by numbers of species, genera, or families. Therefore, one would expect that, if we take account of the step function nature of the biodiversity time path, a premium would be placed on conservation efforts in forest area 2. Solution of the maximization problem accounting for a stepwise progression bears this out: using species again as an indicator of biodiversity, the solution would involve only 33% of conservation efforts in forest area 1 (vs. 42% assuming a linear time path), with 67% of efforts now devoted to forest area 2.

The difference in solutions under linear and step function approaches is perhaps not that striking for the particular example we have chosen, though it is significant. The salient point is that the incorporation of information on threshold effects can affect the decision-making process. Certainly there are cases in which accounting for these effects may have a substantial bearing on the planner's decision, depending on the natural systems and time horizons considered.

5.2. Dynamic illustration 2: the choice of time horizon and biodiversity indicator may have a significant impact on the dynamic solution, but not necessarily in monotonic fashion

Consider once again the allocation of conservation expenditures between a current transitional forest area and a current mid-successional area. Given the knowledge that the biodiversity time path is subject to discontinuities as forests move from one seral stage to the next, how does the choice of time horizon affect the solution to the problem in Eq. (7)? And how does the choice of biodiversity indicator influence the result? We consider three alternative time horizons (50, 100, and 150 years) and three alternative indicators (S , F , and S_b). The solutions to the problem under these conditions are shown in Table 2.

Three main points emerge from Table 2. First, conservation allocation outcomes vary significantly according to choice of indicator and time horizon, from a low of 29% to a high of 55% of total expenditures devoted to forest area 1. Second, the dynamic solutions depend on the time horizon chosen but not necessarily in monotonic fashion. For example, Fig. 3 illustrates how the allocation of expenditures varies according to T when species richness is used as an indicator of biodiversity. The optimal percentage of resources to be devoted to forest area 1 (transitional) first

declines as the time horizon is increased from 50 to 100 years, then rises as T goes from 100 to 150. This is because the expected passage of both forest areas into the late successional stage, which exhibits markedly high biodiversity, is considered to varying degrees according to the chosen time horizon. With $T=50$, passage to the late successional stage is considered for neither forest area, and so the current levels of biodiversity largely drive the result. With $T=100$, passage of forest area 2 to the late successional stage is taken into account while that of forest area 1 is not. As a result, a premium is attached to conserving forest area 2 and the percentage of total expenditures devoted to it rises. With $T=150$, the passage of both forest areas to the late successional is considered, and so emphasis shifts back toward a somewhat higher level of emphasis on forest area 1. While the shifts in expenditures for this illustration may not be dramatic, they are indicative of the implications of choice of T for preservation decisions in general.

Third, the influence of altering T depends on the indicator of biodiversity that is used. For example, using number of bird families as an indicator, conservation efforts devoted to forest area 2 (mid-successional) increase as T goes from

50 to 100 (Table 2), for the same reasons described above for species. However, extension of T from 100 to 150 leaves the solution unchanged with number of families as the indicator, unlike the pattern under the species indicator. This is due to the way in which species appear and disappear as the forest moves through seral stages. Specifically, the number of species may increase or decrease through time without there occurring a change in diversity as measured at higher taxonomic levels. The same kind of pattern can occur for genetic diversity, i.e. if closely related species appear or disappear through time, species diversity may change significantly while genetic diversity does not.

5.3. Dynamic illustration 3: a dynamic approach may differentiate areas that are equivalent from a static perspective

Now consider the allocation of expenditures between two forest areas both currently in the late successional stage but that have different stand ages. Specifically, consider forest areas 1 and 2, which have stand ages of 125 and 250 years, respectively. Assume that these areas display similar numbers of species, genera, and families. The main difference between them is that forest area 2 will evolve into an old growth forest 125 years sooner than forest area 1.

Of course, if the two areas currently are similar in terms of biodiversity, a static approach would give them equal weight regardless of the indicator used. However, one does not necessarily give them equal weight if dynamics are taken into account. The solutions to Eq. (7) for this problem are shown in Table 3. With $T=50$ years, the two areas have equal weight because neither one will have progressed out of the late successional seral stage. With $T=100$ or 150, however, the younger forest area (1) will be accorded a significantly higher percentage of conservation efforts (61 and 66% of the total for $T=100$ and $T=150$, respectively). As the time horizon increases, then, a decision-maker interested solely in maximizing the biodiversity indicator will attach more importance to conserving the younger late successional forest area.

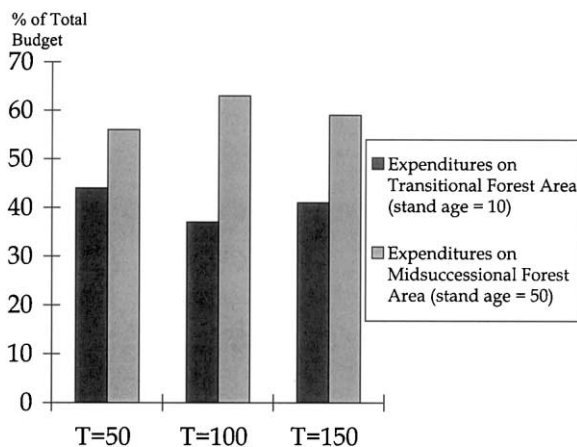


Fig. 3. Allocation of expenditures may be nonmonotonic with respect to time horizon T : dynamic framework using species richness.

Table 3

Allocation of conservation expenditures between two late successional forest areas of different stand age: dynamic framework^a

Time horizon	Relative expenditures by area, using species richness indicator	
	Area of stand age = 125	Area of stand age = 250
50 years	50%	50%
100 years	61%	39%
150 years	66%	34%

^a Each percentage in the table denotes the percentage of total conservation expenditures that will be devoted to the corresponding forest area, according to solution of the dynamic constrained maximization problem defined in the text.

This result may stand at odds with expectations, given that the older forest area (2) will progress to old growth 125 years sooner, and given the importance that society generally associates with old growth forest. The result is driven by the fact that the old growth seral stage is actually less diverse (as measured both by number of species and number of higher taxa) than the late successional seral stage. Therefore, conservation decisions made solely on the basis of anticipated biodiversity will tend to favor the late successional stage over old growth, and therefore result in the conservation of younger forests. This is an issue that may arise in a number of different types of forest systems since evidence suggests similar patterns in a variety of forest types.

Clearly, there may be other reasons to value old growth forest besides numbers of species or higher taxa (Brunson and Shelby, 1992). For example, note that in Table 1 we show that a relatively large number of the species found in old growth were uniquely detected in that forest type. Second, a relative measure such as S_a/S (which prioritizes areas solely according to the percentages of their species collections that are not prevalent at a broader scale) would attach high importance to old growth. Third, individuals may exhibit preferences for recreation in old growth forest because of factors totally unrelated to biodiversity. The counterintuitive result of this illustration certainly is not (and in no way is intended to be) an

argument against conserving old growth. However, it does indicate strongly that decision-makers should clearly and deliberately prioritize conservation objectives on a site-specific basis, as well as recognize that particular objectives may sometimes lead to decisions that run counter to conventional wisdom.

6. Conclusions

We have used data from forest ecosystems to illustrate several key concepts relevant to biodiversity. First, the solution to a static biodiversity preservation problem may depend significantly on the biodiversity indicator used. This is an important concept for decision-makers to understand and assess, particularly at the site-specific level. The use of alternative indicators to examine the multiple attributes of natural systems, and the extent to which those attributes are at risk, can force a useful reexamination of conservation objectives. The choice of final indicators to use as guides may vary greatly from case to case and will depend on the context of the problem and the ecosystem services that are most highly valued by the public.

Second, for any given indicator, dynamic solutions may differ from the static solution, depending on the time horizon chosen by the decision-maker. This forces a reexamination of the timeframes that we wish to take into account when considering future streams of 'biodiversity services', or ecosystem functions and services more broadly. This is a simple concept, but the existing literature does not adequately address it, particularly for cases in which ecosystems are expected to display discontinuous processes in the future. Our analysis also highlights the need for dynamically adaptive management, rather than a long-term fixed formula for conservation, since the portfolio of biodiversity and forest types will continue to change as time passes.

Third, for any given indicator, dynamic solutions can depend on the time horizon chosen, but not necessarily in monotonic fashion. This is a characteristic not common to well-behaved dynamic models and therefore merits special atten-

tion. Fourth, the effect of changes in the time horizon on the dynamic solution is dependent on the indicator used, which reinforces the need to consider multiple proxies.

This manuscript does not deal with choosing any one indicator over another, but rather emphasizes that the choice of indicator certainly does matter and should be linked to conservation objectives. At the same time, the issue of indicator reliability will be important in actual decision-making applications. Reliability is largely a statistical issue and depends on criteria such as sensitivity, specificity, and predictability. A significant literature exists to help guide practitioners on this point (e.g. Murtaugh, 1996; Dufrene and Legendre, 1997; Legendre and Legendre, 1998).

Our analysis is illustrative in nature in that it relies upon an example relationship between conservation effort and conserved biodiversity, rather than an empirically estimated function between these two variables. The impact of conservation effort on any given biodiversity indicator will vary from site to site and potentially through time for any particular site. Future ecological research to examine the biodiversity ‘returns’ from increased conservation activities, as well as the way that this relationship varies by indicator, would be quite useful.

We intentionally have not incorporated uncertainty in any fashion in this analysis, primarily to avoid detracting from the major points of interest. Incorporation of this factor, however, represents an important avenue for further research. For any given natural area, uncertainty exists regarding the future demand for and supply of various ecosystem functions and services. Natural forces, as well as future anthropogenic change (e.g. changes in patterns of adjacent human development or changes in effects from pollutants transported into the area), may change the supply of amenities that the ecosystem offers. However the directions, magnitudes, and timing of such potential future changes, as well as the ways in which the area will respond, are uncertain (King, 1997). In the same way, a host of factors (changes in human population distributions, demographics, preferences for goods and services, and the relative prices of environmental amenities and other

goods) may affect future patterns of demand. Such changes are equally uncertain.

Future research might assess the relative importance of different sources of uncertainty in factors affecting supply and demand. This is likely to be quite site specific. In some instances, uncertainty regarding future demand for environmental amenities may swamp that connected with future ecosystem processes. As mentioned above in connection to forests, catastrophic disturbance (either man-made or natural) can reverse the successional process. In the forests we examined, however, natural widespread disturbances rarely occur and many types of preservation efforts can effectively insulate areas from major anthropogenic effects such as land development. Therefore, uncertainty in ecosystem service supply may be small relative to uncertainty in future demand for environmental amenities. In other types of systems, where disturbance is more likely and vulnerability to disturbance may be higher (some coastal ecosystems may fall into this category), there may be substantial uncertainty in forecasting the supply of ecosystem services for several years into the future.

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