An Introduction to Biodiversity Concepts for Environmental Economists

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Abstract

Biodiversity is a valuable, but poorly understood natural resource. Large scale extinctions resulting from human actions are forecast widely. We present a broad, introductory review of biodiversity concepts. Biodiversity is first defined at the species and community levels. Available methods and approaches for quantifying biodiversity are discussed with specific reference to the spatial scales over which these measures can be applied. Dominant threats to biodiversity are reviewed. Fundamental patterns and processes that underlie ecological production functions are outlined. Differing rationales for biodiversity conservation are given and compared. Finally, the current suite of approaches employed in biodiversity conservation are discussed. Our aim in writing this review is to encourage further, much needed, inter-disciplinary collaboration among economists and ecologists.

Keywords: biodiversity, conservation, ecosystem, endangered species, land-use change
1 What is biodiversity?

Between 3 and 100 million species inhabit the Earth (Heywood 1995). A shorthand description of this great variety of life, ”biodiversity” is a contraction of ”biological diversity”, and was first coined by Walter Rosen for the 1986 National Forum on BioDiversity (Wilson 1988). A typical definition is found in the UN Convention on Biological Diversity:

... the variability among living organisms from all sources including, \textit{inter alia}, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems (UNEP 1992, p. 4).

However this is not a particularly operational definition. We need a way to quantify these different types of variation, and we need to determine an appropriate spatial scale over which to do so.

1.1 Species-level biodiversity

Historically, ecologists have tended to focus on the species level of biodiversity, and have quantified it in two ways:
**Richness**: the number of species in a given area

**Evenness**: the extent to which the number of individuals in each species is similar or different

The contribution of richness to biodiversity is evident. The role of evenness is more subtle. The notion is that in communities of 10 species comprising 100 individuals, for example, a community which has 10 individuals in each species is more diverse than one with 91 individuals in one species and one each of the others. This is because, all else being equal, a rare species will play a lesser overall role in ecological processes than will common ones. Of course, if a rare species is very large, or is particularly effective at modifying the environment, then this distinction may no longer be true.

The *Shannon-Weiner diversity index*, adapted from information theory, measures both richness and evenness:

$$H' = - \sum_{i=1}^{S} p_i \ln(p_i), \quad (1)$$

where $S$ is the total number of species at the site and $p_i$ is the relative abundance of species $i$. However, estimating relative abundances for all of the species in a community can be time consuming and difficult, and is usually not feasible for the rapid assessments performed to set conservation priorities. Thus, in most conservation contexts, *species richness* is typically
used as a proxy for species-level biodiversity. In contrast to the Shannon-Weiner index, this simplification places a relatively high weighting upon rare species.

1.2 Community-level biodiversity

Another important level of biodiversity is the *community* – a suite of interacting species. Different communities may share some species, but the relative abundances and the nature and intensity of interspecific interactions may vary greatly among communities. Indeed, it is this diversity of interactions that distinguishes species in their natural habitat from the same species in a zoo. We lack quantitative measures of community diversity analogous to those for species-level diversity. Instead, conservation biologists often advocate conserving representative samples of *all* distinguishable community types.

Terrestrial communities are usually classified in terms of *vegetation associations*, which are defined in terms of the largest and most numerically dominant plant species. These are easier to map than animal communities (although the boundary between adjacent communities is not always distinct).

Vegetation associations are controlled by abiotic factors such as soil type,
hill slope, aspect (the direction that the slope faces), and climate, as well as biotic interactions among the plant species and with animals. There is also a historical component to community composition. For example, many long-lived tree species are still migrating north in response to the climate change at the end of the last ice age, and have not yet attained their maximum range potential; these migrations are proceeding at different rates for different species (Davis 1976). For a rapidly dispersing species, the current range may represents the best available habitat; for a slow disperser, it may merely represent the best habitat that the species has been able to reach.

Aquatic and marine communities are classified by a variety of variables, including physical factors – water depth; temperature; salinity; nutrient availability; wave exposure; bottom type, etc. – as well as the dominant species of plants or sessile organisms that are associated with the substrate (such as kelp beds or coral communities) (Mumby and Harborne 1999). Far from shore, pelagic communities of highly mobile marine species can move long distances in response to changes in water temperature and nutrient availability. Defining characteristics of these pelagic communities would include geographic range distributions and strong trophic interactions.

Communities are dynamic entities that may change rapidly. Following a disturbance, such as fire, flood, hurricane or intense grazing, the vege-
tation and sessile animal communities can sometimes move through fairly predictable *successional stages* as the bare substrate is recolonized and a se-
quence of ecological interactions allows the previous community to reestab-
lish. Some species can only flourish on freshly disturbed sites, and some
important communities are intermediate successional stages; these would be
lost if disturbance were suppressed. Maintaining a patchwork of different
successional stages can allow a high diversity to exist on a site.

### 1.3 Spatial scales of biodiversity

As well as choosing an organizational level over which to measure biodiver-
sity, one must also choose a relevant spatial scale, because richness increases
with area (see below). Typically one chooses either an economically mean-
ingful scale (the individual land parcel) or an ecologically meaningful one
(habitat zones). Having chosen this “local” scale, there are three aspects
of biodiversity to consider when looking at the landscape (Whittaker 1972;
Schluter and Ricklefs 1993):

\* **α diversity**: the “local” diversity (within each local site, or the average of
such local measures across all the sites)

\* **β diversity**: the change in species composition from one site to another.
The fewer species that the various sites have in common, the higher the $\beta$ diversity.

$\gamma$ diversity: The “total” diversity measured over the entire suite of sites being considered.

By definition, $\gamma$ diversity is a function of the $\alpha$ and $\beta$ diversities within the region. If $\alpha$ and $\beta$ diversities are both low, then so will be $\gamma$ diversity; likewise, all may be high. An intermediate levels of $\gamma$ diversity could correspond either to high $\alpha$ diversity (each site is locally diverse) but low $\beta$ diversity (the sites all have the same suite of species) or to low $\alpha$ diversity (each site is very species poor) but high $\beta$ diversity (all sites are different from one another). For example, Cox (1977) studied bird diversity on two Caribbean islands. Both islands had the same nine habitats, but the larger island had five times the $\gamma$ diversity as the smaller (108 species vs. 20). This was due to a doubling of both $\alpha$ diversity (the average number of species per habitat) from 12 to 28 and of $\beta$ diversity (the inverse of the average number of habitats per species) from 0.19 to 0.43.

1.4 Threats to biodiversity

Anthropogenic threats to biodiversity come in five major forms:
**Habitat conversion.** When land is converted from a wild or semi-wild state to agriculture or urban development, many species are unable to persist on the site. For example, butterfly diversity in the Amazon declines markedly if more than 30% of the forest is converted to agriculture (Brown 1997). This transformation includes the clearing of forest land, conversion of pasture land to cultivation or urbanization, and the filling and draining of wetlands. The introduction of domestic grazers to native grasslands can modify the competitive interactions among the various plant species and severe overgrazing can irreversibly modify the hydrology and soils of the site.

**Habitat fragmentation.** As described below, small areas hold fewer species than large ones, and a collection of isolated habitat fragments may contain less biodiversity than a contiguous habitat of similar size. In addition, species that are not effective at dispersing among the fragments could be at greater risk of extinction. We tend to think of fragmentation as the process of increasing the patchiness of habitat in an otherwise hostile anthropogenic habitat. However, some species can have their movement restricted by as little as a road through otherwise pristine habitat (Trombulak and Frissell 2000). Other species may continue to thrive in developed landscapes.

**Harvesting.** Fishing or logging has a negative impact on the targeted species,
as well as on any species that directly depend on the target species for food or shelter. Certain harvest techniques have broader impacts on the ecological community (Dayton et al., 1995). Fisheries often take large “incidental catches” of non-target species, and trawling can destroy the community that lives on the sea floor. Clear-cut logging has a similar impact to land conversion of forests.

**Exotic species.** Humans have greatly accelerated the movement and introduction of species from one region or continent to another (e.g., Cohen and Carlton 1998). This has included both the deliberate introduction of species with perceived agricultural or aesthetic benefits and accidental introductions of “hitchhikers” on trading activities. Few of these exotic introductions persist in their new environment. Unfortunately those that do are often extremely successful. These exotic invaders can dramatically change an ecological community by being competitively superior or effective predators, and can drive many native species to low densities or extinction (Reid and Miller 1989).

**Climate change.** If temperature and rainfall patterns change to the point that a species can no longer thrive in the sites where it is currently found, then the species will decline unless it can either adapt to the changes or migrate to new, more suitable sites. Faced with rapid climate change, any organism that cannot adapt rapidly or migrate across
the anthropogenically fragmented landscape will not fare well. For example, 5-10% of species in California may be driven extinct if climate warms 4 °F (Morse et al., 1995; Field et al. 1999).

Which level of biodiversity should we be trying to conserve, and at which scale? Any conservation strategy that preserves tracts of land in their natural state (this includes not just protection from conversion, but simulation of disturbance processes, protection from exotics, etc.) will automatically preserve communities, and indeed communities (at least as defined by plant associations) are easier to map on the landscape. However, a focus purely on communities may fail to conserve certain rare species. The scale of focus depends on the social objective involved, and there are conservation goals that map onto all three scales of biodiversity (section 3). Likewise, conservation strategies differ depending on which scale is being targeted (section 4). Before describing these, however, we review the patterns and processes that underlie the ecological production functions.
2 Ecological Production

2.1 Static Patterns

Ecological data are expensive and difficult to obtain. Long time series of population sizes and distributions are only available for a handful of species. Thus, ecologists often observe only a snap-shot of a biological production process, one that represents a particular set of environmental conditions. However, a number of patterns are revealed by data sets of this type in spite of this shortcoming.

One of the most robust and useful patterns has proven to be the species-area relationship. If one graphs the number of species in a selection of sites of intermediate size (e.g., small islands or isolated terrestrial reserves), \( S \), against the area of the sites, \( A \), then the data are often well-approximated by a power-law

\[
S = cA^z
\]  

(2)

where \( c \) and \( z \) are positive constants (Fig. 1a). Moreover, estimates of Figure 1 index \( z \) typically fall within a narrow range for a diverse suite of ecosystems (Rosenzweig 1995).

While the species-area relationship predicts the number of species one expects to find in a site of given size, it tells us nothing about the composition
of the local community. The challenge of predicting community composition opens up a long-standing debate in ecology. One tradition tracing to Gleason (1953) suggests that the set of species found in a site is a random subset of the total regional species diversity. A second tradition tracing to Elton (1933) suggests that ecological communities possess regular and predictable assembly rules. Recent syntheses indicate that both schools of thought were partly correct, and that the degree of predictability in community composition is ecosystem dependent (Cody 1989).

The Gleasonian emphasis on stochastic colonization of sites by species has proven well justified. One lesson to be learned is that the more isolated is a site (or equivalently, the more fragmented is the remaining habitat), the fewer species that one expects to find there. On the other hand, some regular patterns in community structure also emerge (Roughgarden 1989). For example, the species found on isolated sites often comprise nested subsets, with all of the species found on smaller sites also found on larger ones (Fig. 1b; Brown 1995). In this situation, adding a small reserve to a preexisting large reserve would add few new species to the reserved set (low $\beta$-diversity).

These relationships describe interspecific patterns, but intraspecific patterns have also been documented. For example, an examination of spatial distributions of species indicates that they are not distributed homogenously
throughout their ranges (Rapoport 1982; Brown 1984, 1995). Rather, species tend to be patchily distributed with some seemingly suitable habitats left unoccupied. The abundance of species often decreases and the number of unoccupied patches often increases when moving from the center of a species’ range towards its range borders (Brown 1984, 1995).

Descriptions of static patterns, whilst useful, provide insufficient information for most economic studies. Knowledge that a species is found in a site at some time does not guarantee the future persistence of that species in that site. In order to predict the future state of an ecosystem and whether particular species will persist given some management action, one needs to understand the dynamic processes that drive observed patterns.

2.2 Dynamic Processes

The simplest representation of the dynamics of a closed community takes the form,

\[ \dot{N}_i = N_i f^i(N_1, \ldots, N_S) \quad \text{for } i = 1, \ldots, S. \]  

Here it has been assumed that there are \( S \) interacting species in the community and that the per capita growth rate of each species \( f^i \) can depend on all \( S \) species’ densities, \( N_i \) for \( i = 1, \ldots, S \). For a given vector of species’ densities, the relevant partial derivatives indicate whether the interaction between any
two species in the community is (directly) mutualistic ($f_{X_j}^i > 0$ and $f_{X_i}^j > 0$), parasitic ($f_{X_j}^i > 0$ and $f_{X_i}^j < 0$) or competitive ($f_{X_j}^i < 0$ and $f_{X_i}^j < 0$). The special case of a single species grown in monoculture is perhaps best known,

$$\dot{N} = N f(N). \quad (4)$$

When $N$ becomes sufficiently large, $f(N)$ must decline to zero as the population exhausts its available resources. Various functional forms for $f$ have been used (Roughgarden 1997) and they typically show a diminishing return in biological growth per unit stock over larger population sizes, $f'(N) < 0$.

Even these basic representations of populations and communities and their discrete-time analogues display rich and complex dynamics including the existence of single or multiple equilibria, limit cycles, and chaos (May 1981; Murray 1993). While these representations can be informative, it is worth being forthright about all that is excluded. For example, we have excluded all consideration of population structure and of spatial or temporal variation in environmental conditions. We review here three important sources of variability suppressed in Eqn. (3).

### 2.2.1 Spatial variation

To understand how an ecosystem will respond to some land-use change, we must first understand how spatial heterogeneity affects population and com-
munity dynamics. A substantial body of research in ecology addresses this question (Hanski & Gilpin 1997; Hanski 1999; Tilman & Kareiva 1997). This work recognizes that environmental conditions are heterogeneous across all spatial scales (Levin 1992); that habitat patches differ in their isolation, geometry and quality (Pulliam 1988; Hanski 1999; Thomas & Kunin 1999); that individual organisms are clumpily distributed and only interact with their immediate neighbors (Durrett & Levin 1994; Chesson 1998); and that each of these factors can cause population and community dynamics to deviate significantly from those predicted by models of the form given in Eqn. (3). Economic analyses of the exploitation of spatially-structured populations indicate that a failure to consider spatial structure can result in a substantial loss of revenue (Fig. 2).²

²Fig. 2 illustrates optimal harvesting of a spatially structured population or metapopulation; a more complete treatment is given in Tuck & Possingham (1994, 2000). The metapopulation comprises two local populations that exchange individuals through migration. Population dynamics for local population 1 are given by $N_1 = r_1 N_1(1 - N_1/K_1) - m N_1 + m N_2 - h_1$ and similarly for local population 2. Here, $[N_i, r_i, K_i, h_i]$ respectively represent the local population size, intrinsic rate of increase, carrying capacity and harvesting rate in local population $i$. Migration rate $m$ is assumed to be symmetric. The social objective is to choose $(h_1(t), h_2(t))$ to maximize $\int_0^\infty p(h_1 + h_2)e^{-\delta t}$, where $p$ is the price per unit of harvest, and $\delta$ is the discount rate. For brevity, we have neglected harvesting costs and assumed infinite elasticity of demand. The optimal solution comprises an equilibrium, which satisfies the first order conditions $\delta = F_1^*$, and a bang-bang approach path. Fig. 2
Many species rely upon multiple habitat types during their life cycle. Some undergo ontogenetic migrations from juvenile nursery habitats to adult habitats. Others rely on specific areas for reproduction that differ from their typical feeding grounds. Still other species migrate seasonally in response to climatological conditions and changing resource landscapes. Conservation of these migratory species requires conservation of all habitat types on which they depend during the life cycle. Conservation measures aimed at only one habitat type will fail, if the habitats required for other life stages are allowed to deteriorate. Migratory species pose particularly difficult management problems if different life stages cross national or international legislative boundaries.

2.2.2 Temporal variation

The abundance and distribution of populations often fluctuates erratically through time. The simple, deterministic representation of a community in Eq. (3) accounts for endogenously driven fluctuations in population sizes (May 1974; Murray 1993), but neglects unpredictable variations in abiotic factors such as local climatological conditions. Deterministic models could provide poor representations of community dynamics when compared with
noisy time series of actual population data. Short term variation in such time series can prove as important as any long-term trends for assessing potential consequences of management decisions. For example, the data in Fig. 3 indicate a decline in the population abundance of downy woodpeckers (*Picoides pubescens*) at Buckeye Lake, Ohio (years 1935–1970 taken from Ehrlich & Roughgarden (1987), years 1971–1993 from issues of the journal American Birds). One could predict future population sizes from the linear trend alone. However, arguably it would be more meaningful to consider the variation about the trend when making such a prediction. Stochastic representations of population and community dynamics commonly employ autoregressive processes (Ives et al., 1999; Hughes and Roughgarden 2000), Markov chains and diffusion approximations (Nisbet and Gurney 1982; Lande 1993).

A social planner who formulates a management plan that accommodates environmental uncertainty will achieve more success than one who assumes constancy of the environment (Reed 1979, 1984; Roughgarden & Smith 1996; Milner-Gulland et al. 2001; Roughgarden & Armsworth 2001). To incorporate environmental uncertainty into decision-making analyses, one must first assess what information about environmental or population fluctuations is available to the social planner, how accurate this information is and when it becomes available.
Temporal and spatial variability interact in complex ways to determine population and community dynamics. In a population that is restricted to a single site, the long-run population growth rate is measured by taking the geometric mean across years of the annual growth rates. The multiplicative properties of the geometric mean result in this growth rate being greatly depressed by occasional poor years and catastrophic disturbances. In theory, a spatially distributed population can buffer itself against these occasional poor years if the population is spread across sites that experience different local conditions. Essentially, spatial structure allows the population to take a spatial arithmetic average of the environmental conditions in a given year by ‘spreading the risk’ (Bascompte et al. 2002). Whether spatial structure will buffer a population against extinction in this manner depends on the spatial correlation scale of environmental fluctuations relative to the population’s range, on the vagility of the species and on the vulnerability of dispersing individuals (Casagrandi and Gatto 2001).

2.2.3 Individual variation

A further type of variability suppressed in basic models is variation amongst individuals within a population. Individuals vary in their genotypes, phenotypes and behaviors, and such variation can be extremely important in determining population and community dynamics. Using average measures...
of traits can be misleading, because sometimes it is an exceptional few individuals that determine particular phenomena of interest (Clark et al. 2001). Human impacts will interact with this individual variability to determine the ultimate response of population and community dynamics (Fig. 4; Ratner & Lande 2001). 3

Individuals also vary in the timing and success of their reproduction. This reproductive variation causes fluctuations in the population growth rate at small population sizes due to sampling effects and, thereby, can increase the

3Fig. 4 illustrates a simple model of the ecological and evolutionary effects of harvesting on a genetically structured population. Harvesting terms were introduced into a model of density-dependent selection from Roughgarden (1971). The basic ecological model is $N_{t+1} = N_t (1 + r(1 - N_t/K))(1 - qE_t)$ where $N$ is population size, $r$ is the intrinsic rate of increase, $K$ is the carrying capacity, $q$ is the catchability coefficient and $E$ is the harvesting effort. The evolutionary dynamics are given by a one-locus two-allele model without mutation, $p_{t+1} = p_t (p_t w_{AA} + (1 - p_t) w_{Aa}) / \bar{w}$, where $p$ is the gene frequency of allele $A; [w_{AA}, w_{Aa}]$ are the fitnesses of $AA$ and $Aa$ genotypes; and $\bar{w}$ is the mean fitness. Genetic variation was first introduced into $r$ and $K$. Without harvesting $K$-selected genotypes become fixed. Harvesting favors $r$-selected genotypes. Typically, these $r$-selected genotypes will be smaller bodied, fast-growing individuals that may fetch lower prices. Genetic variability was also introduced into the catchability coefficient $q$. Harvesting favors the evolution of genotypes that are least vulnerable to the harvesting method, and thus evolution can potentially raise harvesting costs. Both effects could have major economic consequences and ignoring such effects invites evolutionary externalities.

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vulnerability of small populations to extinction (Nisbet and Gurney 1982; Lande 1993). In recent years, ecologists have moved more towards mechanistic, individual-based models and rely progressively less on simplified mean field approximations.

3 Social Objectives

Given the multitude of processes involved in the production of biodiversity, where should environmental economic research efforts into this area be focused? One method for prioritizing such research is to assess what it is about biodiversity that consumers value.

Many people argue that as a society we have a moral imperative to conserve biodiversity (Leakey and Lewin 1995; Roughgarden 1995), a position embodied in the Endangered Species Act. If one accepts that biodiversity conservation in and of itself is a valid social objective, then one is interested in trying to protect as many species as possible, or \( \gamma \)-diversity.

Some would argue that biodiversity protection is not an absolute moral imperative, because it is only one of several worthy and potentially conflicting social goals (Shogren et al. 1999). These individuals may add that society should weigh costs and benefits of conservation measures within the context
of wider social planning. Thus, biodiversity protection would be justified on the basis of the benefits that society derives from biodiversity.

Direct benefits to consumers from biodiversity arise in different ways. Consumers may derive utility simply from contemplating that certain species exist (Pearce 1993; Goulder & Kennedy 1997). Policies designed to cater to existence values will again favor maximizing $\gamma$ diversity. However, this time the value assigned to different species is likely to be determined by how charismatic they appear to be to consumers.

Conceivably, one could attempt to conserve $\gamma$-diversity in a zoo. However, if consumers do not just value regional biodiversity per se, but value more specifically the conservation of that diversity within relatively undeveloped landscapes, then they value conserving $\gamma$ diversity by conserving $\beta$-diversity.

A quite different case for biodiversity conservation arises from the literature on natural capitalism and ecosystem service provision (Daily 1997; Daily et al. 2000; Balvanera et al. 2001). In this conceptualization, ecosystems are capital assets that provide valuable services to society. Such services include water purification in natural watersheds, prevention of soil erosion and carbon sequestration by standing forests, and recreational services such as ecotourism and bird-watching (Daily 1997). Thus, it is argued that biodiversity will be conserved only to the extent that it delivers a competitive
return on investments in conservation relative to investments elsewhere in the economy (Swanson 1994). Management strategies that favor sustained service provision will not necessarily be those that maximize $\alpha$, $\beta$, or $\gamma$ diversity. Rather, policies would be chosen that favor conservation of species involved in the provision of a service and that facilitate ready delivery of that service to consumers. Managing for service provision would favor protection of natural assets near urban areas and could provide less incentive for protecting resources far removed from human settlements.

An important question then becomes: what is the relationship between biodiversity and ecosystem service provision? This question is one that ecologists have only just begun to answer. However, there is already a large literature that examines the relationship between $\alpha$-diversity and ecosystem functions such as net primary productivity (Loreau et al. 2001). Recently, this literature has focused on a series of manipulative experiments on mesocosm plant communities (Hector et al. 1999, Tilman et al. 2001). While these studies have often reported positive relationships of either species or functional diversity with some ecosystem function, the conclusions have been questioned by other authors (Huston 1997; Wardle 1999). Debate has focused on how one separates effects that are due to species playing complementary roles within a community from sampling effects that can be attributed to a small number of competitively dominant species within the species pool
(Huston 1997; Tilman 1999; Loreau & Hector 2001). When interpreting this literature, we feel that it is important to bear in mind two facts. First, ecosystem function and ecosystem service provision are not equivalent; measures such as total (cross-species) plant biomass will only be of relevance for a small subset of ecosystem services. Second, the literature only concerns the role of $\alpha$-diversity and says little about the potential importance of $\beta-$ or $\gamma$-diversity.

We suspect that there is no general relationship between biodiversity and ecosystem service provision, and that the specifics of the relationship depend on the service of interest. For example, extractive services, such as fisheries and logging, depend directly on the targeted species and indirectly on those species on which the target stock relies for its persistence. However, such services provide little incentive to protect species that do not contribute directly to biomass production in the target stock. Indeed, there can even be incentives for a management agency to eliminate predators and competitors of a target stock (Hartwick & Oleweiler 1998; Roughgarden & Armsworth 2001).

We wish to emphasize one more important direct benefit of conserving biodiversity. Protecting multiple species provides society with a bet-hedge against unforeseen circumstances. For example, a society that was overly re-
liant on monocultured ecosystems would be vulnerable to catastrophic losses in service provision, because of the vulnerability of single species to disease outbreaks (Myers 1997 provides examples for domestic and wild rice). Also, consumer preferences for particular species change through time and species that are valued little today could command high prices in the future (see for example commercial bluefin tuna prices in McDaniel & Gwady 1998). Thus, there is a bet-hedging benefit to conserving γ-diversity and quasi-option values (Arrow & Fisher 1974) could be important when evaluating policies that risk species extinctions.

4 Biodiversity Conservation

Nearly all scientists agree that human activities have dramatically accelerated the rate of species extinction and that the earth will suffer a loss of biodiversity over the next century comparable to the largest mass extinction events in the fossil record (Pimm et al., 2001). Despite the enormous challenges of human population growth and associated global environmental change, scientists also advocate that society can act to reduce that loss meaningfully through well-aimed conservation projects. Designing such projects is currently limited by the paucity of information on the nature and distribution of biological diversity. It is likely that less than 15% of extant species are
known to science and, with the exception of vertebrates, vascular plants and
butterflies, we have only sketchy knowledge of the distribution of described
species (Heywood 1995). However, enough is known about general patterns
of biodiversity and the threats to biodiversity to design effective conservation
programs.

Soulé distinguishes eight different tactics for conserving biodiversity in-
cluding large protected reserves, unprotected but largely undeveloped lands,
extractive reserves with limited sustainable harvest, restoration projects,
zooparks for both indigenous and non-indigenous species, agroecosystem and
agroforestry lands, living ex situ preserves such as zoos, aquaria or gardens,
and germplasm banks (Soulé, 1991). Soulé suggests that the successful mix
of tactics for an area depends on the level of population pressure and politi-
cal instability. For example, large wilderness reserves are most feasible in
areas of low population pressure and high political stability, and extractive
reserves are most appropriate in politically unstable areas experiencing high
population pressure. The literature on biodiversity conservation has tended
to focus either on strictly protected areas or on sustainable resource harvest
on non-reserved lands. Few papers have formally considered potential trade-
offs between biodiversity conservation and economic exploitation across the
spectrum of conservation strategies (Faith et al., 1996).
All societies protect some lands and waters from exploitation and development in order to preserve natural and cultural values associated with those areas. The International Union for the Conservation of Nature (IUCN) Commission on Protected Areas has tallied some 30,000 protected areas covering roughly 13,250,000 km² or 10% of the planet’s ice-free land area, compared to marine reserves that occupy less than 1% of the world’s oceans and coastal waters. Land protection is expanding steadily in most parts of the world. However, most existing protected areas have been established in scenic, rugged and unproductive places that are relatively species-poor and form an incomplete, inefficient and ineffective system of reserves (Pressey et al., 1996; Scott et al., 2001).

The creation of new protected areas remains a largely ad hoc and opportunistic process. However over the past two decades reserve planning has become increasingly data-driven and systematic in identifying systems of nature reserves that would represent all components of the biodiversity of a region most efficiently (Margules and Pressey 2000). Many states and countries have conducted “gap analyses” (Scott et al., 1993), compiling and overlaying maps of vertebrate species and vegetation with land management to evaluate current systems of protected areas and to prioritize species, communities and areas for additional conservation efforts.
A variety of algorithms have been developed and applied to help planners identify additional sites that would most efficiently (that is, with the least cost or area) complete a representative reserve system (Pressey et al., 1997). These algorithms take area-occupancy or abundance data as their input. Area-occupancy data indicate the species (or other elements of biodiversity such as plant community types) that are known to occur in a given set of sites at the present time. In its simplest form, the planning problem can be represented as a maximal covering location problem in which the objective is to choose \( p \) sites from the set of candidate sites, \( P \), that will maximize the number of species (\( Z \)) contained in the reserve system (Church et al., 1996). That is:

\[
\max_{p \in P} \ Z = \sum_i Y_i \quad \text{subject to:} \quad \sum_j X_j = p. \tag{5}
\]

where \( Y_i \) indicates the presence or absence of species \( i \) within a given reserve set—\( Y_i = 1 \) if the \( i^{th} \) species is found within the set of \( p \) sites and zero otherwise; and where \( X_j \) indicates whether site \( j \) is one of the \( p \) sites chosen—\( X_j = 1 \) if the \( j^{th} \) site is chosen and zero otherwise.

This problem can be solved using integer programming methods (Church et al., 1996). A number of refinements have been made to the simple covering problem. These refinements account, for example, for site cost (Ando et al., 1998), connectivity (Possingham et al., 2000) and location and suitability for conservation activities (Davis et al., 1999), and for uncertainty in species
distributional data (Polasky et al., 2000). These explicit procedures and site selection tools identify “minimal” solutions for achieving stated conservation goals that highlight exceptionally important sites and provide a benchmark against which alternative plans can be measured. Perhaps more importantly these tools provide structure, focus and transparency to what are often highly contentious debates among competing stakeholder groups involved in land and water conservation (Pressey et al., 1996). The Nature Conservancy, the world’s largest private conservation organization, now includes regional reserve system design as an integral part of its planning process and has begun applying such algorithms in computer-aided planning support systems (Davis et al., 1999).

The identification of representative reserve systems is a useful exercise, but it is rarely if ever practical to acquire or designate entire reserve networks all at once, meaning that priorities must still be set based on threats and opportunities (Pressey, 2001). At the global scale, analysts have sought to identify “hot spots” of greatest species richness, endemism, rarity and threat (e.g., Pimm and Raven 2000; Myers et al., 2000; Reid, 1998; Dobson et al., 1997). On the face of it, the case for conserving such biodiversity hotspots is compelling: For example, a recent analysis suggests that 35% of all terrestrial vertebrates and 44% of all land plants are restricted to 25 regions comprising only 1.4% of the planetary land surface (Myers et al., 2000). As noted in
Section 1.4, however, patterns of diversity change considerably depending on both the scale and quality of input data and the size of the units used to measure species (Leitner and Rosenzweig 1997; Stoms 1994). At the regional or local scales at which conservation occurs, there is often little concordance in richness patterns among different taxonomic groups (Prendergast et al., 1993; Reid, 1998). Risk to biodiversity may be concentrated in a few areas where human activities leading to extensive habitat loss and high concentrations of endemic species coincide. Some have suggested that these areas offer the best opportunities for efficient conservation (Dobson et al., 1997), however, when land value is considered, these areas may or may not be the ideal areas for large-scale conservation efforts (Ando et al., 1998).

Much conservation focuses on preserving general habitat types such as “lowland tropical rainforest” or “late seral old-growth forest.” This approach is sometimes described as “coarse-filter” conservation because it presumes that most species that depend on the habitat type will be protected accordingly. In contrast, species-based or “fine-filter” conservation is often practiced for rare or endangered species or species of special economic or public interest. Other levels of biodiversity such as genetic diversity are generally not given as much consideration in conservation efforts, and there has been a tendency to dichotomize species-based vs. habitat-based conservation (Noss et al., 1997).
Of course, *in situ* conservation of species ultimately depends on providing adequate habitat to prevent local or regional extinction. Unfortunately, it is difficult to give general answers to questions such as where to put reserves, how big and how well connected to make them, and how to manage them, because the answers are species- and context-dependent. Large carnivores typically require large areas of relatively wild habitat (Noss et al. 1996), whereas rare plants and invertebrates may persist in very localized habitats surrounded by development (Schwartz and Simberloff 1997). In areas that are not extensively developed, much biodiversity can persist on non-reserved or “matrix” land. Thus in rural settings, nature reserves may provide an extra measure of protection to regionally rare or sensitive biota and serve as refuges for harvested species. On the other hand, in regions dominated by agricultural and residential lands, reserves function more like a archipelago of natural areas in an inhospitable ocean of human-dominated ecosystems, and the maintenance of biodiversity is closely tied to reserve system design and management.

Conservation biologists generally advocate a “landscape approach” that conserves large and heterogeneous areas in which ecological and evolutionary processes can be maintained (Scott et al. 1993). Reserve design principles, which are really more rules of thumb than rigorous scientific theory, emphasize the importance of large blocks of habitat (“core areas”) that sup-
port large populations, redundancy (conservation of multiple populations across the range of the species that are not subjected to the same patterns of environmental variation), connectivity between habitat blocks, and reserve buffers (Noss et al. 1997). In practice, reserve design is often tailored to meet the needs of selected species whose habitat requirements are relatively well understood (Lambeck 1997). Conservation plans may focus on particular species that have special legal status (“target” or “trust” species), have high visibility and public support (“flagship species”), are especially important in the ecosystem (“keystone species”), are thought to represent the needs of many other species in the system (“umbrella species”), or are especially sensitive to human activities (“indicator species”) (Caro and O’Doherty 1999). Regional conservation plans are increasingly evaluated for species persistence using tools from population ecology such as population viability analysis and metapopulation models (Lindenmayer and Possingham, 1996; Akcakaya, 2000).

Although conservation theory argues for protecting large areas, in reality, much conservation is now practiced in heavily modified and fragmented landscapes and seascapes where conservation is highly constrained and reserves are typically small and isolated. In such cases the spatial arrangement of reserves, the risk of species mortality in non-reserved lands, and disturbance processes such as wildfire or flooding that affect reserve dynamics may be
critical in determining whether populations can persist (Fahrig, 2001). The
cost of management to maintain species in such settings may soar due to
the difficulties of managing small populations, greater impacts from inva-
sive exotic species, and in some cases the need for deliberate translocation
programs or breeding programs to reduce the negative effects of inbreeding
and to re-populate reserves following catastrophic events like hurricanes and
disease epidemics.

In summary, growing concern over the mass extinction of biodiversity has
galvanized much theoretical and empirical research to improve the efficacy
of conservation efforts. To date most of this research has been undertaken
by ecologists and conservation biologists, in spite of the fact that the prob-
lem is inherently interdisciplinary and requires the perspectives of both so-
cial and natural scientists (Forester and Machlis 1996). Our brief overview
has emphasized conservation on land, but similar efforts are underway for
coastal and marine systems (Murray et al. 1999). There are many limita-
tions and uncertainties to prevailing conservation planning approaches. We
would highlight three in particular. First, conservation programs rarely spec-
ify desired ecological outcomes, for example, maintenance or restoration of
specific ecosystem services or achieving a particular level of protection or per-
sistence probability for species. Clear statement of conservation purpose and
goals is needed in order to prioritize conservation research and practice (Mar-
gules and Pressey 2000). Second, the focus on protecting current patterns of biodiversity does not directly address changes in distribution and abundance associated with global climate change, land use change, and invasive exotic species. Explicit, credible scenarios of social and environmental change must be brought into the planning process. Finally, biodiversity conservation inevitably competes with other social desires for land and water development, resource extraction, and recreation yet conservation analyses rarely consider tradeoffs or solving for multiple objectives in an integrated framework.

5 Conclusion

Our goal in writing this review is to introduce economists who are not already active in research into biodiversity related topics to some of the relevant ecological concepts. By so doing, we hope to encourage further participation and inter-disciplinary collaboration into this important area. Biodiversity in all of its forms is under threat as a result of human actions. To understand better the many and often subtle ways in which human societies depend on their biological resources, to pin-point why those resources are threatened and to implement efficient and dependable measures to conserve these resources for future generations will require a combination of innovative economic thinking with a sound ecological basis. We are heartened by the
exciting contributions in this volume that forge in that direction, as well as by similar inter-disciplinary ventures being lead by the ecological community (see for example Daily 1997). However, we are only just beginning and many challenges that are both daunting and exciting lie ahead.

References


Figure Captions

Figure 1. Distribution of species of reptiles and amphibians in the British Virgin Islands from Lazell (1983). a) Number of species ($S$) plotted against island area ($A$) in hectares. The solid curve is a least squares fit of the power law, $S = cA^z$, giving $c = 1.25$ and $z = 0.30$. b) Island occupancy plotted against area, demonstrating a nested subset species distribution. There are 24 species in total found on the islands, and these are indexed following Lazell (1983) along the vertical axis. Each filled circle indicates the presence of that species on the island of given area.

Figure 2. Present value surface for a harvested 2-patch metapopulation\textsuperscript{2} for all paths that comprise a bang-bang approach from initial condition ($K_1, K_2$) to an equilibrium solution. The family of such paths is parameterized by equilibrial combinations ($N_1, N_2$). Solid curves are contours of this surface and the asterisk indicates the optimal solution. The small circle indicates the optimal solution predicted when neglecting spatial structure and assuming an intrinsic rate of increase of $(r_1 + r_2)/2$. Parameters used: $[r_1, r_2, K_1, K_2, m, p, \delta] = [1.8, 0.2, 100, 100, 0.02, 1, 0.15]$.

Figure 3. Population abundance of the downy woodpecker ($Picoides pubescens$)
from the Christmas Bird Count at Buckeye Lake, Ohio. a) Abundance (\(N\)) through time (\(t\)) plotted along with a least squares linear fit, \((N = -1.54t + 3146)\). b) Two models of the variation about the linear trend. Crosses indicate autocorrelations (\(\rho(l)\) where \(l\) is the lag) of the residuals after the trend is removed. A fitted model that represents the variation with uncorrelated shocks performs poorly; the dashed-dot line shows the resulting Bartlett bands for the 95% confidence intervals (Royama 1992: p. 99). A second model that represents the shocks with a first order autoregressive process performs better. The solid curve shows the expected autocorrelation and the dashed lines show the 95% confidence intervals (Box et al., 1994, p. 32).

**Figure 4**. Ecological and evolutionary effects of harvesting on genetically structured populations\(^3\). Fig. 4ab show respectively the (a) dynamic and (b) equilibrial effects of harvesting for \(r\) and \(K\)-selection. Fig. 4cd show respectively the (c) dynamic and (d) equilibrial effects of harvesting for catchability selection. Two populations were released from small size with genetic variability in either intrinsic rate of increase \(r\) and carrying capacity \(K\) (Fig. 4ab), or in catchability coefficient \(q\) (Fig. 4cd). The populations were unharvested for the first 100 years. Carrying capacity (dotted line) was approached and selection favored the \(K\)-selected genotypes in a); in c), the environment was selectively
neutral. Harvesting began after 100 years. Dashed lines show the new trajectories. Unharvested and harvested equilibria are marked with asterisks and open circles respectively. Mean parameter values (indicated by bold font) in equilibrium for \( r \) (solid, left axis) and \( K \) (dashed, right axis) (Fig. 4b), and \( q \) (Fig. 4d), are plotted as functions of the harvesting effort level. Any amount of harvesting causes the equilibrium mean \( q \)-value to jump from the unharvested values (asterisk) to the harvested value (horizontal line). Parameters used: Fig. 4ab) \([r_{AA}, r_{Aa}, r_{aa}] = [0.5, 0.8, 1], [K_{AA}, K_{Aa}, K_{aa}] = [100, 90, 75]\) and \( q = 0.1\); Fig. 4cd) \([q_{AA}, q_{Aa}, q_{aa}] = [0.15, 0.12, 0.05]\) and \([r, K] = [1, 100]; Fig. 4ac) \( E = 3 \).