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Editorial

Economics of biodiversity: an introduction

1. Introduction

The desire to conserve biodiversity is driving significant aspects of economic policy formation. Some of these policies, such as the Endangered Species Act in the United States (Brown and Shogren, 2003), have real consequences for resource allocation, especially land use. It is therefore appropriate to ask questions about biodiversity—what exactly is it, what are the economic consequences of its loss or retention? As economists, what can we say about biodiversity? These are important and challenging issues, with which our profession is only beginning to grapple (Swanson, 1994; Simpson et al., 1996; Heal, 2000). This special issue of Resource and Energy Economics is a further step in that process: it assembles a collection of articles that, except for one, all have in common a focus of economic analysis on some aspect of biodiversity or its conservation.

The exception is the paper by Armsworth, Kendall and Davis. By three ecologists, this paper provides an overview of what ecologists mean by biodiversity, and of how they make this concept measurable and operational. Readers will quickly see from this that biodiversity is a set of ideas and issues rather than a single precisely-defined quantity. It stands for the total range of biological variability in naturally-occurring organisms, including the variability at all levels from the genetic to the species and community. Nehring and Puppe also address the measurement of biodiversity, though from a very different perspective: they look at axiomatic approaches to defining diversity in the context of phylogenetic trees, trees that show the relationships between ancestor and descendant organisms. Roughly speaking, we expect that organisms may be more different from each other if their last common ancestor is further back. Central to the literature to which Nehring and Puppe contribute is the development of this intuition into an operational measure of diversity.

To an outsider looking in at the biologists’ discussion of biodiversity, or at least to this outsider, it seems as if there are several quite distinct issues that are of concern here. One is that natural ecosystems are complex and highly interdependent, so that small changes can lead to far-reaching and unexpected repercussions. One example is the contribution that the extinction of passenger pigeons may have made to the emergence of Lyme disease as a serious problem in the US (Blockstein, 1998). Another is the impact of eliminating a keystone species, such as sea otters in the California coastal marine environments (Power et al., 1996). In both cases the loss of one species lead to cascading changes that most observers would probably not have expected, changes that were incidentally to the disadvantage of humans.

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Another issue that seems to motivate biologists' concern about biodiversity is the possible social value of the organisms that are being lost. When a species goes extinct, are we losing a unique chemical that could be the basis of a cure for cancer? This raises the issue of the value of biodiversity as a basis for bioprospecting, an issue on which there is an interesting literature already (Simpson et al., 1996; Rausser and Small, 2000) and to which this volume does not contribute. In economists' terms, biologists feel that there are real option values associated with biodiversity conservation. This is a priori a reasonable position—extinction, which is what loss of biodiversity amounts to in its more dramatic form, is irreversible, we are not sure of the value to society of what will be lost through extinction, and we may well learn more about this as time passes. So all the preconditions for real option values are satisfied which is perhaps a reason for being cautious about the loss of biodiversity. In sum, biologists see the loss of biodiversity as destabilizing the natural environment and as the loss of great potential for good.

2. Economic contributions of biodiversity

What in fact are the economic contributions of biodiversity to human societies? Biodiversity provides or enhances ecosystem productivity, insurance, knowledge and ecosystem services. There is some overlap between these concepts, but nevertheless they are helpful as a guide to thinking through the issues. All of them are economically important categories.

2.1. Biodiversity and productivity

How does biodiversity contribute to productivity? There is experimental evidence that plant systems with more biodiversity are on average more productive than those with less. A good illustration of this is work initiated by Tilman et al. (1997) at the University of Minnesota (Tilman and Naeem). He took a number of similar plots of land and planted each of them with a variety of grassland plants, some with a large number of species, some with a much smaller number. Each plot was planted with the same mix year after year, and several indicators of plot performance were recorded. These included the amount of biomass grown and the proportion of the nutrients available that were taken up by the plants. Tilman and others performing similar studies have found that on average over a period of about 20 years plots with a more diverse collection of species performed better than those with a less diverse collection. Similar studies have been conducted for microbial communities, and have found similar results. Again they show that more diverse communities are on average more stable and robust in the face of environmental fluctuations (for a review of this area, see Naeem and Li, 1997).

These studies show that diversity is important in ensuring the productivity and robustness of natural plant communities, and therefore of the ecosystems that are based on them. Diversity also helps natural ecosystems to make the best adjustments to conditions that vary over time or over space. Without the appropriate level of diversity, natural ecosystems cannot adjust to natural variations in the environment.[1]

[1] There is some controversy about the mechanism through which this happens.

Through its role as the raw material in plant breeding, biodiversity also contributes very substantially to the productivity of agricultural systems. New and higher-yielding plant and animal varieties are generated from the natural variation in plants and animals. The great increases in grain yields of the "green revolution" of the 1960s and 1970s, which were responsible for keeping food output growing in parallel with population in developing countries, were largely achieved by use of genetic diversity in the plant populations. There are estimates suggesting that as much as $ 1 billion has been added to the value of the US agricultural output each year for the last half century as a result of plant breeders' use of genetic diversity. Specifically, in the last half century we have seen a doubling in yields of rice, barley, soybeans, wheat, cotton, and sugarcane, a threefold increase in tomato yields, and a quadrupling in yields of maize, sorghum and potato (US Congress Office of Technology Assessment). All of this has been based on and derived from genetic variability in the underlying plant populations. In economic terms, this variability is an asset, and one that has yielded a great return at little cost.

While biodiversity contributes to the productivity of both natural ecosystems and agricultural systems, it does so through different mechanisms. Natural systems benefit directly from a diverse mix of species: agricultural systems benefit from the existence of a pool of genetic variability on which breeders can draw. Agricultural systems are usually monocultures, consisting of a single species grown intensively over a large area, its growth supported by applications of water, fertilizers, pesticides and weed-killers. Farmers manage cropland so as to ensure that crop growth is not limited by lack of water of nutrients, and that the main food crop does not have to compete with other species or with pests in its growth. Farmers create and maintain an artificial environment and then plant a crop that is optimally adjusted to this environment, an approach that is radically different from the natural growth process.

2.2. Biodiversity and insurance

A dramatic illustration of the insurance role of biodiversity comes from the recent history of rice production. The prosperity and comfort of literally billions of people depend on the rice harvest. In the 1970s, a new virus, the grassy stunt virus, carried by the brown plant hopper, threatened the Asian rice crop. This appeared capable of destroying a large fraction of the crop and in some years destroyed as much as one quarter. Developing a form of rice resistant to this virus became of critical importance. Rice breeders succeeded in this task with the help of the International Rice Research Institute (IRRI) in the Philippines. The IRRI conducts research on rice production, and holds a large seed bank of seeds of different varieties of rice and the near-relatives of rice. In this case the IRRI located a variety of wild rice that was not used commercially but which was resistant to the grassy stunt virus. The gene conveying resistance was transferred to commercial rice varieties, yielding commercial rice resistant to the threatening virus. This would not have been possible without genes from a variety of rice that was apparently of no commercial value. Without this variety, the world's rice crop, one of its most important food crops, would have been seriously damaged. An interesting additional detail of this story is that the variety of wild rice that was resistant to the virus was found in only one location, a valley that was flooded by a hydroelectric dam shortly after the IRRI found and took into its collection the critical rice variety. The same story was repeated later in the 1970s, and similar stories have occurred with other food crops, in particular corn in the United States (Myers, 1997). We have every reason to expect that events like these will recur regularly: planting large areas with genetically identical plants greatly increases the chances that once a disease starts it will spread with dangerous speed through the entire area and crop. A recent report by the Council for Agricultural Science and Technology emphasized this point:

> "Because of the increasingly high densities and large areas over which they are now grown, both livestock and crop plants are continually acquiring new diseases and pests, and existing diseases and pests are continually evolving new strains that overcome the defenses of particular breeds or strains. This is exacerbated by the accidental transport of diseases around the world. These diseases and pests destabilize agricultural systems. For instance, areas of western Minnesota and eastern North and South Dakota no longer can produce viable wheat and barley crops because of new strains of scab and vomit toxin for which no crop varieties have sufficient genetic resistance. Indeed, catastrophic attacks of disease, invasions of insects, and climatic extremes have caused wholesale crop destruction and ensuing famines whenever crops had insufficient diversity to provide at least some plants with the ability to withstand the assaults . . .
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> Disease problems, as old as agriculture, are recorded in myth and in written history, and still exist. Red rust on wheat in Roman times, mass poisoning from ergot-tainted rye during the middle ages, the Irish potato famine of the 19th century, and the Southern corn leaf blight in 1970 all were due to insufficient biodiversity in the affected crops. The severity of the 1998 Hong Kong chicken epidemic was likely exacerbated by the lack of diversity in disease resistance as well as by the high chicken densities in the production facilities.
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> A lethal disease of corn, or wheat or rice, were it to appear, would devastate agriculture and human society. The only insurance that society has against such a catastrophe is biodiversity. Genetic diversity within a crop plant or animal species and its relatives might allow resistant strains to be discovered and used. Similarly, a diversity of potential food plants might allow another species to become an effective substitute for a major crop species that was lost to disease." (Council for Agricultural Science and Technology, 1999)

These cases illustrate clearly the insurance role of biodiversity. It is an important defense against disaster in the form of new diseases. The pathogens that cause disease are evolving continually, in an attempt to outwit our defenses against them. A clear example of this phenomenon is the evolution of antibiotic resistance amongst bacteria. The bacteria that cause several once common diseases in humans are now showing resistance to their principal controls, to the great concern of public health authorities. The same is happening with the pathogens that cause disease in crops and in commercial animals. The role of biodiversity in this context is the subject of the paper by Heal et al., who discuss whether individual farmers faced with a choice of crop or animal variety will make a socially efficient choice, given the insurance role played by biodiversity. They also provide a brief overview of the complex debate about whether agriculture is becoming more or less genetically diverse in the face of globalization.

Without reserves of genetic variability we may not be able to develop varieties of our agricultural crops and animals that can resist these new disease varieties. Indeed, it is precisely genetic variability in the pathogens that allows them to develop resistance. Genetic variability means that some of the disease-causing pathogens are naturally relatively unaffected by our defenses against them, which may be in the form of weed-killers, insecticides or vaccinations for livestock. These more resistant specimens are the ones that survive and from which new subsequent generations are bred. So pathogens use against us just the mechanisms that we would use against them if we preserve and use genetic diversity. Without this diversity, we have disarmed unilaterally in the war against our most threatening enemies.

2.3. Biodiversity and genetic knowledge

The third reason why biodiversity is important is that it is a source of knowledge. We can learn from natural organisms how to make chemicals that have important and valuable properties, such as the enzymes that manage the polymerase chain reaction (PCR). This reaction is central to culturing DNA specimens—as in forensic tests used in trials, and in many processes central to the biotechnology industry. Culturing requires an enzyme that is resistant to high temperatures, which were found in hot springs in Yellowstone National Park. The heat resistance of these is now central to the rapidly growing biotechnology industry. There are many less complex examples, as indicated by the fact that 37% by value of the pharmaceuticals sold in the United States are or were originally derived from plants or other living organisms.[2] Aspirin comes from the bark of willow trees: the bark of Yew trees has been used to derive a drug that is effective against ovarian cancer:[3] a derivative of the Rosy Periwinkle flower is being used to cure childhood leukemia. Certain plants and animals are known to produce substances that are highly active pharmacologically, with plants that live in insect-infested areas producing substances that are poisonous to insects, which have been used as the basis for insecticides. Some snakes produce venom that paralyses parts of the nervous system, and others produce venom that reduces blood pressure. Other insects produce anti-coagulants. All of these have been adapted for medical use. There is little that is new in these observations: they form the basis for many traditional medicines, which rely heavily on plants. Shakespeare refers to this in Romeo and Juliet (II:iii):

O! mickle is the powerful grace that lies

In herbs, plants, stones and their true qualities:

For nought so vile that on earth doth live

But to the earth some special good doth give,

Within the infant rind of this weak flower

Poison hath its residence and medicine power.

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[2] Carte (1996).

[3] See Stierle et al. (1993).

2.4. Biodiversity and ecosystem services

I reviewed the role of genetic diversity in providing raw material for selective breeding, the traditional way of developing new crop or animal varieties that are more productive, more disease resistant, hardier, or more desirable in some other way, and also its role in ensuring the productivity of ecosystems and their robustness against diseases and pathogens. Yet there are still other more complex ways in which biodiversity is essential to the proper functioning of ecosystems and to the delivery of the ecosystem services upon which human beings are so dependent.

There are cases in which the full diversity of organisms in an ecosystem is required for that system to function and to provide services to human societies, with the removal or addition of even a single type of organism having extraordinarily far-reaching consequences. Ecologists use the term “keystone species” to describe a species whose removal will cause an entire ecosystem to change substantially. The removal of sea otters from the California coast by hunting for pelts led to far-reaching and undesirable changes in the California coastal ecosystems. Sea otters eat sea urchins, which in turn graze on kelp plants. Without control of the urchin population by otters, the urchins will destroy the kelp beds, completely changing the marine coastal environment. Removal of otters led to a greatly impoverished coastal environment, which was restored in part to its original state with a ban on otter hunting. Another example of the role and impact of a keystone species is provided by the removal of kangaroo rats from an area of the Chihuahuan desert, which led to a threefold increase in the yields of grasses and to far-reaching changes in the desert ecosystem. In this case the rats had played a key role through eating seeds and disturbing the soil, and their removal consequently changed the plant balance.[4]

Not only can the removal of a species led to big changes in an ecosystem, but the introduction of a new species (the so-called exotic species) can also lead to a profound transformation of the system. A dramatic example is the introduction of the rinderpest virus into East Africa in 1890. This initially attacked domestic and wild cattle, and then spread. By 1892, 95% of the wildebeest in the Serengeti region had died, together with most of the domestic cattle. Wildebeest are one of the main grazers and also the main food sources for carnivorous predators (lions, leopards, hyenas) in the Serengeti, so that their virtual elimination led to profound changes in the system. In the 1930s the introduction of a vaccination against rinderpest re-established the original system (Aber and Melillo, 1991). The point of these examples is that we cannot easily tell a priori what species are essential and what are not, so there is often a risk that an apparently small change in a set of species will have effects far beyond those initially anticipated. The degree of interdependence between different species is great, so that human beings may depend on many more species than we would expect from a first analysis of the situation. I am reminded of the words of John Donne, an English metaphysical poet of the seventeenth century, who wrote that

> “No man is an island, entire of itself; every man is a piece of the continent, a part of the maine; if a clod be washed away by the sea, Europe is the less, as well as if a promontory were, as well as if a manor of thy friends or thine own were; Any man’s death diminishes

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[4] See Power et al. (1996).

me, because I am involved in mankind; And therefore never send to know for whom the bell tolls: It tolls for thee."[5]

There is an ecological equivalent to this: no species is an island, entire of itself, not even *Homo sapiens*. Any species' extinction may diminish us, because we depend on many species. To repeat: the loss of even apparently unimportant species can have immensely costly consequences because of the complex patterns of interdependence between species. In the end the loss of an apparently small and unimportant group of species could threaten the provision of ecosystem services that are essential to humanity. The distinguished biologist E.O. Wilson once said of microbes that "We need them but they don't need us." This is why many scientists see a serious risk in the current rate of species extinction: they cannot be precise about the dangers involved but nonetheless believe that there is a real risk of costly consequences. To give this point some substance, let me mention a possible relationship between the extinction of passenger pigeons and the introduction of Lyme disease into American society. When Europeans first arrived in the United States, the passenger pigeon was probably the most abundant bird in the country, with a population estimated in billions. Traveling around in flocks of hundreds of thousands, their passing darkened the sky for many minutes at a time. By 1914 passenger pigeons were extinct, annihilated by a combination of hunting and destruction of their habitat. It seemed unbelievable that an animal so abundant could be reduced to extinction so fast. A possible connection between this extinction and the emergence of Lyme disease events has recently been proposed.[6]

The message of these examples is that it is hard to foresee the consequences of a change in the biodiversity of an ecosystem, with even an apparently small change leading to dramatic alterations in the system's ability to function and to provide the services on which human beings are dependent. Another aspect of this phenomenon is that a particular role in an ecosystem may be played at different times or under different circumstances by quite different plants or animals. The type of tree that stabilizes soil on a north-facing slope at a certain latitude may not grow on a south-facing slope at that latitude, so that a different species is needed there to maintain the physical stability of the system. As a consequence the set of species required for a certain type of ecosystem to function may vary greatly from region to region. In fact, we know of no single subset of species that on their own would serve to operate all ecosystems and provide all ecosystem services in all regions of the planet. So diversity in a given location may increase productivity and ecosystem functions in that location, while diversity at the regional or global level is actually necessary for the operation of important ecosystems in all geographic regions. While individual species may possibly be redundant in some locations, it is possible that at the global scale few if any are really redundant. A clear statement on this is given by Chapin et al. (1997):

> "the abundance of species with similar ecological effects should give stability (resistance and resilience) to ecosystems in the face of increasingly rapid human-induced environmental change. Loss of a keystone species or of all species in a major functional group will, by definition, have large ecosystem effects. Efforts to identify and protect such species and groups often yield demonstrable near-term benefits. Of increasing concern

[5] Cited in Ernest Hemmingway, "For Whom the Bell Tolls."

[6] See Blockstein (1998), I am grateful to Paul Ehrlich for this reference.

is the loss of species that have similar ecosystem effects but differ in their environmental responses. Loss of such species may reduce ecosystem resilience and the capacity to adjust to ever-increasing rates of environmental change. This latter role of diversity is not adequately represented in current international conventions, but it may be one of the most important mechanisms by which we sustain the long-term functioning of ecosystems and the services they provide to society."

3. Conserving biodiversity

It seems from this brief review that there may be real value to the conservation of biodiversity. But how should we go about this conservation? The policy and resource-allocation issue raised by this question make it natural that the majority of the papers in this volume address this issue. Costello and Polasky look at how we should choose which areas to conserve, given that we have a limited budget for conservation and also some uncertainty about which species are present in which areas. This means that the choice of areas to be conserved is a complex stochastic combinatorial optimization problem. Conservation biologists have been studying the choice of conservation areas for many years, but without addressing adequately the cost and opportunity cost issues inherent in making good choices. The paper by Costello and Polasky and its predecessors have brought substantial new dimensions to this literature and tied it more tightly into the framework of economic policy-making. The Pfaff–Sanchex–Kerr paper is complementary to Costello and Polasky, in the sense that it develops an econometric model of the likelihood of an area of land being developed: to be precise, it shows how to estimate a "deforestation index" giving the likelihood that a given area of tropical forest will be deforested. This is strategically important information in the context of reserve planning, as containing rare species and being likely to be deforested are two characteristics that will increase an area's priority on the list of possible acquisition sites.

Brock and Xepapadeas make an important innovation in the economic analysis of conservation issues, studying the conservation of two related and interacting species. The key point here is that species do not exist in isolation: a species is a part of an ecosystem and to conserve the species we have to conserve the system. Indeed, from an economic perspective it is often the system as a whole that is important and not the individual species, although it is often easier to focus public attention and concern on charismatic species, such as pandas and whales, than on the systems of which they are a part. Most economic models of species conservation consider a species in isolation, fisheries models being the classic illustrations of this point. This is like looking to conserve a predator without worrying about its prey—indeed the Lotka–Volterra model is an early example of a model of a multi-species system.

Albers and Muller take a different perspective on conservation policy. Recently, there has been a focus on the integration of conservation and development in poor countries, the countries containing most residual biodiversity. There is often an apparent conflict between conservation and improvements in living standards, as enrichment takes the form of more agriculture, cutting more firewood, and other activities that conflict with the preservation of habitat for threatened species. In integrating conservation and development we are trying to resolve this conflict by finding ways of rewarding local communities for conserving habitat consistent with improvements in their living standards. In a very specific context, this is a manifestation of the traditional public good problem of incentive-compatibility. Indeed, it is clear that biodiversity is a public good, so that in conserving biodiversity we have to wrestle with some of the most complex problems in resource-allocation theory. In general, we expect that markets will tend to under conserve biodiversity, though there are interesting examples of markets effectively integrating conservation and development via ecotourism (Heal, 2001, 2003).

The full consequences of the loss of biodiversity will unfold over years or even decades. The loss is itself a slow process, with a species remaining in existence long after its population and habitat have fallen below the minima needed for long-run survival. Consequently, conservation choices need to be evaluated over long time horizons, with how we handle discounting being of great significance. Settle and Shogren contribute to this issue, investigating the impact of switching from exponential to hyperbolic discounting on the value of a conservation project. Exponential discounting has been the gold standard of intertemporal welfare economics at least since the work of Ramsey (1928) and Hotelling (1931), but behavioral economists have recently suggested that individuals do not discount the future at a fixed rate, but rather at a rate that declines with the degree of futurity. This has potentially serious implications for welfare economics (Heal, 1998; Laibson and Harris, in press) and so for project evaluation, and the Settle–Shogren study is an important case study in this area.

4. Conclusions

Much of the economics of biodiversity remains to be written. There are gaps in our knowledge, many of which will have to be filled by joint endeavors between economists and ecologists. We certainly need to know more about how biodiversity contributes to society. Ecosystem services and natural capital provide a helpful paradigm here. The stock of natural capital, which consists of ecosystems and earth's basic biogeochemical cycles to which they contribute, provides services such as stabilization of the climate within a comfortable and agriculturally productive range (see Heal, 2000; Daily, 1997 for a more comprehensive list of services). These services have undoubted economic value. Through understanding more about the production functions that relate economically important ecosystem services to natural capital, we would be in a better position to understand the value of biodiversity conservation.

Probably what matters most to society is the maintenance of important ecosystem services and biogeochemical cycles. Granted this, the operational question then becomes how much of biodiversity we need to conserve to attain this goal—is this "all" or is it "most" or some well-defined subset? It is probably now too late to conserve "all", so we should hope that is not the answer. Even conserving "most" could by now be a challenge. Nevertheless, most biologists seem to believe that by conserving less than most biodiversity, we expose ourselves to serious risks. These are weighty questions.

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