COMMENTARY

Biological Conservation and Economic Theory

Charles Perrings * and Ann Kinzig **

1. INTRODUCTION

The field of conservation biology was originally developed as the science required to preserve endangered wild species in protected areas. The field has broadened its remit since then, but remains focused on wild living species. Yet, preservation of wild living species is just the tip of the conservation iceberg. The problem of conservation is much more generic than this. It is the problem of what to keep and how long to keep it, what to maintain in some state and what to allow to change, what to use and what to throw away. The protection of natural habitats or watersheds, the maintenance of the population of an exploited species, the preservation of ex situ collections of germplasm, the curation of art or natural history museum exhibits, and the listing of nationally important buildings or monuments are all examples of conservation problems. It is reasonable to ask what principles are at work in deciding what to conserve, and what to convert, independent of the particular conservation problem at hand. It is also reasonable to ask how these principles relate to the biology of threatened species.

In this note we draw on a forthcoming book (Perrings 2019) to consider how the problem posed by conservation biology appears through the lens of economic theory. In particular, we ask how the theory of conservation embedded in the work of Harold Hotelling helps both to deepen understanding of the aims and objectives of conservation biology and to implement the system of triage that must guide conservation efforts in a

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world of limited resources. The evolution of ecological economics as a field has been dominated by debates over what information to privilege in the management of human–environment interactions. Conservation biology has a similar history. We show how Hotelling's work helps anchor the claims made in both fields.

2. HOTELLING'S THEORY OF CONSERVATION

Our starting point is the general theory of conservation contained in Hotelling's paper on optimal extraction of non-renewable resources (Hotelling 1931). In that paper Hotelling provided a simple and intuitive test of when it is optimal to maintain an object, resource, or system in some state and when it is optimal to convert it to an alternative state. Hotelling showed that if the value of a resource when conserved in some state was expected to rise more rapidly than its value when converted to an alternative state, it would be optimal to conserve the resource. By focusing on the expected change in the value of resources in different states, the test allows us to see conservation as one among many alternative future uses. Conservation decisions accordingly reflect all of the factors that influence the value of resources. This includes the factors typically considered by economists such as individual preferences, social norms and mores, property rights and the legal system, technology, and the substitutability or complementarity of goods and services. But it also includes factors that weigh more heavily with others, such as the ecological functions performed by species or their place in the food web, their phylogenetic distinctiveness, and the degree to which they are endangered.

Hotelling saw the emergence of the conservation movement as a response to the perception that natural resources were being undervalued and hence overused. In the light of this he asked what the value of natural resources should be if they were being used in the best interests of society. Hotelling asked, more particularly, under what conditions the owner of some mineral right would choose to extract the ore assuming that the objective of the resource owner was to maximize the present value of the future stream of net benefits to be had from exploitation of the resource. If the value of the resource at time t—what Hotelling called the 'net price' of the resource—is p(t), and if the rate of return on alternative assets is δ , it is intuitive that the answer to this question should involve balancing the rate of growth in p(t) and δ . The Hotelling arbitrage condition does exactly that. In the case of exhaustible resources it holds that the resource owner will be indifferent between holding and extracting the resource if the proportional growth in the value of the resource when conserved is equal to the proportional growth in its value when converted.

$$\frac{\dot{p}}{p(t)} = \delta \tag{1.1}$$

That is, a resource owner will conserve the resource if the expected capital gain of holding on to it is equal to the return that could be had if it were converted.

The Hotelling approach turns out to be broad enough to deal with a wide range of conservation decisions—the decision to hold or sell stocks and bonds is just as much a conservation decision as the decision to hold or sell natural resources. It also makes the decision to harvest or protect wild or domestic populations of fish, mammals, birds, and plants as consistent with the decision to extract non-renewables such as minerals, oil, gas, and fossil water. The difference between renewable and non-renewable resources is that the value of renewables can change for different reasons. As with nonrenewables, the value of the resource can change for any of the usual demand-side reasons. Unlike non-renewables, however, the value of renewables can also change because of changes in the size of the resource itself.

Suppose that a renewable natural resource, the population of a particular species N, grows according to the general relation $\dot{N} = f(N(t), h(t))$. That is, growth is density-dependent—it depends positively or negatively on the size of the resource stock and along with some control, h(t). If the value of the resource is denoted p(t)N(t) it can be shown that the Hotelling arbitrage condition takes the form

$$\frac{\dot{p}}{p(t)} + \frac{\dot{N}}{N(t)} = \delta \tag{1.2}$$

That is, the decision to conserve or convert depends both on the expected capital gain, $\dot{p}/p(t)$, and the expected growth rate in the size of the stock, $\dot{N}/N(t)$. An immediate implication is that the capital gain which warrants conservation *in situ* is smaller, the higher the growth rate of the population of *N*. Conversely, for slow-growing or declining species, conservation will only be warranted if the expected capital gain is high enough.

The consequences of the trade-off between biological growth, value growth, and conservation have been thoroughly explored in the case of fisheries. Clark's conclusion that it could be optimal to drive blue whales to economic extinction depended on the observation that the natural rate of regeneration of the species was low relative to the rate of return on alternative assets (Clark 1973; Clark 1976); however, it also assumed that the low biological growth rate of the species was not compensated by the growth in its value, and that the only thing that prevented the extinction of the species was the increasing cost of accessing whales as their numbers fell (Clark 2006). The example nicely illustrates both the main elements in the decision to conserve living resources, and the points at which different disciplines have traction on the problem.

To see how the relationship between the Hotelling arbitrage condition and the optimal conservation of some natural capital stock, N(t), consider the following simple problem:

$$Max_{h(t)} \int_0^\infty e^{-\delta t} p(t)h(t)dt$$
 (1.3)

subject to

$$\dot{N} = f(N(t)) - h(t) \tag{1.4}$$

A manager chooses the level of harvest of species N so as to maximize the value of harvest. Benefits are discounted at the rate δ , which we take to be equal to the rate of interest on alternative investments. The manager's actions are constrained by the growth rate of the species, \dot{N} .

First, note that the Hotelling arbitrage condition for this problem, equation 1.2, implies that

$$f(N(t),h(t)) = N(t) \left[\delta - \frac{\dot{p}}{p(t)} \right]$$

from which it follows that at the point where the resource owner is indifferent between holding and conserving the resource, the slope of the density-dependent biological growth function, $\frac{df(N(t),h(t))}{dN(t)}$, will be equal to the difference between the opportunity cost of capital and the expected capital gain on the stock, $\delta - \frac{\dot{p}}{p(t)}$.

Now, consider the first order necessary conditions for harvest to be optimal in the problem described in equation 1.3. These include the requirements that

$$p(t) = \mu(t) \tag{1.5}$$

and

$$\dot{\mu} - \delta\mu(t) = -\mu(t) \frac{df(N(t))}{dN(t)} \tag{1.6}$$

where $\mu(t)$ is the shadow value of natural capital (a co-state variable, the multiplier in the current value Hamiltonian for the problem). These conditions together imply that along an optimal harvest trajectory

$$\delta = \frac{\dot{\mu}}{\mu(t)} + \frac{df(N(t))}{dN(t)} = \frac{\dot{p}}{p(t)} + \frac{df(N(t))}{dN(t)} \quad (1.7)$$

But if the resource owner is indifferent between conserving and converting the resource, this is just a restatement of the requirement that the slope of the density-dependent biological growth function will be equal to the difference between the opportunity cost of capital and the expected capital gain on the stock. This does however depend on the equivalence between the price and the shadow value—the true social opportunity cost—of natural capital.

3. HOTELLING THEORY OF CONSERVATION AND CONSERVATION BIOLOGY

How does the Hotelling approach connect to the propositions inherent in conservation biology? As we have already noted, Hotelling himself saw the origins of the conservation movement in the perception that the natural environment was both undervalued and overexploited. Hotelling sought to understand the basis of the value of natural resources, why that value might change over time, and how change in the value of natural resources might influence their conservation. The arbitrage condition applied to living resources or resource systems tells us that conservation depends both on the expected growth in the value of assets if conserved relative to the expected growth in their value if converted, and on the expected physical change in the stocks themselves.

The central tenet of conservation biology as it originally developed was that the value attached by the majority of landowners and landholders to wild species is strictly less than its true value to society—that there is a wedge between the value attached by individuals to wild species and the value of those species to society (Soule 1985). Several reasons were advanced to explain why this has occurred. The most important of these was ignorance about the role played by particular species, and communities of species, and the relation between ecological functioning and the ecosystem services that benefit humans. Ignorance about the effects of reduced diversity of food webs on decomposition, nutrient retention, plant productivity, and water retention, for example, was argued to threaten a number of ecological functions of direct or indirect benefit to humans (Naeem *et al.* 1996). Ignorance about source and sink dynamics was cited as a major reason for the extirpation of many protected sink populations. Failure to protect disproportionately valuable source populations necessarily put associated sink populations at risk, even if those populations were otherwise protected (Mangel *et al.* 1996). More generally, by focusing on single species, populations, or biotopes in isolation from the system that supports them, resource owners paid insufficient attention to critical elements of the wider system (Myers 1996).

A related concern was that decisions that reduced biodiversity tended to be focused on short-term gain, and also that these tended to pay insufficient attention to the longer-term costs in terms of reduced capacity to protect future options against fundamental change. Since the neglect of longer-term costs stems either from ignorance or from the application of high discount rates, and since there is an ethical component to discounting, the undervaluation of species and whole ecosystems was taken to reflect—at least in part—an ethic of myopic greed. By contrast, conservation biology was argued to be concerned about the maintenance of whole ecosystems over the long term. It was claimed that the difference in the values attached by conservation biologists to species reflected a fundamental difference in ethics (Mangel *et al.* 1996).

At the core of the conservation ethic was the proposition that biodiversity has intrinsic value, irrespective of its instrumental or utilitarian value, and that value is 'neither conferred nor revocable' but springs from the fact of the species' existence (Soulé 1985). There are obvious practical difficulties with a concept of value that is independent of human preferences and yet is expected to guide human action. Indeed, many of these difficulties are recognized by conservation biologists themselves (Justus et al. 2009). But if we think of the argument as a statement that there is value to species that stems from their place in the natural system, rather than from their incorporation in a managed production process, then it is quite consistent with the general proposition that nature is undervalued when measured by the market price of harvested species. It is also consistent with the key proposition implicit in the Hotelling arbitrage condition for renewable natural resources: the expected growth in value of natural resources comprises the sum of the expected capital gain in holding those resources in situ and of the value added through their role in the functioning of the natural system.

Many of the original propositions of conservation biology have evolved with efforts to uncover the value attached to the many and varied roles played by genes, species, landscapes, and ecosystems. There is now a more systematic attempt to ask what benefits are lost when there is a change in either species richness or abundance. The notion of intrinsic value still has a place in the language of conservation biologists, but it is increasingly linked to the value deriving from the place of species in the ecosystem rather than their mere existence (Doak *et al.* 2015). The decision to conserve some aspect of the natural system in some state depends on the expected growth in the value of the system in that state, taking account of the role it has in the wider functioning of the system.

While the simple example used to illustrate the Hotelling approach to conservation focuses on a single species, both conservation biology and ecology reinforce the idea that the value of any one species to human society depends as much on its contribution to the functioning of the wider ecosystem as on the specific traits that make it useful in one application or another. Although the wider value of species is sometimes clouded by conservation biologists' insistence on the relevance of intrinsic value, it helps to remind us that for many people a sense of stewardship and moral obligation is a major determinant of the value they assign to the conservation of populations, species, and ecosystems.

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