Extinction, Substitution, and Ecosystem Services

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The loss of services to humanity following extinctions ranges from trivial to catastrophic, depending on the number of elements (populations, species, guilds) deleted and the degree of control each exerted in the system. Most attempts to substitute other organisms for those lost have been unsuccessful, to one degree or another, and prospects for increasing the success rate in the foreseeable future are not great. Attempts to supply the lost services by other means tend to be expensive failures in the long run. A conservative approach to the maintenance of services through minimizing anthropogenic extinctions is recommended. (*Accepted for publication 20 October 1982*)

At this moment humanity is forcing species and populations to extinction at what may well be an unprecedented rate (Council on Environmental Quality 1980, National Research Council 1980). This raises two critical questions. First, what can be predicted about the impact of extinctions of given elements (populations, species, guilds) in ecosystems upon the services delivered to humanity by those systems? Second, to what degree can those elements be replaced without impairing either short- or long-term ecosystem functioning? Economists have paid much attention to substitution for inorganic resources (e.g., Barnett and Morse 1963), but the potential for substituting for living resources has barely been explored.

We hope that this preliminary look at these questions and our conclusions may stimulate the research required to provide the data upon which rules for predicting the success of substitutions can be based. However, we agree with Ehrenfeld (1978) that there are compelling reasons for preserving the biotic diversity of Earth *regardless* of any present or future discoveries made about the benefits people may receive from other organisms.

ECOSYSTEM STRUCTURE AND SERVICES

We use the term *controllers* to refer to the organisms that determine the structure (e.g., species composition, trophic relationships) of the ecosystem and through which the principal flows of energy and materials pass. The term is used broadly, for we recognize that many controllers cannot be identified. One of the two most crucial sets of controllers in all major ecosystems is the one through which solar energy and carbon and other nutrients enter living systems (the producer trophic level). The other set consists of those that release the nutrients bound up in organisms by production for reuse (the decomposer trophic level). Loss of either of these sets brings the collapse of the entire system.

The number of controllers at any given level varies from ecosystem to ecosystem. For example, the trees in a redwood forest or tropical rainforest fix most of the solar energy captured by the system; they also accumulate and retain a large portion of the nutrients. The trees also exercise important control over water and air flows, microclimate, and, through their effect on the albedo and exchanges of CO_2 and water vapor with the atmosphere, macroclimate. In the redwood forest, a single species appears to be the primary controller; in the rainforest, a guild of many species shares control.

Internal configuration is largely controlled by the interactions among the species in the ecosystem. Population sizes and structures are influenced in ecological time by weather (itself influenced by other species), competitors, predators, pollinators, dispersers, seed bed providers, domicile providers, and other factors. In evolutionary time they are determined in large part by climate and coevolution (Schneider 1983), and the plant–herbivore interface has been proposed as the most important in the generation of structure (Ehrlich and Raven 1964). Here, there are usually major and minor controllers, determined by population sizes, physical size of individuals, degree of specialization, precise ecological role, and so on.

The degree of control exercised by a single species is often difficult to evaluate, even when its role is well understood—in part because controllers tend to function in series. For example, many trees depend on mycorrhizal fungi in the soil for nutrients (Wilde 1968). But how much credit the fungus should be given for the many crucial control functions of the tree is difficult to determine. Similarly, the role of the small moth *Cactoblastis cactorum* in Queensland is difficult to evaluate without knowing the history of its presence. One might decide it is a minor component. We know, however, if the moth were removed, millions of hectares would be choked by *Opuntia* cactus, transforming local ecosystems. That was their condition before *Cactoblastis* was imported from the South American home of *Opuntia* to control the cactus plague (DeBach 1974). These difficulties, however, do not mean that important conclusions cannot be drawn about the adverse effects of extinctions on ecosystems and the degree to which substitution can ameliorate them.

EXTINCTION AND ECOSYSTEM SERVICES

Extinctions occur continuously as part of evolutionary and ecological processes Ehrlich et al. 1980), so ecosystems clearly can suffer some rate of extinction without serious degradation of their functional properties. Since the living components are known to be essential to those functions, however, there must also be some rate of extinction that a given ecosystem cannot absorb without undergoing reorganization leading to serious impairment of its functioning from the point of view of *Homo sapiens*.

The immediate impact of the deletion of a single element from an ecosystem obviously can be judged in theory from its quantitative involvement in the control of various functions. Judging the long-term impact is more difficult. For example, the deletion of one member of a controlling guild may or may not result in a significant change in ecosystem function in the long run, even if the species is quantitatively important. Abrupt decline of hemlock from a dominant role in the northeast in prehistoric times (~4800 B.P.) led to important ecosystem changes, notably enhancing lake productivity through greater leaf input Whitehead and Crisman 1978). In contrast, the recent deletion of chestnut did not have a great impact on the ecosystem Good 1968), although it may be too early to tell. Presumably other guild members, in the latter case, have expanded their population sizes, using the resource base left by the deletion. Of course, if all members of a guild are deleted, then there will be a significant and lasting impact on ecosystem function and hence on the services provided.

Deforestation, which is the permanent loss of the guild of dominant trees, and strip-mining, which deletes an entire biota, are classic examples of deletions causing massive disruption of ecosystem services. Strip-mining results in widespread disturbance of aquifers, water pollution, and loss of land from agriculture, support of wildlife, and other uses Wali 1975). The newly exposed areas are prone to intense wind and water erosion (Hodder 1975).

Deforestation cancels numerous services, such as flood control (Revelle 979), erosion prevention, filtration of atmospheric pollutants, and the continuous supplying of firewood and timber Eckholm 1979). The loss of such services can be catastrophic for human populations dependent upon them. Even the

removal of arid-scrub vegetation by overgrazing can be disastrous. This contributed to the degradation of climate-ameliorating services in the Sahel, was a major factor in the large-scale famine there and made the return to moister conditions less likely (Charney et al. 1975). Other human impacts, such as dry deposition of air pollutants, acid rain, and assaults by other toxins may be more subtle but equally catastrophic (Harte 1983, Woodwell 1970, Likens et al. 1974).

Such massive assaults on ecosystems produce a number of well-known syndromes that are accompanied by severe degradation of the public service functions of the systems. By far the best documented is *desertification* (United Nations 1977). Related to desertification, and if anything more serious for *Homo sapiens*, is soil erosion. Recent estimates indicate that unless current rates of erosion are slowed, there will be a monotonic decline in agricultural productivity (Brown 1981). Equally ominous is the trend toward *toxification* of the entire planet (Charney et al. 1975). And, largely as a side-effect of other impacts on ecosystems and of human transport, we are witnessing the *weedification* of the planet. (Of course weeds can and often do play an important role in preserving some ecosystem services).

The ecosystemic effects of large-scale disruption can persist for very long periods. The extinction of the Pleistocene megafauna may have strongly influenced the distribution of the Central American plant species whose seeds were dispersed by the deleted guild of large browser (Janzen and Martin 1982). Whatever the impact of that change on ecosystem services, because of the long generation time of most of the plants (trees and large shrubs), the system has not yet adjusted evolutionarily.

Smaller interventions produce less dramatic disruptions. Consider the practice of using herbicides to kill shrubs following tree harvesting in the forests of the Pacific Northwest to reduce competition with regrowth of the desired trees (Newton 1981). Although tree growth is generally favored in the short term, community productivity may not be in the long term, since certain of the shrubs (e.g., *Ceanothus*) are nitrogen fixers. The setting back of this guild may eventually require a fertilizer subsidy. There are numerous other instances of the substantial consequences of guild reductions in both natural and artificial ecosystems caused by the use of biocides. The Can-

ête Valley disaster in Peru is a classic example. Early successes using insecticides against cotton pests led to larger and larger applications. Predatory insect populations were decimated, and several herbivorous species, freed from predation, were "promoted" to pest status. And, of course, the original pests became resistant. The result: a catastrophic drop in cotton yields (Barducci 1972).

At the other extreme from the massive disruptions, a service may be reduced only imperceptibly after an extinction. Deletion of one of an array of understory plants or of one insect herbivore attacking the trees might make no measurable difference in the delivery of services. Indeed, it might increase some of them. Similarly, to the degree that *Homo sapiens* raises extinction rates above the normal "background" rates, it is automatically disrupting the genetic library service. But in any given case the loss (no matter how serious in the long run) is small in proportion to the total library service and not easily detected. Losses in the genetic diversity of crops and their wild relatives clearly fall in this category (Ehrlich and Ehrlich 1981).

Thus ecosystem services can, in effect, be "killed outright," "nickled and dimed to death," or even enhanced by extinctions. The degree of alteration of services depends on the functional role(s) of the organisms that go extinct and on the pattern of extinctions (e.g., selective deletion from an ecosystem or destruction of most elements simultaneously).

ECOSYSTEM RESTORATION

Increasingly, assaults on ecosystems are of a nature and scale that basic physicochemical conditions are changed. This makes natural succession unlikely or impossible, or extends the time scale of restoration of the original ecosystem beyond the period of reasonable human interest. For example, when a large area of tropical moist forest ecosystem is cleared, climate change and soil and nutrient loss often dictate a pattern of succession that will not soon restore the forest. Confusion about the ease of recovery of such ecosystems is rife because of the often-cited return of moist forests on Krakatoa after that island was leveled by a volcanic eruption (Dubos 1980). But the destruction of the biota on that small island was not comparable to the leveling of large tracts of mainland rain forest. The local climate was not altered, sources of propagules

were very nearby, and the soil was enriched with volcanic ash.

With enough human effort, deserts can be made to bloom and forests to grow in denuded areas of the tropics. But the key word is *enough*, and the key question is whether the replacement can adequately perform the functions of the natural system.

HOW FINE-TUNED ARE COMPONENTS?

Substitutability will, in part, be a function of how closely controllers are fitted to their ecosystemic roles. Some animals are very "fine-tuned." Many parasites are completely dependent on one other species for their existence and have their primary ecological impact on that species. Numerous attempted translocations of vertebrates have failed, in many cases apparently because genetic characteristics were inappropriate to the locality of introduction (Greig 1979).

Populations of many insect herbivore species have made delicate adjustments to both host plants and local conditions. For example, after all the British populations of the large copper butterfly were extinct, a series of attempts was made to introduce stock drawn from Dutch populations. Subtle differences in the ecological requirements of the genetically different populations resulted in failure of the attempted substitution (Duffey 1977). Similarly, checkerspot butterfly populations in the western United States show a high degree of local specialization. Stock from one area often will be unable to recolonize other areas where populations have been exterminated by transitory events (Ehrlich et al. 1975 and unpublished data).

Native Australian dung beetles are fine-tuned for handling the small fecal pellets of kangaroos, other marsupials, and emus. Few can satisfactorily process the moist, large droppings of grazing placental mammals—sheep and cattle—that have been introduced to the continent in huge numbers. This has led to an increase in populations of the pestiferous bushfly (which breeds in unburied droppings), lowered productivity of pasturelands because nutrients remain tied up in the feces, and the creation of a fecal pavement that retards plant growth. Australia has started to introduce African dung beetles in an attempt to solve these problems (Bornemissza 1960, Gillard 1967, Hughes et al. 1978).

Many plant populations are also fine-tuned to their physical environments. A large number of examples have been documented of the precise adaptive responses of plants to the conditions of their local habitat, including specific responses to photoperiod or soil type (e.g., Heslop-Harrison 1964). For example, it is recommended that seed sources for reforestation of douglas fir at a specific site should be collected from areas no further distant from the original site than 110 m difference in elevation, 1.6 degrees latitude and 2.7 degrees longitude (Rehfeldt 1979).

At the opposite end of the spectrum, there are generalists that are relatively insensitive to the disappearance of one or more resources or may have the phenotypic plasticity permitting them to thrive under a wide variety of environmental regimes, e.g., cabbage butterflies, black bears, and coyotes. The moth *Heliothis zea* feeds on an enormous variety of plants in many families. Some plants, such as the reed grass *Phragamites communis*, grow from the polar regions to the tropics (Haslam 1972). Replacing lost populations of such species with ones from elsewhere may be simpler than in more specialized species, unless they, too, prove to be subdivided into many ecotypes that cannot readily replace one another. Unfortunately the degree of ecotypic differentiation in most species remains uncertain.

SUBSTITUTION IN ECOSYSTEMS

The history of introductions gives some insights into the more general problem of substitutions. The most important of these is that a species that is not a controller in one system may turn out to be a major controller in another (Elton 1958). In a coevolved ecosystem, the resources available to a species are determined not only by its physiological capacity to gather these resources, but also on its relationships with competitors and predators. A species removed from its coevolved competitors and predators may reach unprecedented population sizes and have an ecosystem impact to match as, for example, the history of goats introduced onto islands attests.

Most successful weeds are preadapted to invade systems that have already been disrupted by human activities (Mooney and Godron 1983). Successful invasions into natural systems also occur, especially where the invaders represent guilds not previously present in the area. Disruption of island ecosystems by introduced species supplies numerous examples (e.g., Elton 1958, ch. 4).

Ease of substitution would be expected to follow a pattern parallel to that of the impact of loss. Dominant plants are usually long-lived, and even if a suitable substitute is available, restoration of functions dependent on such K-selected organisms is likely to be a long-term process. Furthermore, it has been estimated that every plant species that goes extinct takes with it an average of 10 to 30 other species of organisms (Raven 1976). In the tropical rain forests around Finca La Selva, Costa Rica, the fruit of the canopy tree *Casearia corymbosa* is a resource for 22 species of birds, several of which are entirely dependent on it during one part of the year. If *C. corymbosa* were to disappear, these birds would go also, with ramifications for other trees that depend on the birds for seed dispersal (Howe 1977)[1] and thus on the herbivores dependent on *those* trees, and so on. Species like the *Casearia*, whose loss would start a cascade of extinctions, have been termed "keystone mutualists" (Gilbert 1980). Substitution for a keystone mutualist would obviously be much more difficult than for a species that did not have a unique position in the trophic web.

At first glance, rapid substitution for decomposers might seem relatively easy, since most have short generation times. But, at least in terrestrial systems, most of their extinctions will probably be due to physical-chemical changes in soils. These may be very difficult to reverse, so substitutes will have to function in a different environment. Acid rain, for example, inhibits certain nitrogen-fixing organisms as well as decomposers (Cowling and Linthurst 1981). At low pH, fungi become predominant in the soil, and actinomycetes and other bacteria drop out (Alexander 1977).

Making predictions about substitutions for consumers is more difficult because of the complexity of plant–herbivore and predator–prey interactions in both ecological and coevolutionary time (Roughgarden 1979). Some predators do appear to occupy positions analogous to that of keystone mutualists, and their deletion from a system results in a rapid decay of diversity (Paine 1966). A review of experimental studies of predator removal from natural, predominantly marine, ecosystems, reveals that in most cases other species were lost from the system (Pimm 1980). Equally, removal of herbivores from an ecosystem can often have dramatic effects on plant spe-

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s composition and density (Bartholo-
w 1970). Indeed, the main generaliza-
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pact of the loss of a single consumer
pulation or species from an ecosystem
that it is unpredictable, even though
:oreticians (Pimm 1980) are making
)gress in developing rules for what to
)ect from different patterns of con-
ner deletion. And inability to predict
: consequences of deletion makes
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ich more difficult.

)ne standard of success in replacing
? population or species with another is
viously the degree to which the previ-
s delivery of ecosystem services is
intained. Although this can be rela-
ely easily measured in the case of
ne services (e.g., flood control, genet-
library), it, unfortunately, can be ex-
mely difficult to measure and impossi-
: to predict in others (weather
elioration, pest control, soil genera-
n). In addition, there is the difficult
:stion of stability of the reconstituted
item over time. We don't know how
g to wait before declaring that a sub-
ution has succeeded or failed.

These are obviously questions that de-
ve further consideration and investi-
ion by community ecologists. Here
use, *faute de mieux*, a pragmatic
ssification. A substitution may be
med successful if, after several gen-
tions, the ecosystem shows no obvi-
; deterioration and no human inter-
ition, especially continued inputs of
ernal energy, is required to maintain
services.

SUCCESSFUL SUBSTITUTIONS

n most cases, substitutions appear to
unsuccessful. The number of thor-
;hly studied attempts at substitution
however, small.

es for Trees

Considering the magnitude of the
ses due to deforestation, it is not
prising that attempting to restore for-
ecosystems is a major human activi-
Frequently a single-species tree plan-
ion is substituted for an original mixed
est. The services provided by a forest
one kind of trees, however, may not
equivalent to those provided by an-
ier. For example, it has been estimat-
that shortly after the turn of the
itury, there will be more than a million
:tares of forest plantations in Austra-
, planted primarily with the exotic

Monterey pine (Rymer 1981). It has been
shown that these trees cannot satisfacto-
rily be substituted for native species and
that they lead to reduced energy flow
through the ecosystem, less cycling of
minerals, and a loss of soil nutrients, at
least under prevailing management prac-
tices (Feller 1978, Springett 1976). The
plantations are almost totally unable to
provide the genetic library service of the
forest ecosystem they replace.

Plantation monocultures are also less
likely to be self-sustaining in the long run
than natural forests. Not only is species
diversity likely to increase resistance to
insect outbreaks and epiphytotics, but so
is genetic diversity within species (Ed-
munds and Alstad 1978, Sturgeon 1979).
Polycultures generally do better. The
Kaingaroa Forest of New Zealand, a
multispecies stand of exotic conifers,
supports a wide diversity of native and
introduced consumers (Wilson and Wil-
lis 1975). The potential nutrient loss and
loss of the genetic library function in
temperate-zone exotic plantations, how-
ever, is trivial compared to those losses
when grasses are substituted for tropical
moist forest. Global climatic change that
might result from that substitution (Pot-
ter et al. 1975) could threaten Earth's last
bastion of large, dependable grain sur-
pluses—the prairies of North America
(Poore 1976).

Crops for Prairies

It might be argued that the replace-
ment of perennial prairie grasses by
wheat and corn represents a wholly suc-
cessful substitution. It is true that the
energy capturing function of the ecosys-
tem has been kept and modified in a way
that is of incalculable benefit to human-
ity. But annual crop species, which have
been derived from early successional
species, cannot be maintained without a
continual input of energy and resources.
Annuals allocate less carbon to under-
ground production and thus do not con-
tribute to the generation of soils to the
same degree as perennials. The loss of
the perennial grasses thus results in a
degradation of the site through a loss of
soil nutrient stores, which must then be
replaced by fertilization (Jackson 1980).

Fishes for Fishes

Since 1970 the total oceanic fisheries
yield has increased very little (Brown
1981), which means that per capita yields
have been rapidly declining. Behind this
widely recognized decline, however, is a

less well-known process of species sub-
stitutions. As stock after stock has been
driven to economic extinction, yields
have been maintained only by moving to
the exploitation of species previously
thought to be less desirable or less easily
harvested. This has already led to de-
creased catch per unit effort (Brown
1981). This process of substitution can-
not go on forever. Although the overall
productivity of the sea may not be dimin-
ished by the removal of commercially
valuable fish stocks *seriatim*, there is no
evidence from history or theory to indi-
cate that depletion of one such stock will
lead to the expansion of others that are
equally valuable (Clark 1976, Murphy
1966).

Cattle for African Grazers and Browsers

This substitution has produced disas-
trous consequences in much of semiarid
Africa. The cattle, unlike many ante-
lopes, must trek daily to a water hole.
This both requires energy, reducing meat
yield, and accelerates the downhill spiral
toward desertification. Mixed herding of
antelopes utilizes the habitat much more
efficiently without degrading it (Hopcraft
1979).

Inorganic Substitutes for Extinct Organisms

F. H. Bormann (1976, p. 759) has sum-
marized the problems of substituting
technologies for the loss of services fol-
lowing deforestation:

> We must find replacements for wood
> products, build erosion control works,
> enlarge reservoirs, upgrade air pollution
> control technology, install flood control
> works, improve water purification
> plants, increase air conditioning, and
> provide new recreational facilities.
> These substitutes represent an enormous
> tax burden, a drain on the world's supply
> of natural resources, and increased
> stress on the natural system that re-
> mains. Clearly, the diminution of solar-
> powered natural systems and the expan-
> sion of fossil-powered human systems
> are currently locked in a positive feed-
> back cycle. Increased consumption of
> fossil energy means increased stress on
> natural systems, which in turn means
> still more consumption of fossil energy to
> replace lost natural functions if the quali-
> ty of life is to be maintained.

A similar statement could be written
about substitution for natural pest con-
trol functions with synthetic organic pes-
ticides, natural soil maintenance with

inorganic fertilizers, natural water purification with chlorine treatment, and so on. These substitutions are all unsuccessful because they require a continual energy subsidy; most also only partially substitute for the services originally supplied.

SUCCESSFUL SUBSTITUTION

Although there are numerous examples of unsuccessful substitutions, successful ones are hard to identify. In most cases, at least genetic library functions are degraded by large-scale substitutions, but these are usually not obvious and thus permit the substitution to be rated as largely "successful."

Honeybees for Natural Pollinators

Some 90 crops in the United States alone depend on insects to pollinate them, and 9 others benefit from insect pollination (USDA 1977). Some of these crops, however, can be adequately pollinated by honeybees and thus can be independent of that service from natural ecosystems.

Imported Plants for Native Plants

Many exotic plants seem to replace natives quite adequately in providing all but the genetic library service. In California, ice plants from South Africa function in erosion control, and exotic oleanders provide services on freeway verges where few plants of any kind can survive. Many specially selected street trees provide important services in a hostile environment, substituting for natives that could not adapt to such conditions. The grasslands of California, although now principally composed of annual weeds of Mediterranean origin, are self-maintaining. The weeds have replaced the native herbaceous ecosystems that, at least in coastal regions, were dominated by perennial grasses (Wester 1981). This conversion, evidently induced by overgrazing and drought, has, however, resulted in a substantial decrease in range productivity (Burcham 1957).

What Organisms Are Successful Substitutes?

Organisms that are tough generalists—often "weedy"—are most likely to make successful substitutes if they can supply the needed services. The species and populations that have gone extinct are,

naturally, unlikely to have been generalists. What evidence there is indicates that fine-tuned replacements are usually not available. But introduction of generalists to replace a lost service often presents grave risks of their uncontrolled spread resulting in the loss of other services, such as maintenance of the genetic library.

THE GENETIC LIBRARY

The degree to which genetic library functions can be replaced is especially difficult to evaluate. By looking to the past, one could easily conclude that substitution would be almost impossible. What if the wild progenitors of just wheat, maize, rice, horses, and cattle had been wiped out before domestication? For the last two it might have been a close call, considering the Pleistocene extinctions. And the array of other foods, medicines, industrial products, and esthetic treasures derived from other species is enormous (Myers 1979). Humanity has already withdrawn from the library the very basis of civilization, a priceless benefit.

If one looks to the present, library services seem equally impossible to replace. For example, the continuation of high-yield agriculture will become much more difficult if extinctions of close relatives of crops continue (Frankel and Soulé 1981). It is also clear that to function properly the library must have numerous editions of each "book"—series of genetically distinct populations that can provide the basis for future evolution under either natural or artificial selection. As Aldo Leopold (1953, p. 194) said, it is "the clear dictum of history that a species must be saved *in many places* if it is to be saved at all."

Looking to the future, one might imagine that substitution for the library function of natural ecosystems would become simpler. For instance, genetic engineering may hold some promise of eventually producing new crop varieties with highly desirable properties without reliance on the gene pools of wild plants. In the foreseeable future, however, genetic engineering will not be fabricating substitute organisms to replace those lost from ecosystems. This can be stated with confidence because so little is known of the subtleties of the ecological roles of even prominent organisms. In short, if geneticists could fashion an organism precisely "to order," ecologists would not know what to ask them to make. Indeed, a continuing epidemic of

extinctions will likely do much more to *reduce* the capability of the genetic engineering enterprise than geneticists can do to ameliorate other consequences of the extinctions (Eisner 1981). For now the engineers are confined to manipulating existing genetic material.

CONCLUSION

Aldo Leopold (1953, p. 190) also wrote: "If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering." Unfortunately, humanity has been gambling with its future by saving fewer and fewer of the parts. Therefore, if the tide of extinctions is not reversed, humanity obviously will be required increasingly to attempt substitutions to maintain ecosystem services. Satisfactory substitutes are unlikely to be found at anything like the rate that ecosystems are now being degraded. That situation may change somewhat in the future with advancing knowledge in community ecology (Wilson and Willis 1975). But there is also every reason to believe that the rate of destruction of ecosystems will also increase.

At some point the costs of substitution will almost certainly become unbearable. Therefore, it seems that a conservative approach, emphasizing the careful preservation of ecosystems and thus of the populations and species that function within them, is absolutely essential. The ways of accomplishing this are the subject of a growing literature in conservation biology (Soulé and Wilcox 1980) and even economics (Fisher 1981).

252

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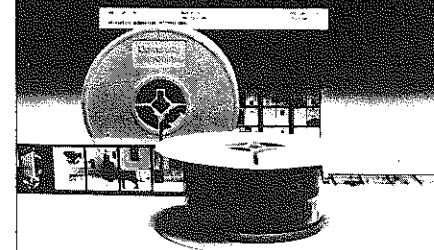
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