PART III

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# LINKAGES AND EXTERNALITIES

Can we ever really conclude that a species is expendable? While it is straightforward to identify a research protocol that provides evidence for the value of a species or of biodiversity in general, using science to conclude that a species is expendable seems unbearable to many ecologists and evolutionary biologists. This final section reveals the difficulty that leading ecologists experience when asked to consider a judgment that some species might in fact be expendable.

First, Leigh points out that our current understanding of the interdependencies among species is so limited, and falls so short of the deep understanding required, that questions about "expendability" are staggeringly naïve. He examines the web of influences among tropical species, uncovering numerous surprises that could be detected only with the use of long-term and intensive field studies. Leigh scolds modern ecology for its under-appreciation of detailed natural history, which in his view dooms ecology to shallow and erroneous assessments of species expendability.

Morris focuses his attention on the value of the pollination services provided by various species that visit flowering plants. He uses data

from a wide range of studies on patterns of pollinator visitation to quantify the consequences to the plant of losing any given pollinator species. Specifically, Morris asks whether infrequent pollinators might be expendable from the plant's point of view. Even this more narrowly defined question proves difficult to answer, and Morris's analyses reveal that even species that are infrequent visitors to plants have value.

Root goes further toward a possible verdict of "expendability" in recounting his studies of rare herbivorous insects. He points out that after lengthy study (and the sort of detailed natural history that Leigh champions), some goldenrod insects would seem to be truly ecologically expendable. Root backs away from this potentially shocking conclusion, however, by reminding us that studies of plant-herbivore interactions are replete with examples of host shifts and evolutionary change. He points out that if a taxon represents a proper species with a unique evolutionary lineage and hence a unique (and unpredictable) future, then evolutionary (rather than ecological) considerations imply that the taxon is not expendable.

Palumbi arrives at this same conclusion but starts from the perspective of an evolutionary biologist rather than a community ecologist. Specifically, Palumbi extends Root's caution about evolutionary potential by describing several examples of rapid species evolution that in turn altered the nature of species interactions and hence a species' ecological role. Once we admit that ecologically significant traits of species can evolve rapidly, then a species' value is not so easy to dismiss—especially given the dramatic anthropogenic disturbances that currently impact our planet. Today's ecologically trivial species could be tomorrow's keystone species.

Perhaps it is not surprising that the contribution that most seriously grapples with the issue of setting priorities for conservation comes from a group of ecologists who work on salmon recovery for the National Marine Fisheries Service. Federal agencies and other "on-the-ground" conservation efforts consistently face the reality of limited funding, and hence the need for rational guidelines to be used in making choices about what to save. Ruckelshaus, McElhany, and Ford in this section ask which populations of endangered salmonids might be given lower priority for protection (or recovery). Although populations are one step below the species level, their approach is germane to questions of "expendability" for any unit. A quantitative constraint (minimum "services" that must be provided) is specified, then the contribution of different collections of populations is assessed. Academic researchers would probably be troubled by the willingness of these conservation practitioners to establish priorities for protection, but if science does not establish those priorities for sal-

mon, economics will. Ruckelshaus et al. find that the greatest obstacle to developing rational priorities for population protection is an inadequate understanding of the frequency, magnitude, and impact of catastrophes and how this impact is mediated by evolutionary responses. The same obstacle would probably be true of species expendability, since so many of the arguments for biodiversity ultimately rest on the value of "buffering," "redundancy," and "insurance" in the face of dramatic change.

Finally, Power and Flecker analyze a remarkable data set that describes the specificity of insect-vectored plant diseases for the species they infect, and for the host insects that vector these diseases from plant to plant. We forget sometimes that pathogens are species as well, and that any discussions of biodiversity and the value of species need to consider pathogens. What makes Power and Flecker's chapter so interesting is the completeness of the data set and the number of species it involves (1673 viruses). For most taxonomic groups or associations of species, it would be impossible to compile such a definitive list of direct interactions. One interesting result of Power and Flecker's analyses is the notion that diseases may be vulnerable to the loss of their vectors (because they are carried by few vectors), which in turn could have broader implications for plant population dynamics in the wild.

The most striking feature of the chapters in this section is the general reluctance of scientists to deem any species to be more or less important than another. If ecological studies fail to find an important role for a species, for instance, then evolutionary arguments are invoked. The problem is that "importance," and conversely "expendability," are value-laden terms that have implications for environmental policy. The discomfort we feel in using a word such as "expendable" or "redundant" with regard to any species suggests that policy regarding biodiversity (or extinctions) must be founded on general principles rather than on a case-by-case justification for each species. Or, perhaps ecologists need to admit to themselves, as well as to others, that there are ethical dimensions to the discussion that contribute to their unwillingness to deem any species expendable.

At the same time, it is essential that ecology develop the ability to predict the consequences of particular species additions or losses, so that such gains and losses can be managed for the best possible sustainable future. Reactive conservation, which emphasizes the maintenance of all biodiversity and of "natural pristine systems," can decide on its course of action without regard to the detailed roles of species. However, proactive conservation, which emphasizes providing for a future natural world that is likely to differ from any historical vision of pristine, will require the sorts of insights developed in this volume, and inspired by Bob Paine's career.

CHAPTER 12

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## Social Conflict, Biological Ignorance, and Trying to Agree Which Species Are Expendable

*Egbert Giles Leigh Jr.*

**D**eciding which species are expendable is a singularly contentious question, at three levels. First, posing it looks very like sitting in judgment on God's Creation. One need not be religious to be wary of this sort of pride. Second, if we do choose to sit in a judgment seat that belongs to Another, how do we decide what aspects or functions of ecosystems should be preserved or enhanced? Finally, if we are not put off by the orgy of self-centeredness involved in deciding what *we* want from ecosystems, how do we discern whether a particular extinction will bring on consequences that we deem unacceptable? A look at the fossil record tells us that any number of species have gone extinct. Except for major crises such as those that ended the Paleozoic and Mesozoic, we can rarely see how these extinctions threatened their ecosystems. The extinction of the American megafauna at the end of the Pleistocene must have caused major changes in at least

some ecosystems (Janzen and Martin 1982), but human beings responded to these changes quite readily, even creatively. The invention of agriculture seems to be among these responses (Piperno and Pearsall 1998). At the moment, our ecological understanding is usually far too crude to allow precise judgments of which extinctions would matter.

To decide what species, if any, are expendable, we must consider two issues:

1. Suppose we knew our biology. What criteria are appropriate for deciding which extinctions are unacceptable? In other words, what features of the world ecosystem must we preserve?
2. What kinds of biology do we need to know to preserve the essential features of our ecosystem? To know how the extinction of different species affects their ecosystems requires knowing how ecosystems are organized and the many ways we depend on them.

## How Do We Decide What Features of the World Ecosystem to Preserve?

What are our responsibilities toward our environment and the other species in it? Because traditional religions have played a crucial role in maintaining harmony between human beings and the order of nature, in societies as different as the Achuar of Amazonian Ecuador (Descola 1993), the Amuesha of Amazonian Peru (Santos-Granero 1991) and traditional China, let us begin with two traditional answers. The scriptures of Judaism, Christianity, and Islam proclaim us lords and stewards of God's creation, responsible to God for its integrity (Nasr 1996). Moreover, God made wonderful wild animals that are living praises of their Creator, although they are without any conceivable use to human beings (Psalm 104; Job, chapter 38:36 through chapter 41). Theoretically, this view would not allow us to proclaim any species expendable. Nonetheless, although God is concerned for young lions, who are said to seek their food from Him (Psalm 104:21), the Bible recommends no particular human provision for their survival or welfare. Instead, good stewardship means preserving harmony between human beings and the order of nature. Preserving this harmony requires harmony between human beings and God. Because Adam rebelled against God, he was told "cursed is the ground because of you; in toil you shall eat of it all the days of your life; thorns and thistles shall it bring forth to you . . ." (Genesis 3:17–19). Harmony between human beings and nature centers on the responsible

*use* of land, with due regard to the interests of poor neighbors and even of wild animals (cf. Exodus 23:10, Leviticus 25:1–7). Indeed, harmony between humans and nature *requires* a modicum of social justice: social injustice leads to ruin of the land (cf. Isaiah 5:8–10).

Let us now turn to a very different traditional voice. The Makuna, hunter gatherers and swidden agriculturalists of Amazonian Colombia (Århem 1996), are much more dependent on the integrity of wild nature than were the Hebrews of the Torah. Perhaps as a result, the Makuna consider themselves parts of nature—or nature as an integral part of society. They view hunting as a carefully regulated exchange among humans, animals, and the animals' Spirit Owners. Before an animal is hunted, the shaman must negotiate consent from its Spirit Owner. When the animal is killed, the shaman must despatch the spirit of the slain animal to its species's "birth house" so that a new young of the species may be born. Overhunting is punished by disease or death in the hunter's community. It is the Makuna's job to maintain harmony with the forest animals and their Spirit Owners, which are members of the society of which humans are only a part. Maintaining this harmony involves the avoidance of overhunting. Here again, the maintenance of harmony among humans and other forest denizens is the primary goal: the avoidance of extinctions would simply be a by-product.

As the impact of the ecological crisis on the rural poor of Third World countries increases and becomes increasingly evident, the ideal of human beings as stewards of God's creation, working for the common good of the creation as a whole, is being put forward as a fundamental principle to govern relations between humans and their environment (Hall 1990; Nasr 1996; Northcott 1996).

Of course, answers reeking of theism or the spiritual value of harmony with nature will not satisfy everyone. Secular answers about our responsibilities come in two basic kinds. First, a person who, like Paine, has devoted a lifetime to understanding the ecology of a setting of striking natural beauty, does not wish this beauty to disappear from the face of the Earth. Many ecologists, and other lovers of nature, would consider an extinction unacceptable if it threatens the integrity or beauty of some natural system. To what extent these systems can or should be restored to their pristine condition is, however, a contentious issue. Not everyone who wishes to keep developers out of Yellowstone wants to see it filled with grizzly bears. Not everyone who wishes to keep the central California coast "unspoiled" welcomes the return of abalone-eating sea otters. Even the biologists of Barro Colorado Island might have misgivings about repopulating that island with bushmasters. Suppose that we could recreate the Pleis-

tocene megafauna à la Jurassic Park: how many farmers would wel-
come the opportunity to share their crops with marauding mammoths?
Agreeing on what beauties of nature to defend, or restore, is not easy.

Second, others would manage the world ecosystem to further hu-
man well-being. This goal is very vague. People disagree on how
much human well-being depends on access to natural beauty, how
much natural ecosystems can tell us about the management of artifi-
cial ones, and what sorts of economic sacrifice are appropriate to
maintain clean rivers or clean air. Even when there is agreement in
principle, disputes occur. Although no one wants global warming,
some do not or will not see the connection between fuel use or forest
destruction and global warming; others ask whether local attempts to
reduce carbon dioxide emissions will merely subsidize cheaters else-
where in the world, or wonder how much one should sacrifice to
reduce the suffering that global warming may cause others. (How
much do citizens of Denver care about the flooding of London or
Bangladesh?) No one wants to see the world fisheries ruined by over-
exploitation or destructive fishing techniques. Yet ruinous fishing
techniques are used, on the assumption that competitors will use
them anyway. Dysfunctional forms of competition, often excused by
expressions of despair over the prospect of fair regulation, are a major
obstacle to intelligent conservation planning.

Where there is a sufficient sense of community, intelligent conser-
vation is possible. The exceptional sense of community among the
inhabitants of Monteverde, Costa Rica, enabled them to preserve over
10,000 ha of nearby rainforest and its fauna—one of tropical Amer-
ica's most striking conservation successes (Nadkarni and Wheel-
wright 2000; Leigh 2001). This success stemmed from several factors:
(1) the infectious example of sustainable, profitable land use by immi-
grant Quakers; (2) the Quakers' effort to transform Monteverde into a
community meant to seek the good of each member, farmer, or town
dweller, where community decisions were reached by consensus after
all views had been heard and considered; (3) a communal reserve of
ridgetop forest set aside by the Quakers to protect the area's soil and
water supply, which became a tourist attraction; (4) a Quaker cheese
factory that paid fair prices for all comers' milk, providing the basis
for a widely shared prosperity—which allowed community members
to profit from the increasing numbers of visitors to the reserve by
building hotels and eateries for them, a circumstance that increased
support for more reserves.

Unfortunately, few societies approach the Quaker ideal of social
harmony. Indeed, in most tropical countries, as in the United States,
social conflict, latent or blatant, is the biggest single obstacle to con-

servation (Bruenig 1996). Western society now seems particularly prone to conflict. Capitalists are promoting an aggressive, often heedless, economic competition; Marxists are promoting conflict among classes; and other groups are responding with violence. These conflicts are spreading all over the world. A tragedy of the commons (Hardin 1968) is most likely when social harmony does not reign among its users (Netting 1976, 1993, pp. 172–178). A community of interest in protecting a commons is weakest, and least effective, when there is high turnover among its users. Yet the free market capitalism currently in fashion increases turnover within neighborhoods by seeking a mobile labor force that is willing to move where the money is. A worldwide tragedy of the commons becomes inevitable when the poor feel that they are paying the expenses of conservation with no prospect of sharing in its benefits, and when the rich and their governments are indifferent to their plight. Communities cannot decide how to maintain harmony with nature when they are riven by such conflicts: it is like trying to safeguard the good of one's country when fighting a desperate civil war.

## How Can We Decide Which Extinctions Will Compromise Our Chosen Goals?

Currently, the most effective, and appropriate, argument for preventing extinctions is Aldo Leopold's: we should not discard any part of an ecosystem before we know its function. Academics might question the implied analogy between an ecosystem and a machine designed for a purpose. Nonetheless, we are just beginning to learn the many ways we depend on natural ecosystems, the variety of their aspects on which we depend, and the range of services natural ecosystems provide (Daily et al. 1997). Natural ecosystems provide models for forest managers. For example, disturbances that occur normally in natural forests suggest appropriate cutting regimes for managed ones (Bruenig 1996; Kohm and Franklin 1997). Natural ecosystems also provide us with medicines, and our crops with genes that enhance pest resistance and organisms that control pest populations. They provide small farmers living near forests with protein, firewood, and construction materials. They moderate regional climates and regulate global temperature. All too often, we learn the importance of some ecosystem service only when human activities begin to compromise it.

Resources for conservation are limited, however, so we will inevitably be confronted with choices of what to conserve. Ideally, such

decisions presuppose an understanding of how the extinction of a species affects its ecosystem and how biodiversity influences ecosystem function. How can we answer such questions?

### What Can We Learn from Treating Ecosystems Holistically?

The most important lesson of holistic ecology is that ecosystems are organized—adapted—for functions that enhance their productivity and the diversity of their species (Leigh and Vermeij 2002). This principle will not help us identify which species are expendable, but it strengthens Leopold's argument for conservation and helps us see through some of the methods proposed for demonstrating the importance of biodiversity.

How can we recognize whether ecosystems are adapted? Knowing nothing of how adaptation evolves, Aristotle argued that organisms are adapted—organized—to grow and reproduce because visibly mutant organisms are usually less functional than their normal counterparts (*Physics* 199b 1–4: see Barnes 1984, p. 340). Fisher (1930, p. 38) expressed a similar view:

> An organism is regarded as adapted to a particular situation . . . only in so far as we can imagine an assemblage of slightly different situations . . . to which the animal would on the whole be less well adapted; and equally in so far as we can imagine an assemblage of slightly different organic forms, which would be less well adapted to that environment.

Aristotle's remark and Fisher's definition provide a criterion that allows us to decide whether ecosystems are adapted.

We imply the "adaptedness" of ecosystems when we say that disturbance usually injures them. Is disturbance injurious? Here, I can only sketch relevant kinds of evidence. One mark of ecosystem adaptedness is the naturally occurring ecosystem properties that cultivators desire but must strive to obtain. For example, a good soil embodies a host of seeming contradictions. It is soft enough for roots to penetrate yet cohesive enough to stay put. It keeps the nutrients and an appropriate amount of the water entering it from leaching or draining away yet allows plants to suck them out when needed. Even when holding abundant water, it allows air and carbon dioxide to circulate through it (Bruenig 1996; Marshall et al. 1996). A natural forest protects its soil and usually improves it. Deforestation usually increases erosion rate and decreases the soil's thickness, fertility, and ability to hold water (Stallard et al. 1999). Careful cultivation of deforested land can pre-

serve the soil and its quality (Bruijnzeel 1990). Such care, however, presupposes an understanding of the land that usually reflects generations of experience with the land, and a long-ripened traditional knowledge of it. For humans to preserve the integrity and quality of soil as well as natural forest does is an achievement that does not happen by chance.

Another mark of ecosystem adaptedness is the radical degradation that often results from human disturbance (Leigh and Vermeij 2002). In many tropical areas, for example, careless or incompetent land use has led to the replacement of diverse forest by depauperate monodominant grasslands (Jacobs 1988, p. 252; D'Antonio and Vitousek 1992). Similarly, killing off the megafauna in eastern Siberia led to the replacement of grassland by much less productive moss tundra, whose limited transpiration causes waterlogging of the soil (Zimov et al. 1995).

These marks suggest not that ecosystems are optimally designed but that they are sufficiently adapted that major disturbance usually compromises their productivity or diversity. Ecosystems are not units of selection. Although Leigh (1999, chapter 9) and Leigh and Vermeij (2002) consider various mechanisms that may adapt ecosystems, how ecosystems adapt is one of the great mysteries of biology. Here, I demonstrate the adaptedness of ecosystems without explaining how this adaptedness evolves.

Trying to assess the effects of extinction or the relevance of biodiversity by treating ecosystems holistically, however, has been unfruitful. Comparative studies of productivity, biomass, and nutrient cycling provide no general criteria for identifying those species whose extinction matters most. In terrestrial ecosystems, different species affect soil quality and nutrient cycling very differently, thanks to the differing chemistry of their fallen leaves and twigs, the presence or absence of nitrogen-fixing nodules on their roots, and the like (Hobbie 1992; Bruenig 1996; Silver et al. 1996). It is clear that some species are more expendable than others; the problem is finding general criteria to identify which species matter most. Holistic studies have been particularly unsuccessful in assessing how diversity affects ecosystem function. Wright (1996) concluded that in tropical forest the ecological roles and functions of different plant species overlap so completely that the extinctions of a few plant species would have no impact on productivity, biomass, or nutrient cycling. Vitousek and Hooper (1994) found that, beyond a relatively low threshold value, further increases of plant diversity had no effect on a soil's content of nitrogen or organic matter. All this must be true, yet such results are a grossly inadequate basis for making decisions about conservation.

   Many holistic studies fail because they are too "schematic"; they neglect the many and various demands on natural ecosystems. Those who have studied natural ecosystems in fluctuating environments have learned something about the relevance of biodiversity. Diverse grasslands recover more quickly from drought or unusual grazing pressure—and maintain steadier production in the face of environmental variation or normal grazing levels—than do species-poor grasslands (McNaughton 1985, 1994; Tilman 1996).


## To Predict the Effects of Extinction, We Must Know How Ecosystems Work

To assess the effect of an extinction, we must know how the relevant ecosystem is organized. This means knowing how its populations are regulated or controlled, how its species can coexist, how its species depend on each other, and how the ecosystem responds to invading exotics or severe fluctuations in its physical environment. These criteria sound obvious and elementary. Yet some have tried to assess the importance of biodiversity by studying artificial, simplified ecosystems (experimental or theoretical) whose development was not shaped by natural selection. However, in so far as natural communities are adapted systems whose species are mutually adjusted, these studies are irrelevant. Moreover, they sometimes overlook crucial factors. One such study of how biodiversity affects ecosystem properties (Tilman et al. 1997) considers only communities of primary producers. This study cannot tell us how, for example, tree diversity defends tropical forest against its enemies (Ridley 1930, p. xvi: Regal 1977).
   On the other hand, mechanistic ecological studies, designed in light of how natural selection works, can provide a much clearer idea of how extinctions affect ecosystems, and can sometimes even suggest which extinctions matter most. Such studies should also consider which features allow ecosystems to resist invaders, because these same features render communities less susceptible to the extinctions such invaders can cause, and because invasions can tell us how an ecological community is organized. Paine (1974, 1977) learned much about the ecological organization of the rocky intertidal at Tatoosh by causing "extinctions" of selected species in experimental plots. Paine was also fascinated by the often radically disruptive consequences of species introductions (Zaret and Paine 1973; Paine and Zaret 1975). Indeed, invasions by exotics are also informative probes of the ecological organization of natural ecosystems. Next, consider how a knowledge of how populations are regulated, how species coexist, how they

depend on each other, and what factors influence an ecosystem's ability to resist invaders sharpen our vision of what extinctions are most damaging and why biodiversity matters. I focus primarily on tropical forest, but the lessons of Tatoosh, like the lessons from the extinctions on newly created islets, are never far from my mind.

### How Understanding Population Regulation Can Identify Indispensable Keystone Species

Paine (1984) knew as well as anyone that many features of ecological systems are governed by competition either for food or for a means (e.g., space) to procure it. In Neotropical forests, most vertebrate herbivores are limited by seasonal shortages of fruit and new leaves (Leigh 1975, 1999; Leigh and Windsor 1982; Smythe 1986). Many of these herbivore species depend on a few "keystone" sources of fruit to survive these seasons of shortage. The extinction of one or more of these keystone species would be especially disruptive of their ecosystems (Terborgh 1986).

The competition of predator and prey (or herbivore and food plant) for resources in the prey's body, a process much studied by Paine (1966, 1969b, 1971, 1974, 1976, 1980, 1992; Paine and Vadas 1969) plays a crucial role in the regulation of many populations. A keystone predator is a species whose extinction would cause major changes in the structure and ecological organization of its community (Paine 1969a). Paine (1966, 1974) showed experimentally that on the weather coasts of the northeastern Pacific, the sea star *Pisaster* keeps beds of the mussel *Mytilus californianus* from spreading into the lower intertidal. By limiting the spread of mussels, *Pisaster* makes space for a diversity of algae and sessile animals in the mid-intertidal. Because its activities maintain species diversity in the rocky intertidal, *Pisaster* qualifies as a keystone predator.

Over the long term, keystone predators can affect the evolution of ecosystem properties. In the northeastern Pacific, sea otters limit subtidal populations of sea urchins (*Strongylocentrotus* spp). Where sea otters are absent, sea urchins devastate kelp beds. Where sea otters limit urchin populations, luxuriant kelp beds develop (Estes and Palmisano 1974: Estes and Duggins 1995). The resulting increase in nearshore productivity supports animals as different as harbor seals and bald eagles (Palmisano and Estes 1977). By making this increased productivity possible, sea otters qualify as keystone predators. Before human beings nearly finished them off, northeastern Pacific sea otters had long consumed enough sea urchins to reduce the kelps' need for

antiherbivore defense. In New Zealand, however, kelp-eating herbivores are food limited, not predator limited. Thus, New Zealand kelps contain much higher levels of antiherbivore toxins, and New Zealand herbivores are much more tolerant of these toxins than are their counterparts of the northeastern Pacific (Steinberg et al. 1995). There is a fairly strict tradeoff between a plant's growth rate and the effectiveness of its antiherbivore defense (Coley 1988; Kitajima 1994). Thus, sea otters have presumably favored the evolution of faster growing, more productive kelps.

Tropical forests need the help of birds and other insectivores to limit populations of insect herbivores (Leigh 1975, 1999). Leigh and Windsor (1982) originally inferred this need by comparing insect consumption by birds, as inferred from the numbers, weights, and diets of Barro Colorado's birds, with leaf consumption by insects. It takes about 250 kg dry weight of foliage to feed the 25+ kg dry weight of insects eaten by birds in tree canopies per ha per year (Leigh 1999). This amount represents up to half the foliage eaten by insects other than leafcutter ants (which birds do not eat). Other researchers are now becoming interested in the extent to which predators limit populations of insect herbivores (Coley and Barone 1996; Bernays 1998; Letourneau and Dyer 1998). How important is this "third trophic level" to the maintenance of the luxuriance of tropical forest? Are specific keystone predators involved in protecting the forest?

*Forest Fragmentation as a Tool for Understanding How Forest Populations Are Regulated*

Forest fragmentation, especially the creation of forested islands by new reservoirs, provides a new tool for understanding how different terrestrial populations are regulated. The smaller the island, the more of its predator populations go extinct. Populations that explode when these islands are cut off from the mainland must lack the factor that limits them on the mainland, often a predator that died out when the island was created. By causing extinctions of different sets of predators on different islands, forest fragmentation provides terrestrial ecologists with their nearest counterparts to the exclusion experiments of the intertidal ecologist.

Forest fragmentation can suggest the existence of previously unsuspected keystone species. On newly created 1-ha islands in Lake Guri, Venezuela, leafcutter ant colonies are extraordinarily abundant. These islands average over 2 mature colonies per ha, 20 times their density on the mainland (Terborgh et al. 1997). On these islands, leaf-

cutter ants severely limit the density and diversity of seedling recruitment (Rao et al. 2001; Terborgh et al. 2001). Something other than food supply, presumably some predator, must limit the abundance of leafcutter ants on the mainland. This predator would, accordingly, be a keystone species protecting forest diversity (Rao 2000).

What might this keystone species be? Terborgh et al. (1997) note that on the mainland, army ants, Ecitonini, limit populations of many litter arthropods and forest floor ant species. A 1-ha or even a 10-ha island, however, is too small to maintain even a single colony of army ants. Even though most species of army ant cannot harm an established leafcutter colony (Swartz 1998), they do destroy young colonies (C. Ziegler, pers. comm.). Can they limit the recruitment of new colonies? This question is testable.

Herbivore populations can explode on small islands for other reasons. In Venezuela, capybaras are common on certain islands of Lago Guri (Terborgh et al. 1997), perhaps because the nearness of water makes the habitat favorable. Some 1-ha islands in Lago Guri have one or more resident howler monkeys, *Alouatta seniculus* (Terborgh et al. 1997). Monkey populations normally regulate their numbers socially, through the dispersal of young, to levels that allow a troop to compete effectively with others for food when it is scarce. These islets offer no opportunity for dispersal, but they do protect the monkeys from competing troops. These monkeys only need to survive food shortages: they do not have to be strong enough to repel competing troops. Thus, they maintain unusually high population densities on these islets.

In sum, herbivore pressure must be several times higher on the Guri islands than on the surrounding mainland (Terborgh et al. 2001). Does this heavy herbivore pressure favor better defended, slower growing plants? Studies are on foot to find out. Work in another set of forest fragments suggests that forest fragmentation does favor slower growing, more herbivore-resistant plants. Small forest fragments surrounding Malaysia's Pasoh Reserve are being taken over by plants with low photosynthetic capacity and explosively dispersed seeds that do not travel far from their parents (Thomas 2002). Low photosynthetic capacity presumably reflects low nitrogen content in the leaves (Zotz and Winter 1994), which makes the leaves less attractive to herbivores (Coley 1983). Moreover, poorly dispersed plants, which are likely to grow close to conspecifics and are thus easily found by their pests (Ridley 1930, p. xvi), must therefore be better defended against herbivores (see below). By eliminating other limits on herbivore populations, fragmentation may favor a less productive vegetation.

*We Must Know How Species Coexist to Protect Biodiversity*
*and Predict the Effects of Extinction*

Competition favors biodiversity insofar as the "jack of all trades is master of none" (MacArthur 1961)–that is to say, insofar as there are trade-offs between the ability to exploit different foods or habitats (Fisher 1930, p. 126). Among plants, a famous trade-off allows light-demanding pioneers of clearings and shade-tolerant trees of mature forest to coexist (Pacala and Rees 1998).

To learn which management strategies best protect biodiversity, one must know what trade-offs maintain biodiversity. For example, if pioneers and mature forest species coexist because there is a trade-off between the ability to colonize new clearings and the ability to oust competitors (Skellam 1951), then devoting even small patches of forest to agriculture can cause the extinction of those mature forest species whose balance between colonization (recruitment) and mortality is so delicate that it will be overset by wasting some of the seeds on permanently cleared fields (Tilman et al. 1994). On the other hand, if coexistence between pioneers and persistents is driven by the trade-off between growing fast in high light and surviving in shade (Kitajima 1994; Pacala et al. 1996), limited agricultural disturbance is much less threatening.

Pests and pathogens appear to play an integral role in allowing species of tropical tree to coexist (Janzen 1970). First, I review evidence for this proposition, then I show how this tree diversity affects ecosystem properties. Monocultures everywhere are liable to devastating pest outbreaks (Dethier 1976), particularly in the tropics (Ridley 1930). In natural settings, too, pest pressure is much more intense in the tropics. Insect activity is spread much more evenly through the year in the tropics than further north (Wolda 1983). The dry season reduces tropical pest populations less sharply and predictably than winter sets back their high-latitude counterparts. Accordingly, young tropical leaves are eaten much more rapidly, despite being much more poisonous, than are the young dicot leaves of temperate-zone forests (Coley and Barone 1996; Coley and Kursar 1996). Moreover, in most plant species, the greatest damage is inflicted by specialist pests (Barone 1998). In the tropical forest of Barro Colorado Island, Panama, saplings of most tree species survive better and recruit more abundantly per conspecific adult, the greater the proportion of the trees within 10 m, young and adult, belonging to other species (Wills et al. 1997). A plant species appears to suffer most from pest pressure where it is most abundant (Wills and Condit 1999). Therefore, "pest pres-

sure" is presumed to promote diversity among tropical trees (Ridley 1930; Janzen 1970; Connell 1971).

In everwet forests, no dry season lowers pest pressure (Wolda 1983), and the proportion of tree species with animal-dispersed seeds is highest. Ceaseless pest pressure appears to create a high premium on dispersing seeds away from the mother tree and its associated pests. Tree diversity is highest in these everwet forests (Gentry 1982, Leigh 1999), as expected if pest pressure maintains it.

How does the role of pests in maintaining tropical tree diversity relate to the properties of tropical forest ecosystems? Cushman (1995), echoing a widespread doubt, questioned whether studies in population biology enhance understanding of ecosystem function. I explore the intellectual bases for concluding that pest pressure maintains tree diversity and that tree diversity is an essential condition for the productivity and luxuriance of most tropical forests.

A crucial assumption of Ridley's (1930) proposal—that pest pressure enhances plant diversity—is that when a species is rare enough, the abundance of a consumer dependent on it declines. Together with its counterpart assumption—that when the consumer species is abundant, abundance of the victim species declines—this assumption is fundamental to the theory of predator-prey cycles (Volterra 1926, 1931; Rosenzweig and MacArthur 1963; Bulmer 1976). Experiments have abundantly verified that the numbers of a consumer dependent on a single victim species decline when the victims are rare enough (see, for example, Gause 1935; Maly 1969, 1978).

Another assumption implicit in the pest pressure hypothesis is that, to increase its density, a herbivore-limited species must strengthen its antiherbivore defenses. This proposition seems too obvious for serious attention. Nevertheless, in a simple Volterra model of two victim species limited by the same consumer, the victim species that can support the most consumers without declining prevails. Improved defenses are often favored, but only if the abundance of consumers increases as a result of the increased victim abundance (Appendix 12.1). This theory is good enough to predict that in rivers and streams with two or four trophic levels, primary producers are much rarer than those with one or three trophic levels (Wootton and Power 1993). The theory may also apply to grasslands protected by their grazers from encroaching trees. It makes no sense, however, for forests, which are adapted to reduce the herbivore load.

A plant population does benefit from improved antiherbivore defenses if its numbers are regulated in part by plant density. Improved defenses presumably reduce the herbivore's ability to find its host, the proportion of host plants it can use, or its capacity to digest what it

eats. Any of these changes increases the density of host plants required to maintain a specialized herbivore population in equilibrium. Competition with other plants limits the increase a plant population derives from improved antiherbivore defenses. Instead, improved defenses reduce the per capita mortality inflicted by the herbivores (see appendix 12.1). If the defenses are good enough that the herbivores cannot maintain themselves on the density of host plants supported by the environment, the new defenses will put the herbivores out of business.

The advantage of rarity as an escape from specialist herbivores and the role of defense in maintaining a host plant's density in the face of its pests jointly imply that the rarer a plant species, the lower the proportion of its productivity lost to pests specializing on that species, or the lower the proportion of its resources this plant must devote to defense against specialist pests to ensure its survival. Thus, the more diverse a forest, and the rarer each of its component species, the fewer resources need be devoted by this forest's plants to defense against specialized pests. Since, even in diverse tropical forest, most damage is inflicted by specialist pests (Barone 1998), rarity must allow most plant species to reduce their total investment in antiherbivore defenses.

The pest pressure hypothesis has ecosystem implications, because reduced investment in antiherbivore defenses allows faster growth (Coley et al. 1985). There is abundant evidence for Coley's thesis. Comparisons among plant species in the wild show that saplings of fast-growing species are eaten more and invest less in antiherbivore defenses such as tannins, other phenols, and lignins than saplings of slower growing species (Coley 1988). In the laboratory, *Cecropia peltata* seedlings with tannin-rich leaves are less vulnerable to armyworms (*Spodoptera* sp.) but where herbivores are absent, seedlings with tannin-poor leaves produce more foliage (Coley 1986). In a field experiment with *Psychotria horizontalis* on Barro Colorado, cuttings with tannin-rich leaves were eaten less than low-tannin counterparts when exposed to the full range of the island's herbivores. Tannin-poor cuttings, however, had faster intrinsic growth, so a cutting's total weight gain was not correlated with the tannin content of its leaves (Sagers and Coley 1995). Among clones of these cuttings in a nearby, protected enclosure, tannin-poor plants grew faster than their tannin-rich counterparts (Sagers and Coley 1995).

Intense antiherbivore defenses not only slow plant growth, they impose other costs. For example, plant species that cannot escape their enemies by being rare are more likely to have defenses that damage the soil. Better defended plants have longer lived leaves that

are defended by long-lasting compounds such as tannins and other phenols, which break down slowly (Coley 1988). These toxins hinder decomposition and nutrient recycling (Waring and Schlesinger 1985). High concentrations of these toxins in leaves and wood can injure the soil (Whitmore and Burnham 1969; Reich et al. 1995); although the extent of this damage has yet to be quantified. Nonetheless, it is becoming increasingly apparent that the tree diversity created by pest pressure makes a forest more luxuriant and productive (Corner 1964; Leigh 1994, 1999).

### How Species Depend on Each Other: Keystone Mutualists

Ecosystems are webs of interdependence. We must know these interdependences to assess the consequences of an extinction, since a species whose extinction entails the extinctions of many dependent species is not expendable. Moreover, to preserve a species, we must know those species and habitats on which it depends. Discovering the interdependences that maintain the integrity of tropical forests and other ecological communities presupposes an interest in natural history that is second nature to Paine, but which most research ecologists dismiss as not science. These interdependences are surprising, complex, and varied (Bond 1994b). Near Gothic, Colorado, for example, red-naped sapsuckers excavate cavities in fungus-infected aspens that two species of swallow require as nest sites. They also drill holes in willows, the sap from which supplies abundant nourishment to several bird species and a few mammals (Daily et al. 1993). Moreover, interdependences no one ever thought about can be crucial. Vast oyster reefs in Chesapeake Bay previously filtered the equivalent of one third of the bay's water every day. Although from 1750 onward, farming was increasing the amount of nitrogen and phosphorus draining into the bay, these oyster reefs kept the bay's water clear. Mechanical harvest dredges destroyed these oyster reefs between 1875 and 1910. The resulting "ecological extinction" of oysters was followed by sharp increases in phytoplankton, sedimentation of organic matter, incidence of anoxia on the bay bottom, and crashes in the benthic fauna (Jackson et al. 2001).

Tropical forests depend on animal pollinators to maintain tree diversity, which in turn preserves their productivity and luxuriance. Plant species that use animals to convey their pollen to conspecifics can survive when made rare by pests; they can accordingly divert resources from anti-herbivore defense to faster growth. Conifers and other wind-pollinated species, however, are reliably pollinated only

when conspecifics are nearby. Insofar as wind-pollinated species must be common where they occur they must invest heavily in antiherbivore defense. The natural pesticides in the fallen leaves of wind-pollinated conifers injure the soil (Waring and Schlesinger 1985). Similarly, seed dispersers help maintain tree diversity in mature tropical forests by allowing large-seeded tree species to disperse far enough from their parents to escape their pests (Leigh 1994; Tiffney and Mazer 1995).

Some pollinators and seed dispersers are replaceable. The extinction of others, such as elephants (Alexandre 1978), leads to the extinction of some of the plants they serve. Indeed, the extinction of a few animal species favored by hunters could greatly reduce the diversity of tropical trees by eliminating crucial seed dispersers (Emmons 1989). Moreover, the multiplicity of relationships involving pollinators and seed dispersers ensures that no tropical forest, and certainly no single tree species, is an island sufficient unto itself. Most pollinators and seed dispersers rely on a diversity of plants to maintain themselves. Some depend on access to several different habitats to avoid seasonal shortages in each one: they migrate seasonally from one to another, according to where the resources are (Loiselle and Blake 1991).

The mutualism through which each species of fig tree has its own species of pollinating wasp transforms fig trees into keystones for their forests (Corner 1940, Herre 1996). These minute pollinating wasps, each of which matures within the confines of a single fig seed, are truly remarkable. Several fig species maintain extraordinarily high genetic diversity because their trees can attract pollinators from more than 10 km away (Nason et al. 1996, 1998). To maintain these pollinators, however, some trees of each fig species must be coming into fruit all year round. The year-round availability of their fruit makes neotropical figs a keystone resource for all sorts and conditions of animals (Terborgh 1986), including a guild with 10 species of fruit-eating bats (Kalko et al. 1996). Their pollinators allow some fig species to survive when very rare indeed. Perhaps this is why fig trees grow so fast, produce such productive and edible foliage (Zotz et al. 1995), and rot so fast when dead: "By leaf, fruit, and easily rotted wood fig plants supply an abundance of surplus produce" (Corner 1967, p. 24). Indeed, fig trees support many species other than frugivores (Zeh and Zeh 1992a, b; 1994).

Indeed, the evolution of pollinators capable of seeking out flowers of a particular species triggered the explosive diversification of angiosperms by allowing the evolution of a great variety of relatively rare, presumably fast-growing, angiosperm weeds (Crepet 1984). These plants occupied scattered openings and disturbed sites (Wing et al.

1993), crowding out slower growing gymnosperm seedlings. Similarly, "domesticating" mammals and birds to serve as seed dispersers enabled large-seeded angiosperm trees to invade mature coniferous forests, replacing a depauperate, slow-growing vegetation by a fast-growing, diverse one (Tiffney 1984).

### Forest Fragmentation, Mutualism, and the Diversity and Productivity of Tropical Forest

Forest fragmentation can reveal the variety of mutualisms that maintains tree diversity and forest productivity. Creating Gatun Lake in central Panama by damming the Chagres River severed many islands from the surrounding mainland by 1914. Islands of less than 1 ha have lost agoutis and other mammals (Adler and Seamon 1991). On those <1 ha islands that have been forested ever since their severance from the mainland, tree diversity has dropped precipitously since 1914 (Leigh et al. 1993). Four tree species are spreading on these islands, all with large seeds. Seeds of three of these species, and late-falling seeds of the fourth, are not attacked by insects. On Barro Colorado, seeds of some other large-seeded species, now absent from or not regenerating on these islands, escape destruction by insects only if buried by agoutis (Smythe 1989; Forget and Milleron 1991). Fragmentation into such small islands is clearly catastrophic for tree diversity. Does this happen because agoutis are keystone animals for maintaining Neotropical tree diversity? This thesis is in urgent need of further testing.

Fragmenting tropical forests may reverse the direction of angiosperm evolution. Many pollinators and seed dispersers no longer visit small islands (Cosson et al. 1999), thereby reducing these islands' plant diversity. In the area surrounding Malaysia's Pasoh Forest Reserve, fragmentation has favored the tree species that do not need animals to disperse their seeds or whose leaves have low photosynthetic capacity (Thomas 2002). Disrupting mutualisms with pollinators and seed dispersers degrades the diversity and productivity of tropical forest. Natural tropical forest ecosystems are adapted to maintain diversity and productivity. To preserve these qualities, pollinators, seed dispersers, and other mutualists must be protected.

### What Invasions by Exotics Reveal about Natural Ecosystems

Natural ecosystems that are exposed to repeated invasions become resistant to invasion (Elton 1958), presumably because they no longer

offer unused or poorly used sources of energy for invaders to exploit (Leigh 1971). Ecosystems that were invaded rarely in the past, such as oceanic islands, are notoriously susceptible to introduced species (MacDonald et al. 1991). In part, this is because their species were not exposed to effective competition. Exotics are spreading in Mauritius and Reunion, even though native forests, with their strong wood and even canopy, readily resist cyclone winds that devastate the exotics. Apparently, the reproductive capacity of the exotics, whose seeds are often dispersed by introduced birds, far outweighs the superior survival of the natives. An abundance of unexploited resources, or a totally open niche, can make an isolated ecosystem catastrophically vulnerable to invasion. Guam lacked nocturnal carnivores until the brown tree snake was introduced in 1950. This snake has become abundant, causing many extinctions and utterly transforming Guam's ecosystem in the process (Fritts and Rodda 1998). Diversity in itself provides no immunity against invasion. The astonishing diversity of Lake Victoria's species flock of haplochromine fishes did not block the initial onrush of predatory Nile perch, but it appears to have provided the fish community sufficient resilience to avoid utter extinction (Goldschmidt 1996). The diversity of South Africa's fynbos has not protected it from invasion by more productive nitrogen-fixing acacias from Australia (Macdonald 1984; Witkowski 1991).

Exotic invaders are relatively rare in mature tropical forests on continents (Rejmánek 1996). Of the 42 species of exotics listed by Rejmánek (1996) as successfully invading mature tropical forest, 21 are invading forests on oceanic islands, 14 are invading forests of East Africa, which are both somewhat isolated and rather degraded, and 2 are invading forest fragments in Singapore that are less diverse than the extensive forests elsewhere in Malaysia.

Even in the continental tropics, however, land abuse offers footholds for invaders that indirectly threaten natural forest. During the Vietnam War, seeds of the aggressive southeast Asian grass *Saccharum spontaneum* established in Panama. This grass has occupied untended, open places, where annual fires late in the dry season have transformed it into a low-diversity "dysclimax" inhospitable to most wildlife. This grass now occupies fields that formerly would have been colonized by pioneer trees and undergone forest succession (Dalling and Denslow 1998). It takes great labor, and some luck, to replace these grasslands by forest. Open areas elsewhere in the world have also been occupied by aggressive grasses whose annual fires exclude trees (D'Antonio and Vitousek 1992). These grasses transform ecosystem restoration from something that happens naturally to an achievement demanding abundant human labor.

Can extinctions open ecological communities to destructive take-overs by aggressive species? In Indonesia, the grass *Imperata cylindrica* has taken over thousands of hectares of misused land, forming sterile monospecific grassland (Jacobs 1988). In Nepal's Royal Bardia National Park, however, deer, rhinoceros, and elephant maintain diverse, nutritious grazing lawns in the midst of a grassland dominated by *Imperata cylindica* but including other grasses (Karki et al. 2000). These grazing lawns include *I. cylindrica* and *Saccharum spontaneum*, the aggressive pest grasses of Indonesia and central Panama. In Indonesia, the extinction of large herbivores has helped transform *I. cylindrica* from a member of a diverse ecosystem into a pest.

## Concluding Remarks

This essay has two aims. One is to remind biologists that social conflict, whether latent or blatant, is the biggest single obstacle to sound conservation. Suppose for a moment that we were Laplacean demons, able to assess the ecological consequences of each and every extinction. Would this circumstance really cause society to close ranks behind conservation? As the world seems organized to destroy any sense of community among human beings, a greater knowledge of biology is not likely to make it easier for society to agree on conservation policy.

The essay's second aim is to show that, like any other aspect of conservation planning, deciding which species, if any, are expendable depends on understanding the ecological organization of natural communities and how the balance of nature works (Ehrlich 1994). This is a tall order: can we learn enough to assess the effects of eliminating a species?

Just as field experiments were crucial tools for understanding the ecological organization of rocky intertidal communities and identifying some of its keystone species, so the pseudoexperimental approach of studying the effects of forest fragmentation is revealing the ecological organization of intact tropical forests and identifying keystone species essential to their integrity.

An interest in natural history is crucial to the assessment of expendability. Natural history is unpopular nowadays. The student who showed that some tree species need agoutis to bury their seeds out of reach of insect pests (Forget 1994) came to Barro Colorado only because political events in Panama frightened away higher ranking applicants. In ecology, the "stone the builders rejected" often "becomes the head of the corner" (Ps 118, v. 22). In other words, preconceived

notions of what is important often prove to be deceptive. Whether we can learn enough natural history to predict the effects of most extinctions is, however, an open question.


## Appendix to Chapter 12

Let $N_1$ and $N_2$ be the population densities of two species, 1 and 2, limited by the same species of consumer, whose density is $C$. In the simple theory of Volterra (1931),

$$\frac{dN_1}{dt} = r_1 N_1 - a_{1C} N_1 C = a_{1C} N_1 \left( \frac{r_1}{a_{1C}} - C \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 - a_{2C} N_2 C = a_{2C} N_2 \left( \frac{r_2}{a_{2C}} - C \right),$$

where $r_i$ is the logarithmic rate of increase of species $i$ in the absence of consumers, $a_{iC} N_i N_C$ is the rate at which the consumer species eats victims of species $i$, and $r_i / a_{iC}$ is the number of consumers victim species $i$ can sustainably support. The consumer's abundance increases to the level the more tolerant victim species can support (i.e., the larger of the two quantities $r_1 / a_{1C}$ and $r_2 / a_{2C}$). The victim with smaller $r_i / a_{iC}$ is forced to decline to extinction as the consumer's abundance increases beyond what it can sustainably support. A victim species benefits from improved antiherbivore defenses that reduce $a_{iC}$, only if this change increases the number of consumers it can support.

Now assume that the victims are limited in part by their own density. Suppose that only the first victim species is present, and that

$$\frac{d\ln N_1}{dt} = r_1 - b_1 N_1 - a_{1C} C$$

$$\frac{d\ln C}{dt} = \lambda a_{1C} N_1 - m,$$

where $b_1$ represents the impact of a unit increase of victim density on its per capita rate of increase, $\lambda$ represents the increase in consumer population per unit of victim consumed, and $m$ is the per capita death rate of consumers in the absence of victims. If there are no consumers, $N_1$ equilibrates at $r_1 / b_1$. On the other hand, if consumers are present, their population just maintains itself (i.e., $d\ln C / dt = 0$) when $N_1 =$

$m/\lambda a_{1C}$). The smaller $\lambda a_{1C}$ (i.e., the less effectively the consumer finds suitable victims or the less effectively it digests them), the larger the density $\overline{N}_1$ of victims required to sustain the consumer population in equilibrium, and therefore the smaller the per capita mortality $a_{1C} C = r_1 - b_1 \overline{N}_1$ inflicted on victims by consumers. If antiherbivore defenses are so effective that $m/\lambda a_{1C} > r_1/b_1$, competition limits victims at a level too low to support the consumer species.