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Maintenance of Diversity in Tropical Forests

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IN A WORLD LESS HELLBENT on exhausting its natural resource capital, a prescription for the maintenance of diversity in tropical forests would be simple: leave them alone. Nature itself is the best guardian of tropical forests, having created and nurtured them over millions of years. It is only when we insist on tampering with nature that diversity is threatened.

Whether we like it or not, human tampering with the works of nature is a fact of life that is likely to be with us for the foreseeable future. Nature will not be left alone to serve as her own best guardian; instead, conservationists and biologists will be called upon to play an increasingly active role in managing parks and reserves for the maintenance of diversity. Where a policy of benign neglect has been the practice, a conspicuous loss of species can be the result, as has recently been demonstrated for parks in East Africa (Soulé *et al.* 1979) and in the western United States (Newmark 1987). This suggests than an interventionist approach may be required, but, unfortunately, we do not yet understand enough about the causes of species loss to be able to counteract them.

One can say with certainty that there are chains of cause and effect that lead to species loss, though at this point we can follow the links only part way to their conclusion (Wilcox & Murphy 1985). The chain begins with the incursion of industrial man into natural landscapes, and continues with the fragmentation of the habitat into smaller and smaller subdivisions. Species loss accompanies or quickly follows habitat fragmentation. This has been demonstrated in the disappearance of migratory songbirds from woodlots in the deciduous forest region of the eastern United States (Whitcomb *et al.* 1981, Wilcove *et al.* 1986, Terborgh 1989), in the absence of many resident breeding birds from remnant fragments of the south temperate forest of Saõ Paulo State in Brazil (Willis 1979), in the extinction of birds on Barro Colorado Island, Panama (Willis 1974, Karr 1982b) and in the rapid loss of birds, primates, butterflies, army ants, and euglossine bees in isolated forest fragments in Amazonian Brazil (Lovejoy *et al.* 1986). The decline of species diversity in fragments is thus a well-established empirical fact.

Increasingly, conservationists are going to be called upon to mastermind rescue operations designed to preserve as much diversity as possible in severely fragmented ecosystems. A case in point is that of the Atlantic coastal forest of Brazil. Once forming a continuous belt over 2000 km long from Bahia in the north to Rio Grande do Sul in the south, the primary forest has been reduced to less than 10 percent of its original extent. What remains of it is contained in scattered fragments, nearly all on private land, and very few larger than 1000 ha (10 km^2) in area (Fonseca 1985).

The Atlantic coastal forest is home to numerous endemic plants and animals, among them the renowned golden lion tamarin and wooly spider monkey, and the little known soft-spined porcupine. The future persistence of these and many other species in the remaining small habitat fragments is severely in doubt. For a very rough estimate of what to expect, one can refer to a rule of thumb for islands at equilibrium: the species number is halved for each reduction in area of 90 percent (Wilson pers. comm.). Since most remaining fragments of the Atlantic coastal forest individually comprise less than 0.1 percent of the original forested area, their ability to retain diversity is roughly $0.5 \times 0.5 \times 0.5 = 0.125$ or $\leq$one-eighth that of the intact forest. Clearly, this is not an encouraging prognosis, and one can hope that the island biogeographic analogy leads to an overly pessimistic prediction (*e.g.*, Simberloff & Abele 1982). Nevertheless, it would be foolhardy to assume a more optimistic scenario in the absence of evidence to the contrary.

The case of the Atlantic coastal forest is among the most desperate in the world, but other situations are rapidly developing that are not far behind. The once extensive forests of Cuba and Hispaniola have

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been reduced by more than 90 percent; the forests of Madagascar are down to 8 percent of original cover and continue to shrink with each passing year; the rain forest of west Africa is almost gone and the remaining patches have little or no protection; much the same can be said for the forests of the Philippines. Short of captive propagation in zoos and arboreta, the prevention of dramatic waves of extinction in all these areas will require a highly sophisticated knowledge of how to manage diversity in habitat fragments, a knowledge we do not now possess. Our ignorance of this important subject should define the agenda of conservation biology for the next decade and beyond.

In the following pages, I shall review what we currently know about the consequences of fragmentation in the context of three questions. Can we identify the mechanisms of species loss in fragmented habitats? If so, what steps can be taken to counteract the effects of fragmentation? If landscapes could be managed to optimize the goals of retaining diversity and providing for human needs, how might they be organized? Ultimately our success or failure in maintaining tropical diversity will depend on how well we answer these questions and put the knowledge into practice.

A MATTER OF SCALE

Before we proceed to the question of why diversity declines in forest fragments, we should first consider the matter of scale. Scale is crucial to the issue of fragmentation, and often not adequately considered. A fragment of a given size may provide perfectly well for one species and be wholly insufficient for another. If we were to be lucky, we would find that the species with the largest spatial requirements would be among the least critical to maintaining the stability of ecosystem function, so that their loss from small and medium-sized fragments would have few consequences for the retention of other species. If we were to be unlucky, we would find that these same species would play indispensable roles in the long term maintenance of diversity. The limited evidence now available suggests that luck is not with us.

To illustrate the differential effects of scale, I shall use the ecosystem most familiar to me, that of western Amazonia. There, one finds macroscopic animals whose spatial requirements vary by over six orders of magnitude (Table 1). At the lower end of the scale are invertebrates capable of carrying out their entire life cycles within the space occupied by one tree. Invertebrates involved in complex dependencies and mutualisms with both larval and adult food plants, such as the *Heliconius-Passiflora-Gurania* system described by Gilbert (1980), might need as much as 10 ha to meet all their requirements on a long-term basis. Representing the opposite end of the scale are a number of highly mobile birds and mammals that function as top predators, seed predators, or seed dispersers. These species cannot maintain breeding populations in areas of less than many thousand hectares, yet their loss from smaller patches may have serious consequences for the persistence of many other species with far more modest spatial requirements.

TABLE 1. *Spatial scales relevant to Neotropical organisms.*

Organism unit	Area occupied by one reproductive unit (ha)
Ant colony	<0.01
Butterfly food web	2–10
Troop of howler monkeys	25
Bird-specialist on treefall openings	30–100
Community of spider monkeys	150
Troop of squirrel monkeys	500
Scarlet macaw	>1000
Jaguar	5000
Herd of white-lipped peccaries	>10,000
Fruit crow	>10,000

MECHANISMS OF SPECIES LOSS IN HABITAT FRAGMENTS

Fragmentation leads, over a range of time scales, to a variety of effects, both physical and biotic. Migration and dispersal patterns are disrupted, population sizes and gene pools are reduced, ecosystem inputs and outputs can be altered by the modification of adjacent areas, exotic species gain access to previously insulated habitat, the creation of edges modifies the physical microenvironment, and this in turn can lead to accelerated tree mortality and the penetration of nonforest species into forest habitat (Lovejoy *et al.* 1986). Consequences such as these are inevitable and will occur independently of more direct human impacts such as increased frequency of fire, intensified hunting pressure, exploitation of natural products, introduction of grazing stock, inadvertent poisoning of plants and animals via spillover of agricultural chemicals applied to adjacent lands, stream pollution and siltation, etc. Isolated habitat fragments are thus exposed to a

myriad of hazards, any and all of which can potentially contribute to species loss (Janzen 1986).

Over the long run, the activities of humans adjacent to, but outside of fragments, especially smaller ones, may do more to accelerate species loss than the operation of internal biological processes. Inclusion of the human element adds such complexity and unpredictability to the problem of understanding the consequences of fragmentation that the intrinsic biology of the matter almost becomes lost. For this reason I shall restrict my remarks to biological processes and, like an ostrich with its head in the sand, ignore any further consideration of the human element.

Direct effects of fragmentation

DETERMINISTIC LOSS.—Reduction in the area of a habitat has the immediate consequence of drastically reducing the effective population sizes of many of the included species (*cf.* Table 1). Some of these, including those with the lowest intrinsic population densities, and those requiring large home ranges or territories, may immediately find themselves without adequate living space. A single adult jaguar, for example, needs 30 to 50 km² simply to maintain itself (Schaller & Crawshaw 1980). A nature preserve the size of Barro Colorado Island, Panama (16 km²) thus cannot possibly maintain a population of jaguars. This may seem like a trivial example, but the number of species of birds and mammals in the Neotropical forest that require at least 10 km² for the completion of their life cycles is not trivial. No one can say exactly how many such species there are, but certainly they number in the dozens. It follows that Neotropical forest fragments of less than 10 km² will suffer the instantaneous loss of a whole array of area demanding species.

LOSS TO INBREEDING DEPRESSION.—A second type of deterministic loss results when populations are reduced below the threshold of genetic viability. The population may persist for several generations while it steadily loses ground due to lowered fecundity and viability (Frankel & Soulé 1981). This type of population loss can be documented in zoos, but in most cases would be undetectable in the wild (Ralls *et al.* 1979).

STOCHASTIC LOSS.—Works on conservation biology have placed great emphasis on the process of stochastic population loss–local extinction when normal fluctuations in numbers reduce a population below some minimum size needed for recovery (Leigh 1975, 1981). Again, the diagnosis of this type of population loss in nature is difficult, except perhaps in the aftermath of a hurricane or other natural disaster. Recently, Karr (1982a) has discovered that many of the bird species known to have disappeared from Barro Colorado Island, Panama show higher than average population fluctuations on the nearby mainland where they are still present. While this is a very interesting finding, it does not preclude a contributory role of deterministic factors (see below). More generally, in the context of isolated parks and reserves, it remains to be shown whether stochastic or deterministic processes predominate in the overall dynamics of species loss.

TRUNCATION OF THE HABITAT MATRIX.—Most natural landscapes are a mosaic of recognizably distinct habitats: uplands, flood plains, marshy wetlands, etc. Fragmentation almost invariably results in a biased sampling of the landscape mosaic, such that fragments will primarily represent only one or at most a few of the regionally available habitat elements. Such fragments may initially contain species that require missing habitats on a seasonal basis, or that are able to reproduce at levels above the replacement rate only in missing habitats (Erlich *et al.* 1980, Terborgh & Winter 1980). Again, one can point to the example of Barro Colorado Island, an erstwhile hilltop that lacks permanent streams and which now lacks a suite of bird species that is associated with permanent streams on the nearby mainland (Karr 1982b).

INTRUSION OF EDGES.—The creation of edges is an inevitable consequence of fragmentation. Where interior forest is suddenly exposed to open pasture or agricultural land, dry winds and light will penetrate the understory, and the canopy becomes vulnerable to windthrow. Alteration of the physical environment leads in turn to changes in the species composition and structure of the vegetation. If high rates of tree mortality result from fire, desiccation or windthrow along the windward edge of a forest fragment, a wave of modification can potentially propagate deeply into the stand (Lovejoy *et al.* 1986). Such major changes in the vegetation are likely to have repercussions in the animal community.

Changes in physical parameters and their biological consequences are not the only effects of introducing edges into continuous habitat. Nonforest species are given the opportunity to exploit the habitat. Janzen has described the invasion of dry

forest in Santa Rosa National Park, Costa Rica by plant species typical of weedy pastures (Janzen 1986). Some of these plants have penetrated hundreds of meters into the forest, presumably carried there as seeds by animal dispersal agents. The effects of high levels of alien seed import on the populations of plant species native to the forest have not yet been documented.

The expansion of edges with the fragmentation of the eastern deciduous forest of the U. S. has exposed breeding birds, especially migratory songbirds, to the double jeopardy of abnormal numbers of nest parasites (brown-headed cowbirds) and nest predators. Cowbirds feed in open country, but readily penetrate as far as 400 meters into closed forest in search of hosts (Brittingham & Temple 1983), while predation rates on artificial nests in small and medium-sized forest fragments are many times higher than in the interior of a large national park (Wilcove 1985). A similar result has been obtained on Barro Colorado Island in Panama (Loiselle & Hoppes 1983), suggesting that the tropics may not be immune to local buildups of what Michael Soulé has termed "mesopredators" (Soulé *et al.* 1988).

Indirect effects of fragmentation

We come now to a topic that lies at the cutting edge of contemporary ecological research, one that I predict will prove to be of central importance to conservation biology. By "indirect effects," I refer to the propagation of perturbations through one or more trophic levels in an ecosystem, so that effects are felt in organisms that may seem far removed, both ecologically and taxonomically, from the subjects of the perturbation.

The role of predators in regulating the relative and absolute abundances of their prey species is an elementary type of indirect effect. The first dramatic demonstration of this was by Paine (1966) in his landmark study of the removal of a predatory starfish, *Pisaster*, from a marine intertidal food web. Following experimental removal of the starfish, a diverse community of chitons, limpets, bivalves, and barnacles gradually collapsed, as the mussel, *Mytilus californianus*, a superior competitor for space, crowded out other species. While this result deservedly drew much acclaim, it was tacitly presumed by many ecologists that predators could play such a major structuring role only in space-limited ecosystems, such as the intertidal zone. A similarly pervasive role for predation in terrestrial ecosystems was argued in a famous paper that appeared even earlier, but convincing evidence was lacking and few researchers gave the matter more than passing thought (Hairston *et al.* 1960).

After a lapse of nearly a decade, several theoretical ecologists more or less simultaneously seized upon the idea of "apparent competition" in which an inverse density relationship between two prey species is mediated, not by the exploitation of a common pool of resources, but by the intervention of a selective predator (Levine 1976; Holt 1977, 1984; Vance 1978; Vandermeer 1980). These papers gave new impetus to the notion of indirect effects in terrestrial ecosystems.

In the vanguard of what is likely to become a flowering of empirical studies on indirect effects is the experimental megaproject of James Brown, Diane Davidson, and their collaborators on the structure of desert granivore communities. This team subdivided a 20 ha tract of Chihuahuan desert in southeast Arizona into 24 fenced 0.25 ha exclosures. Experimental treatments included the removal of large kangaroo rats (*Dipodomys*), removal of all rodents, poisoning of granivorous ants, and the elimination of all granivorous rodents and ants (Davidson *et al.* 1985). The responses to these treatments were slow to develop, taking two or more years to reach their fullest expression, but the magnitudes of the induced changes leave no doubt as to the pervasive action of indirect effects in this system.

Rodent removal led to increases of up to 1000-fold in the densities of some large-seeded plants, the seeds of which are normally harvested by kangaroo rats and pocket mice. The increased density of large-seeded plant species led in turn to intensified competition with small-seeded plants, which suffered consequent declines as their small seeds put them at a disadvantage in the race to accumulate biomass with the onset of rains. Thus, while seed-eating ants and rodents compete on a year to year basis, through their sharing of a common pool of food resources, over the longer term they engage in what Brown *et al.* (1986) refer to as an "indirect mutualism" (Fig. 1). This is because the presence of ants alone would favor vegetation composed of large-seeded species (because ants eat small seeds), while rodents acting alone would depress the abundance of their large-seeded food plants and promote the dominance of small-seeded species. By competing on the short term and depressing the number of seeds of all sizes remaining in the soil to germinate, ants and rodents together maintain a balance of large-seeded and small-seeded plants, and thus mutually assure each other's food supply. The chain of interaction thus runs reversibly from rodents through large-seeded plants to small-seeded plants

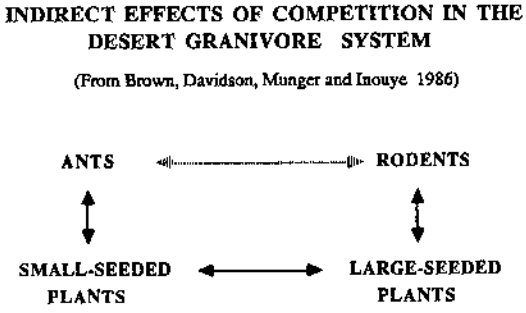

FIGURE 1. Schematic showing direct and indirect effects in the desert granivore system. (Modified from Brown *et al.* 1986.)

to seed harvesting ants. This is more than a mere predation effect; it is an interaction that structures a major segment of the plant and animal community of the Chihuahuan Desert ecosystem.

INDIRECT EFFECTS IN THE NEOTROPICAL FOREST.—If seed predators can play such a decisive role in structuring the desert ecosystem, what is the likelihood that they are similarly crucial to regulating the plant species composition of tropical forests? Aside from scattered, largely anecdotal reports (*e.g.*, Temple 1977), this remains an entirely open question. Perhaps the daunting proposition of having to identify the seedlings of scores of little known tree species has deterred investigators from initiating the required experiments.

Despite the current lack of direct evidence, some pieces of the puzzle have recently come to light, and by fitting these together, we may be able to assemble a picture, which, though incomplete, may nevertheless prove interpretable.

The first piece of the puzzle concerns the role of carnivores in regulating the densities of vertebrate seed predators. The three top terrestrial carnivores of the Neotropical forest, jaguar, puma and ocelot, have been studied at Cocha Cashu Biological Station in southeastern Peru by Louise Emmons (1987). Analysis of scats showed that the mammalian prey consumed by jaguar and puma generally weigh more than 1 kg, while most of those consumed by ocelot weigh less. If one looks at the representation of prey (> 1 kg) in the diet of jaguar and puma, a striking consistency emerges. When the occurrence of each type of prey in the diets of the predators is ranked relative to that of the most prevalent species, the proportions coincide astonishingly well with the relative abundances of the species in the environment at large, as determined by direct census (Table 2). This implies that the cats are acting as ideal searchers, *sensu* MacArthur and Levins (1964), in that they are taking prey nonselectively in strict proportion to their respective availabilities.

The interpretation of this result is rather subtle, because the various prey species differ in their intrinsic fecundities (Robinson & Redford 1986). High fecundity species, such as capybara and collared peccary, are capable of producing more prey biomass per individual female per year than low fecundity species such as paca, agouti, and coatimundi. This implies that the high fecundity prey species largely determine the carrying capacity of the environment for their felid predators (Terborgh 1988, 1990; Janson & Emmons 1990). A relatively high density of predators can then drastically suppress the abundance of less productive prey species, given the nonselectivity of their harvest. Here we have a perfect example of "apparent competition" (*e.g.*, Holt 1977). The more abundant peccaries become in this system, the more certain other species, such as agouti and coati, are forced into decline. Instead of shared resources, it is the cats that mediate the interaction.

So far we have an *a priori* interpretation that may appear highly speculative to some readers. The interpretation, however, does lead to a prediction,

TABLE 2. *Abundances of large terrestrial mammalian prey species at Cocha Cashu, Peru and their representation in scats of jaguar and puma.*[1]

Mammal	Densities in area		Relative no. in scats	
	No./km²	Rel. no.	Jaguar	Puma
Tayassu (peccary)	5.6	108	200	
Myoprocta (acouchi)	5.3	102		
Dasyprocta (agouti)	5.2	100	100	100
Agouti (paca)	3.5	67	67	75
Mazama (deer)	2.6	50	67	
Hydrochaeris (capybara)	1.6	31	33	

[1] From Emmons (1987).

TABLE 3. *Densities of terrestrial mammals of adult weight > 1 kg at Cocha Cashu, Peru and Barro Colorado Island, Panama.*[1]

	No. individuals per km²		
	Cocha Cashu	Barro Colorado Is.	BCI/CC
Didelphis marsupialis (opossum)	20	47	2.4
Dasypus sp. (armadillo)	4	53	13
Silvilagus brasiliensis (rabbit)	+	7	*ca* 7
Dasyprocta sp. (agouti)	5	100	20
Agouti paca (paca)	4	40	10
Nasua narica (coati)	+	24	*ca* 20
Tapirus sp. (tapir)	<0.5	0.5	>1.0
Tayassu tajacu (peccary)	6	9	1.5
Mazama + *Odocoileus* (deer)	2.6	2.7	1.0

[1] Compiled from Emmons (1984) and Glanz (1982).

namely, that if one could examine this system in the absence of felid predators, greatly increased abundances of the low fecundity prey species would be expected. In fact, an ideal situation does exist, and it happens to be at one of the very few Neotropical forest sites other than Cocha Cashu at which mammal densities have been measured. Once again, it is Barro Colorado Island, which, as mentioned above, is too small to harbor large felids such as jaguar and puma, although it does carry a healthy population of ocelots (Glanz 1982).

When one compares the densities of prey species weighing more than 1 kg as adults at Cocha Cashu and Barro Colorado Island, the contrast is nothing less than stunning. The abundances of nearly the whole spectrum of medium-sized terrestrial mammals are from 8 to more than 20 times greater on Barro Colorado Island (Table 3). These differences go beyond any likely measurement errors or effects of uncontrolled between-site variables, other than the presence vs absence of large felid predators. Included among the species showing the largest "releases" are paca and agouti, both major seed predators (Smythe 1986).

Now, if I may be permitted the luxury of some deductive speculation, this result could suggest, in parallel with the Chihuahuan desert study, that a superabundance of large vertebrate seed predators on Barro Colorado Island might be depressing the regeneration of large-seeded plants. To prove the point one would have to conduct appropriate seed predator exclusion experiments at both Cocha Cashu and Barro Colorado Island. Since this has not been done, is there anything more that can be said?

In fact, there is. In an act of far-sighted inspiration, a team of three investigators took it upon themselves several years ago to examine the tree species composition of some tiny islets (>0.1, <2.0 ha) in Lake Gatun, Panama (Putz *et al.* 1990). Like Barro Colorado, these islets were former hilltops that were isolated when the Chagres River was dammed to make Lake Gatun. Early air photographs show that the islets in question were cloaked in mature forest shortly after the canal was opened, so one can safely presume that their vegetation was then equivalent to that of forested hilltops on Barro Colorado Island and the nearby mainland. Today, 70 years later, the vegetation of those islets is drastically different, being composed principally of large-seeded trees, such as *Protium* (Bursuraceae), *Swartzia* (Leguminosae), *Scheelea* and *Oenocarpus* (Palmae). What is significant about these islets is that they are too small to maintain populations of the major terrestrial seed predators: squirrels, peccaries, agoutis, and pacas. Though other interpretations are possible, the prediction has been upheld that in the absence of the major terrestrial seed predators, large-seeded plants seem to better small-seeded species in the competition for establishment.

The final picture that emerges when we assemble all the pieces resembles that derived from the desert granivore system, except that an additional carnivore trophic level has to be added on top (Fig. 2). The chain of interaction then extends from the top carnivores (jaguar, puma) to the larger terrestrial seed predators (peccary, paca, agouti), to large-seeded trees (*Dipteryx, Protium,* etc.) that compete for establishment with small-seeded trees whose seeds are eaten by mice, rats, and tinamous, that are in turn the prey of ocelot, owls, and diurnal raptors. Direct interactions occur reversibly along the length of this chain, and indirect interactions link all the other components (diagonal lines omitted for simplicity).

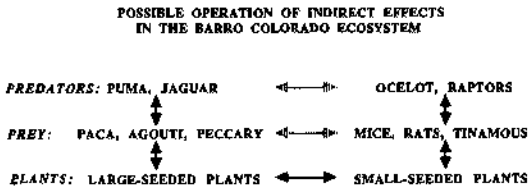

FIGURE 2. Schematic showing direct and indirect effects in the Barro Colorado Island, Panama ecosystem. (Diagonal lines representing further potential indirect effects have been omitted for simplicity.)

If all this has any truth in it, the implications for the future management of diversity in tropical forests are quite profound. Distortions in any link of the interaction chain will induce changes in the remaining links. So long as the perturbations are mild and of short duration, the system can probably recover, although the time needed for the restoration of prior states may have to be measured in tree generations. By the same token, major alterations in the processes of tree regeneration will essentially be invisible to the casual observer for perhaps decades. What must be guarded against then is the complete loss of one of the links. If that were to happen, the whole system could fall out of balance with consequent repercussions for both the plant and animal communities.

By far the most vulnerable link is that represented by the top carnivores. We have eliminated puma and wolf over most of North America with unknown consequences. The counterparts of these species are already disappearing over large portions of the Neotropics and elsewhere in the world. It is important that we better understand the role these animals play in maintaining diversity, before their removal, like that of the starfish *Pisaster*, leads inexorably to the drastic simplification of tropical forest ecosystems.

Where top predators have been extirpated, it may be impractical to reintroduce them. Once they have gone, it may be impossible to reverse the chain reaction leading to loss of diversity. Perhaps by hunting vertebrate seed predators, humans can attempt to substitute for the missing carnivores, but one can doubt that even with the best of intentions, man could ever replace the guiding hand of nature.

AMELIORATION OF THE EFFECTS OF FRAGMENTATION

This brings us to the question of what can be done to ameliorate the effects of fragmentation. The answer, I believe, lies in comprehensive planning at the level of whole watersheds, landscapes, and regions. The piecemeal approach of creating scattered parks and reserves for essentially serendipitous reasons should become a thing of the past.

Some portions of the earth are inherently better suited for human exploitation than others. My own state of New Jersey provides a good example. Its population density is the highest of any state and rivals that of Bangladesh. Nonetheless, New Jersey still contains habitat for bear, beaver, and bobcat. How is this possible? Wildlife persists in New Jersey because hunting is strictly controlled, and because the human population is concentrated in a belt of fertile soils that runs diagonally from southwest to northeast through the center of the state. Formerly a region of productive farms, for which New Jersey became known as the "Garden State," the fertile soil belt has lately been taken over for urban and industrial use. One does not find bears in this part of New Jersey.

The bears live in the northwest section of the state where there are thousands of hectares of forested hills and mountains that are too steep and rocky to support agriculture. The few people that live here occupy narrow, finger-like valleys that run between the parallel ridges. The low density of both people and roads assures the continued coexistence of man and wildlife.

Occupying much of the southeastern third of the state is another nearly empty region, known as the "Pine Barrens." Here, a deep deposit of Pleistocene sand creates a sterile and edaphically xeric substrate that gives rise to acidic blackwater rivers. A few "pineys" cut pulpwood, gather pine needle mulch, and cultivate blueberries and cranberries in the barrens, but the economic rewards of these activities discourage all but the most die-hard country folk. The pine barrens have remained sparsely settled into the 1980s, despite their proximity to New York and Philadelphia, because the fire hazard is so great that insurance companies will not write policies for homeowners.

In spite of its high population density, New Jersey has not become a wasteland for wildlife. Economic forces have dictated land use patterns which assure that only the most productive portions of the landscape are dedicated to intensive use. Nearly half of the state, where the terrain is too steep or the soil too poor for agriculture, has remained forested, and thanks to some accidents of nature, most of the forest is in two large and nearly contiguous blocks. Because of this, nature survives in New Jersey.

If there is a lesson in this for the tropics, it is that development should proceed with foresight. It should not just be allowed to happen, as it does when "highways of penetration" are built into wilderness. Desperate people will accept any land that is made available. The responsibility for exercising judgment as to the suitability of a particular landscape for sustained occupancy should not be forced upon peasant farmers. It should be the province of national planning and development organizations in conjunction with the major international lending agencies. The tropical counterparts of the steep rocky ridges of northwestern New Jersey and the sterile and fire-prone pine barrens should not be opened for settlement, but should instead be set aside as forest reserves, because light forestry and watershed management are among the few types of land use that can be sustained in such fragile environments. Where such zones of low productivity are large, as they happen to be in New Jersey, entire ecosystems can be maintained essentially intact as havens for diversity.

Adequate land use planning prior to development can help assure the minimization of fragmentation. The portions of the landscape that are truly appropriate for intensive and sustained use have mostly been preempted for human purposes already. Surviving tropical wilderness areas constitute residual lands that heretofore have been subject to light shifting use by native peoples, or simply passed over as having inferior development potential. It is important that this fact be appreciated by governments and development agencies, for the future of tropical diversity will depend crucially on the institution of enlightened policies for managing these fragile lands.

PRESCRIPTION

Marginal lands should be off limits for intensive development. Promote light, extensive forms of use as the only rational and sustainable alternative to the continued generation of degraded wasteland. Regulate hunting, either directly via licenses, bag limits, open seasons, etc., or indirectly via strict controls on arms and ammunition. Retain top predators wherever possible as indispensable regulators of ecosystem balance. Maintain maximum interconnectedness of wildlands to minimize fragmentation. This can be accomplished in hilly terrain by managing the backbone of the landscape for watershed protection, and in level terrain by sparing galleries along watercourses.

By following these simple admonitions as guiding principles in development, it may be possible to achieve an equilibrium between man and nature in the tropical world. By ignoring them, we can be assured of an undesirable outcome.

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