Winner of the John Burroughs Medal for Natural History Writing and the Helen Bernstein/NY Public Library Award for Excellence in Journalism

THE SONG OF THE DODO

BY THE AUTHOR OF MONSTER OF GOD AND THE FLIGHT OF THE IGUANA

ISLAND BIOGEOGRAPHY IN AN AGE OF EXTINCTIONS

DAVID QUAMMEN

"Stunning."—BARRY LOPEZ, AUTHOR OF ARCTIC DREAMS

THE HEDGEHOG OF THE AMAZON

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WE'RE A SPECK in the sky above the jungle of jungles. Below, but not far below, is an unbroken expanse of canopy that stretches away vanishingly in every direction: Amazon forest. The ceiling today is low and gray, the terrain beneath us looks sublimely inhospitable, and our noisy little two-engine plane is thumping along gamely at about five hundred feet, a precarious altitude where the air is as curdy as soured milk. We're headed north from the city of Manaus. Occasionally the plane lurches twenty or thirty feet upward. Or it sinks. It buffets like a kite while we try to concentrate our attention on the ground. About an hour of flying under these circumstances, I know from experience, is as much as my stomach will tolerate.

"If the pilot gets lost," Tom Lovejoy shouts above the engine's baritone whine, "we could end up in Venezuela." Then he gives me his chipmunk grin.

From where we sit, dangling above it, the forest seems nothing more than a magnificent abstraction of flatness and chlorophyll—cryptic, monotonous, green. That's at first glance, anyway. But the magnificent abstraction conceals a magnificent wealth of particulars, and with second and third glances I can discern some detail. The greenness resolves into hundreds of different shades, representing hundreds of different tree species. Here and there it's punctuated by the crown of one individual tree blossoming gaudily in yellow or magenta. Steam rises in cottony plumes from some spots, where the wet exhalation of plant metabolism is putting vapor back into the sky. "Fifty percent of the rainfall in Amazonia is generated by the forest itself," Lovejoy tells me. It seems only logical that an ecosystem so grandly intricate, so organismic, should have its own breath.

I crane my face to the window. Scenery reels by like a Bach fugue at 78 rpm. The vomit-alarm glands underneath my jawbone begin tingling. The gentle bucking of our low-flying little plane isn't the problem; the problem is that I've been staring too long at the ground. If I relax and breathe deeply, if I lose myself in the spectacle, I can possibly avoid tossing my heavy Brazilian breakfast onto Dr. Lovejoy's shoes.

I notice five macaws, large and blue, gliding in formation above the trees. I see no other wildlife, only foliage and steam. The forest canopy covers everything like a tent. There don't seem to be any gaps—no glades, no savanna, no ponds. No splits in the green uphol stery revealing brown-water or black-water rivers. Not hereabouts, anyway. Only treetops. The great junction of the Rio Negro and the mainstem Amazon has fallen away behind us. Even the clay-red slash of road leading out of Manaus, our first line of orientation from the airport, has gone its own way—and we've gone ours, on a more abstract path. There's nothing much below us except plants and animals in unimaginable profusion. There's nothing much ahead of us, as Lovejoy has said with such dire satisfaction, except more plants and more animals and then Venezuela.

The plane banks. The ground rises toward us from one side. We sweep down, straighten, and pass low, as though on a bombing run. This would be murder on my balky stomach if I weren't distracted by a new set of sights. As I watch, the canopy comes to an abrupt edge. The forest is suddenly gone. Beneath us now, instead, is a different sort of landscape. We have crossed an ecological boundary.

We're over the zone of clear-cut. We're looking at near-naked Amazon clay covered thinly with weeds. The tropical earth is as bare as a shorn ewe.

I see a stubble of tree stumps. A few charred logs lie crisscrossed in slash piles, remnants of the fires that took everything else. The sawyers and burners have done their work thoroughly. They have destroyed much more than trees. Besides removing the rainforest, they have removed the conditions that make rainforest possible: the darkness, the humidity, the shade-loving understory vegetation, the various flying and climbing beasts, the big predators, the small prey, the leaf litter, the soil fauna, the protection from wind and from erosion, the mycorrhizal fungi, the chemical nutrients, the pulsebeat of ecological interactions. The wet breath of the forest is gone too.

Now the plane banks again, tipping my window toward another peculiar sight. Standing up out of the scorched clear-cut is a small patch of intact forest, almost perfectly square. It looks like a piece of shag carpet tossed down on a dirt floor.

"That's a ten-hectare reserve," says Lovejoy.

We're in the airspace above Fazenda Esteio, the same hardscrabble cattle ranch surrounding the reserve where I'll later chase *Pithecia pithecia*—those leaping monkeys marooned in their tiny fragment of forest—with Eleonore Setz. Right now I'm getting a much different perspective on a similar fragment. The ten-hectare patch is known to Lovejoy as Reserve #1202. In the terms more familiar to most of us, it's a twenty-five-acre piece of woefully isolated tropical forest. It constitutes one unit within a mammoth enterprise that Lovejoy himself launched, back in 1979, to explore the dynamics of ecosystem decay. He has brought me up here today for an overview of the world's largest experimental study of the principles and implications of island biogeography.

Reserve #1202 is just one of many. Other such patches of forest lie scattered amid the clear-cuts of Fazenda Esteio, and still others on neighboring ranches, each one peculiarly rectilinear and ranked within an orderly gradation of sizes: one hectare, ten hectares, a hundred hectares, a thousand. This one, at ten hectares, is roughly the size of four city blocks. It's an island of jungle in a sea of man-made pasture. It was isolated in 1980, carefully preserved amid the scorched desolation, and since then it has been intensively studied. Around its perimeter I notice a well-worn trail.

Our plane lifts through another banked turn and back over the area from a different angle. Now into view comes a second island, still smaller. This one is barely more than a tuft of trees. Like the first, it's outlined by a square trail, but the patch itself is no longer square. It's tattered like an old flag. Sunlight and wind have parched and eroded it. Trees have fallen—tall rainforest trees, stout-trunked but shallowrooted, incapable of enduring such exposure. The canopy is full of gaps. The shade-loving understory vegetation has shriveled.

As the plane dips us down for a close pass, I see movement just outside the patch. Aha, I think, Amazon fauna. I prepare myself eagerly for a glimpse of a monkey, or a tapir, or with great luck maybe even a jaguar.

Wrong. What I've spotted are cows.

They are white as bone. A native rainforest herbivore couldn't afford whiteness—it would need camouflage—but these beasts aren't native. They are oblivious to the local realities of predation and defense. Spooked by our engine noise, they lumber around stupidly.

"That's a one-hectare reserve," says Lovejoy.

Even from this height, I can tell that the one-hectare patch is a husk of its former self. What changed it? Not chain saws, not fire, not cattle—not directly, anyway. Within its surveyed perimeter, it has been carefully protected against those factors. What changed it was sheer insularity.

Beyond the particulars of these two reserves stands a more general question: Is there a quantifiable, and therefore predictable, relationship between insularization and doom?

What is the threshold of ecosystem decay? What is the lower limit of ecological cohesion for a parcel of landscape? If a one-hectare fragment is too small to sustain itself, if a ten-hectare fragment is also too small, then how much is enough? Stated otherwise, in Tom Lovejoy's language: What is the minimum critical size of a piece of Amazon rainforest?

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DURING THE earlier years, from 1979 onward, Lovejoy and others called it the Minimum Critical Size of Ecosystems Project. In Brazil there was also a Portuguese name, suggesting a less narrow focus: Projeto Dinâmica Biológica de Fragmentos Florestais. That translates, by easy cognates, to the Biological Dynamics of Forest Fragments Project. It could mean many things.

Actually, it has meant many things. Over the course of its history, Lovejoy's enterprise has encompassed a number of major subprojects and smaller studies: on the local snake fauna, on bats, on primates, on rodents, on the solitary bees, on the social spiders, on the distribution and ecology of palms, on such important tree families as the Lecythidaceae and the Sapotaceae, on the reproductive biology of strangler figs, on soil nitrogen, on microclimate and plant-water relations within the reserves, on seedling regeneration along the reserve edges, on lizards, on frogs, on beetle diversity, on symbiotic relationships between ants and plants, on stream dynamics, on the role of fungi in rotting leaves, on various aspects of the bird fauna. Eleonore Setz's work on the little population of *Pithecia pithecia* is another of the many discrete studies. A recent report lists thirty different topics of research. The phrases "ecosystem decay" and "minimum critical size" appear nowhere on that list, though they represent the original, transcending agenda.

In the late 1980s the English name of the project was changed, under some pressure from a special review committee, so as to suggest wider purposes and to achieve semantic congruence with the Brazilian version. Now it's officially the Biological Dynamics of Forest Fragments Project. Lovejoy himself liked the old name, and so do I. The old one was narrow, yes, but also more vivid, and it gave a better sense of the project's theoretical roots. Those roots include the species-area relationship, the equilibrium theory, the early efforts by Jared Diamond and others toward applying island biogeography to the design of nature reserves, and the conundrum that became known as SLOSS.

Single large or several small? That question had been argued, argued again, argued bitterly and to a point of logical impasse, when Lovejoy got the idea of addressing it by means of a giant experiment.

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"THE FOX KNOWS many things," wrote Archilochus, a Greek poet of roughly 700 B.C., "but the hedgehog knows one big thing."

The hedgehog is more familiar on our side of the world as a porcupine. And the one big thing that it knows, of course, is the value of being prickly. The fox, a predator well armed with teeth and claws and speed and wit, but smallish and gracile, is obliged to be more versatile.

Forty years ago, the intellectual historian Isaiah Berlin wrote a memorable essay titled "The Hedgehog and the Fox," using that pair of animals to illuminate what he considered a bifurcation within the novelist Leo Tolstoy. Berlin suggested that the published works of Tolstoy show a certain two-mindedness, reflecting a tension between the great writer's natural disposition and his conscious convictions. On the one hand, here was a creative genius gifted with wondrously acute powers of observation and invention; on the other hand, a philosopher chasing the ultimate single answer. Tolstoy's particularized, pluralistic view of human history stood opposed to his theoretical, monistic beliefs. As he looked at the world, part of him saw Oneness and part of him saw Many. So Tolstoy himself, according to Isaiah Berlin, using the categories of Archilochus, was at once both a hedgehog and a fox. Besides fitting the categories onto Tolstoy, Berlin also applied them more broadly. The intellectual particularist Balzac, for instance, was a fox. Pushkin, Herodotus, Joyce, also foxes. Singleminded visionaries such as Dante and Dostoyevsky and Nietzsche were hedgehogs. It isn't that hedgehogs don't also see the multifariousness of life and experience; but like Tolstoy in writing *Anna Karenina,* they see it in light of a single big idea.

By this standard, Tom Lovejoy can be considered the hedgehog of tropical ecology.

Lovejoy is a soft-spoken fellow in early middle age, deceptively youthful in appearance, deceptively easygoing in manner. He doesn't come across as a man of grand obsessions. He looks as well scrubbed and ingenuous as a graduate student from Indianapolis, though in fact he's the scion of a wealthy Manhattan family and bears an unmitigated Ivy League pedigree. He is presently counselor to the secretary of the Smithsonian Institution, which makes him an influential science maven with a broad mandate. In the offices and boardrooms of Washington, he wears a bow tie. He claims that dangling neckties collect gravy stains and are more of a nuisance than bow ties. But you and I know that there is simply a bow tie sort of person—quirky but smart, unassailably self-confident, sublimely immune to the vagaries of fashion, rooted in New England—and Lovejoy is one. On the streets of Manaus, during an Amazon downpour, he deploys a collapsible umbrella. But when he hikes into the forest, his khakis are trail-weary and his boots are old. His Portuguese is fluent. His ear for the local birdsong is expert. He knows a forest falcon from a caracara, a hoatzin from a sunbittern, and one species of antshrike from another. He has been commuting to the Amazon since 1965. That was just after he finished college and before he got rolling on his doctorate.

Professional ecology is a small world where paths commonly cross. Lovejoy, like Robert MacArthur, did his Ph.D. under the broad, owlish wing of G. Evelyn Hutchinson at Yale, though Lovejoy was eleven years younger than MacArthur and arrived after he had left. Also like MacArthur, Lovejoy approached theoretical ecology by way of a solid empirical grounding in ornithology. For his dissertation research, Lovejoy spent a few years netting and banding birds in the forest near Belém (formerly Pará, the coastal Brazilian city where Alfred Wallace had established his earliest base), at the mouth of the Amazon. Eventually his notebooks would document seventy thousand individual bird captures. He was looking at patterns of diversity and abundance among bird species within forest communities, a topic that could be traced straight back, beyond MacArthur, to Frank Preston.

There was a further coincidence between Lovejoy's early career and the work of Robert MacArthur. Before he ever visited Brazil and fell in love with the country, Lovejoy had taken part in an ornithological expedition to East Africa, where he noticed that isolated mountain forests seemed to constitute ecological islands above the grassy plains. He had passingly contemplated shaping his dissertation around that. But it wasn't an irresistible idea at the time; it didn't seem hugely resonant. MacArthur and Wilson had not yet transformed the conceptual framework of ecology, and islands weren't the commanding paradigm they would shortly become.

"My first awareness of island biogeography was when I was in Belém, about 1967 or '68," Lovejoy recalls, "and this Harvard graduate student showed up with a copy of the book." By "the book" he means, without need to specify, *The Theory of Island Biogeography.* "Hot off the presses. I'll never forget that. And it was all very interesting. But it didn't particularly apply to anything I was doing." Not at that moment, it didn't. Later it would.

In 1973 Lovejoy became program director of the United States branch of the World Wildlife Fund. Today WWF-US is a vast corporate organization that performs the function, among others, of funneling money to small conservation projects all over the world. Back when Lovejoy signed on, it was still small itself, but even then it played a role in grant disbursal. Lovejoy's job involved reading and assessing the grant proposals. He had the help of one secretary. Funding would flow, or not, on the basis of his judgments. Many of the proposed projects involved statutory set-asides of habitat—that is, the designation of new parks and reserves. So, at just over thirty years old, he found himself making consequential recommendations about which parcels of the planet's richest ecosystems might be protected and which, by default, might not. He remembers two essential questions that had to be answered about such protected parcels. Where should they be? And how *big* should they be? He wanted to base his advice on the best available scientific wisdom. He read the early journal literature on applied biogeography. Then came SLOSS.

"I began to realize," he says, "that there was this rather serious problem relating to how you design a conservation area."

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THE SLOSS debate went public in 1976, when Dan Simberloff and a colleague named Lawrence Abele published a short paper in *Science,* voicing their concern over the recent vogue of applied biogeography. What made them uneasy was this business of deriving neat principles of reserve design from MacArthur and Wilson's theory. They cited Diamond's paper "The Island Dilemma" and pointed also to the brief but prominent essay by Robert May, "Island Biogeography and the Design of Wildlife Preserves," which had run in *Nature.* They quoted May's statement that several small reserves "will tend to support a smaller species total" than will a single large reserve of equal area. Not so fast, said Simberloff and Abele.

The theory itself hadn't been broadly enough proven, they warned, to justify such confident application. And the most basic principle being offered by May, Diamond, and others—that nature reserves should always consist of the largest possible continuous area—might not be correct. It didn't follow necessarily from the theory. Some of the same evidence cited on behalf of the single-large option could also be adduced to support the several-small option. It was all premature, according to Simberloff and Abele. The complex decisions involved in reserve design weren't reducible to a half dozen sleek principles. Furthermore, given the cost and the irreversibility of ambitious conservation programs, any half-baked application of a threequarters-baked theory could conceivably do more harm than good.

Simberloff's own stance here is an interesting matter. Back in the late 1960s, as Ed Wilson's graduate student, he had virtually been present at the creation of the equilibrium theory. Sweating his way through the Florida mangroves, he had helped gather experimental data that lent support to that theory. He seemed at the time to believe in the theory's predictive (as well as its descriptive) value. Was he contradicting himself, then, when he criticized its application in 1976? Not necessarily. But if his scientific convictions hadn't changed, his emphasis had. His attitude was subtly but firmly different from just two years earlier, when he had stated in print that island biogeographic theory might indeed "aid in the preservation of the earth's biotic diversity." He wasn't now repudiating the equilibrium theory. He was just cautioning that it might not fit all island ecosystems quite as well as it fit the Florida mangroves, and that it didn't provide any simplistic guidelines for conservation.

To some degree he was reacting against what he saw as the others' careless haste. Another factor was new data. Simberloff and his coauthor Abele had each been involved with recent field studies casting doubt on the notion that a bigger reserve is invariably better.

Simberloff had gone back to the mangrove islands—not just to the general area, but to the same individual clumps that he and Wilson had fumigated. In late 1971, with the original experiment finished, he had altered a few of those islands, cutting channels through the root tangle and the canopy. His cuts reduced the total area only slightly, but a new level of fragmentation was introduced. Each mangrove island was now a tiny archipelago of islets. How would that fragmentation affect the total number of arthropod species supported on a given archipelago? Simberloff had waited three more years, allowing the islets again to equilibrate; then in the spring of 1975 he had returned for another census. His results were equivocal; a single large mangrove island did not always support more species than several small ones. He found a case in which four severed fragments combined for a higher total of species than the original island. In another case, two severed fragments supported fewer species than they had as a single intact island. Simberloff announced these mixed results in his 1976 paper with Lawrence Abele.

Abele's own fieldwork on marine ecosystems had turned up a similar situation. His "islands" were heads of coral, and the resident species were marine arthropods dependent for habitat on one coral head or another. Abele had found a consistent pattern: Two small coral heads harbored more arthropod species than one large coral head of equal total area. Abele's field results were intricate and equivocal, like Simberloff's, but their net significance was to challenge the categorical postulate that a big island is always richer than two small ones.

Given the long history of species-area studies and the recent excitement over the equilibrium theory, it seemed heretical. Simberloff and Abele might as well have announced that the pope *isn't* Catholic and the bear *doesn't* always shit in the woods.

What could account for the reversal against expectations? Simberloff and Abele mentioned some factors: (1) size of the mainland pool of species, (2) lack of differences in dispersal ability among the mainland species, and (3) competition between species. Each of those factors could contribute, for complicated reasons, toward a situation in which two small islands would contain more different species than a single large one.

Another potential factor—not mentioned by Simberloff and Abele in their 1976 paper but destined to figure eventually in the SLOSS debate—was habitat diversity. If two small islands offer three different types of habitat between them, and one large island offers only two types of habitat, the pair of small islands might conceivably harbor more species.

Or possibly not. And possibly a single large island might contain more habitat types, not fewer, than two small islands. Possibly the habitat factor and others might determine that, in a given situation, large size and lack of fragmentation do indeed support greater diversity. Simberloff and Abele granted such possibilities. In the real world, islands are various. The principles of reserve design as enunciated by Diamond, on the other hand, assume a certain uniformity. The point that Simberloff and Abele wanted to make, they explained, was not that several small reserves are necessarily preferable to a single large reserve. Their point was that the species-area relationship (as subsumed into MacArthur and Wilson's theory) gives no guidance as to what is preferable, and that each situation should be judged on its own details.

"In sum," Simberloff and Abele concluded, "the broad generalizations that have been reported are based on limited and insufficiently validated theory and on field studies of taxa which may be idiosyncratic." Even within a context of formalized scientific discourse, those words don't sound especially harsh. But the paper's effect was incendiary.

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"WHEN THAT was published," one biologist has told me, "that was sort of like dropping a match in some very dry tinder. I think it's no overstatement to say there was an explosion of rebuttals to that."

The Simberloff-and-Abele paper appeared in January 1976. In September, *Science* ran a set of responses by six different authors, including Jared Diamond and John Terborgh. Diamond's came first. He noted Simberloff and Abele's accusations about prematurity, insufficiently validated theory, idiosyncratic field data. He acknowledged that Simberloff and Abele had posited circumstances in which several small reserves might seem preferable to a big one. And he wrote: "Their reasoning from their assumptions is correct but minimizes or ignores much more important conservation problems. Because those indifferent to biological conservation may seize on Simberloff and Abele's report as scientific evidence that large refuges are not needed, it is important to understand the flaws in their reasoning." The debate was on.

Among the flaws, Diamond argued, was their emphasis on the fact that two small islands sometimes contain more species than a large one. It might be true in certain circumstances, wrote Diamond, but it was irrelevant. How so? Because the sheer number of species present on some island or group of islands, or within some wildlife reserve or group of reserves, was not the real issue. The real issue was how an island or a reserve might affect extinction or preservation of particular species in the larger context. And in the larger context, not all species are equal.

Why aren't they equal? Because some species live in much greater jeopardy of extinction than others. The rare species, the highly specialized species, the less competitive species, and the species having low aptitude for dispersal and colonization—all these species might be missing from a reserve system if the reserves were numerous but small. Meanwhile the common species, the generalists, the good competitors, and the adventurous species would most likely be present. Diamond acknowledged that several small reserves might very well contain a large number of species, but most or all of them, he argued, would belong to that second category: the good travelers, the feisty competitors, the generalists. Those are precisely the species least in need of protection. They are resourceful and tolerant of disruption. They are abundant in all sorts of landscape. They are resistant to extinction. They might survive even without any system of reserves. The species most needing protection are members of the first category: the specialists, the less competitive creatures, the reluctant travelers. "A refuge system that contained many species like starling and house rat while losing only a few species like ivory-billed woodpecker and timber wolf," Diamond wrote, "would be a disaster."

He rejected Simberloff and Abele's rejection of his design principles. Idiosyncratic, my eye. Premature, my ass. Of course his language was muted, but that was the spirit. Biologists had better alert themselves, Diamond concluded, to this island dilemma.

John Terborgh and the other responding authors made similar arguments. Terborgh even declared that the logic of Simberloff and Abele, if accepted uncritically, "could be detrimental to efforts to protect endangered wildlife." That comment seems to have stung.

In the same issue of *Science,* Simberloff and Abele were allowed the last word. They repeated their charge about inadequate data. They repeated their assertion that the species-area relationship offers no generalized guidance. They alluded, now, to the factor of habitat diversity. Raspberry to you guys and the island dilemma you rode in on, said Simberloff and Abele, though not in precisely those terms.

They also reacted to Terborgh's stinging comment. "We regret being cast as the bêtes noires of conservation," they wrote. But they didn't retreat. "Our conclusion still stands: the species-area relationship of island biogeography is neutral on the matter of whether one large or several small refuges would be better."

The audience for this debate was other biologists. Among them, Tom Lovejoy had reason to be especially interested.

"I WOULD READ these papers. I would discuss it with people. The controversy was raging," says Lovejoy. "And it was upsetting, in a way. Because it was intuitively obvious that some species need large areas, and if you're going to protect them, you just have to *have* large areas." Big-bodied predatory mammals, for instance. A population of jaguars or wolves or tigers simply can't sustain itself within the confines of a small area.

On the other hand, Lovejoy admits, Simberloff and Abele were correct in pointing out that island biogeographic theory provides no logical basis for assuming that large reserves are necessarily better. "Because the theory merely treats all species as being equal," he says. It makes numerical assessments, not qualitative ones. It predicts that the equilibrium number of species on a large reserve should be greater than the equilibrium number on a small reserve, but it doesn't distinguish between a large reserve full of common species and a large reserve full of rare species. It doesn't take account of whether a species harbored in one reserve is desperately jeopardized throughout the rest of the world. It knows a big island from a little island but not an ivory-billed woodpecker from a starling.

The SLOSS debate was made doubly complicated, then, by the fact that it entailed two closely linked issues: (1) What is the optimal strategy for designing nature reserves? and (2) What does the equilibrium theory say, if anything, about the optimal strategy for designing nature reserves? One issue was mainly practical, the other mainly intellectual. Lovejoy, a pragmatic conservationist, cared more about the first than the second.

"I used to discuss it and worry about it a lot, with my scientific colleagues," he recalls. He came to believe that conservation planners like himself needed more than just theory and argument. They needed data. Specifically, they needed data on the structure of ecological communities and the pernicious phenomenon that Diamond was calling relaxation. They needed answers to a handful of technical-sounding but crucial questions:

- What exactly happens when a sample of habitat, newly isolated, relaxes to equilibrium? Species are lost, yes, but which species?
- Are the losses random, or are they determined by aspects of the community structure of the ecosystem?
- Will a particular nature reserve give long-term protection to those species in greatest jeopardy? Or will the reserve lose its jeopardized species over a short span of time while maintaining its populations of species that don't badly need protecting?

- Will several small reserves, offering similar habitat, all lose the same species and save the same species? Or will they vary randomly from each other, preserving assemblages of species that are different and complementary?

These questions hadn't yet been answered—not by Simberloff's work in the mangroves, not by Brown's study of Great Basin mountaintops, not by other empirical investigations, and certainly not by the early phase of SLOSS.

Lovejoy himself viewed the SLOSS debate with some wariness. "It may be my political nature, but I've never gotten into the middle of that pissing match," he says. "Simply because I didn't see what could be added to it. I thought it would be better just to go out and try to get data." But how?

Then, just before Christmas in 1976, Lovejoy was invited over to the National Science Foundation for a brainstorming session with a few other biologists, one of whom was Dan Simberloff. "We were sitting around, talking about this problem," Lovejoy recalls. "And all of a sudden, in one little lump, this project leaked into my mind."

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"THIS WAS one of those brilliantly simple ideas," says Rob Bierregaard, a younger biologist who became Lovejoy's first recruit to the Minimum Critical Size of Ecosystems Project.

Bierregaard has known Lovejoy since 1969. They went to the same prep school, some years apart, and were inspired there by the same science teacher, a remarkable man named Frank Trevor. It was on Trevor's recommendation that Bierregaard had met Lovejoy—back when Bierregaard was a freshman at Yale and Lovejoy still a graduate student—and through Lovejoy in turn he was introduced to G. Evelyn Hutchinson, the eminent ecologist who had been Robert MacArthur's mentor. During his undergraduate years Bierregaard studied ecology under Hutchinson, and in Bierregaard's recollection that opportunity was "sort of like taking your catechism from God." The linkage among Hutchinson, MacArthur, Lovejoy, and Bierregaard, with Frank Trevor hovering beneficently nearby, is more than an artifact of old-boy-network dynamics within professional science; it's a major chain of influence in the history of modern ecology, from pioneering theory to pioneering applications.

Lovejoy was just back from his two years of doctoral fieldwork when he met Bierregaard at Yale, and he hired the undergrad as a student assistant to do the computer chores on his dissertation data. After Bierregaard finished his own doctorate, Lovejoy hired him again—this time at the World Wildlife Fund in Washington, where Bierregaard made five hundred bucks a month and lived rent-free in Lovejoy's basement. The consummate right-hand man, he would eventually serve eight years as field director of Lovejoy's Amazon project. Bierregaard above all other people is entitled to call the MCSE idea simple, since he played such a big role in its complicated day-to-day implementation.

"Somebody had to go in," says Bierregaard, "and find out what really happens with this whole process of ecosystem decay in fragmented habitats." Lovejoy's brainstorm, in late 1976, offered a way to do it.

The crucial questions by then had come into focus. The difficult part was devising a workable but sufficiently grand experimental structure. It had to be much broader in scope than Simberloff and Wilson's project among the mangroves. It had to consider larger fragments, a richer ecological community, a longer time scale. And it had to incorporate before-and-after surveys of the species that were resident on each fragment, not just guesswork about what species *might* have inhabited some land-bridge island before its isolation, back in the mists of the Pleistocene. The new enterprise would need to be different from any ecological field experiment ever done. It would need to be wildly ambitious but economical. Tom Lovejoy, the pragmatic conservationist with the theoretical education, saw those requirements clearly. He also happened to know about a certain provision in Brazilian law.

This provision (let's call it the fifty percent provision) related to tax structure and land rights in the Amazon region, including that area known as the Manaus Free Zone, which encompassed a handful of ranches such as Fazenda Esteio. Under the Free Zone incentives, big swaths of rainforest on Fazenda Esteio and elsewhere were being cleared to plant pasture for a few scrawny cattle. But the fifty percent provision stipulated that fifty percent of the forest on any given fazenda had to be saved. In effect, it mandated the insularization of scattered rainforest fragments. Lovejoy's idea was to make scientific virtue out of legal necessity. With a little painless cooperation from the ranchers, maybe the mandatory insularization could be shaped into an experiment.

There was nothing so esoteric about that. Like other brilliantly simple ideas, though, it seemed obvious to everyone else only after the first hedgehog had thought of it.

The next step was a long campaign of persuasion. Lovejoy flew down to Manaus and started jawboning. He talked with scientists at Brazil's National Institute for Amazonian Research (INPA, by its Portuguese acronym), in particular Dr. Herbert Schubart, who was intrigued enough to become his collaborator. He talked with Brazilian conservationists, including Maria Tereza Jorge de Padua, at that time in charge of the country's national parks. Schubart and Jorge de Padua helped him with entree to others. He explained his idea to officials at SUFRAMA, the Manaus Free Zone Authority. He also visited some of the ranchers. With his diplomatic charm and his fluent Portuguese, Lovejoy coaxed people into sharing (or at least indulging) his vision. He created a broad partnership. And eventually it was agreed: The destruction of forest, destined to happen anyway, would be arranged so as to incorporate certain patterns. A remnant here, a remnant there, a bigger remnant over there… and the rest clear-cut.

Some of the remnants would be square, their edges linear and abrupt. They would be measured out with decimal precision, spanning a progression of sizes: one hectare, ten hectares, a hundred, a thousand. A vast tract of man-made pasture, hospitable only to cows, would surround the patches of untouched jungle. Those patches would be studied, both before and after isolation, by scientists whom Lovejoy, Bierregaard, and Schubart would enlist. There would be multiple replicate patches, for purposes of comparison—so that results from a ten-hectare patch could be matched against those from a one-hectare, from a hundred-hectare, or from another ten-hectare patch in a different location. Across two or three decades of study, the patches would yield information about the phenomenon of ecosystem decay.

Although the conceptual outline was vast, reflecting the size of the issues to be addressed, the execution phase began modestly, reflecting the size of Tom Lovejoy's disposable resources. At first Rob Bierregaard was the only staff person, and his operating budget was minuscule. “When I had the project set to go,” Lovejoy remembers, “I brought him down, introduced him to people, and said, ‘Here you are, Rob. See what you can do.’ “

Bierregaard recounts it in somewhat more vivid terms. “Lovejoy just abandoned me,” he says amiably. “We went to Belém, and I met some people there, and he said, ‘All right, get on a plane, go back to Manaus, charter a plane, do an overflight of the area where the sites are. And work with Schubart.’ “Bierregaard rewrote the project proposal in order to get government approval, and Schubart translated that into Portuguese. They submitted it. “This was the middle of Carnival,” says Bierregaard. “The theme in Manaus for Carnival was Disneylandia. Here I was going to Carnival in Brazil, my first time out of the country, I was really gonna get some Latin American culture—and there were Mickey Mouse costumes coming down the Carnival avenue. It was also in the peak of rainy season. So somehow I had to charter a plane, I had to talk to the ranchers, and all this on the Portuguese one has in about two months of working with some tapes. Unfortunately I’d stopped one chapter before the past tense. It was terrible.”

But when Carnival was over and the Mickey Mice ended their capering, the problems turned out to be solvable. Official approval was granted a half-year later. Eventually he would be able to reminisce—even in Portuguese, using the past tense—about those hard early days.

Bierregaard established his field presence in September of 1979. He spent $245 that month, and offered a long explanation in his first financial report as to why he had been so profligate. He opened a vest-pocket office in Manaus and, in October, purchased a vehicle. The surveying of reserve sites had begun, but so far there had been almost no clearing of forest. The reserves were like those hilltops on the Bassmanian peninsula during the last low-water episode of the Pleistocene: islands-to-be. But this time, when insularization occurred, a team of ecologists would be watching.

A few months later Lovejoy himself came back down from Washington. He was encouraged by what he found. Bierregaard had adapted fast. Things were happening. It was still just the humble start of what would grow into a vast project—with a $700,000 annual budget and a sizable roster of scientists, support staff, interns (young volunteers from the United States, Brazil, and elsewhere), and Brazilian woodsmen—but Lovejoy could see his idea becoming reality. He and Bierregaard took off together into the forest. They hiked up a long trail to the site of what would later, after the cutting and burning, become one of their insular reserves. “It was beautiful,” says Lovejoy. “Big ground birds would fly up from the trail as we came along. Finally we stopped. And he built us a little fire, getting it started in the damp wood by using a bit of old tire for tinder, as they do in the jungle.” Bierregaard heated up two cans of *feijoada,* the dark, beanrich Brazilian stew. Then he pulled out a miniature bottle of wine that he'd saved from his last airline flight. "And sitting there in the jungle," says Lovejoy, "we drank a toast to that biology teacher back at our prep school." Frank Trevor had died some years before. He had always dreamed of a visit to the Amazon.

"I HAVE a tendency to start things," says Lovejoy, "and then get other people to do the follow-through." Sensitive to the realities of collaborative effort and national pride, he corrects himself: "—other people to *help with* the follow-through."

It's a few days after our flight over the project aboard the little plane. In the meantime we have gone back out on foot. We have hiked down a path, away from the clear-cuts, deep into an area of undisturbed forest, where I've had the chance to appreciate its magnificent wealth of particulars at close range. We have walked through a wilderness of filtered green light, surrounded by gauzy humidity, buzzing and hooting sounds cast forward against deeper silence, toucans rustling in the canopy, hummingbirds and azure-winged morpho butterflies in the few sunny openings, cotingas, screaming pihas, epiphytes, lianas, leafcutter ants marching in long processions through the understory, discreet lizards, lichens, fungi in bright pastels. We have slept at a field camp, in hammocks, and heard the sibilant roar of howler monkeys filling the night like a choir of Harpies. For dinner and breakfast we have eaten *caldeirada,* an aromatic Brazilian chowder of river fish and cilantro. And on top of the *caldeirada* Lovejoy has fed me as much information as I could swallow. Now there's a respite for digestion.

"As a kid I was known as an instigator," Lovejoy adds. "Always starting things, getting in trouble." He pauses again, surrendering to a reflective smile. "Evidently it's carried over into adult life."

With Bierregaard installed as field director, the Minimum Critical Size of Ecosystems Project grew. Other scientists came to do fieldwork on the site. Lovejoy himself spent most of his time in Washington, at the World Wildlife Fund offices, and from there he provided guidance and support. On the fazendas north of Manaus, more than twenty reserves were laid out in the midst of what was still forest. Simple field camps were established. Ecological surveying began. The first question that had to be answered was: What species of animals and plants inhabit these demarcated squares before any isolation occurs? To find out, the researchers deployed mist nets for birds, traps for small mammals, binoculars for primates, and all manner of other techniques for collecting and identifying fauna and flora. The project's budget increased, so did support staff, and more woodsmen and interns were sent out to help gather data. The first isolates were created during the dry season of 1980: a one-hectare patch and a tenhectare.

The understory, outside the patch boundaries, was cleared by machete. Fallers with chain saws took down the trees. The jackstraw debris of timber and slash was left to go crisp for a few months; then it was torched. The fire raged and died. The two patches remained, rectilinear islands of green in an ocean of charcoal. One of those patches was Reserve #1202, the ten-hectare square that Lovejoy showed me from the plane. I wasn’t aware at the time, with my stomach gone burbly, that I was looking down on such a swatch of scientific history.

Phase two of the fieldwork started at once. Bierregaard and others went back out with their mist nets and their traps, this time to study the consequences of insularization. Some early results were published in 1983 and 1984, under the joint authorship of Lovejoy, Bierregaard, and a few colleagues. Those results were dramatic but not surprising.

First and most obviously, both reserves had lost their large predators. The jaguar, the puma, and the margay cat were no longer present. Why not? In addition to the noxious commotion of chain saws and flames, which had probably helped scare them away, there was an ecological reason: The reserves were too small to provide adequate cover and food for such big-bodied predators.

The paca, the deer, the white-lipped peccary, and the other sizable prey were likewise gone. Inadequate forage, inadequate security, inadequate something or other. The precise ecological details are unknown; what is known is that those species hadn’t found what they needed.

The primate populations were also affected. The ten-hectare reserve had contained a band of golden-handed tamarins *(Saguinus midas)* before isolation. Not long after, they came down from the trees and hightailed it off across the clear-cut. Two bearded sakis *(Chiropotes satanus)* also found themselves isolated within the ten-hectare patch. Unlike the tamarins, the sakis were canopy-dwelling creatures unaccustomed to ground travel. Their lonely confinement on such a small island must have been hard for these two individuals, since bearded sakis ordinarily live in large groups and travel wide circuits through the forest, feeding on fruits and seeds. The two trapped sakis couldn’t do that. Within the reserve, only one tree was in fruit, and before long they had eaten it clean. Then they disappeared, first one, then the other. Maybe they died of starvation. Maybe, pushed to extremes, they came down and made a run for it. No one knows.

A third primate species within the ten-hectare area was the red howler monkey *(Alouatta seniculus),* which had the advantage of being folivorous. Leaf eaters, like cows, can usually find something to eat. Still, the howlers had trouble. At first there were eight. By 1983, they had been reduced to about five, and the skeleton of a young male had turned up on the forest floor.

Among birds, a peculiar trend had appeared just after isolation: a higher capture rate in the mist nets, suggesting increased population density within the reserves. The likely explanation was that these patches of forest had assumed short-term significance as lifeboats, artificially crowded with birds displaced from the clear-cut terrain. If that was so, the increase in bird density wasn’t expected to last, since the habitat of the reserves couldn’t support it. And it didn’t last. Within a year, bird density had fallen back to normal in the tenhectare reserve and was lower than ever in the one-hectare.

The avifauna of each reserve continued declining. The declines were notable not just numerically but also in terms of which species were disappearing—the ant-following birds particularly. These are species of the understory that eat insects spooked up by columns of army ants on the march. Some ant followers are versatile enough to find food by various methods, but others (such as the white-plumed antbird, *Pithys albifrons,* and the rufous-throated antbird, *Gymnopithys rufigula)* are specialists, depending utterly on the armies they follow. No ants, the antbirds don't eat. Both the white-plumed and the rufousthroated antbirds seem to require a largish feeding area—large enough that they share it with at least a couple of ant colonies putting their armies on the march daily. And even a single colony of these ants requires a modestly big area of its own. With a half-million mouths to feed, one hectare isn't sufficient. After six months of isolation, therefore, army ants were gone from the one-hectare reserve, and the whiteplumed and rufous-throated antbirds were gone too. By the end of a year, three other species of ant-following birds had been lost. They had followed the ants to oblivion.

Among butterflies, the shade-loving species of the deep forest became rare, some disappearing altogether. Meanwhile the number of light-loving species (such as those flashy blue morphos, adapted to forest gaps and edges) increased. This represented turnover, in MacArthur and Wilson's sense. Even with no net loss of species, turnover among the butterfly fauna was a hint of corrosive changes.

Some of those changes involved the vegetation. Trees along the perimeters of the reserves had received unaccustomed exposure to sunlight, drying, and winds. With their leaves scorched, with their inherently weak root structures subjected to extraordinary stresses, they began dying and falling. Sometimes a falling tree took another tree with it, and every new gap offered another channel for the intrusion of sunlight and winds. Light-tolerant species, including weeds from the pasture, invaded. Hot breezes reduced humidity and raised temperatures within the reserves, drying leaf litter on the forest floor. Near the center of the ten-hectare reserve, the number of standing dead trees increased dramatically. And beyond being stressed, some of the plants were downright confused: A mature tree of the species *Scleronema micranthum* came into flower six months out of sync with the rest of its species. Vulnerable in a season of scarcity, it lost a large part of its seed crop to seed predators. The forest had commenced to unravel.

The ecosystem was in decay. Species were vanishing, relationships were disrupted, even climatic conditions had gone bad. The lesson of these early data was unmistakable. A tiny patch of Amazon rainforest—one hectare, say, or even ten—could not maintain its existence in isolation. It just wasn't big enough to sustain itself.

Then what *was* the minimum critical size? If that question had any meaningful answer, it wouldn't come quickly or easily.

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WHILE Lovejoy was launching his experiment, the SLOSS debate continued, with Jared Diamond conspicuous on one side and Dan Simberloff on the other.

Throughout the decade that followed their 1976 exchange in *Science,* the familiar arguments were repeated and some fresh ones were added. Each side gathered partisans. At issue was not just one question of reserve design strategy, single large versus several small, but also such broad matters as whether the species-area relationship was profoundly instructive or not, whether the equilibrium theory was scientifically valid or not, and whether either of those two concepts had any relevance to conservation.

Journal papers appeared in quick succession. Even as cited in the usual shorthand format whereby professional ecologists know and remember them, they pile up into a longish list: Gilpin and Diamond (1976), Abele and Patton (1976), Brown and Kodric-Brown (1977), Simberloff (1978), Diamond (1978), Abele and Connor (1979), Connor and Simberloff (1979), Gilpin and Diamond (1980), Simberloff and Connor (1981), and dozens more. Each of those papers was full of elaborate logic and conviction. Many were besmeared with math. Some also contained facts. Scientists characteristically fight out their battles in the journal literature—lobbing papers back and forth like flaming arrows—and that's how these scientists fought SLOSS. It didn't go on as long as the War of the Roses, it didn't spill as much blood, but it was something more heated than a cordial discussion among colleagues.

The specifics were intricate and tendentious. I recommend them as a cure for insomnia. A few salient themes did arise from the welter of voices, and those few are worth mentioning. Habitat diversity was one.

Representatives of the Simberloff camp argued that habitat diversity is far more significant than sheer area in determining how many species can exist in a given reserve. A handful of different habitat types will support many more species than a large zone of homogeneous habitat, and the best way to preserve a handful of habitats is with a handful of smallish reserves.

Representatives of the Diamond camp disagreed—but they disagreed obliquely, not diametrically. They didn't deny the significance of habitat diversity. In fact, Diamond himself had emphasized habitat diversity just a few years before, in a study of bird species turnover on the Channel Islands. But now Diamond and others found it reasonable to propose that, for practical purposes, the laborious inventorying of habitat diversity can be ignored. In the real world of speedy ecological destruction caused by humanity on the march, they suggested, a shortcut conservation method is justifiable, even necessary. They were thinking of planners like Tom Lovejoy, obliged to make consequential decisions on the basis of incomplete ecological data. Under those circumstances, according to the Diamondites, the sheer area of a proposed reserve is a highly significant datum. It can be taken as a rough gauge of both species abundance and habitat diversity.

No it can't, said the Simberlovians. Presume to make such an equation, they said, and you're closing your eyes to the texture of ecological reality.

The fine points of this controversy filled dozens of pages in the *American Naturalist, Biological Conservation,* the *Journal of Biogeography,* and other journals. Which side was right? It's anybody's call. In caricatured form (and angry debates do tend toward caricature), the opposing views became known as the "habitat-diversity hypothesis" and the "area-per-se hypothesis," despite the fact that few Diamondites would have agreed that "area-per-se" was an accurate label for their position.

Taking up another issue, the Simberlovians pointed out that several small reserves would offer insurance against certain forms of catastrophe. If a typhoon or a forest fire struck one small reserve among a scattered system of several, the other reserves would probably be spared, whereas the same typhoon or fire might sweep straight across a single large reserve and eradicate whole populations of plants and animals. If a virulent disease took hold in a large reserve, it might likewise spread widely, while several small reserves would offer the protection of quarantine. An exotic predator, like the tree snake on Guam, might also cause more damage within a single large reserve. The same predator would need to accomplish several successful colonizations, each one against high odds, in order to terrorize several small reserves. Don't put all your eggs in one basket, the Simberlovians were in essence arguing.

The Diamondites, for their part, noted that a single large reserve would offer greater security within its interior, while several small reserves would suffer proportionately more disturbance along their edges. A large reserve, too, would be necessary to save large-bodied and wide-ranging predators, such as the jaguars and pumas of the Amazon. And a large reserve might provide a margin of safety against climate change; if one region of the reserve became too dry or too hot for a given species, that species might be able to move to a wetter or cooler region without being stopped by a boundary. A small reserve would afford no such migrational latitude.

So it went: pro and con, argument counterbalancing argument. Small reserves might be more cost-effective for saving tropical insects and rare plants, which tend to be localized within small pockets of habitat. A careful selection of small reserves might harbor more plant and animal species than one large reserve, and those scattered reserves might even cost less, in total, than a single continuous parcel of land. On the other hand, many plants and animals within small reserves might represent common and widespread species not really needing protection. One large reserve might contain fewer species overall but more species that are rare and jeopardized. On the other hand, small reserves might… On the other hand, a large reserve might… And so on.

All these assertions are summarized in the subjunctive—things that *might* happen, rather than things that had happened or indisputably would—because the SLOSS debate by its nature was hypothetical. And the deep text beneath much of the hypothetical arguing was the equilibrium theory of MacArthur and Wilson.

A large reserve might receive more immigrations and endure fewer extinctions, according to Diamondite logic. Why? A large reserve presents a bigger target to dispersing individuals—hence a higher immigration rate. A large reserve supports large populations, thereby buffering each species against the dangers of rarity—hence a lower extinction rate. Of course a higher immigration rate combined with a lower extinction rate results in a larger number of species at equilibrium. Q.E.D., said the Diamondites.

B.S., said the Simberlovians. There you go again with MacArthur-and-Wilson.

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THEY FOUGHT to a standoff. As the conflict continued and the lines of alliance and opposition became clear, the arguments grew progressively more rancorous and abstruse. But despite all its vehemence, not every aspect of what Tom Lovejoy calls “that pissing match” was relevant to our interests here. One portion that *was* relevant involved a biologist named Michael Gilpin.

Gilpin, based at UC-San Diego, is a pal of Ted Case, the swashbuckling herpetologist of the Gulf of California, with whom he shares a certain robust personal style. You wouldn’t mistake Gilpin for a corporate lawyer; more likely you’d take him for a high school track coach. Like Case, he’s an aging athlete who sees no reason why stiffening joints and cholesterol and a forty-seventh birthday should consign him to sober-sided adulthood. His laugh, sounded often, is a full-hearted, high-pitched bray. He reads widely, plays hard, thinks fast but deeply, and his world remains larger than science, though his scientific world is large. My own intermittent multiyear interview with Mike Gilpin has been conducted in kayaks, on ski lifts, while jogging along city streets, in the cab of an old truck crossing Nevada by night, at campsites in the Montana backcountry, and over more than a few glasses of beer. He also competes in triathlons, but for that foolishness he’s on his own.

Gilpin was trained originally as a physicist and worked in the 1960s for Hughes Aircraft, “developing lasers to blind Viet Cong,” as he puts it cheerily. That life was unappealing, so he dropped out for the Peace Corps. After a few years in the Mideast he returned to the United States and found himself diverted toward the science of ecology by watching Paul Ehrlich one night on the *Tonight Show.* Ehrlich was talking about human population growth, the extinction of species, and what amounted to ecosystem decay. Gilpin took it to heart. He went to grad school in ecology and finished a doctorate quickly.

Reborn as an ecologist, he showed a special talent for computer modeling. He also performed well in collaborative matchups with other ecologists. He did some abstruse theoretical work in population genetics, he studied the dynamics of predator-prey interactions and competition between similar species, but then he came into contact with “two real good island biogeographers” who helped shift his interests in that direction. One was Ted Case. The other was Jared Diamond. Strong in math, masterly as a computer programmer, Gilpin during the SLOSS debate made a good partner for Diamond and a worthy opponent for Dan Simberloff.

His work with Diamond, contra Simberloff, came to focus eventually on something called the “null hypothesis.” This was a hot little battle fought out parenthetically to the larger war.

The null-hypothesis controversy was somewhat more purely scientific than the matter of SLOSS. It concerned deductive procedures and their philosophical underpinnings. But it did contain some practical implications of its own. Its starting point was a study, published by Diamond in 1975, of bird distributions and community structure on fifty islands of the Bismarck Archipelago, just east of New Guinea.

The Bismarck bird distributions were irregular, a messy patchwork of avian rosters differing from one island to the next. Amid the messiness, though, was a hint of order. Certain species or combinations of species appeared to be mutually exclusive. Diamond considered that significant. Among the factors determining these distributions, he concluded, was interspecific competition. Some of the bird species just couldn't coexist with some others. Competition made it impossible for them to live sympatrically. They had prevented each other from colonizing their respective islands.

Or maybe not. In a 1978 paper Simberloff attacked both Diamond's methods and his conclusion. It would be more parsimonious, Simberloff argued, to entertain a null hypothesis before seizing on the hypothesis of competition. What was that null hypothesis? Randomness. Maybe the Bismarck distributions, which seemed to reflect competition, in reality reflected nothing but chance. The human mind is always eager to see meaningful pattern, after all, even where meaningful pattern doesn't exist. We compose the stars of the night sky into hokey, connect-the-dots constellations. We imagine that we've caught sight of animal shapes in the clouds, flying saucers in swamp gas, a conspiracy behind every witless assassination, and the future in tea leaves. Simberloff suspected Diamond of making the same sort of credulous leap. He urged skepticism. If sheer chance was sufficient to explain those bird distributions, Simberloff argued, then Diamond's claim that the data reflected a more causal process (namely, competition) was superfluous and logically unacceptable.

From that start, the null-hypothesis dispute rolled forward through time and across journal pages, with Mike Gilpin joining Diamond's side and a biologist named Edward F. Connor co-authoring papers with Simberloff.

Diamond, the bird ecologist, had collected much of the Bismarck data during his arduous field expeditions in the New Guinea region. He himself had done the original, seat-of-the-pants analysis. But with Gilpin's collaboration he could go further. Gilpin, the math jock and wizard programmer, was capable of holing up in his house and writing a thousand lines of ingenious computer code before he emerged again into daylight. Using an early-model Vax computer, he pushed the analysis of Diamond's Bismarck distributional data to new levels of statistical sophistication.

Simberloff and Connor had their own durable, synergistic partnership, which gave a certain two-against-two symmetry to the flamingarrow battle of the papers. A Connor-and-Simberloff paper would appear, offering new and more trenchant criticisms of the original Diamond work; that paper would be answered by a Diamond-and-Gilpin paper, to be answered in turn by a Simberloff-and-Connor, which a Gilpin-and-Diamond would then rebut. It got testy. They derided each other's mathematical competence. They used exclamation points, which are rare! and drastic! in scientific literature. They accused each other of malpractice. It's slapdash and illogical, claimed Simberloff and Connor, to embrace the competition hypothesis without first having disproved the null hypothesis. No it isn't, argued Gilpin and Diamond. And furthermore, they said, your "null" hypothesis ain't so perfectly null. It contains hidden assumptions that introduce ecological bias. Does not, said Connor and Simberloff.

There was a bit of repetitive bickering, as well as formidable displays of ecological ratiocination and computer-aided statistical hotdoggery. Translate the whole thing into theological terms and it looks roughly like this: Diamond and Gilpin were rational Unitarians, Simberloff and Connor were devoutly agnostic.

Do you hunger for a detailed account of who said what and how the other guys answered? My own working hypothesis is that you don't. But I wanted at least to mention this business for two reasons: because Mike Gilpin will reappear later, in a context more directly germane to the extinction of insularized populations, and because some knowledge of the null-hypothesis controversy is prerequisite to appreciating what confronts me as I knock on Dan Simberloff's door.

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SIMBERLOFF'S office is in a nondescript building on the campus of Florida State University, in Tallahassee. It stands near the end of a cinderblock corridor. Though the surroundings are drab, the door itself is festooned with newspaper clippings. One headline catches my eye:

IMAGE ON TORTILLA DRAWS CROWDS TO HIDALGO HOME

The copy reads: "They come alone or in groups to view a tortilla in a foil-lined cup above a home altar. Candles flicker while people wait in a darkened parlor for a chance to see for themselves what all the fuss is about." Hidalgo is a small town on the Mexico side of the Rio Grande. The fuss, it seems, is about a provocative pattern. Whether that pattern might be meaningful is a question the newspaper reporter has left to others. "They want to decide first-hand if the story is true, if an image of Jesus Christ did miraculously appear on the last tortilla made by Paula Rivera, a Hidalgo housewife, on February 28." Some academics are content with Gary Larson cartoons on the office door. Dan Simberloff's humor seems a little more dry and pointed. What this clipping represents, of course, is the continuation of the null-hypothesis argument by other means.

There are a half-dozen more in the same vein. JESUS' IMAGE DRAWS CROWDS AT FOSTORIA, reads the headline above a report about dark smeary shapes on the side of a soybean-oil storage tank in Ohio. VIRGIN MARY'S "IMAGE" DRAWS FAITHFUL, CURIOUS, reads another, announcing the case of an Arizona woman who found Our Lady of Guadalupe in a yucca plant. WOMAN MOVING G.E. JESUS is a good one, involving a Tennessee lady who declared she was on a mission from God. The mission was to move her General Electric freezer, upon which she had discovered a facsimile of Christ's visage, to a site where the public could more conveniently venerate it. "Arlene Gardner insists that God chose her appliance to reveal the face of Jesus, but some of the 3,000 viewers who have seen it in recent weeks say it looks more like country singer Willie Nelson." That last part seems especially implausible. Why would God trouble himself to make Willie Nelson's face appear on a freezer?

I suppose it's worth stating that I'm not making this up. We're dealing strictly with facts—or, to be slightly more accurate, with reallife newspaper journalism. We're dealing with the data on Dan Simberloff's door. Maybe the best of his headlines is MIRACULOUS FACE APPEARS ON SCROTUM! "IT'S A MIRACLE!" SAY EXPERTS, about which the details can be left to your fertile imagination. Simberloff has also posted a story about a Moslem man in England who found Allah's name written inside an eggplant. Somewhere in western Asia, no doubt, the face of Mohammed has shown up in a chapati, though Simberloff so far doesn't seem to have gotten wind of that one. But there is another account of Jesus revealing himself in his favorite medium: "Maria Rubio was rolling a tortilla for her husband's dinner last fall when she noticed that the skillet burns on the tortilla resembled the mournful face of Jesus Christ, crowned with a wreath of thorns. Since then, 8,000 curious pilgrims, most of them Mexican-Americans, have trekked to the Rubios' small stucco house in rural Lake Arthur, N.M., to view what they consider a sacred icon."

Standing at Simberloff's door, my head swims with questions. For instance: corn or flour? I would love to read my way through the full dossier, but I'm already late for my appointment and I don't want him to catch me lurking outside. So I knock.

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A FRIED tortilla is data. An oval shape of oil-darkened splotches represents pattern. To assume that the pattern is meaningful—that it's a face, that in fact it's the face of Jesus made manifest as a miraculous message—is to adopt a theory about the pattern within the data. Dan Simberloff has strong convictions on the general subject of theory.

"Maybe I haven't been blunt enough," he tells me.

He's alluding to his writings on SLOSS, his role in the nullhypothesis controversy, and his published criticisms of what he considers the overzealous application of MacArthur and Wilson's theory. "It's hard for me to believe that I *haven't* been blunt enough," he adds. "But theory can cause a lot of trouble."

It has led to some disastrous mistakes, Simberloff says. And besides the actual disasters, there have been some near misses. He mentions a handful of cases in which bad conservation decisions were barely averted when the prevailing theory was successfully challenged. Officials in Costa Rica, for instance, were going to give up on jaguars and harpy eagles because they had read somewhere that rarity to a certain precise degree (fewer than fifty individuals) dooms a species to extinction. Their jaguars and eagles were already that rare, so they were inclined to abandon all hope. Simberloff knows of similar situations in Australia, where state governments were prepared to eliminate protection for certain species, based on theoretical notions suggesting that the species were irremediably rare.

Another notable triumph for wrongheaded theory, in Simberloff's view, occurred when the United Nations Environmental Programme, the International Union for the Conservation of Nature, and the World Wildlife Fund adopted—in their joint *World Conservation Strategy* document of 1980—the reserve-design principles that Jared Diamond had promoted in "The Island Dilemma."

And there's the case of Israel. "I've done some work in Israel, on leaf-mining insects," says Simberloff. "When I was there in '85 or so, a man from the Nature Reserves Authority came to see me. He was desperate. And here's what he was desperate about. Israel has a wonderful system of nature reserves in a country where it's very hard to *keep* nature reserves." They have more than two hundred reserves, he says, though the country itself is smaller than Maryland. Furthermore, a large portion of the Israeli citizenry seems to care fervently about nature. Like the English, Simberloff explains, Israelis have a strong proprietary affection for the remnants of their own native fauna and flora. Most of those reserves are adjacent to bodies of water, where the ecological communities are rich. Many of them were established decades ago, back when Israel itself had just gained statehood. For years there had been squabbling between the Nature Reserves Authority and two interests that wanted the reserves disestablished: agriculture and the military. Agriculture coveted the sites for their water, and the military wanted them for strategic reasons. But the political pressures had been resisted; the reserves kept their protection. Then, just about the time of Simberloff's visit, a new factor threatened to tip the balance.

"They read, both the military and the agricultural interests, that small reserves are not able to preserve viable populations. And almost all of the reserves in Israel are very small. So at a cabinet-level meeting they said that the weight of scientific evidence shows that these are worthless anyway, and what's the good of them? And they wanted me to go and look at their reserves, and then to provide some scientific support. You know, it was utter bullshit," he says.

The Israelis had caught wind of SLOSS. They were swayed by the argument that a number of small reserves are necessarily inferior to a few large ones—the same argument that Simberloff dismisses as "a cocktail-party idea having the trappings of science."

I'm inclined to agree with him on one point, among others: It seems unlikely that he hasn't been sufficiently blunt.

"I could give you other examples," he says. "The theory that doesn't really have strong empirical support can be very dangerous." In the dangerous class he includes not just Jared Diamond's reserve-design principles but also the equilibrium theory itself. Theory in any branch of science entails a risk of detachment from reality, but especially so in a science as multifarious as ecology. If the theory is applied in decision making that affects how humanity treats portions of the world's landscape, the risks and the consequences are still greater. "It's not like, at worst it's neutral. At worst it's *bad.*"

The proper way to bring science into conservation planning, Simberloff says, is with detailed ecological studies of particular species in particular places, not by applying grandiose theories. The term for what he favors is *autecology,* embracing an imperative to learn the ways of the creature itself, and the immediate relationships that connect it to its place, before drawing conclusions about the overall structure of the community to which the creature belongs. This contrasts with *synecology,* attending more to the community dimension and the sort of organizing principles that Diamond saw among the Bismarck Archipelago birds. Although the difference between the two is only a matter of emphasis, it's a clear enough difference to be significant. Autecology, Simberloff's preferred approach, tends to be more descriptive than theoretical, and descriptive ecology is out of fashion. Some people are still doing that sort of work, he says, but they don't get enough credit from their colleagues and they don't exert enough influence on conservation policy. Too many other ecologists are in a hurry to generalize. Too much attention goes to the hotshot theories.

"It's sad. There's an element of physics envy in all of this," Simberloff tells me. "That's what is really at issue here. Conservationists and conservation scientists feel that unless they can point to a theory—and the more quantitative it is, the better—they won't be able to get people to respect their views and ideas." The people whose respect is so crucially at issue are government bureaucrats, conservation administrators, and politicians, as well as scientific colleagues. In order to be heeded in the councils of policy, some ecologists believe, they've got to deliver deductive conclusions in concise mathematical form. "And it's too bad, but ecology isn't that kind of science."

I ask: Is this the legacy of Robert MacArthur?

No, Simberloff says. He finds that explanation too simple. MacArthur happened to be a very, very smart guy who came along at the right time, but the yearning to mathematize ecology was already in the air. If it hadn't been MacArthur, it would have been someone else a couple years later.

How did you yourself become disenchanted with the equilibrium theory? I ask.

"Well, you know, it goes back to, I don't know …" And he diverges from there into a roundabout answer, leaving me to continue wondering: back to where?

To the very beginning, presumably. Simberloff after all is the fallen archangel who had stood at the right hand of Ed Wilson while Wilson and MacArthur were creating this particular universe. That's one way of seeing it, anyway, admittedly a little melodramatic. Dan Simberloff himself is not inclined to melodrama. His mind makes razorclean, ruler-straight cuts. His nostalgia, if any, is not on display to every visiting journalist. Having cast his memory backward, he starts over.

"I'm sort of viewed as a professional crank," he says truly. "I'm disenchanted with lots of community ecology. And my disenchantment to some extent with the equilibrium theory stemmed from the same source. That is: Modeling is fun, sometimes it produces elegant structures, but there is a tendency to reify models. To take them as nature, when really all they are is proposed abstractions of nature. I'm concerned when a literature begins to develop on the models themselves, rather than on nature." There's a long history of such airy theorizing in the journals of ecology, he says. Too much conceptual scat-singing, too little observed data. Far too little experiment. "And the equilibrium theory, it seemed to me, was increasingly that sort of beast. That is, Ed and I did that experiment to try to test it directly." They went to the mangroves. They censused real arthropods on real islands under the real Florida sun. They not only tested theory against reality; they did it with data from a controlled, focused, carefully manipulated situation. They found a way to convert small bits of functioning ecosystem into a rigorous experiment. "Not many other people did."

This brings us around to Tom Lovejoy's experiment in the Amazon, for which Simberloff professes a guarded admiration. The original idea was a great one, he says. The execution has been mixed. Too bad that the experimental conditions aren't more precisely controlled. Too bad that there aren't more replicate patches. "But hell, no one had done anything like that before. So it was a neat thing to do." And it has produced some good work. He mentions a herpetologist named Barbara Zimmerman, who happens to be one of his own doctoral students. Zimmerman's study of frog species on the reserve sites, he says, tends to show that habitat diversity is more important than sheer area. Based on those findings and others, she's a skeptic. She thinks that the application of equilibrium theory to conservation, and the notion that a single large reserve will always be better than several small ones, are hooey. But her results have come out of Lovejoy's big experiment, and that's good, Simberloff says.

We talk for two hours about these matters and others. He loses me occasionally with his brisk, concise explanations of intricate scientific ideas, and at one point he shows impatience with my obtuseness. Like Robert MacArthur, Dan Simberloff is clearly a very, very smart guy. And he knows it. He is perfectly civil and cooperative but, unlike Ed Wilson, he doesn't squander his charm on strangers. It would be easy to make a faulty judgment of the man. He possesses a dangerous critical intelligence, yes. He's blunt, yes. He would gladly cut the throat of an ill-conceived idea and swat down an innocent misstatement like a fly. He seems to care zip about what most people think of him. He despises ecological theorizing when it's done irresponsibly, which in his view is most of the time. He values fieldwork, autecology, and experiment. He seems curt and unemotional. It would be easy to conclude, as some among his peers evidently have, that he cares far more for sleek scientific rigor than he does for the natural world. I might have reached that conclusion myself. But somehow our conversation swings back to his work on the mangrove islands. He has been down there a few times since the 1970s, he tells me. It's not so far from Tallahassee. He still has some ideas that he would like to pursue in that experimental context. But he hasn't been to the site now for five years.

"I'll tell you why I stopped working there," he says, though I haven't asked.

With each trip, he would notice another diner or trailer park or some other touch of human encroachment upon the natural landscape. "It became very depressing to work down there, because I could see the Florida Keys going to hell around me," he says. Then, casting back again to the early days of his work with Ed Wilson, he shares a story.

"After we figured out roughly what I was going to do, I guess in '65 or '66,1 went down and spent quite a while in the Florida Keys. Getting to know the system, scouting out islands that we might be able to use, et cetera. There was an island at that time near Seven Mile Bridge—it was the third island to the west of Seven Mile Bridge, the first substantial island—called Ohio Key, for some reason, I don't know. It had a lot of forest. No one lived on it. And fringing mangrove swamp. Off that swamp there were two islands that in our notes would be called E4 and E5, if I remember correctly. And I practiced censusing those islands. We may have practiced fumigating one of them, I'm not absolutely sure." He and Wilson also made a collection of snails from the two islands. Ed still has the snail shells in a box, says Simberloff, and uses them to illustrate certain points when he teaches evolution. In a purely symbolic, sentimental way, these two tiny islands off the edge of Ohio Key were special.

Simberloff came to know them intimately. “I mean, they were my first mangrove islands. They were about a third the size of the ones we ended up fumigating. They each had about twenty-five species.” They stood just beside Ohio Key, no farther away than from here to the door, he says, gesturing. That proximity made Ohio Key itself seem a bit special. Relative to E4 and E5, it was the mainland.

“And then in the mid-1970s,” he says, “I don’t remember the exact year, I was driving down to one of the field sites for those later experiments. I came off Seven Mile Bridge, passed over the first key, it was called Little Duck Key, and the next key, which was Missouri Key. Normally, from Missouri Key I would see the trees of Ohio Key. Instead of Ohio Key I didn’t see *anything.* Then, when I got to the end of Missouri Key, I could see that the reason was, there were no trees there. The entire key, which would have been in the range of four acres, had been leveled and cleared. It was now all crushed coral. It had been turned into a trailer park.”

It was renamed Holiday Key, Simberloff says drily. “And it was too new even for there to be trailers there. So, there was this one central place, a trailer that was the store, and then there were all these stanchions, you know? For hooking trailers. And off this gleaming coral monstrosity were my two islands, E4 and E5. They were still sitting there.”

By now I see where the story is headed and, despite my wariness, I’ve begun to like Dan Simberloff. He’s not just smart as a cobra. He’s also complicated. It would be easy to assume that his sleek scientific rigor and his adamantine empiricism are incompatible with a deep love of nature. But that, after all, would be just another theory.

“I was so …” He pauses.

He starts again. “I drove right over it into the next key, which is Bahia Honda, where the state park is. And I pulled over, and I cried. I couldn’t handle it. It was just so sad. And it so epitomized what was happening in the Keys.”

Simberloff knows, better than most of us, that the same sort of thing is happening on islands and mainlands all over the world. But sometimes the most personalized losses seem the most dire.

“That’s why I stopped working there,” he says.

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BARBARA Zimmerman's article on Amazon frogs, which Simberloff mentioned as we talked, was co-authored by Lovejoy's own field director, Rob Bierregaard. It was published in 1986. It's a provocative paper on several counts, and my own copy shows multiple layers of chicken-scratch notations from the half-dozen times I've read it over the years. Although it does carry Bierregaard's name, Zimmerman is the first author, and the frog data derive from her work. Really it's two papers in one: an analytical section on habitat requirements among thirty-nine species of frog, and a section devoted to arguing that the equilibrium theory holds no relevance whatsoever to conservation.

Like her mentor Simberloff, Zimmerman is a confirmed autecologist. She believes that the best route toward conserving frogs is the laborious, incremental, muddy-footed study of—what? yes, of course—frogs. She disbelieves ardently in theoretical shortcuts. Nearly three years of fieldwork convinced her that the survival of frog populations within the Amazon reserves depends on contingent details of available breeding habitat, not on reserve size. She identified three types of critical habitat, each of which supports different frog species: large streams, small permanent pools, temporary pools. The supply of those habitat types within the various reserves, she found, does not correlate with reserve area. In other words, ironic as it may seem, Zimmerman's involvement with the Minimum Critical Size of Ecosystems Project persuaded her that the very concept of minimum critical size (at least as an abstraction detached from particularities of habitat on a given site) is vacuous.

Maybe that's not so ironic, in fact. Maybe it's just science properly done, wherein conclusions based on empirical data don't always conform to initial assumptions.

Forget about sheer area, she argued. Forget the surveyor's boundaries. A hundred-hectare reserve containing a rich supply of breeding habitat will have more conservation value than a five-hundred-hectare reserve containing little. If you want to protect amphibians, she said, then ignore all those species-area curves, ignore $S = cA^z$, ignore the notion that only a big reserve is a good reserve, and focus your protection around streams and puddles.

This was the lesson of the frogs. In the paper's other section Zimmerman and Bierregaard made a broader claim. Cast in regretful tones, it sounded almost elegiac. "Because of the similarity between islands and nature reserves, there were great hopes that the equilibrium theory of island biogeography would produce guidelines for the design of nature reserves." What became of those hopes? Punctured, deflated, squashed. What became of applied biogeography? Nothing. What happened to the equilibrium theory itself? Ecologists got tired of reading about it. "The inescapable conclusion," according to Zimmerman and Bierregaard, is that MacArthur and

Wilson's theory "has taught us little that can be of real value planning real reserves in real places."

Dan Simberloff must have been gratified when he read this. Jared Diamond, presumably not. Tom Lovejoy stood apart from the pissing match, as always, and tried to stay dry. His project was still young and more data would come. The lesson of the frogs wasn't necessarily the lesson of the birds or the monkeys or the beetles. But because its narrow assertions are based solidly on experimental results, and because its broader argument is cogently stated, the Zimmerman-and-Bierregaard paper may have seemed, to some biologists, almost terminally persuasive. Was the SLOSS debate settled, then?

No. Probably SLOSS will never be settled, only eclipsed by newer frameworks of dispute. In the meantime, anyway, there was another interesting voice to be heard. A young man named William Newmark had entered the discussion.

NEWMARK wasn't associated with the Lovejoy project. His scientific ideas hadn't been shaped among Florida mangroves, New Guinea birds, or Amazon frogs. He worked in a chillier setting.

In the mid-1970s, Newmark came out of the University of Colorado with a degree in political science. Even as an undergraduate doing a poli sci major he had taken a smattering of ecology, and in one of those courses he had gotten his first exposure to the notion of ecological insularity. "This was in '74," he says. "I can distinctly remember the lectures, talking about island biogeography and saying that there may be some application to nature reserve design." MacArthur and Wilson's equilibrium theory was mentioned at least passingly in the course. Soon afterward, Newmark switched to biology, finished another bachelor's degree in that, and then started a graduate program at Michigan. While researching his master's thesis, a modest project concerning data collection within the Yellowstone ecosystem, he discovered that the archives of Yellowstone National Park contained faunal sighting records dating back through earlier decades of the park's history. The records told which species of animal had been seen when. They also told, implicitly, when certain species had stopped being seen. It was a potentially revealing body of information.

Newmark learned that the same sort of information existed for other parks too. Historical sighting records had found their way piecemeal into a wide range of chronicles, reports, and checklists. From those sources, Newmark realized, a patient researcher could compile a fuller set of checklists, indicating which animal species had been present in a given park when the park was founded and at various times since. In 1976, for instance, it was a matter of record that Yellowstone harbored moose and elk and bison and two species of deer, ravens and bald eagles and Clark's nutcrackers, mountain lions and lynx, bobcats and wolverines, black bears and grizzly bears, badgers and coyotes and ermine, among other species. How closely did that list match the list from, say, sixty years earlier? In 1916 there were moose and elk and bison and… virtually the same list, with a single addition: wolves. The gray wolf, *Canis lupus,* had been present in the old days but was now gone.

The sorry tale of wolf eradication in Yellowstone has little pertinence to island biogeography (and much pertinence to a benighted brand of wildlife management known as "predator control," once practiced by even the National Park Service), but it exemplifies the more basic fact that rosters of fauna within American national parks have been subject to change. Some species, once present, are later absent. And campaigns of active extermination aren't the sole factor responsible for such disappearances. Insularity is another. That wasn't lost on William Newmark.

Having finished his master's thesis, he was shopping for a doctoral topic. He remembered the sighting records. "I don't think I would have probably chosen the dissertation topic if I hadn't by chance run across these checklists when I was working in Yellowstone." He remembered also what he had heard, in the ecology course back at Colorado, about MacArthur and Wilson's theory. And he was aware that Jared Diamond, among others, had noted a parallel between nature reserves and islands. Newmark in response felt the same sort of empirical hankering as Tom Lovejoy: It would be nice to get some data on the relationship between insularization and ecological change. He decided to use faunal sighting records, from Yellowstone and other parks, for a study of that relationship.

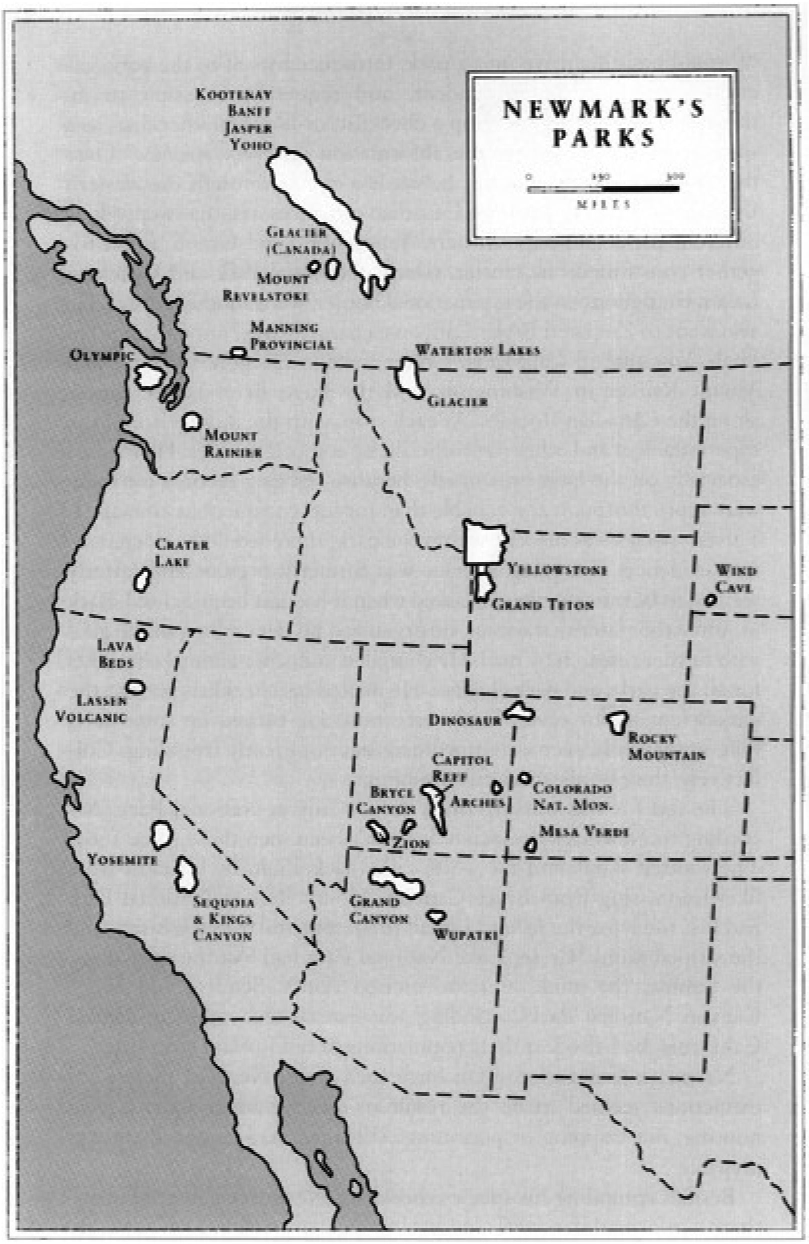
His working premise was that national parks are analogous to land-bridge islands. They represent bounded areas of natural landscape, formerly connected to much larger areas, that have become (or are in the process of becoming) insularized within an ocean of human impacts. They may be younger than Tasmania, they may be larger than Barro Colorado, they may be surrounded by wheat fields and fenced pastures and towns and highways instead of by water, but ecologically the situation is similar. If his premise was correct, Newmark guessed, certain patterns might appear in the sighting records.

He left Ann Arbor in autumn of 1983, headed west. "I was driving a small Toyota station wagon and I was sleeping in the back of it," he says. "I would basically drive into a park, introduce myself to the park scientists, the park superintendent, and request permission to go through their files and develop a checklist, or use their checklists as a starting point, and gather this information on every species." Over the course of several months, he made a circuit through the western United States and up into two Canadian provinces, visiting twenty-four different parks and park clusters. Yellowstone and Grand Teton together constituted one cluster. Glacier National Park and Waterton Lakes, contiguous on the international border, were another cluster. He also went to Zion and Bryce Canyon (separate parks, not clustered) in Utah, Yosemite in California, Crater Lake in Oregon, Olympic and Mount Rainier in Washington, and the huge Banff-Jasper cluster along the Canadian Rockies. At each stop, with the indulgence of the superintendent and other park officials, he combed the files. He focused especially on the larger mammals, because sighting records for them were more thorough and reliable than for less conspicuous animals. If a given species was present within the park, there would be documentary evidence. If a given species was formerly present and latterly seemed to be missing, then he asked when it had last been sighted. Back in Ann Arbor later that winter, he organized his data, filling in the gaps with further research by mail. He compiled uniform mammal checklists for all the parks and park clusters. He mailed his checklists back to the park scientists for review and correction. He turned up some facts that, individually, seemed unfortunate but not greatly troubling. Collectively, their implication *was* troubling.

The red fox was missing from Bryce Canyon National Park. According to Newmark's research, it hadn't been seen there since 1961. The spotted skunk and the white-tailed jackrabbit, by his tally, were likewise missing from Bryce Canyon. Mount Rainier National Park had lost the lynx, the fisher (a small predator similar to a weasel), and the striped skunk. Crater Lake National Park had lost the river otter, the ermine, the mink, and the spotted skunk. Sequoia and Kings Canyon National Parks, standing adjacent to each other in central California, had also lost their populations of red fox and river otter.

Newmark found more than forty such cases. None of these local extinctions seemed to be the result of direct human activity—not hunting, not trapping or poisoning. Whatever had caused them was invisible.

Besides compiling his species checklists, Newmark gathered quantitative information concerning habitat diversity within each park. He also took note of the size of each park and the year it was established. Species diversity, habitat diversity, area, age—on this body of data he performed a battery of mathematical analyses. Then he looked for larger patterns, and found some. Eventually he wrote a doctoral dissertation that turned heads in the scientific community, which not many doctoral dissertations do.



In early 1987 he published a summary of his results in *Nature.* Because *Nature* is an august journal and science writers watch it for leads, Newmark's findings made news in the wider world. The *New York Times* ran a story under the headline SPECIES VANISHING FROM MANY PARKS. The *Times* reporter, without troubling his readers with chatter about island biogeography, announced that mammal species were disappearing from North America's national parks "solely because the parks—even those covering hundreds of thousands of acres—are too small to support them."

The full dissertation had meanwhile achieved some circulation in photocopy form. From the first set of photocopies were taken further photocopies, grainy and bad, like home dubs from a bootleg recording of Bob Dylan performing half-drunk at a local bar. Word spread that this newcomer named William Newmark, whoever he was, had done an important bit of work. He had discovered evidence of ecosystem decay among

America's own treasured national parks.

In the dissertation, Newmark had written:

> Several predictions follow from the hypothesis that nature reserves are analogous to land-bridge islands. These are: (1) total number of extinctions should exceed total number of colonizations within a reserve; (2) number of extinctions should be inversely related to reserve size and; (3) number of extinctions should be directly related to reserve age.

The three predictions came right out of Frank Preston's discussion of samples versus isolates, as further developed in MacArthur and Wilson's theory and as interpreted for application in Diamond's "The Island Dilemma."

A nature reserve, by its essence, is a sample of landscape that is destined to become an isolate. The total number of extinctions "should exceed total number of colonizations" because immigration will be impeded. The number of extinctions "should be inversely related to reserve size" because (a) reserve size will determine population size for each species and (b) small populations face special jeopardies. The thrust of these first two predictions is that a newly delineated reserve will temporarily hold more species than its equilibrium number but that the surplus will progressively be lost, and that the losses will be comparatively great if the reserve is comparatively small. As time passes, species will continue being lost until the reserve has "relaxed" to a new equilibrium. The reserve age will be relevant as a rough estimate of how much time has elapsed since the sample became an isolate and, therefore, how far its loss of species has progressed.

Do the parks of North America conform to those predictions? Scrutinizing the fourteen western parks and park clusters for which records were most complete, Newmark found that they did. Bryce Canyon National Park, Lassen Volcanic National Park, and Zion National Park were the three smallest on the list. According to his research, they had each lost close to forty percent of their larger mammal species, either through direct human persecution or through insularization. Newmark factored out the species lost by direct human persecution—such as the gray wolf, which had been extirpated intentionally from Bryce Canyon, as it had from Yellowstone—and showed the subtotals of those extinctions with no apparent cause except insularization. Of this sort, Zion had suffered five. Lassen Volcanic, six. Bryce Canyon, with the smallest area, had suffered not quite so many extinctions—four—but Bryce Canyon is also a younger park than the other two. Maybe its time would come.

The largest park clusters had suffered the fewest losses. Yellowstone and Grand Teton together, twenty times as big as Zion, had lost nothing but the wolf.

Newmark's mathematical tests showed that the inverse correlation between extinction and area was statistically significant. In plain words, large parks had consistently lost fewer species than small ones. And young parks had also lost fewer species than old parks (though the correlation of those variables wasn't quite so strong). He concluded that the fourteen parks and park clusters had experienced "a mammalian faunal collapse," most likely caused by insularization. That was the essence of what he published in *Nature,* and that's what the *New York Times* carried.

Newmark had reaffirmed Preston's warning, given twenty-five years earlier: "If what we have said is correct, it is not possible to preserve in a State or National Park, a complete replica on a small scale of the fauna and flora of a much larger area."

The dissertation itself made another remarkable point, concerning the issue of habitat diversity versus sheer area. In one phase of his data analysis, Newmark had totaled up the checklists for each park and park cluster, and against those totals he had set a question: Were the differences in mammalian richness best explained by sheer area or by habitat diversity? Area is an easily measured quantity. Habitat diversity is less easily measured, since it involves complex and blurry gradations, but Newmark tried to touch at it indirectly by way of some other parameters—latitude, elevational range, plant diversity. Among those three, plant diversity might seem the most pertinent, since vegetation is such an important component of animal habitat. But he found that plant diversity didn't correlate significantly with the number of mammal species within each park. Latitude didn't correlate either. These results are notable. They tend toward refuting the habitat-diversity hypothesis, propounded by the Simberlovians during the SLOSS war. An argument in rebuttal can be made: that Newmark's three parameters missed the essence of habitat diversity. Still, it's interesting that, of the three, only elevational range showed a significant correlation with species number. And the strongest correlation that Newmark found was between species and sheer area.

The large parks contained more mammal species than the small parks—that much wasn't unexpected. What was unexpected, at least by some biologists, was that the best predictor of species diversity was sheer area, regardless of park-to-park differences in elevational range, latitude, or vegetation. This gave new support to the area-per-se hypothesis, which some Simberlovians had so persuasively reviled. It set Newmark's North American park mammals in counterbalance to Zimmerman's Amazon frogs. For conservation planners like Lovejoy, it had serious implications. But it never made the *New York Times.*

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"THERE IS ONE idealized will-o'-the-wisp goal, which we may or may not achieve," Lovejoy says over coffee at a hotel in Manaus. "Which I think is the ultimate goal for conservation anyway. Which is to have intact, fully diverse ecosystems persisting in reserves." He chooses his words carefully, even when his syntax is loose, and the most crucial of several crucial words in this statement is "persisting."

He's not talking merely about the miniaturized reserves of his Amazon project. He's talking about real nature reserves throughout the world. It's one thing to mark off an isolate of some ecosystem, hang a sign saying MINUSCULE NATIONAL PARK, post wardens to guard the boundaries from encroachment, and call it protected. Whether the species and relationships within that isolate persist over time, after the landscape all around it has been trashed, is another thing.

Take this central Amazon ecosystem as a test case, Lovejoy says. Consider the species diversity, just among trees. Assume that any tenhectare sample amid the continuous forest supports about three hundred tree species. "I want ultimately to be able to define a national park size so that, a thousand years from now, somebody can go in and sample ten hectares and *still* come up with three hundred species of trees. And draped around all that is the invertebrate diversity and everything else"—ants, ant-following birds, frogs, peccaries, butterflies, monkeys, jaguars. "I'm not interested just in the preservation of individual species. But of the whole system. And that's… you know, I may not achieve that. But that's what I'm thinking about."

He admits that the project has had setbacks. Fewer reserves have been isolated than he had hoped. Changes in government policy have eliminated the fiscal incentives for cattle ranching in the Manaus Free Zone, so the ranchers are no longer clearing much land for new pasture—which is good for the forest but bad for Lovejoy's experiment. Second-growth vegetation has sprung up in some of the clear-cuts, blurring the line (in both a physical and a conceptual sense) between isolated reserves and continuous forest. And there have been the routine hassles inherent to tropical field biology. Equipment has been hard to maintain. Funding has been insecure. Research permit renewals have been subject to bureaucratic delay. Leishmaniasis, a nasty disease carried by tiny crepuscular flies, has taken a toll on fieldworkers.

And the research results have proven more complicated than Lovejoy foresaw. The area effect, the distance effect, habitat diversity, edge effects, small-scale changes in climate, relationships between species, and the vagaries of chance are all implicated in the biological dynamics of forest fragments. Even after more than a decade, there's no simple message. Although the enterprise has yielded insights on the problem of ecosystem decay, ideally it would have yielded more. Still, Lovejoy doesn't seem discouraged.

"In a funny kind of way, we could have been sitting there in the forest drinking *cachaça"* for all these years, he tells me, "and the project would have had some real benefit." *Cacha ç a* is that old sugar cane moonshine used by Alfred Wallace for pickling specimens. What Lovejoy means is that the emblematic value stands to some degree independent of the empirical results. The Minimum Critical Size of Ecosystems Project has been recognized broadly throughout the scientific and conservation communities as a single visionary idea, not just a collection of loosely related studies. "Its existence has influenced people to think about the problem, around the world, and respond by setting aside bigger areas."

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LEAVING Lovejoy in Manaus, I return to the forest. I want to see it again from a perspective less Jovian than the view from a low-flying plane. I've arranged to spend a few days at one of the field camps, looking over the shoulders of two bird-banding interns named Peggy and Summer.

The self-mocking label by which these interns refer to themselves, Peggy and Summer and the others, is "bird slaves." They are generally young people with a bit of scientific training, or at least serious birdwatching skills, who have signed on to trade their labor for a tiny stipend and a chance to spend time in the Amazon. Peggy has a degree in earth sciences and environmental studies from UC-Santa Cruz. She has worked previously for the Peregrine Fund. Summer is a nonscientist with a streak of New Age idealism. Her previous experience includes eight years with a collective that ran a natural-foods bakery in Berkeley. Ever since she was a girl, Summer tells me, she wanted to come to the Amazon. "I have these throwback Neanderthal genes," she says, meaning it literally for all I can tell, and she feels them urging her to escape civilization for a more primitive life in the wilderness. She was inspired to volunteer for this bird-slaving tour of duty by her concern over rainforest destruction. But when she finally arrived here and began work, she admits with admirable candor, she found the forest terrifying. "I was scared shitless. It was just kind of a mental attitude. Then, after three months, I started to relax a little. Now I'm getting better." In response to my questioning, both Peggy and Summer declare that they have no thoughts whatsoever about the theory of island biogeography. As far as they are concerned, this project pertains to the ecology and preservation of the Amazon. Isn't that enough?

Well, yes. Okay. On one scale of judgment, it certainly is. Whether that scale of judgment encompasses the real significance of Tom Lovejoy's enterprise is a question that, for the moment, can be set aside.

Before dawn on the first day, we start walking. I follow them up a dark trail and out into a clear-cut, where the second-growth vegetation is short, thick, and weedy. Our destination is a hundred-hectare reserve. The two women wear headlamps powered by large battery packs and I carry a dippy little flashlight. We scuff along, ankle-deep in fallen *Cecropia* leaves as big as busted umbrellas. We step across dead logs, from the soggy flanks of which sprout lewd fungal growths in unearthly colors. The trail is slippery and narrow, a machetecarved tunnel through the weed zone. Then we enter the reserve itself, where the canopy is high and the understory is more open.

Lianas dangle down like a galleon's rigging. Capuchin monkeys yelp in the distance. Toucans and macaws shift from perch to perch overhead. The tree trunks are patterned with lichens and termite tracks. Epiphytes sit high in the limb crotches. From somewhere nearby comes the wolf-whistle call of a screaming piha. Although I catch glimpses by lamplight, my hearing tells me more than my vision. Memory supplies some ecological detail, and imagination adds a few beasts of its own.

I place my steps cautiously. I've heard Peggy mention that she surprised a sizable bushmaster (the world's largest species of viper, *Lachesis mutus,* famed for its propensity to strike without warning) at twilight on one of the trails. "Yeah, you could hardly miss it," she said. "A two-and-a-half-meter bushmaster, you're not likely to step on it." A snake so big and lethal that you couldn't set your foot on it in the dark? This leap of logic marks Peggy for an optimist, in my view, and as a pessimist I'm glad to be following ten paces behind while she walks point.

Beating the dawn is crucial for tropical bird banders. Their mist nets must be opened and ready by first light, when the birds begin moving. But working before dawn also exposes the banders to the crepuscular flies that carry Leishmaniasis. The disease is curable though ugly, I've been told, and the cure is ugly too: a series of injections of antimony. For protection I'm relying on long sleeves, pants tucked into boots, drugstore insect repellent, and fool's luck.

Peggy and Summer stop walking and I stride up beside them, still unaware that we've reached the net line. The fine nylon mesh is invisible until I've nearly smoodged my face into it. I flinch, from the same arachnophobic instinct that made me edgy on Guam. The central Amazon harbors at least one species of tarantula big and cocky enough to prey on birds. It may be the same species that Alfred Wallace knew and collected (another measure of his heroic fortitude) for its charm as a specimen. Rob Bierregaard too has seen one, in a mist net just like this, where it had killed a tangled bird before he could intervene. Mercifully, there's no sign today of the bird-eating spider. If there were, I'd probably push my head into its clutches and get wrapped up like a sulfur-rumped flycatcher.

The net line transects the reserve like a stutter of hyphens across a page. The nets are strung permanently on poles, so that each morning they need only be opened. Peggy and Summer and I set to it. Within a few minutes, we have deployed the whole line, a diaphanous barricade stretching three hundred meters through the forest. Then we vacate the area, crossing a sumpy blackwater stream and climbing a low slope. There, at the far side of the reserve, Peggy sits on a log. Get comfortable, she advises me.

The headlamps and batteries come off. The first hint of daylight leaks down through the broken canopy and then, soon, beams of sunshine. We're in the edge zone, where direct light and sun-loving species have begun penetrating the forest. A hummingbird appears before us to hover and gawk.

The hummingbird, a shiny little creature, has two tail feathers as long as toothbrushes. *Phaethornis superciliosus,* says Peggy, who knows a thousand things by their names.

After an hour we return to the nets. Peggy gently untangles the first bird. She soothes it, examines it, measures it. At a glance she and Summer both know it's a cinnamon-crested spadebill, *Platyrinchus saturatus,* of the Tyrannidae family. Its wide bill is adapted for scarfing small insects. This individual is a recapture, previously banded and released. Back at the office in Manaus, it's already on the computer. Now the fact of its lingering presence, and the details of its current condition, will be added to the file.

Peggy handles it deftly. She puffs feathers aside with a tickle of breath, checking the skin for parasites. She dictates to Summer: sternum configuration, percentage of fat, amount of body molt, wing length, tail length. Summer records the data. So do I, in my own notebook, without knowing why. My gut tells me only that there's something important, something preciously real, about such specificity. The tail length is twenty-five millimeters. The wing length, fifty-three millimeters. Body molt, none. Band number, 24998. The bird weighs ten grams.

Peggy opens her hand. For a moment the dainty brown spadebill sits dazed on her palm, heart pumping furiously, and I have time to wonder about its future. How long can *Platyrinchus saturatus* maintain itself in a hundred-hectare reserve? Will this species eventually disappear, like the margay cat and the golden-handed tamarin? Will it follow the birds that follow the ants? Will it prove to be ecologically desolate in the absence of solitary bees? Will it suffer terminally from the rupture of some other mutualistic relationship? Will it die back to a state of precarious rarity, then damage itself with inbreeding, lose its adaptive vigor, and be finished off by a minor accident? Or is one hundred hectares of insularized habitat all the universe that a population of cinnamon-crested spadebills will ever need?

And furthermore: Will the Lovejoy experiment answer these questions?

The bird flies suddenly, vanishing into the forest. *"Ciao"* Peggy says. Yes, I think. Goodbye and good luck.