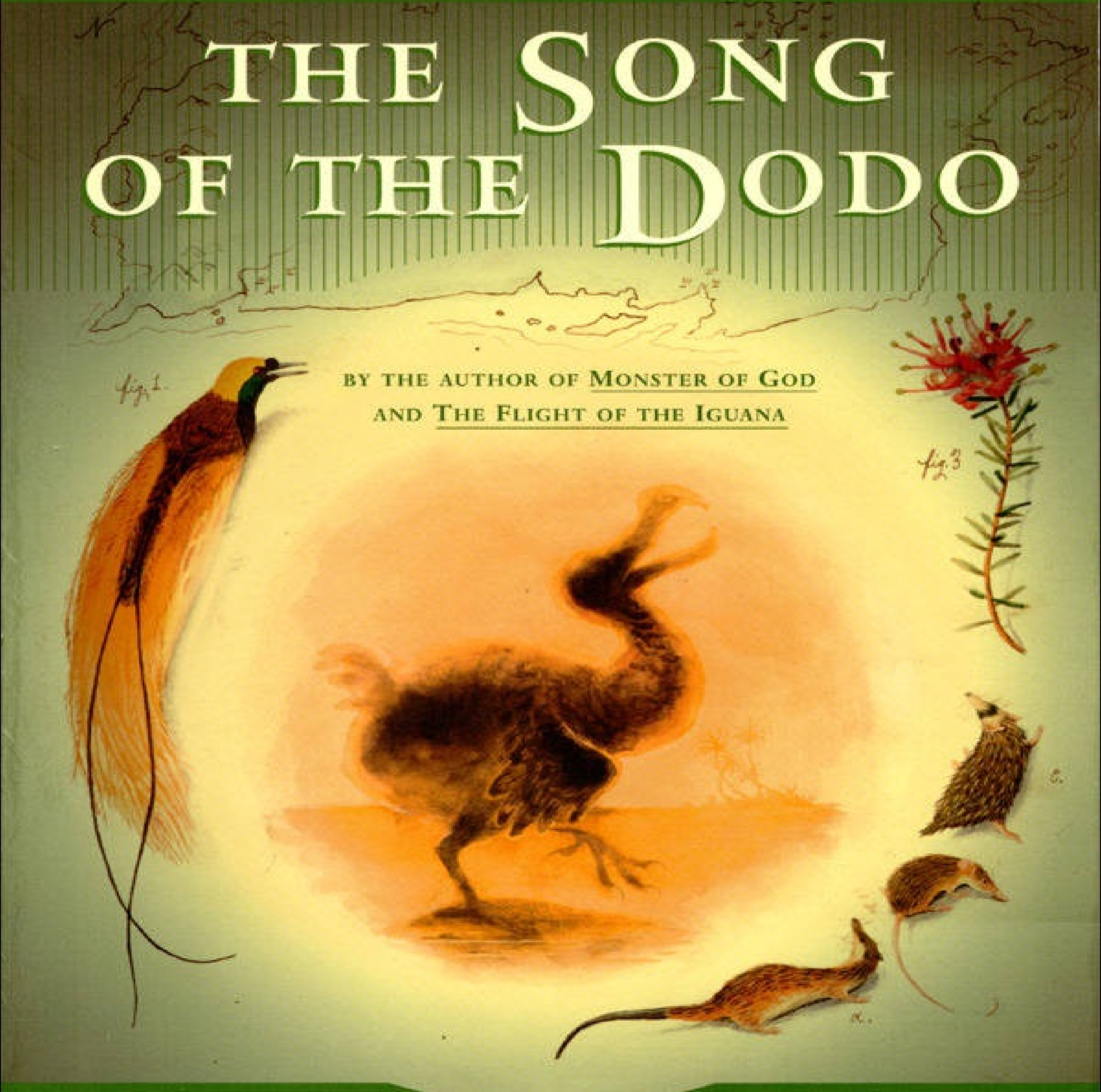
Winner of the John Burroughs Medal for Natural History Writing and the Helen Bernstein/NY Public Library Award for Excellence in Journalism

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 COMING THING

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IN 1967 Princeton University Press published a small, dense, eyecrossingly mathematical book that I've already mentioned, *The Theory of Island Biogeography.* It was the first in a series that Princeton intended to bring out under the collective rubric Monographs in Population Biology, and its premier position in that series hinted at the fact that this drab little volume concerned itself not just with islands and not just with biogeography.

Population biology, at that time, was still a new label for a new combination of scientific concerns and perspectives. It had subsumed a number of disciplines that, throughout earlier decades, earlier centuries, were generally treated as distinct: evolutionary biology, taxonomy, biogeography, ecology, the demography of plant and animal species, genetics. During the 1930s and 1940s, evolutionary biology (as descended from Darwin and Wallace) had at last become informed by and integrated with genetics (as descended from Gregor Mendel, of whose work Darwin and Wallace were ignorant), largely through the efforts of such men as Sewall Wright, R. A. Fisher, J. B. S. Haldane, and Theodosius Dobzhansky. Also during that era, taxonomy had been added to the synthesis, thanks much to Ernst Mayr and George Gaylord Simpson. By the 1950s, a great ecologist and teacher named G. Evelyn Hutchinson, born British but latterly fetched up at Yale, had started to bring a modestly mathematized style of ecology into conjunction with those other elements. Hutchinson's own research specialty was limnology, the study of lakes. It was a canny choice for an ecologist of his bent, in that lakes are neatly bounded ecosystems, relatively small and relatively impoverished, and therefore lend themselves well to relatively thorough ecological investigation. They share that with islands—not surprisingly, since a lake is the reverse image of an island. But the similarity between lacustrine and insular ecosystems isn't what puts G. Evelyn Hutchinson into this story. Among the graduate students who would go on to add luster to Hutchinson's reputation as a teacher—foremost among them, in fact—was a young man named Robert MacArthur, born in 1930.

After finishing a master's degree in mathematics, MacArthur had turned to ecology, arriving at Yale in 1953 for a doctoral program under Hutchinson's guidance. By 1955 he had published a paper in *Ecology.* By 1957 he had produced a provocative theoretical contribution that appeared in the *Proceedings of the National Academy of Sciences.* His dissertation work, a study of community structure and niche partitioning among different species of warbler, also yielded a paper for *Ecology,* which appeared in 1958 and became recognized as a minor classic. Young MacArthur was a hot prospect. He possessed the right combination of talents and ambitions to make a big impact at that particular time on that particular field. He was formidably bright, restless, almighty curious, innovative, and mathematically proficient. He loved the natural world, especially birds, but he had no interest in spending his life as a descriptive field naturalist. He cared about ideas and deep mechanisms, about order and explanation, not just about creatures and landscape. He was eager to change the very character of ecology.

MacArthur felt that the science of ecosystems should venture beyond description. It shouldn't limit itself to collecting and indexing facts. It should find broader patterns in the natural world, and from those patterns it should extract general principles. It should measure and count and perform calculational abstractions that would illuminate the essential amid the contingent. It should construct mathematical models that would function as usefully as a slide rule. It should be vigorous enough and bold enough to make predictions. It should offer theory. Olof Arrhenius, Henry Allan Gleason, and a few other ecological researchers had made modest efforts in that vein. So had Hutchinson himself. And Frank Preston had begun ringing the bell of canonical distribution just as MacArthur reached his scientific adulthood. But ecology as generally practiced was still a loose-jointed, descriptive, nonquantified, nontheoretical enterprise.

MacArthur began to teach. He continued to publish interesting papers. His reputation blossomed. In 1965, after several years at the University of Pennsylvania, he accepted a professorship at Princeton, his role there to include the overall editorship of the Monographs in Population Biology, which offered promise as a forum for the newfangled ecology that he favored. MacArthur would co-author the first monograph himself. By that time he had met and begun sharing ideas with another young scientist, Edward O. Wilson.

Wilson was a myrmecologist, a specialist on the biology of ants. He had grown up in the South, a nature-loving boy who collected insects and kept snakes, spending much of his time alone in the woods and swamps of Alabama and northern Florida. He had become interested in ants by the time he was nine, and soon after that he began doing precociously serious myrmecological fieldwork. Why ants? To some degree it was their inherent fascination, to some degree it was a choice urged by necessity. "I had use of only my left eye," Wilson explains in an autobiographical essay published in midcareer. The right eye "was mostly blinded by a traumatic cataract when I carelessly jerked a fish fin into it at the age of seven." With only monocular vision, he had found it hard to watch birds or mammals in the field. But the left eye was very acute, especially for fine detail at close range. "I am the last to spot a hawk sitting in a tree, but I can examine the hairs and contours of an insect's body without the aid of a magnifying glass." Many young boys collect insects; this one-eyed boy was doing real science.

At age thirteen Edward Wilson began a rigorous study of certain ant groups in the Mobile area and made his first publishable observation. Several years later, with adolescent earnestness, he decided that he should pick an entomological specialty.

Based on the challenge and opportunity they offered, he chose flies (the order Diptera), in preference to ants. But it was 1945 then, and World War II had interrupted the supply of insect pins, which came mainly from Czechoslovakia. Since ants are best preserved in small vials of alcohol rather than mounted on pins, Wilson switched back to them—and has never regretted it. "In a sense, the ants gave me everything," he declares. His highest career aspiration at that age was to be a government entomologist, "to ride around in one of those green pickup trucks used by the U.S. Department of Agriculture's extension service" and help farmers cope with their crop pests. But he had a first-class scientific brain, as it turned out, which carried him from the University of Alabama to the University of Tennessee and then to Harvard. The particular attraction of Harvard, as put to him, was that its museum held the world's largest collection of ants. "Get a global view," an older colleague had told him; "don't sell yourself short with entirely local studies." When he met Robert MacArthur, in late 1959, Wilson had recently returned from a long stint of fieldwork in the tropics.

His skills and his interests were complementary to MacArthur's. Whereas MacArthur had shifted from mathematics to mathematical ecology, Wilson was a taxonomist and a zoogeographer. He had made extensive collections in New Guinea and Australia, on the island of New Caledonia, in the New Hebrides, on Fiji. He knew more about the Cerapachyinae and the Ponerinae subfamilies of ants in Melanesia than any man-jack on Earth—what they looked like, how they made their livings, which species lived on which islands. Like MacArthur, though, he was interested in more than the description of natural history phenomena. As his head and his field notebooks filled with ant data, Wilson had begun to see patterns. For example: The number of ant species on an island tended to correlate closely with island size.

Wilson's brainload of purely descriptive data seems to have helped bring on an existential headache. In 1961, feeling mildly depressed and unsure about his professional direction, he took a sabbatical. During this getaway from Harvard he went to South America. He loved fieldwork as much as ever, and the rainforests of Surinam, to his great pleasure, were rife with previously unstudied ants. He also visited the islands of Trinidad and Tobago, just offshore from Venezuela. Trinidad is large, Tobago is small. On Trinidad he found more species of ant than on Tobago.

Pondering the descriptive sort of work he had been doing, Wilson yearned for something more. "It just didn't seem enough to continue enlarging the natural history and biogeography of ants," he confides in his short memoir. "The challenges were not commensurate to the forces then moving and shaking the biological sciences." His recent acquaintance with Robert MacArthur and some other young mathematical ecologists, and his awareness of G. Evelyn Hutchinson's work, had persuaded Wilson that "much of the whole range of population biology was ripe for synthesis and rapid advance in experimental research; but this could only be accomplished with the aid of imaginative logical reasoning strengthened by mathematical models." He was a mediocre mathematician, by his account, with no training beyond algebra and statistics. So during his brooding summer in Trinidad and Tobago, besides collecting ants, he taught himself some calculus and probability theory out of textbooks. Returning to Harvard, he enrolled in a mathematics class and sat conscientiously, as an associate professor, in a small desk among a crowd of undergrads. Eventually, after further remedial classes, he had enough math to feel comfortable. Meanwhile he began a collaboration that would take him beyond the descriptive.

"In 1962 Robert H. MacArthur and I, both in our early thirties, decided to try something new in biogeography," Wilson relates. "The discipline, which studies the distribution of plants and animals around the world, was ideal for theoretical research. Biogeography was intellectually important, replete with poorly organized information, underpopulated, and almost devoid of quantitative models. Its borders with ecology and genetics, specialties in which we also felt well prepared, were blank swaths across the map." Wilson told MacArthur that he thought biogeography could be made into a rigorous, analytical science.

There were striking regularities in the welter of data, Wilson said, that no one had explained. The species-area relationship, for instance. More particularly, the recurrent ratio to which Philip Darlington had called attention: With each tenfold decrease in area came roughly a twofold decrease in species diversity. Among the ant species of Asia and the Pacific islands Wilson had noticed another pattern. Newly evolved species seemed to originate on the large landmasses of Asia and Australia and to disperse adventurously from there out to the farflung islands. As those dispersing species colonized small and remote places such as Fiji, they seemed to supplant the older native species that had gotten there before them. New species were continually arriving, old species were continually going extinct, and the net effect was… no gain or loss in number of ant species. It looked to Wilson like some sort of natural balance.

Yes, said MacArthur, an equilibrium.

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"HE WAS MEDIUM tall and thin, with a handsomely angular face," as Wilson remembers MacArthur. This was written a decade after MacArthur's early death. "He met you with a level gaze supported by an ironic smile and widening of eyes. He spoke with a thin baritone voice in complete sentences and paragraphs, signaling his more important utterances by tilting his face slightly upward and swallowing." Although it may not have been a complete sentence when MacArthur first spoke the word "equilibrium" to Wilson, presumably he tilted up his face.

"He had a calm understated manner," Wilson continues, "which in intellectuals suggests tightly reined power. Because very few professional academics can keep their mouths shut long enough to be sure about anything, MacArthur's restraint gave his conversation an edge of finality he did not intend. In fact he was basically shy and reticent."

To that portrait, subjective and affectionate, Wilson adds a statement that stands as dead accurate: "By general agreement MacArthur was the most important ecologist of his generation."

The two of them brainstormed together during 1961 and 1962 over this notion of a biogeographical balance. They scrutinized Wilson's ant data from Melanesia. They looked at patterns of distribution among bird species in the Philippines, Indonesia, and New Guinea, which they extracted from published work by Ernst Mayr and others. They referred back to Darlington's enumeration of beetle and reptile species on the various Antillean islands, and they looked into the case of Krakatau, for which there were those historical records of recolonization by animal species after the cataclysmic purge. They read Frank Preston's recent paper on the canonical distribution of commonness and rarity, finding it essentially in agreement with their own views. They grew convinced that the species *lost* from an island, during a given span of time under ordinary circumstances, are roughly equal in number to the species *gained* by the same island over the same span of time. Unless the island itself is very recent in origin or has undergone a sudden disruption, the rates of losses and gains tend to cancel each other out. The result is a dynamic stability. The *number* of resident species remains steady while, with one species replacing another, the roster of *identities* changes continually.

Just how are species lost from an island? By local extinction. And how are they gained? Two ways: (1) by speciation, when a single old species splits into a pair of new species, and (2) by immigration, when a species arrives and becomes established. MacArthur and Wilson suspected that the second of those two, immigration, is vastly more frequent than the first. Speciation could be disregarded, then, and the equilibrium they envisioned could be expressed as a balance between immigration and extinction. It's worth repeating that extinction in this context refers usually to the local extinction of a population, not to the global extinction of a species. Mainlands or neighboring islands, having supplied the flow of transoceanic immigrants, supply still more as extinctions occur.

MacArthur and Wilson drew a simple, vivid graph that showed two sloping lines forming an X: the immigration line coming down, from left to right, and the extinction line going up. The downward slope indicated that immigration events tend to *decrease* in frequency as an island becomes crowded with species. The upward slope indicated the converse—that extinction events tend to *increase* in frequency with increasing crowdedness. Each of the lines was curved slightly, into a gentle concave sag, indicating subtle changes in the rate at which immigration decreases and extinction increases on an ever fuller island. In midgraph, the lines crossed; their crossing point marked equilibrium. The number of species corresponding to that graph point is the island's normal complement of species, remaining roughly constant through time. At least that's what MacArthur and Wilson hypothesized.

They also created an intricate mathematical model—a long sequence of differential equations capable of accepting numerical data at one end and, like the canning line in a pickle factory, emitting a conveniently transmogrified product at the other end. The product of this canning line was predictions. The model foretold particulars of equilibration (how much elapsed time? how many species?) on a given island.

MacArthur and Wilson then co-authored a paper, which the journal *Evolution* published in 1963. Titled "An Equilibrium Theory of Insular Zoogeography," this paper contained the essence of their concept, lucidly presented, but for one reason or another it didn't have the immediate effect of turning the whole science of ecology sideways. That was still to come.

They weren't finished with the theory. They expanded the range of supporting data to include plant species as well as animals. They added some discussion of related topics—the process of colonization, the process through which an island community might resist colonization by new species, and also a bit about evolution on islands. Four years later, their expanded version became volume one of the Princeton monographs, published as *The Theory of Island Biogeography.* The slight change in title, from the article to the book, suggested a major increase in confidence and scope.

The new title even sounded a little presumptuous. *An* equilibrium theory of island biogeography had become *the* theory of island biogeography. It wasn't actually the only such theory; the scientific literature was already lightly peppered with theoretical notions concerning the biogeography of islands. But none of the others was so forceful, none was so detailed, and none ever proved so influential. The title's presumption was vindicated. This was the book that changed things.

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To SOME people, few but vocal, Edward O. Wilson is a bugbear, infamous as the leading enunciator of a branch of science called sociobiology. To others, he is famous and much admired for the same reason. Yes, it's the same Edward O. Wilson who published *Sociobiology: The New Synthesis* in 1975, daring to suggest that human social behavior might be partly shaped by evolutionary genetics. That phase of his life and career is a story in itself (how he was accused of inventing pseudoscientific justification for a racist and sexist status quo; how he was denounced in print by leftist intellectuals and on the placards of angry young demonstrators; how he achieved the unwelcome distinction of having a pitcher of water dumped on his head, by one of those demonstrators, while addressing the American Association for the Advancement of Science), but it's not the story I'm telling. To still other people, more recently, Edward O. Wilson is a brilliant polymath and an elegant writer, a statesmanlike voice of warning about global losses of biological diversity, a wise elder to the conservation movement. And among his entomological colleagues, he is a towering authority on the taxonomy and behavior of ants.

Aware of all those Wilson personae, I'm interested in still another. To me he's the sole surviving member of the MacArthur-and-Wilson partnership, and therefore a maker of history. He's the one living human best qualified to explain how such an informal and seemingly peripheral field as island biogeography became so formalized and so central to the science of ecology. He's also, as I discover, a generous, mild, and unassuming man. He offers me three hours of intellectual hospitality from the middle of his busy workday as calmly as a goodhearted Methodist minister visiting the sick. "Please call me Ed," he says. "And I'll call you David, if I may."

His office, on an upper floor of Harvard's Museum of Comparative Zoology, is a large, cheerful room decorated in memorabilia and ants. Unlike the ants that come and go through my own office, his are in cages. The cages are neat plastic units arrayed on long lab tables. Some of them, no doubt the ones holding tropical species, are warmed gently by red electric bulbs. An oversized bronze sculpture of an ant, big as a lobster, sits on a pedestal bearing an award inscription. An old Georgia license plate, a nonsense memento of the sort that arrive in the mail as gifts, reads HIANTS. And the skull of a sabertooth cat (or a facsimile cast, anyway) rests on a table, offering a note of mammalian relief to the myrmecological theme.

Far up on the left wall hangs a row of imposing, black-framed photographs: five venerable men. Are they Ed Wilson's distinguished predecessors here at the Museum of Comparative Zoology? That's my guess; and I succeed in identifying one of those faces as William Morton Wheeler, a great American ant maven of the early twentieth century. The rest are strangers to me. Five dignified elders, they glower down on everything. Has the Harvard administration issued these photos as mandatory office decor, like the unctuous shot of the president in every post office? On the opposite wall, ironically contrapuntal in identical black frames, five ants glower back.

Far across the room, inconspicuous beside Wilson's small desk, hangs another photo: the young Robert MacArthur.

Before we get serious about islands, Wilson hosts me to lunch. From his office refrigerator he pulls out turkey sandwiches, bottles of lingonberry juice, and paper-wrapped pieces of baklava, all of which he seems to have shopped for at some local deli himself. He apologizes, this eminent man, this wonderful lunatic of politeness, for the food's not being fancy. But the turkey is fine and the lingonberry juice has come all the way from Finland. As we stuff our faces we talk ramblingly about the politics of scientific funding (especially ecology versus molecular biology, with ecology getting short shrift) and about the sociopolitical challenge of conserving biological diversity. Both those related subjects concern him deeply. But the Finnish juice gets us off on a digression about Scandinavian surnames, and he voices curiosity about mine.

It's Norwegian, I answer. The original version, before Ellis Island—so I've been told, anyway—translates roughly as "cow-herder" or "cow-man." I suppose that could be stretched to "cowboy," if a person liked the ring of the word, which I don't. Besides, I say, in Norway there's no swaggering ethos involving horses and dip tobacco and pointy boots. My prattle on the subject moves Wilson to confide that he has always chafed at the ordinariness of his own name. If it had to be WASP, he says, at least it could have been something more robust. Such as Stonebreaker, he muses. Curling his mouth to a little smile, he stares into space and repeats, Stonebreaker. I imagine it: *Dr. Edward O. Stonebreaker, the renowned ant expert and sociobiologist, announced today at Harvard that he would no longer use the name Wilson and that, furthermore, no Marxist yoyos would ever again dump water on* HIS *head.*

But he doesn't seem to be a man of grudges, or of ponderous selfimage. The joke of this jokey name is one that he plays on himself. Yes, he decides, Stonebreaker would be his choice, because it so nicely suggests generation upon generation of big-muscled, stolid ancestors, some of them wearing manacles at the ankle. He chortles.

After the baklava, we carry coffee cups to a seminar room just up the hall from his office. Anticipating the focus of my questions, he has offered to show me some slides. What he means, I discover, is that he'll give me a private lecture on the origins and development of the MacArthur-and-Wilson theory. A projector sits ready. Wilson clicks up the first slide and then, triggered by that image into an outpouring of scientific and personal reminiscence, talks for almost an hour before clicking on to the next.

The slide shows two young men, dressed for tropical fieldwork, on a sun-scorched cay of white sand. One of the two, thin and angular, wears chinos and deck shoes and a red-and-white baseball cap with the brim pulled low, barely revealing a three-day beard.

"MacArthur always hated to be photographed," Wilson tells me.

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IN THE LATE 1940s and the 1950s, Wilson says, G. Evelyn Hutchinson gathered around himself at Yale a small circle of extraordinary graduate students, to whom he was teaching evolutionary theory and "stressing over and over again that ecology needs an evolutionary twist." It was an unconventional approach back then, when ecology and evolution were still generally treated as separate and the integrated perspective of population biology had only begun to take hold. Hutchinson and these particular students were cutting a little deeper than others, says Wilson, in exploring how evolutionary adaptation played a role in the dynamics of complex communities. Anyway, one of the Hutchinsonians was a young fellow named Larry Slobodkin, who had just written a little ecology textbook expounding the quantitative model-building approach to evolutionary problems.

Wilson himself, up at Harvard, wasn't part of Hutchinson's circle. He had not yet met MacArthur or taken his South American sabbatical. But he knew Larry Slobodkin, and they got along well. Since their interests meshed, he and Slobodkin started planning a joint project.

Slobodkin had some of the mathematical skills that Wilson lacked, as well as a firm grounding in ecological theory. Wilson for his part was strong on myrmecology, on biogeography, and on speciation theory. "Slobodkin and I saw that we could put these two bodies of knowledge and these approaches together, and maybe do a book on population biology," Wilson recalls. They had even discussed it with a publisher. "Then Slobodkin hesitated. He said, 'We really need a third author' "—a specific fellow, a certain mathematician whom Slobodkin had in mind—"'because he's just so damn good. He's so brilliant and he's the coming thing in ecology and full of ideas. I want you to meet Robert MacArthur.' "During a conference in December of 1959, they did meet. "And he and I hit it off immediately," Wilson says.

I gaze at the young man in the red-and-white cap, now famous, now departed, whose image remains frozen on Wilson's screen.

MacArthur was just back from a postdoctoral year at Oxford. He struck Wilson as "a somewhat ethereal, delicate, slightly Anglicized American who clearly was thinking deeply about these subjects." Also, just as clearly, he was ambitious to do something exciting and drastic in population biology. Fine; so was Ed Wilson. They quickly became friends, started a dialogue through the mail, and traded ideas toward that proposed three-author book. Wilson even drafted a few chapters. But then for some reason the friendship between Slobodkin and MacArthur went sour—it was Slobodkin who took a dislike to MacArthur, by Ed Wilson's recollection, and MacArthur who felt wounded—so the book project fell apart. Wilson himself went off on that sabbatical and began his remedial studies in math. When he returned north, his attraction to quantitative methodology was stronger than ever, and he resumed the contact with MacArthur. They met when they could, at conferences, at the University of Pennsylvania when Wilson was invited down there to speak, at MacArthur's summer home in the small town of Marlboro, Vermont. They had "runaway conversations about biology—about the future of population biology and so on." They were young and energetic, dreaming the sort of wild plans that energetic young men often dream. But these two weren't just young and energetic. Though Ed Wilson doesn't say so, they were also disciplined, scientifically sophisticated, and extraordinarily smart.

They hankered to collaborate on some project or another. "And I felt that the main collaborative effort would be in biogeography, because that was my passion." Wilson was mesmerized by the biogeographic patterns that he had found among his own field data on tropical ants and had read about in the works of Darlington, Mayr, and others. He was especially intrigued by species-area curves. "I became increasingly interested in them because to me they represented, possibly, an equilibrium. They represented some kind of law." He and MacArthur talked a good deal about what they saw as "the balance of nature."

The old photo of MacArthur still shines before us. Without a good fan in the projector, this precious slide would have long since suffered meltdown.

"Okay," says Wilson, "now I'm coming up to the crunch." He has told the story before, in some of his classes, but never to a smaller or more interested audience. "Slobodkin drops out," he says. "Mac-Arthur and I become thick as thieves. We're now enchanted by the idea that something really important might be done with biogeography. So I keep saying, 'Biogeography, that's the field of the future.' Balance of nature. Equilibrium and so on. We're looking at those curves. Then in '62, the summer of '62, after talks in Pennsylvania and Marlboro, at his summer house, I get through the mail a little two- or three-page letter with the equilibrium model—the crossed lines—from MacArthur. And he says, 'I think that's the way the whole thing might be approached.' And I look at this thing. And I say, 'Yes, that's it.' "

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THE EQUILIBRIUM theory of island biogeography is not a piece of conceptual art. It's a tool. MacArthur and Wilson developed it for two reasons: to explain and to predict.

Although its mathematical details are egregiously complicated, its essence is simple. Think of it as analogous to your digital watch. You don't need to comprehend the circuitry on a silicon chip in order to read the time. Probably you have even mastered the task (after a trialand-error struggle, if you're like me) of setting the little alarm tweeter and using the stopwatch function. Meanwhile you've preserved your happy ignorance of the chip. Yes? The deal with this equilibrium theory is similar. MacArthur and Wilson's 1963 paper, in which the theory was first presented, contains a moderate amount of arcane mathematical circuitry. Their book, from 1967, contains an immoderate amount. You and I are gonna ignore it. We're interested in telling time and in using the tweeter, not in the how-to of electronic digital engineering.

Two patterns of real-world data served as the starting points for the theory, which was devised to account for them jointly.

First pattern: the species-area relationship. The ants that Ed Wilson knew so well, on islands of the western Pacific, showed a nicely regular version of that relationship. There were more ant species on the bigger islands, fewer ant species on the smaller islands. The carabid beetles and the reptiles and amphibians of the Antilles showed other neat versions of the species-area relationship, as Darlington had reported. The land birds of certain Indonesian islands showed still another. In each case, larger islands contained more species than smaller islands, and when the numbers of species were graphed against the sizes of the respective islands, the graph points arrayed themselves (with a little logarithmic jiggering) as a straight line. Despite its straightness, as you'll recall, the line was what scientists call a curve. The slope of each species-area curve could be expressed as a decimal number, which varied from one group of islands to another.

To restate the slope business in plain English: Among some island groups, the big islands contained *many* more species than the small islands, while in other island groups, the big islands contained only marginally more species than the small islands. Frank Preston had said as much in his 1962 paper, as MacArthur and Wilson acknowledged (though Preston had been talking mainly about sample areas, not isolates). The equation offered by MacArthur and Wilson for the species-area relationship was the same one that Preston had credited to Arrhenius: $S = cA^z$. The exponent z represented the slope of the curve—that is, the extremeness of the correlation between species number and island size within each group of islands. That exponent took one value for Antillean beetles, another value for Indonesian birds, still another for ants of the western Pacific. Every set of islands was different, though not *too* different; there did appear to be some inherent consistency in the degree to which big islands contained more species than small islands. The average slope value among the cases presented by MacArthur and Wilson was roughly 0.3—just another number to you and me, but a benchmark to anyone studying the interplay of species diversity and area.

The second pattern underlying MacArthur and Wilson's theory, like the first, had long been familiar to biogeographers: Remote islands support fewer species than less remote islands.

This pattern shows itself in several different ways. An island of some given size, if located near a mainland, generally supports more species than a similar-sized island far offshore. Also, a small island near a large island (for instance, one of the satellite islands around New Guinea) generally supports more species than a small island with no big neighbor. And finally, an island that is part of a small island archipelago, though far from the nearest mainland or big island, generally supports more species than a solitary island equally far from major neighbors. In each case, the species richness correlates inversely with the degree of isolation.

MacArthur and Wilson's predecessors had commonly explained that pattern in historical terms. Remoteness was an impediment that only eons could overcome. Impoverishment together with remoteness suggested that an island's history had been relatively brief. Colonization of any new oceanic island took time—vast sweeps of time, if the island was remote—and remote islands were generally not ancient enough to have acquired great richness of species. So said the historical hypothesis.

But MacArthur and Wilson suspected that history wasn't the answer. Time was the limiting factor only during the earliest period on a new oceanic island, they believed, and most of the world's island ecosystems had long since come to maturity, to a state of balance, to equilibrium, with the number of species on each a reflection of ongoing processes, not historical circumstances. The ongoing processes that most shaped the balance, they argued, were immigration and extinction.

On page 21 of their book MacArthur and Wilson reprinted the sagging-X graph to illustrate this ahistorical theory. The immigration curve slopes downward from the left. The extinction curve slopes upward to the right. The decrease in immigration rate and the increase in extinction rate are graphed not against elapsed time but against the number of species present on a given island. As an island fills up with species, immigration declines and extinction increases, until they offset each other at an equilibrium level. At that level, the rate of continuing immigration is just canceled by the rate of continuing extinction, and there is no net gain or loss of species. The phenomenon of offsetting increase and decrease—the change of identities on the roster of species—is known as *turnover.* One species of butterfly arrives, an other species of butterfly dies out, and in the aftermath the island has the same number of butterfly species as before. Equilibrium with turnover.

This sagging X of crossed curves became the most renowned and provocative graphic image in the ecological literature. It or its variants would eventually show up in countless books and papers. It would be fervently saluted by many ecologists and fervently denounced by quite a few others. If Preston's canonical curve was the bell heralding change, MacArthur and Wilson's equilibrium figure was the flag of revolt.

Their conceptual model does explain the two patterns of real-world data, and its explanatory power is what made it forceful. Small islands harbor fewer species than large islands—why?—because small islands receive fewer immigrants and suffer more extinctions. In MacArthur and Wilson's schema, that's known as the area effect. Remote islands harbor fewer species than near islands—why?—because remote islands receive fewer immigrants and suffer just as many extinctions. That's the distance effect. Area and distance combine their effects to regulate the balance between immigration and extinction. It all fits together ingeniously.

The sagging-X figure as it appeared in the book was just a generalized version of specific equilibrium graphs that can be drawn for specific islands. The curves will be steeper for some islands than for others, because of particular localized circumstances. As the steepness varies, the crossing point shifts downward or up (indicating a lower or higher turnover rate, at equilibrium) and leftward or right (indicating a lower or higher number of species, at equilibrium). When either curve is especially steep—reflecting the fact that immigration decreases especially sharply or extinction increases especially sharply—their crossing point shifts leftward, toward zero. The shift means that, at equilibrium, in this particular set of circumstances, there will be relatively few resident species.

In other words, high extinction and low immigration yield an impoverished ecosystem. To you and me it's just a dot in Cartesian space, but to an island it represents destiny.

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WEEKS went by. MacArthur had mailed Wilson his little sketch of the crossed lines and Wilson had said eureka; but the full theory, with its supporting arguments and math, was not yet on paper. Then one day they were sitting together near the fireplace in MacArthur's living room, as Wilson recollects, with notes and graphs spread out before them on a coffee table. This was late 1962. They felt satisfied that their equilibrium model gave a good explanation for the two real-world patterns. But that wasn't enough. Both patterns—one reflecting the distance effect, one the area effect—were relatively uncomplicated, and some alternative theory might account for them equally well. MacArthur and Wilson needed further evidence. They needed to show an intricate match between what their theory said and what *was*.

MacArthur suggested a way. Using the mathematical machinery of their theory, they could calculate how quickly a newborn island should approach equilibrium, and how that rate of approach should correspond to the island's eventual rate of turnover. The numbers would be different for each different newborn island. They should pick one and try it. Having made the calculations, based on the actual area and remoteness of their chosen island, they could compare their theory-derived answers against empirical data. The theory would be either supported or contradicted. It was a good suggestion with one practical drawback: Newborn islands are rare. And not many have ever been scientifically studied during the approach to species equilibrium. So there wasn't much empirical data available. Lonely nubs of fresh lava, cooling like slag in midocean, don't often attract ecologists.

At this point Ed Wilson had an idea. Let's look at Krakatau, he said.

Wilson himself had never been there and didn't propose to go, but he knew something about Krakatau from the literature. He knew that the great eruption of 1883 had killed everything, leaving only a cauterized mound, and that the ash had barely settled before spiders and insects and fern spores began arriving to fill the biological vacuum. He knew that the cauterized mound was effectively a newborn island. He recognized that this mound (under its new name, Rakata) could offer a well-documented case of an island's approach to equilibrium. It was as close to a theory-testing experiment as two eager young biogeographers could get.

So MacArthur and Wilson began calculating. They focused on birds. Extrapolating from a species-area curve for the avifaunas of other Asian islands, they figured the number of species that Rakata should support at equilibrium. They figured how much time should have been necessary, after the sterilizing explosion, for Rakata to reach that equilibrium. They figured what the turnover rate should be at equilibrium. Baldly put, their projections were:

- equilibrium number: thirty species

- time to equilibrium: forty years
- turnover: one species per year

Then they went to the empirical data.

After the earliest biological expedition, led by Professor Treub back in 1886, Rakata had been visited and surveyed again a number of times, notably in 1908, 1921, and 1934. The data from those surveys had been summarized in a Dutch journal paper of 1948. Consulting it, MacArthur and Wilson found that Rakata in 1908 had supported just thirteen resident species of bird. Recolonization had barely begun. Between 1908 and 1921, they found, the number of bird species rose to twenty-seven. Then it leveled off. Between 1921 and 1934, there was no net change, with just twenty-seven species recorded again. That suggested a form of stability, dynamic or otherwise. Among the twenty-seven bird species identified in 1934, though, five of the old species were gone and five new species had replaced them. That was turnover. Equilibrium had arrived within roughly four decades, it seemed, and the equilibrium number was roughly thirty, as predicted. True, the turnover rate appeared to be lower than their projection, but not so much lower as to discourage MacArthur and Wilson.

"We were very excited," Wilson tells me. "We said, Good Lord, here was the first time that you could come up with a bare-ass model like that, of what an equilibrium would look like, and you actually have a case where you can measure equilibrium and turnover, and it seems to fit."

Three decades later, the fit of the Krakatau data to the MacArthur-and-Wilson model continues to be a point of dispute. Is it a stretch, is it a pinch, or is it a stunningly good match? Ecologists are still making expeditions to Rakata, still surveying the bird species, totaling the number, gauging the turnover; and they are still comparing their findings against the coffee-table calculations of MacArthur and Wilson. Why do those other ecologists bother?

They bother because the equilibrium theory of island biogeography has been so successful at capturing minds. For much of the past thirty years, it has defined an important framework of research and debate within the world of professional ecology.

And the Krakatau case contributed vividly to its success. Wilson's idea about looking at those data had paid off. "But that didn't make me satisfied," he adds. "I said, What we need is a whole system of Krakataus."

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"THERE'S *nothing* more romantic than biogeography," Ed Wilson says with quiet passion, and in the spell of the moment, by God, I almost believe him.

The aura of romance has been embodied by scientists like Philip Darlington, who was one of Wilson's early role models at Harvard. Darlington, when he wasn't living the cloistered life of a beetle taxonomist and a curator, was "a tough character, a real macho field person," as Wilson recalls him. Phil Darlington would march in a straight line through the thick of a tropical forest—off the trails, up and down the mountains, following only his compass—in order to collect beetles. That was the way to get the real fauna, the deepwoods fauna, he advised Wilson. Another formidable predecessor was William Diller Matthew, a paleontologist based at the American Museum of Natural History, who studied the biogeography of extinct mammals and made field expeditions to places like Java, Mongolia, and Wyoming. Earlier still, before Matthew and Darlington, there were what Wilson describes as the countless heroic, Kiplingesque naturalists of the past. He doesn't mention Alfred Wallace by name and he doesn't need to, since we both know that no single human fits the "heroic, Kiplingesque" description more aptly.

Wilson's paean is leading us toward a point. Yes, biogeography was always romantic, physically challenging, enlivened by adventurous field trips to exotic locales. But intellectually it was a muddle. Amorphous, disorderly. It lacked quantitative rigor. It made no use of the experimental method. But in the early 1960s Wilson had begun to believe that maybe it could be transformed.

While working with MacArthur on their equilibrium theory, he became energized by that prospect: to recast biogeography as an experimental science. Keep the romance, dispose of the muddle. Apply some mathematical rigor. Endow it with a capacity, not just to describe and to explain, but to predict. The potential was enormous. One problem, though. He himself couldn't play a substantive role in any such transformation, Wilson knew, if he never left urban Massachusetts.

"So I said, I've got to get into the field."

He wasn't as young and unfettered as he'd been during his fieldwork in Melanesia. He had more responsibilities: a family, a professorship at Harvard. He couldn't just gallivant off to some tropical archipelago for months that would stretch into years. But he longed to create an important field experiment on the equilibrium aspect of biogeography. He knew it would be possible, he says now, "if I could just find the right place for it. I kept poring over maps of the United States, you know, places I could get to quickly. And there it was: southern Florida."

During the summer vacation of 1965 he took his family to Key West. He got hold of a fourteen-foot boat with an outboard motor. He began exploring the little universe of mangrove islands that speckled the shallow blue waters south of the Everglades.

There were thousands of these mangrove islands, more than any mapmaker had ever bothered to name. Florida Bay was full of them and, still farther south, the Key West area had its own share—tiny tufts of greenery punctuating the saltwater flats out beyond Boca Chica, beyond Sugarloaf Key, offshore from the Snipe Keys and Squirrel Key and Johnston Key, out between the Bob Allen Keys and the Calusa Keys, north of Crawl Key, north of Fiesta Key, all the way back to Key Largo. They bulged up dark against the bright sea horizon like bison grazing a frost-covered prairie. Wilson cruised his boat among them.

He saw that many consisted solely of vegetation, lonely clusters of mangrove standing knee-deep in the shallows. The red mangrove tree, *Rhizophora mangle,* is a water-loving and salt-tolerant species that thrives in such circumstances. It supports itself on a single main trunk and a constantly thickening network of prop roots, broadening outward, stabilizing its stance in the underwater muck, gradually claiming more area. A small mangrove island might comprise just a single tree, or it might include several red mangroves with a black mangrove taking security in their entanglement. The whole cluster might be hardly much bigger than a beach umbrella.

An island so minuscule, lacking dry ground, couldn't support any large-bodied terrestrial animals. It would be devoid of mammals and probably also of reptiles. But there would be tree-dwelling arthropods—mainly insects and spiders, with maybe a few centipedes, millipedes, isopods, scorpions, pseudoscorpions, and mites. In such a tiny and simplified ecosystem, the diversity would be modest and the population sizes would be small. A few dozen different species, a few thousand individuals. One determined scientist could collect and identify virtually every creature.

Wilson was determined.

He returned in 1966 with a young grad student named Dan Simberloff, another in his long series of mathematically proficient collaborators. Together, Wilson and Simberloff designed a project that would become the first experimental test of the equilibrium theory—and, for that matter, one of the first gambits in experimental biogeography of any sort. It would become famous for its logical elegance, for its results, and for its gonzo methods. The idea was to pick a few of the smaller islands and census them completely, identifying every species of resident arthropod; then to empty each island of its animal life, as Rakata had been emptied by the eruption; finally, to monitor what happened next.

Would recolonization occur? Yes, certainly. Wing power and wind would bring adventurous arthropods back, filling the zoological vacuum.

Would it happen quickly or slowly? Would the rate correlate with an island's remoteness? Would the number of species on each island eventually settle at an equilibrium? If it did, would the new equilibrium number be roughly the same as what Wilson and Simberloff had found originally? And would there be turnover? At what rate? Would it all conform to predictions from the theory? Those were the ultimate questions.

The immediate question was, How the hell are we going to empty an island?

They hired National Exterminators, of Miami. The men of National became intrigued with this challenge and rose to it. They erected scaffolding and towers above the muddy-bottomed shallows. When the initial censusing was finished, they wrapped each island in a huge tent of plasticized nylon. (Although the avant-garde artist Christo later gained fame for wrapping parcels of landscape, including islands, his debt to Ed Wilson, Dan Simberloff, and National Exterminators has not generally been noted by art historians.) Then they filled the tent with Pestmaster Soil Fumigant #1, a pesticide gas consisting mainly of methyl bromide. Methyl bromide is lethal to arthropods, and under some circumstances it will also hurt red mangroves; but Wilson and Simberloff arranged for the fumigations to be done at moderate dosages, administered nocturnally when air temperatures were lower, and with those considerations the trees remained healthy. The gas treatment lasted a few hours. The insects and spiders fell dead, the tent came off, the gas blew away, and the island was suddenly empty of animal species —but otherwise unchanged.

"This is where Dan Simberloff carried the heavy part of the work," Wilson says. "Dealing with the company, being there, supervising most of the fumigation. And beginning the monitoring afterward."

Here in the seminar room, Wilson's slide carousel reawakens. The shot of the camera-shy young man blinks away and new images start to appear. Click: a mangrove island. Click: The island is wrapped with dark plastic. It looks like a giant tomato plant inside a Hefty bag on a night when the gardener expects frost. Click: closeup of a beetle. At least in the visual dimension, we have now moved beyond Robert MacArthur.

This Florida work entailed some peculiar difficulties, Wilson tells me, besides just the problem of fumigation. He and Simberloff got buzzed by helicopters. It was the Coast Guard, checking them out, "because there were a lot of anti-Castro Cubans in the area, and they were using these islands, we were told, as weapons caches." The Coast Guard patrols were alert for anyone out on the flats who didn't look like a fisherman. It's easy to imagine how Wilson and Simberloff, two guys from Harvard wearing field khakis, climbing around in the branches of a mangrove or up to their shins in the shallows, causing giant black tents to occlude entire islands, might have provoked some suspicion. The mud was another thing, says Wilson. It sucked at their ankles like bathtub caulk. They sank, they stuck. Simberloff got a brainstorm and made some large plywood paddles for himself and Wilson to wear like snowshoes. The paddles were drilled full of holes, supposedly to relieve the suction. "But you couldn't move in them," says Wilson. "I jokingly referred to them as simberloffs. I'd say, 'Our simberloffs aren't going to take us anywhere.' Dan didn't seem to care for that joke very much. But he was really giving it his best."

After the fumigations, Wilson traveled back and forth to Harvard but Simberloff stayed in the area for a year, monitoring the recolonization process. He worked beastly hard, according to Wilson. Because the new populations were so small, and because the point was to study living ecosystems in a state of renewal, Simberloff and Wilson couldn't simply collect arthropods and carry them away for identification. They had to make their identifications by sight or take photos and then release each individual arthropod unharmed. What with the tree-climbing and the mud and the climate and the identification problems, the project demanded an acrobatic entomological taxonomist who was immune to sunburn and despair, proficient with a camera, and blessed with big feet. History doesn't record Dan Simberloff's shoe size, but he coped. During the course of the experiment, Wilson says, Simberloff transformed himself from an urban-raised mathematician into a very good field biologist.

And the results were gratifying. "To my absolute delight, and to Dan's delight, because this was going to be his thesis," Wilson says, "we watched the numbers of species rise to what was obviously equilibrium within about a year." That was true on three of the islands, anyway. Each of those three was recolonized quickly. On each, the species diversity rose to a temporary peak, then settled back down and stabilized at a lower level. The stable levels were nearly identical to what each island had supported before fumigation. Here was strong confirmation for the idea of equilibrium.

On a fourth island, meanwhile, recolonization happened more slowly. That island was the most remote. It eventually came to an equilibrium of its own, but its equilibrium number was lower than on the less remote islands. So the distance effect was confirmed too.

After two years, the four islands were censused again. Each island still held about the same number of species as it had after the first year—but some new species had been added, some old species had disappeared. Immigration was continuing, offset by extinction: turnover.

It was a nice bit of science, and it brought Simberloff his doctorate. He and Wilson together published three papers on the project in *Ecology,* for which they received an award from the Ecological Society of America. The work became quietly famous among other ecologists and biogeographers. It lent empirical validation to the equilibrium theory at a time when that validation was crucial. The mangroveexperiment papers—coded in dry scientific format as Wilson and Simberloff (1969), Simberloff and Wilson (1969), and Simberloff and Wilson (1970)—began turning up among the source citations of other scientists' journal articles, along with MacArthur and Wilson (1967). The theory gained credence from its applicability to the mangroves, and its adherents began to see a great breadth of other possible applications, most notably in the realm of conservation planning. This all seems ironic, in retrospect, given the role that Dan Simberloff would later play—as preeminent critic of the application of the equilibrium theory to conservation problems.

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AFTER THE publication of *The Theory of Island Biogeography,* in 1967, Robert MacArthur had five years to live. He continued teaching at Princeton. He wrote fifteen more papers. He helped found the journal *Theoretical Population Biology.* He played his editorial role in the Princeton monograph series. In 1968 he went down to the Keys and visited Wilson, who had another sabbatical and was spending it there. Wilson took him out to see some of the mangrove islands, in which Dan Simberloff was still climbing around. They talked excitedly, MacArthur and Wilson, about island biogeography as a quantitative paradigm and where it might possibly lead. MacArthur was always a great talker, and conversation with his students and his colleagues was one of the chief ways he exerted his magic influence. Sometimes the conversation involved scribbled equations, groping efforts to put nascent ideas into the crisp language of mathematics. Not many ecologists could match his mathematical sophistication. But mathematics for MacArthur was only a means toward the larger goal: understanding how evolutionary processes and ecological tensions combine to shape biological communities.

One theme underlay most of his work. This theme—it seems almost a truism now, but MacArthur himself considered it worth stating—was the search for patterns. He emphasized patterns and equilibria and ongoing processes, while de-emphasizing the sort of one-time, contingent events that figure in historical explanations. Where lies the distinction between those two types of explanation, the process-oriented and the historical? A historian pays special attention to the differences between phenomena, because they shed light on historical contingency. "He may ask why the New World tropics have toucans and hummingbirds," MacArthur wrote, "and parts of the Old World have hornbills and sunbirds." The hornbills of Africa and Asia are large-bodied, omnivorous birds with huge beaks, allowing them to fill roughly the same ecological niches as the toucans of tropical America; likewise the sunbirds of Africa and Asia are small-bodied, bright-colored nectar drinkers, filling roughly the same niches as American hummingbirds. The history-minded biogeographer wonders why hummingbirds, not sunbirds, have occupied the suitable niches on a given continent. MacArthur himself was more interested in the similarities among phenomena, because similarities reveal the workings of regular processes. He was more inclined to wonder why hummingbirds and sunbirds, despite their different ancestries and their independent histories in two different regions of the planet, are so similar. I've already quoted MacArthur's statement that to do science "is to search for repeated patterns, not simply to accumulate facts," and the patterns that especially concerned him were the patterns of biogeography.

The geographical distribution of animal and plant species had utterly captured his interest. The subject was full of deeply interesting questions. Why did such-and-such a community contain *these* species but not *those?* Why did such-and-such species live *there* but not *here?* Answers existed, MacArthur knew, and those answers were important, he believed. Of course the best of the earlier biogeographers, Darwin and Wallace, had also searched for repeated patterns and sought answers for the deeply interesting questions those patterns raised; MacArthur was merely continuing their tradition while inventing new methods. In his early career he had been a mathematician and later he labeled himself an ecologist, but during the final years, according to Wilson, he preferred to think of himself as a biogeographer. For most of the twentieth century, biogeography had been descriptive, not theoretical; it hadn't maintained the standard of profound provocation that Wallace and Darwin had set. Robert MacArthur, like his distinguished Victorian predecessors, was a biogeographer with a hungry ambition toward theory. One of his last field projects was a study of niche breadth and total abundance among the birds of Puercos Island, off the south coast of Panama. The birds of Puercos were not surpassingly significant in themselves. But they embodied patterns, and maybe the patterns were telling.

Sometime in 1972, MacArthur's illness was diagnosed. The romance ended.

He had renal cancer. It progressed quickly. He went up to the house in Vermont and, working against time, with no access to libraries, produced a short volume titled *Geographical Ecology: Patterns in the Distribution of Species,* summarizing his own final view of what mattered most in ecological science. He gave special thanks in the preface to Ed Wilson, who "showed me how interesting biogeography could be and wrote the lion's share of a joint book on islands."

By late autumn, MacArthur was home again in Princeton. Although he and Wilson had pursued different projects since their collaboration, the friendship remained strong. Ed Wilson tells me of their last conversation. He had heard that MacArthur was low, so he telephoned. "I knew he was dying. I didn't realize he was within hours of passing on."

"What did you talk about?" I ask.

It was just the same sort of chat as he'd had with MacArthur many times. They discussed ecology. The future prospects, the unanswered questions, the personalities. "We talked about recent developments in the field, and we gossiped about who had his head screwed on right," Wilson says. MacArthur barely mentioned his own illness, ignoring it as though he had a hundred years to live, and he and Wilson rattled on about other matters. The call lasted half an hour. Wilson made notes immediately afterward, thinking not so much about deathbed wisdom from a historic personage as about his own later sentimental interest. He stuffed the notes into a file, he says, and hasn't looked at the file in two decades. He seems to prefer trusting his memory. Memory knows things that notes could never remember.

About those notes: "I took them down as to what we said, and as to what we thought of certain people, and this and that. And that was it. I mean, there was no… We didn't inject sentiment." What he seems to mean is that true emotion, of which there was plenty, is often wordless. "Or say farewells. I didn't really expect that it would be that quick, anyway. That was it."

The death of MacArthur as perceived by Wilson—that *can't* be it, I think. There's undoubtedly more. There's surely some little human detail, incidental, piercingly vivid, so poignant that even memory chooses not to remember it. I want to say: Let's look at the notes. Let's see what it is you've forgotten. But of course I don't.

By now I've cored the heart out of Ed Wilson's workday, and it's time to let him escape back into the present. I've caused distraction enough, not least by reminding him of the note file. The file is still around somewhere, presumably in the ant-filled office, where the photo of Robert MacArthur hangs like a private icon. "Someday I'll pull that out and read it," Wilson says, "and may have a different perspective. I might even do that. I think I will do that. I've been meaning to pull it out for some time now," he says.

"It wouldn't hurt to read it," he says, though neither of us is entirely convinced.

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MACARTHUR was dead but the theory lived. It grew steadily more influential among the professional community of ecologists and population biologists. You never caught wind of this at the time, neither did I, no reason we would have, but journals like *Ecology* and *Evolution* and the *American Naturalist* were full of it. The science of ecology was undergoing a revolution, some people said. Invigorated by the new techniques of mathematical modeling, shaken out of its conceptual timidity, liberated from its plodding obsession with merely cataloguing the particulars of natural history, ecology was in upheaval. It was finally becoming a theoretical, predictive science. The preeminent revolutionist had been Robert MacArthur, according to this view, and his most resounding battle whoop was *The Theory of Island Biogeography.* Not every ecologist agreed that the book was ingenious, persuasive, and useful—but those who didn't agree still found MacArthur and Wilson's equilibrium theory hard to ignore. It was the coming thing.

One way to measure its growing influence is from the record of its citation by other scientists. A citation record, like a set of career stats in *The Baseball Encyclopedia,* is a sequence of crabbed, coded entries into which can be read a whole vista of failure or success. Each journal paper in ecology (as in most other branches of science) concludes with a selective bibliographical list, usually labeled "references" or "literature cited." Cited works are any that have been alluded to by author and date in the text of the paper, the implication being that these were especially helpful—or anyway inspirational, or maybe just provocative because of their adamantine dumbness—to the author citing them. Such citations serve to unify and focus the scientific discourse. They specify just which ideas and which sets of data stand as relevant background to the ideas and data in a piece of new work. The sheer frequency with which a scientific book or paper is cited reflects the breadth of its influence. Citation records are therefore a good way of keeping score. And scientists do keep score.

Like those baseball statistics, citation records have their own encyclopedic repository. It's the *Science Citation Index,* a series of big, boring volumes, supplemented annually. Every instance of citation for virtually every scientific book or article published within recent decades is encoded in one of those volumes, which stand collectively ready to serve as a scholarly resource (or as one wall of a hurricane bunker) at your local university library. So from the *Science Citation Index* we can track the influence of MacArthur and Wilson's theory.

First there's the short version, "An Equilibrium Theory of Insular Zoogeography," published as a journal paper in 1963. It attracted little notice. In 1964, only two other scientific papers acknowledged it. Just six citations the following year, just seven the year after. The paper showed no sign of becoming a runaway hit.

In 1967 came the book. In 1968, while the world pondered student revolutions not scientific ones, and Denny McLain won thirty-one games for the Detroit Tigers, *The Theory of Island Biogeography* collected a mere five citations.

But then its spell began to take hold. The numbers climbed, plateaued, climbed again. In 1969, the book was cited more than two dozen times. Most ecological publications don't ever receive such attention. In 1970, twenty-nine citations. It drew around thirty in each of the next few years, then in 1974 it surged up to seventy-nine. Word was out. Ecologists had started muttering to one another about insular equilibrium, immigration versus extinction, the area effect, the distance effect, turnover. In 1976, ninety-four citations. I know the exact number because, peering through the low rim of my glasses at maddeningly tiny print, I have counted them. In 1977, more than a hundred. Still rising in 1978. These were the glory years for MacArthur and Wilson's model. Island biogeography was no longer a subject on the fringe, interesting chiefly to Kiplingesque beetle taxonomists. It had become one of the central paradigms of ecology. In 1979, the book was cited by other scientists 153 times, an exceptional total. Its influence still hadn't peaked.

In 1982, Willie Wilson of the Kansas City Royals (no relation to Ed Wilson of Harvard) batted .332. He led the league. That same year Reggie Jackson, playing for the Angels, hit thirty-nine home runs. He was flaunting his escape from the Yankees. With the Oakland A's, Rickey Henderson stole 130 bases in 1982, more even than Lou Brock at the height of his powers. Also that year, one decade after Robert MacArthur's death, *The Theory of Island Biogeography* was cited 161 times.

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WHY DID THE book have such impact on ecology and population biology? Not because islands were so important, but because *The Theory of Island Biogeography* brought the island biogeography paradigm to the mainlands.

MacArthur and Wilson had made that point on their first page. They quoted Charles Darwin's early hunch that the zoology of archipelagos "will be well worth examination." They noted that patterns of species distribution on islands had played a major role, from Darwin's time onward, in the development of evolutionary theory. They added an important observation:

> Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galápagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats.

They meant that literal islands, surrounded by water, are only one sort of insular situation. Also to be considered are virtual islands, surrounded by other kinds of barrier.

"Consider, for example, the insular nature of streams, caves, gallery forest, tide pools, taiga as it breaks up in tundra, and tundra as it breaks up in taiga," wrote MacArthur and Wilson. Taiga is subarctic conifer forest. Tundra is treeless plain. In the far north, they dapple into each other along the border zone, forming paisley and polka-dot patterns. A tree-dwelling species of animal that inhabits a small dot of taiga surrounded by tundra is effectively insularized. Consider also lakes, which are insular for the fish and amphibians that inhabit them. Consider mountaintops, which are cooler and wetter than the surrounding valleys, and which often support utterly different plants and animals. The equilibrium theory was directed at all these situations.

The new mode of thought began to show itself promptly. In 1968 an imaginative ecologist named Daniel H. Janzen published a short piece in the *American Naturalist* titled "Host Plants as Islands in Evolutionary and Contemporary Time." For an herbivorous insect, he noted, each individual plant represents an island of habitat. Janzen had read and absorbed MacArthur and Wilson more quickly than most of his colleagues.

In 1970 David C. Culver published a paper subtitled "Caves as Islands." Culver brought equilibrium theory into his analysis of the biotas of certain West Virginia caves. Also in 1970 François Vuilleumier published a study of bird species on "páramo islands" of the northern Andes. *Páramo* is a type of meadow-and-scrub vegetation that occurs at around 10,000 feet on some peaks of the Andean chain, isolated there between the snow line and the tree line. Since páramo constitutes a distinct botanical community, with each patch supporting bird species distinct from the birds of the lower-elevation forest, Vuilleumier chose to analyze his páramo data in insular terms: area effect, distance effect, slope of the species-area curve. The slope of that curve, he reported, fell nicely within the narrow range of slope values that MacArthur and Wilson had described in their own collection of examples. About the same time, S. David Webb produced a paleontological study that also paid its respects to MacArthur and Wilson. Webb considered North America itself as a single vast island (fully isolated when the Bering and Panama land bridges were submerged) and found that, over the past ten million years, the diversity of North American land mammals had held roughly at equilibrium, with turnover.

Webb's study, and Culver's, and Vuilleumier's, and Janzen's, served as quiet indicators that the new mode of thought was taking hold. Another study in the same vein attracted wider attention, partly on the strength of contrariety. This one was "Mammals on Mountaintops: Nonequilibrium Insular Biogeography," published by James H. Brown in 1971. Brown announced, politely but firmly, that his research results did *not* fit the theory.

Brown's "islands" were forested mountaintops poking up out of the Great Basin desert. The Great Basin is generally dry, low, austere, and flat, an ocean of sagebrush spread across that huge region of the American West bordered roughly by Las Vegas, Mount Whitney, Reno, Boise, Pocatello, and Salt Lake City. Protruding above the sage-purple plains are some forest-topped ranges of mountains. At their higher elevations, above 7,500 feet, these mountains get cool temperatures and enough rainfall to support piñon and juniper woodlands. They also support certain species of small mammals that can't live on the plains below. The northern water shrew *(Sorex palustris),* for instance, doesn't inhabit the lowlands of central Nevada; but it does survive as an isolated population in the moist heights of the Toiyabe range. The pika (*Ochotona princeps)* needs a subalpine climate, nutritious highland grasses for food, and slopes of talus for shelter; it's absent from the sage flats, where it can't find those essentials, but it does exist in the Ruby Mountains southeast of Elko. Besides the northern water shrew and the pika, Brown found the ermine, the Uinta chipmunk, the yellowbelly marmot, the bushytail woodrat, and nine other species of small mammals on mountaintops within the Great Basin. These were all boreal species, normally native to cold forests of the north.

Brown outlined seventeen mountaintop islands, most of them in Nevada, each one rising separately from that vast swale of sage between the Sierra Nevada in California and the Rockies in Utah. The Sierra and the Rockies, offering large zones of high-altitude habitat and source populations for the boreal mammals, represent mainlands relative to the insularized mountaintops. For each of his islands, Brown gathered the familiar sorts of data: area, distance from mainland, list of species in residence. Like the other researchers, he made charts. He drew species-area curves. He saw patterns, and from the patterns he deduced meaning. But the patterns and the meaning in this case were different.

These mountaintop mammals, Brown concluded, were not descended from immigrants who had crossed the sage. Instead they were relicts, left behind when their habitat dried up around them.

Their ancestors had arrived sometime in the Pleistocene, maybe fourteen thousand years ago, maybe earlier, during one of those glacial episodes when cooler and wetter climatic conditions had allowed piñon-and-juniper woodland to spread across lower elevations. The low-altitude woodland had formed a network of habitat linking the solitary mountaintops to the Sierra and the Rockies. While the cool conditions endured, the small boreal mammals enjoyed broad distribution throughout that habitat. Then the last ice age ended and the climate changed. The network dissolved into fragments. The boreal mammals were extirpated from the lowlands, but they survived (at least for a while) in their highland enclaves. The pika and the bushytail woodrat and the northern water shrew found themselves stranded—just as the brown bandicoot and the wombat had been stranded, at about the same time, on those land-bridge islands between mainland Australia and Tasmania.

The area effect showed strongly in Brown's data. The larger islands of mountaintop habitat supported distinctly more species than the smaller islands. So Brown's species-area curve was fairly neat. But it seemed unusually steep; the slope of the curve (as derived from that familiar species-area equation) was above the upper end of the range that MacArthur and Wilson had described. This meant that the species-area correlation for Brown's mountaintop islands was not just consistent, it was severe. A big mountaintop held not only more north-country mammal species than a small mountaintop, it held *far* more.

The distance effect, on the other hand, was nonexistent. Proximity of each island to either the Rockies or the Sierra, the habitat mainlands, signified zilch. There was no inverse correlation between distance and species number, as the equilibrium theory said there should be. The Stansbury Mountains, rising just forty miles west of the Rockies (in Utah), held only three species. The Panamints, just fifty miles east of the Sierra (in southeastern California), held only one. Some of the more remote islands, of about the same size, contained more species than those less remote islands. So distance was irrelevant to diversity. What did that mean?

It meant that immigration wasn't contributing to the species richness of *any* of the islands. The little mammals weren't achieving new colonizations across the Great Basin—not occasionally, not rarely, not ever. The pikas and water shrews and chipmunks and woodrats weren't so vagile and adventurous as reptiles and birds often are. With their high metabolic requirements, their tiny footsteps, their vulnerability to stress and predation, they had no chance in hell of crossing a forty-mile stretch of sagebrush. The barriers to dispersal and establishment were unbreachable. Brown said it clearly in his summary: "Apparently the present rate of immigration of boreal mammals to isolated mountains is effectively zero."

MacArthur and Wilson had tried to free ecology from historical explanations, but this was a case in which history couldn't be ignored. The distribution patterns represented artifacts of historical circumstances rather than manifestations of timeless processes. Colonization had happened during the Pleistocene—historical fact. Then the climate changed, the habitat split into fragments, and the mountaintop populations were trapped—historical fact. Immigration came to a halt—historical fact. During the subsequent ten millennia, Brown guessed, it had been solely a matter of survival (for some populations) and (for others) extinction.

Without immigration, there can be no immigration-extinction equilibrium. That's why Brown's title announced a "nonequilibrium" case of island biogeography. He was not so much refuting the MacArthur-and-Wilson model as he was using it to highlight an alternative sort of situation.

Instead of turnover, Brown found only extinction. Slowly but irreversibly, one species after another had been lost from each island, and those losses weren't offset by gains. When the Stansbury Mountains lost their last ermine, no Uinta chipmunks arrived to compensate. When the Panamints lost their last yellowbelly marmot, no incoming pikas made up the difference. The species number for each island didn't hover at equilibrium; the species number only went down. Insularization, for the Great Basin mountaintop communities, entailed an inexorable decline in diversity.

Does this sound ominous? Does it sound familiar? The same phenomenon would eventually be known by various labels, one of which is ecosystem decay.

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BROWN'S PAPER IN 1971 was an early hint of what would soon become an important trend: using the equilibrium theory to illuminate matters of habitat fragmentation and species extinction on the continents.

MacArthur and Wilson had presaged that trend with a comment in their first chapter:

> The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization.

The breaking-up process, they added, was "graphically illustrated by Curtis's maps of the changing woodland of Wisconsin," which maps they reprinted in the book. The Curtis maps gave visual force to MacArthur and Wilson's point that this theory of islands was not just a theory of islands.

John T. Curtis, a professor of botany at the University of Wisconsin, had studied the progressive destruction of native forests and grasslands during the decades since white settlers had invaded the Midwest. His work appeared in 1956 as one chapter of a volume titled *Man's Role in Changing the Face of the Earth.* The book's reach was global, but Curtis himself had focused on a single small unit of land: Cadiz Township of Green County, Wisconsin. It was a square tract measuring six miles on a side. Curtis had depicted its botanical transformation with four dated maps: one each for 1831, 1882, 1902, and 1950.

Back in 1831, before settlers began clearing it, the area had been covered with deciduous forest dominated by basswood, slippery elm, sugar maple, oak, and hickory. What would later be Cadiz Township was in those years a hardwood wilderness that Daniel Boone or John Muir could have loved. By 1882 it had become a patchwork of rectilinear woodlots within a larger matrix of cropland. By 1902, as mapped by Curtis from historical records, the forest patches had grown smaller and fewer. By 1950 they were still further reduced. These last parcels of woodlot in mid-twentieth-century Cadiz Township resembled a sprinkling of cracked pepper on a bare china plate. One sneeze, it seemed, and they'd vanish.

Curtis's maps were arresting. Like time-lapse photography from high overhead, they revealed the relentless diminishment whereby a mainland expanse was chopped into largish islands, then nibbled down into tiny ones. The remnants were too dinky to support much in the way of large-bodied, forest-dependent animals. The maps showed how human enterprise and human population growth had reduced one square of wild landscape to dysfunctional bits. And of course Cadiz Township of Green County, Wisconsin, was only a small model of the world.

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THE SAME SORT of pattern that Curtis had documented in Wisconsin was envisioned on a broader scope by Jared Diamond. One place he saw it happening was New Guinea, and that caused him special concern.

Diamond, our man of the elephant-eating komodos and the birdextinction tally, is a dauntless field ecologist who began making ornithological expeditions to New Guinea in 1964. He was just out of graduate school with a doctorate in physiology. The prospect of settling into a one-track career as a lab researcher on membrane physiology, his professional specialty, seemed too narrow. He had other aspirations and talents. Since boyhood, he had been a serious birdwatcher. He was blessed with a strong constitution and a fine ear for birdsong, the two requisites for doing ornithology in the tropics. Just by hiking and listening, matching the bird calls he heard against the aural field guide in his brain, he was capable of surveying the avifauna of a forest—even, he discovered, a forest so dense and difficult as those of New Guinea. During that first visit, the island captured his lifelong devotion.

"New Guinea is my intellectual roots," Diamond says. He feels as though he was born there. "Half of my emotional life goes on in New Guinea. Cut off from New Guinea, I would feel like Rachmaninoff cut off from Russia." Diamond came from a musical family, which might go some way to explain the acuity of his birding ear.

By the early 1970s he had become alarmed over the rate at which humans were destroying tropical rainforest. It was occurring not just in his beloved New Guinea but also in the Amazon, Malaysia, Madagascar, Central America, West Africa, the Philippines, and elsewhere. It took two basic forms, very different in socioeconomic character but similar in result: large-scale timber extraction by corporate entities, and small-scale slash-and-burn agriculture by hungry people. Diamond himself had seen it in both forms.

At the end of an otherwise arcane paper on equilibrium theory as applied to bird diversity, published in 1972, he mentioned the problem. Throughout the tropics, he wrote, rainforest "is being destroyed at a rate such that little will be left in a few decades. Since many rainforest species cannot persist in other habitats, the destruction of the rainforests would destroy many of the earth's species and would permanently alter the course of evolution." He wasn't the first biologist to voice that concern, but Diamond added a gloomy insight, extrapolated from MacArthur and Wilson's work:

> The governments of some tropical countries, including New Guinea, are attempting to set aside some rainforest tracts now for conservation purposes. If these plans succeed, the rainforests, instead of disappearing completely, will be broken into "islands" surrounded by a "sea" of open country in which forest species cannot live.

The likely result of establishing those refuges, he warned, was the same as occurs on peninsular bits of landscape when they become isolated as land-bridge islands: Rare species suffer extinction and overall species diversity falls. It happened on Flinders Island and King Island in the Bass Strait, and on Brown's mountaintop islands in the Great Basin. It happened on Barro Colorado in Panama. It could happen, Diamond argued, to any patch of ecosystem that became insularized—for instance, to a nature reserve or a national park.

Although Diamond didn't cite him, Frank Preston had made the same point a decade earlier in his discussion of samples versus isolates. To refresh your memory: "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."

Diamond's term for the phenomenon was *relaxation to equilibrium.* The sort of equilibrium to which he alluded, of course, was MacArthur and Wilson's, and the relaxation was actually a loss of species, as the species number came to equilibrium again at a new, lower level commensurate with the new, smaller area of the insular patch. It was another way of saying ecosystem decay. Diamond's phrase might be mistaken to imply stoical indifference—*relaxation* does sound languid and soothing—but indifferent is one thing that he wasn't.

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IN 1974, the upheaval initiated by MacArthur and Wilson entered its next phase. The equilibrium theory by then had been published, widely noticed, and empirically tested. It had been projected onto a variety of natural situations—Janzen's plant islands, Culver's cave islands, Vuilleumier's páramo islands—and had helped to illuminate them. Intellectually, it was a success. The next phase was more practical: applied biogeography. Could the theory be used for problem solving in the real world?

A small handful of scientists, speaking up individually, suggested that it could. In their view, it was pertinent to the fate of natural landscape and wild creatures all over the planet. At a time when humanity was cutting forests and plowing savannas at a rapid pace, when habitat everywhere was becoming fragmented and insularized, the equilibrium theory embodied minatory truths. It was not just an interesting set of ideas—it was goddamned important. If heeded and applied, it might help save species from extinction. Conspicuous amid this chorus of opinion was Dan Simberloff.

Simberloff declared in print that the work of MacArthur and Wilson, along with the obscure papers by Frank Preston, had "revolutionized" biogeography with the suggestion of dynamic equilibrium. "Island biogeography has changed in a decade," Simberloff wrote, "from an idiographic discipline with few organizing principles to a nomothetic science with predictive general laws." He was a bright young man with a recondite vocabulary. "Idiographic" to "nomothetic": He meant that MacArthur and Wilson had succeeded just as they had hoped to, transforming biogeography from a descriptive endeavor into one that could articulate some of nature's governing rules. Yes, the theory brought fresh insight to the ecology of islands; but still more significant, Simberloff added, was that it also addressed insularized habitats on the mainlands. "We can therefore use island biogeographic theory to further our understanding of a variety of evolutionary and ecological phenomena and even to aid in the preservation of the earth's biotic diversity in the face of man's ecological despoliation."

Simberloff's statements appeared in 1974. Jared Diamond was saying much the same thing. That agreement, as you'll see, was a notable and fleeting convergence.

The following year Diamond published a journal article titled "The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves." It would become one of his bestknown papers. Because it represented a culmination in the development of these ideas, and because it triggered such vehement reaction, "The Island Dilemma" is worth looking at in detail.

Like Simberloff, Diamond believed that MacArthur and Wilson had touched off a "scientific revolution." One aspect of the revolution was a heightened awareness that insularity can occur under natural conditions on the mainlands: a mountaintop, a lake, a tract of wood-land surrounded by meadow. As humanity chops the world's landscape into pieces, those pieces become islands too. A nature reserve, by definition, is an island of protection and relative stability in an ocean of jeopardy and change. So the dynamics of parks and reserves can be described—and predicted—by equilibrium theory. The theory, according to Diamond, yields a handful of serious implications.

On his way toward examining the implications, Diamond revisited some of the theory's logical and empirical underpinnings: the species area equation and Darlington's tenfold-to-twofold ratio, among others. He invoked Vuilleumier's páramo islands in the Andes, as well as Brown's work on mountaintop mammals of the Great Basin. He nodded in the direction of Krakatau. He described the mangrove experiment by Simberloff and Wilson. He also drew on his own study of "relaxation times" for the satellite islands around New Guinea. He noted the high rate of extinction on Barro Colorado. This body of evidence and theory, as Diamond viewed it, led to certain conclusions about the survival prospects of species in isolated reserves, such as:

- A reserve newly isolated will *temporarily* hold more species than its equilibrium number—but that surplus of species will eventually disappear, as relaxation to equilibrium occurs.
- The rate at which relaxation occurs will be faster for small reserves than for large ones.
- Different species require different minimum areas to support an enduring population.

At the end of the paper he offered a set of "design principles" for a system of nature reserves, including:

- A large reserve can hold more species at equilibrium than a small reserve.
- A reserve located close to other reserves can hold more species than a remote reserve.
- A group of reserves that are tenuously connected to—or at least clustered near—each other will support more species than a group of reserves that are disjunct or arrayed in a line.
- A round reserve will hold more species than an elongated one.

Besides stating them verbally, Diamond presented his design principles graphically, in a figure suggesting tiddlywinks on parade. Circles of various sizes and in various spatial arrangements were shown as a menu of dichotomous options. Each pair was labeled with a letter: principle A, principle B, and on up to principle F. The clear visual message was that some patterns of insularity, in the abstract and in reality, are more damaging than others.

Diamond made two claims about his design principles: that they were applicable to conservation planning and that they derived from MacArthur and Wilson's theory. Although both claims were controversial, the first met especially strong challenges. Some ecologists rejected the whole notion of imposing abstract solutions on such various situations; and some who accepted a few of the principles were unwilling to swallow the whole group. There were quibbles about principle F, reservations about E, qualifications that should be added to C—but none of the others provoked such heated and lasting disagreement as the one Diamond listed as principle B.

Four little tiddlywinks were "worse" than one big tiddlywink, according to Diamond's graphic figure. But were four small reserves, in the real world, necessarily worse than a single large one? That question would be argued for a decade. The argument would grow bitter and personal. It would acquire a handy label: SLOSS. The acronym stood for "single large or several small." During the late 1970s it would become ecology's own genteel version of trench warfare.

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THE CHORUS of opinion about applied biogeography rose to fullness in 1975. Besides Diamond's paper, there were conspicuous statements by John Terborgh, Robert M. May, and others.

May's appeared in *Nature,* under the title "Island Biogeography and the Design of Wildlife Preserves." He allied himself with Diamond on the single-large-or-several-small question. "In cases where one large area is infeasible, it must be realised that several smaller areas, adding up to the same total as the single large area, are not biogeographically equivalent to it," May wrote. Rather than being equivalent, the small areas "will tend to support a smaller species total."

Terborgh, an old friend and kindred soul of Jared Diamond's, agreed. His scrutiny of the Barro Colorado situation and his fieldwork in other tropical forests had helped persuade him that the equilibrium theory was both scientifically valid and applicable to conservation planning. He paid homage to MacArthur and Wilson, noting that "the methods and the way of thinking they developed are extensible to a much larger range of situations, including the design of faunal preserves." Terborgh was not so specific as May on the SLOSS question, but he argued that the equilibrium theory implied a need for leaving corridors of habitat as connections between reserves—as Diamond had warned in another of his design principles. Terborgh further noted that if reserve planners hope to save large-bodied predator species, the planners had better make their reserves huge.

Ed Wilson joined the chorus. Along with a collaborator named Edwin O. Willis (whose long-term study of the Barro Colorado birds had made him an important influence on Terborgh's thinking also), Wilson co-authored a paper on applied biogeography, proposing many of the same principles as Diamond. Wilson and Willis's piece was published as the final chapter in a multi-author volume, derived from a somewhat historic symposium held at Princeton in November of 1973.

The choice of Princeton as the venue for that symposium, and the date, were significant. One year had passed since the death of Robert MacArthur, and the meeting was a memorial event. The participants included Jared Diamond, James Brown, Robert May, Edwin Willis, John Terborgh, and a handful of other ecologists of the new mold, as well as G. Evelyn Hutchinson and Ed Wilson, all of whom had cause to pay homage. The book appeared several years later as *Ecology and Evolution of Communities.* It was dedicated to MacArthur.