For Terry Erwin,
pioneer in biodiversity
with warm regards
EO Wilson

BIODIVERSITY

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EDITOR'S FOREWORD

The diversity of life forms, so numerous that we have yet to identify most of them, is the greatest wonder of this planet. The biosphere is an intricate tapestry of interwoven life forms. Even the seemingly desolate arctic tundra is sustained by a complex interaction of many species of plants and animals, including the rich arrays of symbiotic lichens. The book before you offers an overall view of this biological diversity and carries the urgent warning that we are rapidly altering and destroying the environments that have fostered the diversity of life forms for more than a billion years.

The source of the book is the National Forum on BioDiversity, held in Washington, D.C., on September 21–24, 1986, under the auspices of the National Academy of Sciences and Smithsonian Institution. The forum was notable for its large size and immediately perceived impact on the public. It featured more than 60 leading biologists, economists, agricultural experts, philosophers, representatives of assistance and lending agencies, and other professionals. The lectures and panels were regularly attended by hundreds of people, many of whom participated in the discussions, and various aspects of the forum were reported widely in the press. On the final evening, a panel of six of the participants conducted a teleconference downlinked to an estimated audience of 5,000 to 10,000 at over 100 sites, most of them hosted by Sigma Xi chapters at universities and colleges in the United States and Canada.

The forum coincided with a noticeable rise in interest, among scientists and portions of the public, in matters related to biodiversity and the problems of international conservation. I believe that this increased attention, which was evident by 1980 and had steadily picked up momentum by the time of the forum, can be ascribed to two more or less independent developments. The first was the accumulation of enough data on deforestation, species extinction, and tropical biology to bring global problems into sharper focus and warrant broader public exposure. It is no coincidence that 1986 was also the year that the Society for Conservation Biology was founded. The second development was the growing awareness of the close linkage between the conservation of biodiversity and economic development. In the United States and other industrial countries, the two are often seen in opposition, with environmentalists and developers struggling for compromise in a zero-sum game. But in the developing nations, the opposite is true. Destruction of the natural environment is usually accompanied by short-term profits and then rapid local economic decline. In addition, the immense richness of tropical biodiversity is a largely untapped reservoir of new foods, pharmaceuticals, fibers, petroleum substitutes, and other products.

Because of this set of historical circumstances, this book, which contains papers from the forum, should prove widely useful. It provides an updating of many of the principal issues in conservation biology and resource management. It also documents a new alliance between scientific, governmental, and commercial forces—one that can be expected to reshape the international conservation movement for decades to come.

The National Forum on BioDiversity and thence this volume were made possible by the cooperative efforts of many people. The forum was conceived by Walter G. Rosen, Senior Program Officer in the Board on Basic Biology—a unit of the Commission on Life Sciences, National Research Council/National Academy of Sciences (NRC/NAS). Dr. Rosen represented the NRC/NAS throughout the planning stages of the project. Furthermore, he introduced the term *biodiversity*, which aptly represents, as well as any term can, the vast array of topics and perspectives covered during the Washington forum. Edward W. Bastian, Smithsonian Institution, mobilized and orchestrated the diverse resources of the Smithsonian in the effort. Drs. Rosen and Bastian were codirectors of the forum. Michael H. Robinson (Director of the National Zoological Park) served as chairman of the Program Committee, organized one of the forum panels, and served as general master of ceremonies. The remainder of the Program Committee consisted of William Jordan III, Thomas E. Lovejoy III, Harold A. Mooney, Stanwyn Shetler, and Michael E. Soulé.

The various panels of the forum were organized and chaired by F. William Burley, William Conway, Paul R. Ehrlich, Michael Hanemann, William Jordan III, Thomas E. Lovejoy III, Harold A. Mooney, James D. Nations, Peter H. Raven, Michael H. Robinson, Ira Rubinoff, and Michael E. Soulé. David Johnson at the New York Botanical Garden was very helpful in verifying some of the botanical terms used in this book. Helen Taylor and Kathy Marshall of the NRC staff and Anne Peret of the Smithsonian Institution assisted with the wide variety of arrangements necessary to the successful conduct of the forum. Linda Miller Poore, also of the NRC staff, entered this entire document on a word processer and was responsible for formatting and checking the many references. Richard E. Morris of the National Academy Press guided this book through production.

The National Forum on BioDiversity was supported by the National Research Council Fund and the Smithsonian Institution, with supplemental support from the Town Creek Foundation, the Armand G. Erpf Fund, and the World Wildlife Fund. The National Research Council Fund is a pool of private, discretionary, nonfederal funds that is used to support a program of Academy-initiated studies of national issues in which science and technology figure significantly. The NRC Fund consists of contributions from a consortium of private foundations including

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Finally, and far from least, Frances M. Peter marshalled the diverse contributions in the present volume and was essential to every step of the manuscript editing process. The cover for *Biodiversity* was derived from a forum poster designed by artist Robert Goldstrom.

E. O. WILSON

CHAPTER

13

THE TROPICAL FOREST CANOPY
The Heart of Biotic Diversity

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A few years ago in a short paper in the *Coleopterists Bulletin*, I hypothesized that instead of the current estimate of 1.5 million species on Earth, there were 30 million species of insects alone (Erwin, 1982). This hypothesis was based on collections of beetles from tropical forest canopy samples in Panama (Erwin and Scott, 1980), rather than on the catalog counts of taxonomic names used in all the earlier estimates. I used simple arithmetic based on actual numbers of beetle species in my samples, estimated numbers of tropical forest tree species given me by the leading botanists, and a conservative estimate of the host specificity of tropical forest canopy insects. Host specificity in this sense means that a species in some way is tied to the host tree species and cannot exist without it.

This reestimation of the magnitude of life on Earth got a lot more coverage than I anticipated and began the usual controversy of right or wrong. Those engaged in the controversy, most of whom never read this obscure paper in the *Coleopterists Bulletin*, in a way actually missed the point of the paper. Consequently, I now want to take the opportunity to clarify the situation.

Science, at least in natural history, proceeds from casual observations, usually in the field or on museum specimens, to the erecting of hypotheses and finally to the testing of those hypotheses. Repeated failure to prove a hypothesis false lends support to the possibility that it may be true. For the 30 million species of insects hypothesis, which was based on a brand new set of observations never before available to scientists, I suggested that testing must begin by refining of our knowledge about host specificity of insects in tropical forests.

In a subsequent paper, analyzing data from the canopies of four different forests in the central Amazon around Manaus, Brazil, I showed that 83% of the beetle species in the samples were found in only the samples of one of the types of forest, 14% of the species were shared between two, and only 1% of the species of beetles was found in all four forest types (Erwin, 1983a). This added fuel to the "numbers" controversy, because of the numerous types of forest known to exist in the Amazon Basin alone and the fact that the analysis was based on more than 1,000 species of beetles, a fairly substantial data base. At this point, I turned my attention to the now well-refined sampling techniques of insecticidal fogging of forest canopies at the Tambopata Reserved Zone in the southeast corner of Amazonian Peru. I developed these techniques for the purpose of testing the main hypothesis regarding biological diversity in tropical forests and the subhypothesis that host specificity is a main feature of the lifestyle of tropical canopy insects. The following paragraphs provide some glimpses of the Tambopata Canopy Project, some preliminary observations on the fauna itself, and what I believe to be the status of the 30 million species hypothesis. With a data base of a million specimens (we'll get to the number of species later), it will take a long time to complete the data analysis from just 1 year of collecting.

THE PROBLEM

It has been predicted that in 25 to 30 years, much of the humid tropical forest could be gone or severely converted (see Raven, this volume, Chapter 12). Between 25 and 40% has already been lost to misguided human exploitation. The best estimate is that an area the size of Honduras is being lost or converted each year, and by the year 2000 some popular accounts have predicted that a million species will become extinct. Although I regard such guesses as a bit low, a point discussed later in this chapter, they mean that in our generation we, the only species on Earth with the mental capacity to reason, will see the virtual disappearance of contiguous tropical forests and probably the extermination of more than 20% of the diversity of life on Earth, and we humans will have caused it.

THE HISTORY

The Amazon basin (Figure 13-1) has the richest biota on Earth. There are several factors involved, not the least of which is the sheer size of the basin. We must start the historical analysis with the Amazon basin as it was on the western portion of the megacontinent Gonwanaland some 100 million years ago. The biota of today is a result of many events that occurred after two supercontinents, South America and Africa, rifted, and South America drifted in a westerly direction. As this occurred, the uplift of the Andes began. This wonderful mountain chain, extending from Venezuela down into Chile, became a dike that reversed the western flow of all the rivers of Gonwana, turning them around and beginning their flow to the east. In the last 40 million years, this event has caused a mosaic of habitats, the fine-grained resolution of which we have no comprehension at this time. As I am discovering in some of my work in Peru, the fine-grainness of habitats is far, far greater than what the botanical classifications have led us to believe. We need

from the botanists a better picture of tree species distribution and habitats, and of the small communities made up by these tree species microdistributions.

During this 40 million years of Andean orogeny, there were three uplifts of crystalline rock across the Amazon, represented by the red arches in Figure 13-1. The two gray areas in the north and south are bedrock, the Guyana and Brazilian Shields. From this perspective, we now see the development of this mosaic of habitats, defined by the meandering river systems of the Amazon basin itself. The study of these rivers and the areas between them offers an interpretation of the events of the past (Erwin and Adis, 1982).

A mosaic component that extends throughout the Amazon basin is the oxbow lake, a lake formed when a loop of a river becomes isolated from the river as a result of sedimentation. The formation of an oxbow lake is the first stage in succession that culminates in forest. This small "island" of aquatic life will soon become an island of grassy life, which will then become an island of palm tree life and so on until it returns to climax inundation or upland forest of some type. During succession, it may be crosscut by another twist of the river or another small river, which will then subdivide it into four successional stages each with a different time differential. This kind of successional evolution on a massive 6-million-square-kilometer area is but one of the features that has provided the evolutionary pathway for Amazonia's fantastic diversity.

What we see today from the air is a forest canopy that extends more or less unbroken across those 6-million-square kilometers, except for the rivers, the hy-

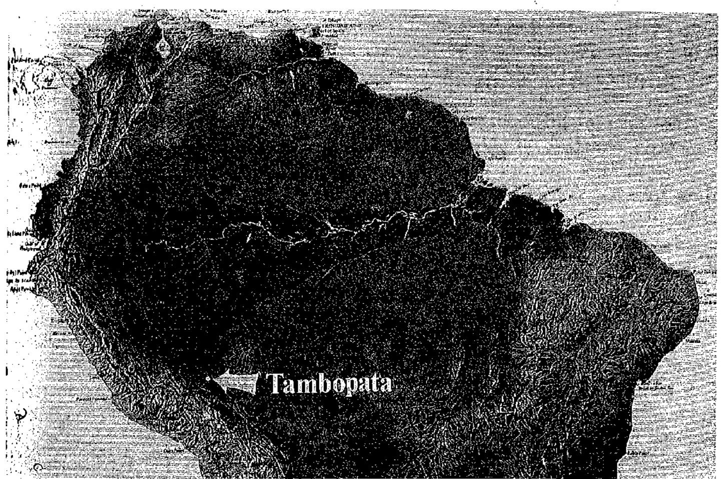

FIGURE 13-1 The South American land mass. The Guyana and Brazilian Shields are shown in gray; the hatched areas represent the three arches of crystalline rock.

droelectric projects, the Rondonia project, and various other development projects that are starting to break up that vast expanse of forest. From the air, one can detect even finer and finer mosaics. It is very easy to pick out the trees in blossom, the trees with tough dark-green leaves, trees that lost their leaves during the dry season and are now getting a new flush of very light pale leaves (the ones the insects like to eat the most), and vines that reach up into the canopy to spread their leaves over the tree leaves or intermingle them with the leaves of the canopy trees. All 150 or more species of canopy trees or vines per hectare contribute to the mosaic. There is an intermingling of leaves between two species of trees, between the vines and the trees, and between one tree overshadowing the other, resulting in the creation of microenvironments for the little creatures that are so important in providing the richness of the world's biotic diversity.

Depending on forest type, the tops of the trees range from 15 meters to as high as 55 meters. Tambopata was chosen for my preliminary studies because logistically it is very difficult to get equipment and people into a virgin rain forest, keep them there for long periods, and get the material back to the museum to study it under the microscope. The average length of the beetles in the canopy is about 2 to 3 millimeters, so one needs pretty good facilities to make detailed studies. Tambopata served the logistic purposes as well as another purpose—approximately 11 different types of forests are found within walking distance. That seemed like too much to handle during 1 year, so only five were selected for intense collecting. In each of these five forests, we selected three 12-meter-square plots (Erwin, 1983b).

All 15 plots were sampled in the early rainy, late rainy, early dry, and late dry seasons. The data collected included tree canopy sizes, species of trees, and exact location of the collecting trays. All this information has been computerized and allows museum specimens to be traced back to the actual square meter of rain forest where they were collected. This gives us the opportunity to return in subsequent years and resample in order to see what the canopy, or what the forest in general, is doing over long periods. Long-term cycles have been largely overlooked, except by a few researchers for only a few species. My research team is now beginning to computerize the canopy in three dimensions so that we can describe exactly where these insect species reside in the canopy.

Beyond this data set, we also have the branching patterns, the leaf structure, and other details of microhabitats. It has taken a long time to develop our data collections, because we have paid attention to the finest details. I am trying to look at the canopy habitat through the eyes of these 2- to 3-millimeter-long beetles.

To date, we have analyzed about 3,000 species of beetles from only five plots. When we complete our analysis, we will have a large data set. A comparison of the tree composition of the different kinds of forest has shown that the forest in Manaus and two of our upland terra firma forests contain entirely different tree families. There are more big trees in the Peruvian sites than in the Manaus sites. Perhaps that accounts in part for the larger size of the insects in the canopy in Peru than in Manaus.

Only 2.6% of the species are shared between Manaus and Tambopata (Figure 13-2). This seems reasonable, because the two sites are 1,500 kilometers apart.

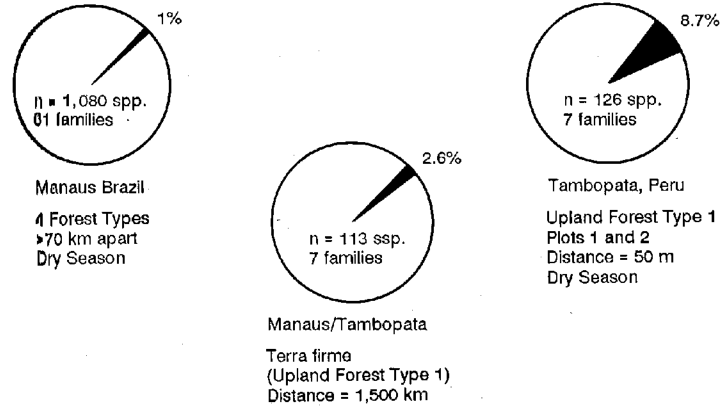

FIGURE 13-2 Pie diagrams of shared beetle species among forests in Peru and Brazil in percent of fauna.

But we found that of the 1,080 species analyzed, there was only a 1% overlap of species in all four forest types in Manaus (Erwin, 1983a).

Data collected during three seasons for two forest plots in the same type of forest 50 meters apart in Tambopata indicate that only 8.7% species are shared. When we add the fourth season data (which will come in shortly), we predict that the percentage of shared species will drop.

Figure 13-3 is a cumulation species curve, which shows the increase in the number of species as we increase the samples. After this figure was made, some more samples were analyzed and the curve became much steeper. These data are just from Plot 1 in Upland Forest Type 1 (Erwin, 1985). The 3,000 species already analyzed amount to more than all the samples from Brazil.

A canopy beetle is shown in Figure 13-4. In fully describing the distribution of these insects in time and space in the tropics, we should think in terms of more than 30 million, or perhaps 50 million or more, species of insects on Earth. A large number of species are tied only to certain forest types that are found on very small patches of soil deposited differentially through time by the vast and meandering Amazon River system. The extermination of 50% or more of the fauna and flora would mean that our generation will participate in an extinction process involving perhaps 20 to 30 million species. We are not talking about a few endangered species listed in the Red Data books, or the few forbish louseworts and snail darters that garner so much media attention. No matter what the number we are talking about, whether 1 million or 20 million, it is massive destruction of the biological richness of Earth.

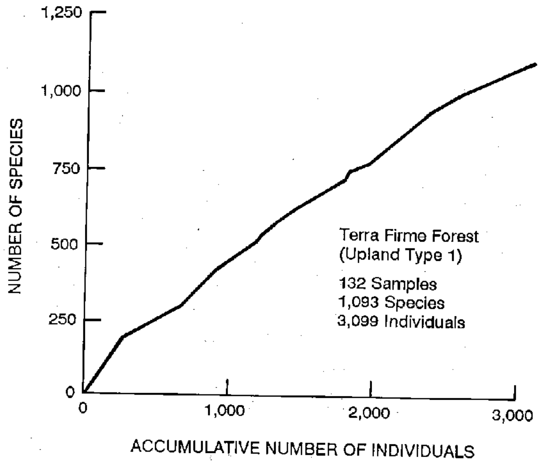

FIGURE 13-3 Numbers of species accumulated per square meter sample in 12-meter-square plot (119 square meters sampled) in Upland Forest Type I at Tambopata Reserved Zone, Peru.

FIGURE 13-4 *Agra arrowi* Liebke, a member of the top predatory carabid beetle group in tropical forest canopies.

We are rapidly acquiring a new picture of Earth, and it is crammed with millions upon millions of nature's species on the verge of being replaced by billions upon billions of hungry people, asphalt, brick, glass, and useless eroded red clay baked by a harsh tropical sun. Many driving forces of evolution have affected carabid beetles and much of the other life on this planet. Very late in the scale of geologic time, a new driving force, humans, appeared. There is little question in my mind that Isaac Asimov (1974) in his wonderful *Foundation Trilogy* may have been particularly visionary when he described the planet Trantor, a sphere of steel and concrete; a hollow joke of its former self. Could Trantor be future Earth? Perhaps; perhaps not. Perhaps the biocrisis can be avoided. Human beings are starting to pay attention to the problem, and we're a very resilient species and have a lot of good ideas. But do we have the resolve to rise above profit and greed?

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