By **Klaus Bachmann** (text) and **Christian Ziegler** (photos)

A Unified Formula for Biodiversity

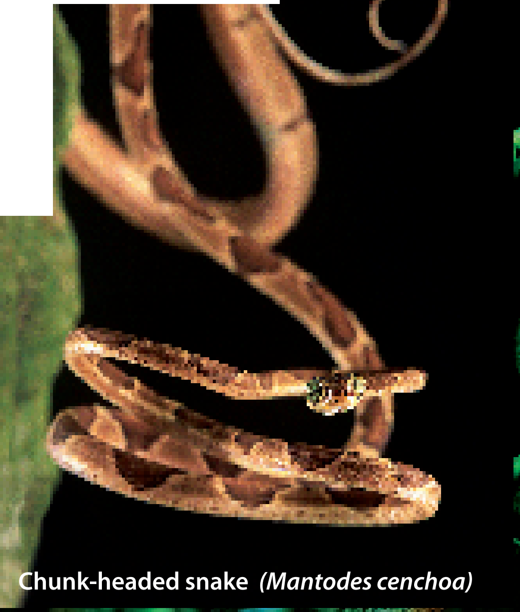
It is one of the greatest puzzles in biology: why do so many more plant and animal species flourish in the tropics rather than in the cool North? American ecologist Stephen Hubbell suggests an answer, in the form of a succinct equation that many of his colleagues deem sacrilegious. But his theory has a solid foundation: the world's largest forest census, in which millions of trees were counted, time and again, for almost 30 years.

[+] 50 ha

The crucible of the global tree count: in 1980, Stephen Hubbell created the first research plot, 1,000x500m in size, on Barro Colorado Island. Since then, trees on 37 additional plots worldwide have been measured every 5 years. GEO documents plots in Panama, Borneo and Thailand.

Panama

300 species of trees grow on the research area in Panama—offering sanctuary to 140 kinds of birds.

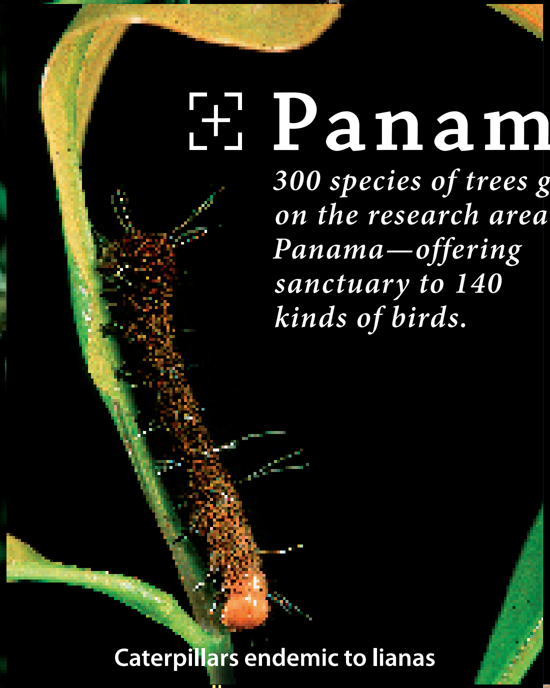


Chunk-headed snake *(Mantodes cenchoa)*

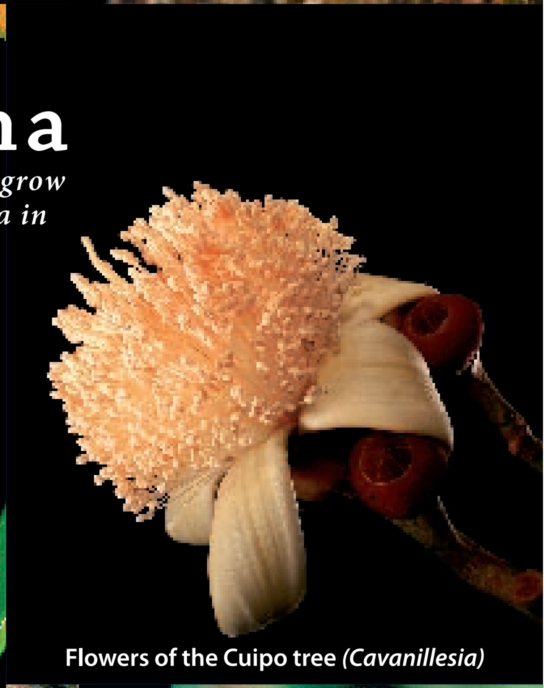
Fig-tree fruits

Spectacled owl *(Pulsatrix persipicillata)*

Brazilian Dutchman's pipe *(Aristolochia gigantea)*



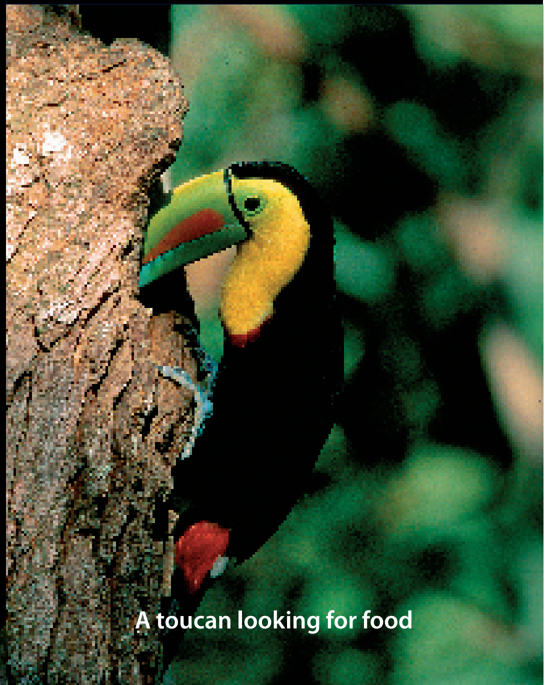
Caterpillars endemic to lianas



Flowers of the Cuipo tree *(Cavanillesia)*

Green iguana *(Iguana iguana)*

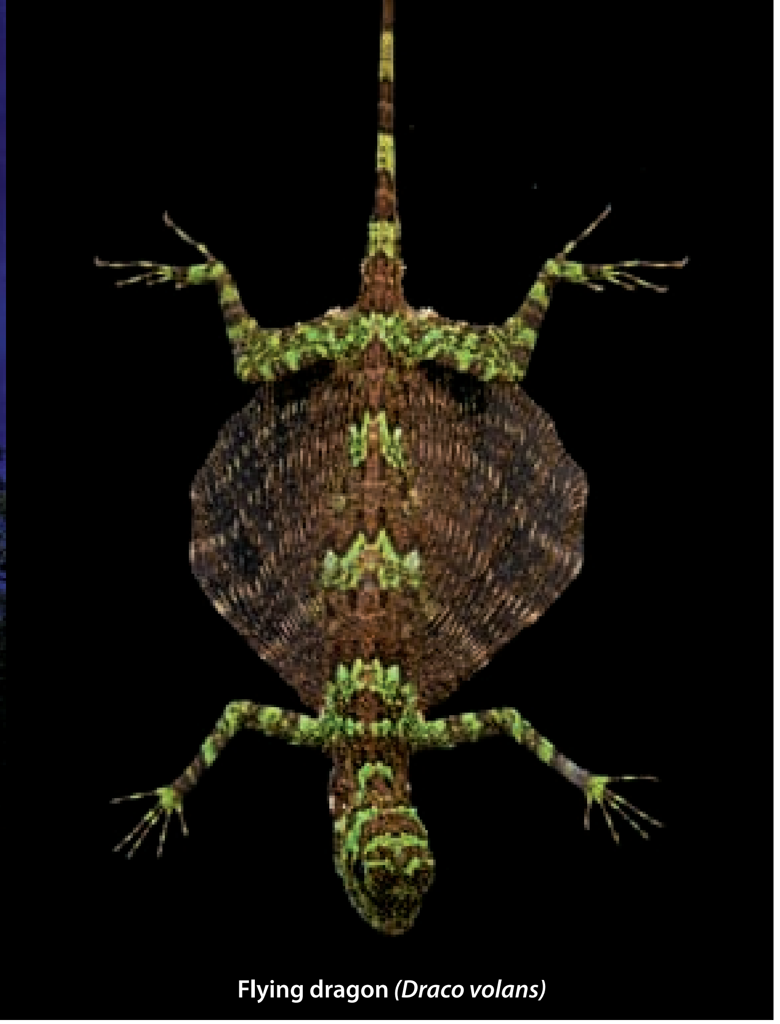
Psychotria in bloom



A toucan looking for food

Measurements in the rainforest: the census workers determine the circumference of every tree and bush which has a diameter of more than 1cm at chest-height. In the first survey, each plant gets a metal marker with an identification number. Trunks with buttress roots are measured above the outgrowth.

Dipterocarpaceae



Flying dragon *(Draco volans)*

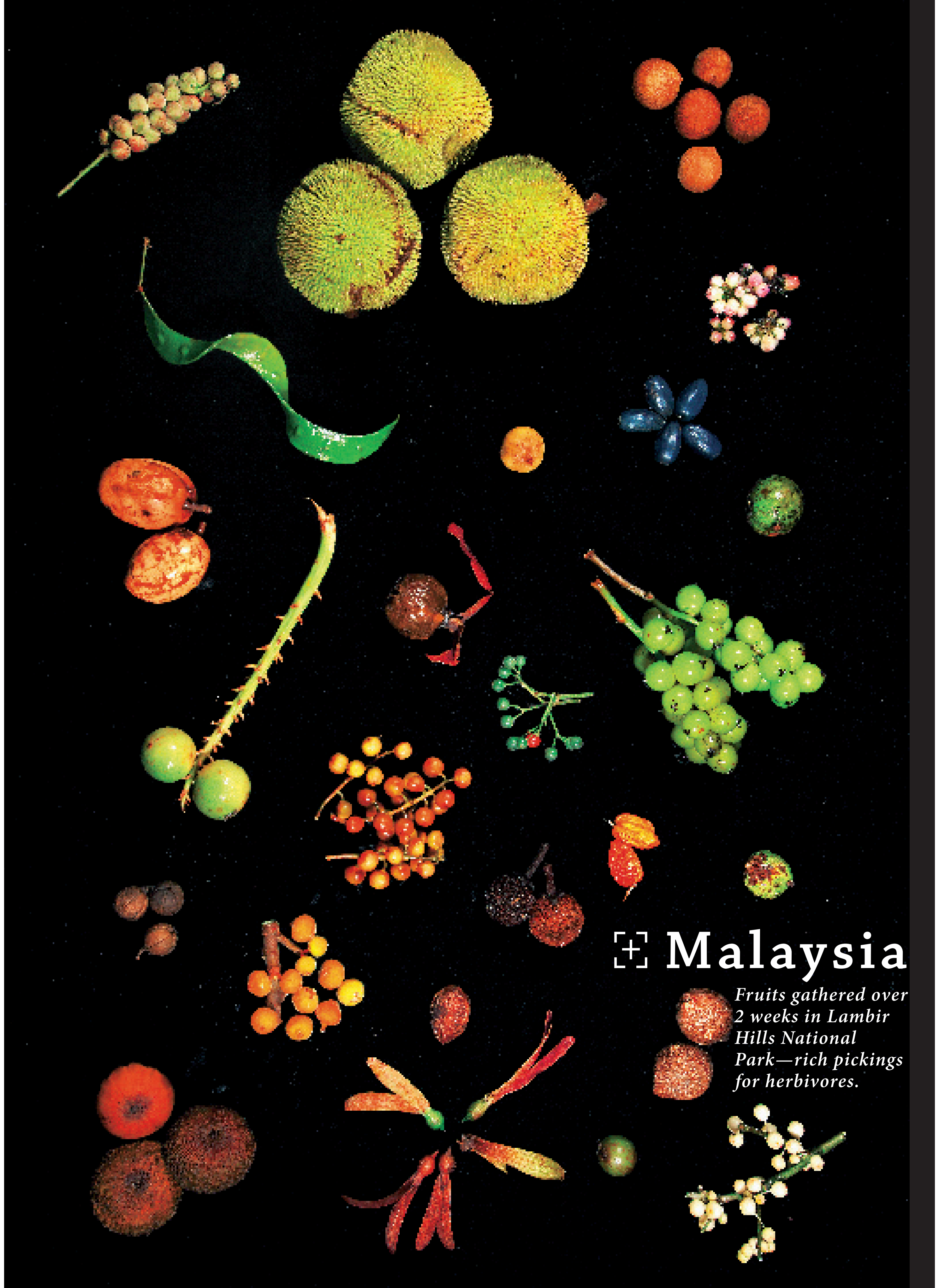
Grid 24/22, which is 20m^2 and sits on a hill on Barro Colorado Island, in the middle of the Panama Canal, is marked by warning tape. Mario Bailon, an agriculture student, places a measuring tape around the trunk of a palm that bears the number 076. He calls out, “142mm!” to his team-mate, who is making notes on a clipboard. The data from the most recent census shows that, as is typical of its type, the palm has not grown wider in the last 5 years but has grown taller. A few meters further on, tree 078: it was 15mm at its last measurement, and is now broken at knee-height. Note on the chart: 0.

The next tree is a newcomer that has fought its way up. Long, thin leaves with a smooth border and black dots identify it as *Trichilia tuberculata*, the third-most common species in the forest. It’s a tree that, with any luck, will make it to the canopy and directly into the sunlight. Mario ties a metal plate to the trunk, marking the plant as number 332. Its position is measured and registered on the chart.

Like Mario and his companion, a handful of other teams are on the move in this warm, humid rainforest to record and identify a total of 210,000 trees and bushes within a 50-hectare area. The census workers require 2 days to cover a 20m^2 field, about 9 months for the entire area. 1,250 grids in all.

But this is just one of 38 research plots across 19 countries. These plots form a unique global observation network that will track the dynamism in forests, and record the changes in the green cover. Altogether, 3.5 million trees representing 7,500 species grow on these plots of land—approximately 10 per cent of the tree flora on earth. The researchers carefully examine, count, measure and catalogue these millions at 5-year intervals: a Sisyphean task.

It is the most extensive forest census ever



Malaysia

Fruits gathered over 2 weeks in Lambir Hills National Park—rich pickings for herbivores.

Winged fruit tree *(Hopea odorata)* with a fig (Ficus)

Centipede (Chilopoda)

undertaken; an extremely complex task—and an expensive one. More than 40 institutes and research organisations all over the world are involved in maintaining and monitoring these pieces of land, and in procuring the necessary resources. It costs between 70,000–350,000 euros (Rs48.5–243 lakhs) to establish each 'plot' and its initial tree count.

The laborious and sometimes tedious work of measuring and cataloguing is an essential step in approaching the larger issue, which is to attack what Dr Stephen Hubbell, an ecologist at the University of California, Los Angeles (UCLA), calls "the Mount Everest of biology."

The question is this: how does nature maintain the remarkable diversity of species found in the tropics? And, considering the issue on a global scale, why do so many more tree species grow in the humid, warm forests around the equator than in the temperate zones of the world?

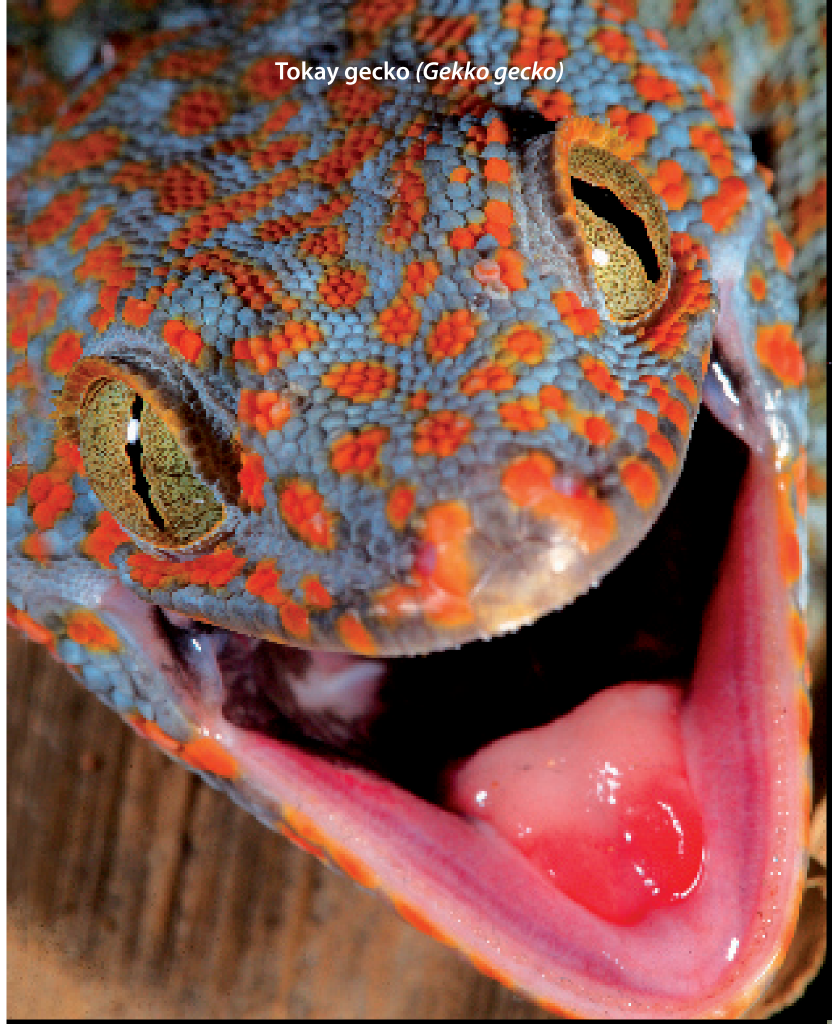
Not to forget, these are plants that in turn offer a habitat to innumerable lianas and epiphytes. Plants whose sap feeds countless insects, whose leaves are then eaten by hordes of bugs, whose fruits feed bats and birds, apes and rodents. A diversity, in other words, that creates ever more diversity.

In contrast, the flora and fauna of the cool North are positively paltry! For each 4.2 million km^2 of the temperate regions in North America, Europe and Asia, there are as many species of trees as can be found on $0.5km^2$ in the Amazon or in Borneo. Less than 300 species of birds breed in central Europe, whereas 890 species have been discovered in Panama alone.

In temperate zones, it is easy to distinguish the various species of trees in forests dominated by oak, beech, fir and pine. But to identify the 300 species that exist just on Barro Colorado Island requires considerable botanical knowledge.

The diversity of tropical nature is only matched by the variety of explanations for it: there are over 30 hypotheses on the origin of biodiversity, depending on how the often-related theories are demarcated from each other.

At a small, spartan study in a log cabin in the Santa Monica Mountains, west of Los Angeles, Dr Hubbell is at his desk, brooding over the forest



Tokay gecko *(Gekko gecko)*

Jeweled flower mantis *(Creobroter gemmatus)*

Thailand

The forest in this research plot is drier and not as rich in tree species. There are 70 reptile species here.

Moss fern (Selaginella)

Wild ginger *(Zingiber thorelii)*

data. Since he has no appointments at UCLA today, he immerses himself in the mysteries of abundance. Equations, curves and graphs flit across the large computer monitor that dominates the room.

At 67, Hubbell has poor eyesight and has to move closer to the screen. "My entire life revolves around trying to understand this diversity," says the ecologist. The grey-haired professor is one of the 'big shots' in his field, as they say in the USA. Without him, the worldwide network of 50-hectare plots of land would not exist; his unique theory has injected new momentum into his field of research.

Hubbell's career started off in 1979. At the research laboratory of the Smithsonian Tropical Research Institute (STRI) on Barro Colorado Island, he met the young botanist Robin Foster, now considered one of the world's experts on tropical flora. Foster had documented the island's plants for his doctorate. Hubbell and Foster came up with an ambitious counting project: to create an inventory of all the trees on 50 hectares of land whose trunks had a minimum diameter of 1cm at chest-height, and to follow the fate of each plant for several decades.

India

India has also been participating in the global observation network of forests since 1988—with a 50-hectare plot in the Mudumalai Wildlife Sanctuary in Tamil Nadu. The forest here is comparatively dry and is home to 76 species of trees. The ground is covered with a luxuriant carpet of grass: ideal terrain for elephants.

It was a bold new approach. Until then, researchers had limited themselves to an area of 1 hectare, and solely to large trees. But Hubbell and Foster believed that they could gauge the dynamism of a rainforest more effectively by including a correspondingly large number of younger trunks.

Five months later Hubbell walked through the undergrowth with two students, measured a piece of land 1km long and 0.5km wide, and drove 20,000 metal rods as border markers into the red earth. Then the tree count began. It took the researchers 18 months to complete the pilot project.

The result was the marking of 235,338 trees, the "seed capital" of an organisation that has fired up the world of ecology in an unexpected way.

"Many people laughed at me at the time," recalls Hubbell. Colleagues visited the forest and reproached him, saying it was useless to map such a huge area. "But we carried on," says Hubbell. His blue-grey eyes have a peaceful, steady look, but carry a hint of the tenacity behind his gentle demeanour. In that respect he resembles the plants that hold out in the shade of a tropical forest until an opening emerges—a gap in the canopy—and then forcefully aim for the sun.

After the publication of his initial findings, Hubbell found more comrades-in-arms. Colleagues realised that his approach offered the chance to formulate the rules of biodiversity in forests.

They set up new plots in Southeast Asia, India, Africa and South America, and fed their databases with various numerical values for analysis. Hubbell calls the global observation network a "fantastic machine for scientific discoveries."

With the information the 'machine' spewed out in the 1990s, Hubbell formulated what he called a 'Neutral Theory' of biodiversity. As it contradicted the prevailing theories, it came as a considerable shock to the field of ecology.

Biologists had earlier explained diversity through the concept of 'ecological niches.' Each species uses natural resources in a unique manner, thus surviving contiguously without challenging one other. To avoid competition, some plants develop strategies to manage with a little light, while others flourish in full sunlight. One takes the help of bees to pollinate; another uses bats. *Vive la différence!*

This system resembles a society based on the division of labour. For example, more people can make a living from automobiles if they specialise. Apart from the traditional car mechanic, one person would offer a tyre service, another would deal with the electrical systems and a third, the paint work. Along these lines, ecosystems function like finely balanced mobiles, in which only the best have a place, a 'niche.' This also means that each species has a stabilising function.

"Forget the niche," Hubbell says provocatively, "it will happen by coincidence." His calls his theory 'neutral' because, above all, he sees the similarities between species. The needs of plants in a forest can overlap, and the competition that arises because of this does not determine the ecosystem's dynamism.

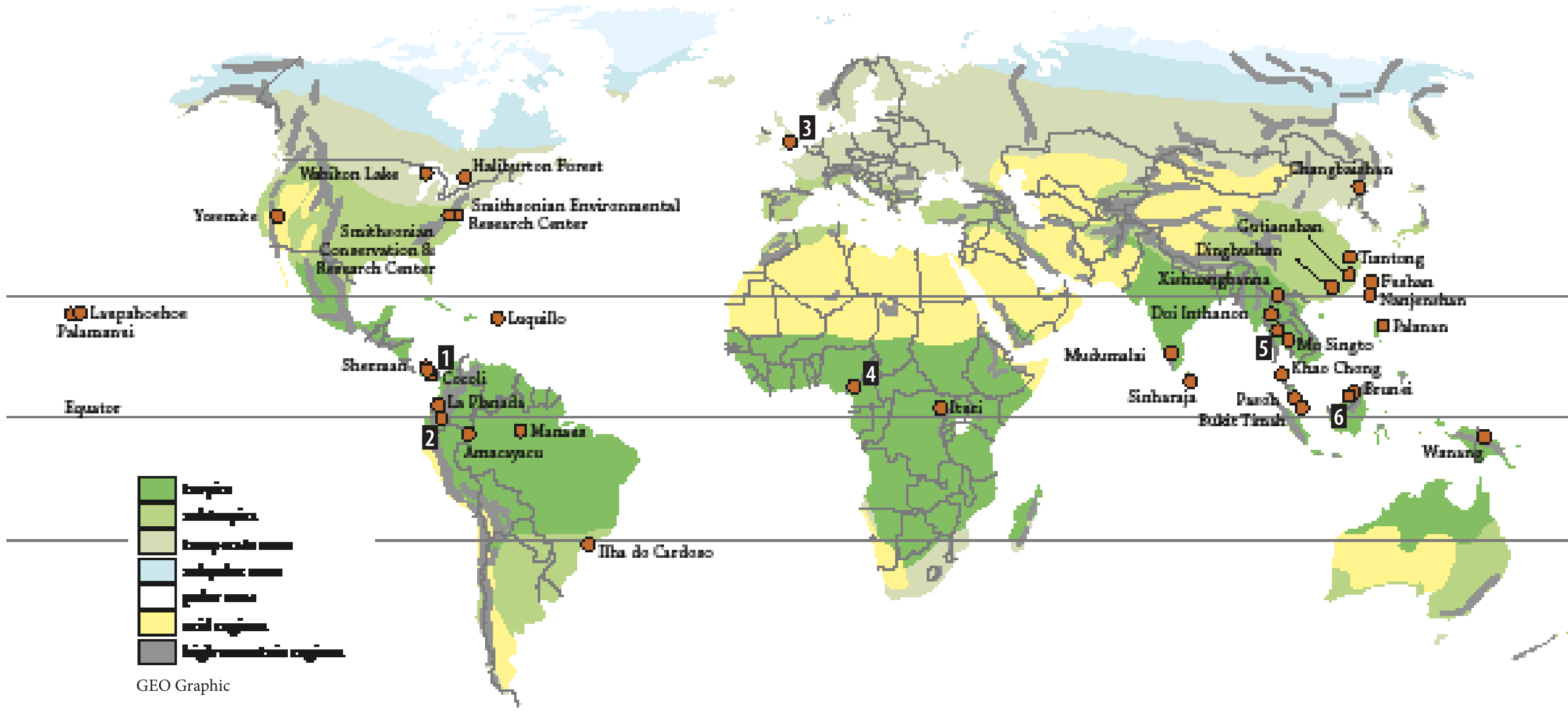
He feels a forest does not consist of species that have found perfectly separated niches: rather, it is a wild mixture that has nothing to do with balance. Only coincidence determines if a species is found in a particular area: if, thanks to a stroke of luck in the course of evolution, a species emerged right there; if fate carried its seeds from a neighbouring region; if, due to pure coincidence, the plant managed to survive catastrophes like storms or fires.

Hubbell doesn't believe that any firmly bound systems exist. According to him, a forest resembles a kaleidoscope whose colourful stones arbitrarily arrange themselves in new patterns with each twist.

On the face of it, Hubbell's theory contradicts

Counting Trees

The census of 38 plots in the tropics and in temperate zones throws light on the biological dynamism in forests.



GEO Graphic

1 Barro Colorado Island / *Panama*	50 hectares	208,400 trees	299 species
2 Yasuni *Ecuador*	50 hectares	151,300 trees	1,114 species
3 Wytham Woods *Great Britain*	18 hectares	16,300 trees	23 species
4 Korup *Cameroon*	50 hectares	329,000 trees	494 species
5 Huai Kha Khaeng *Thailand*	50 hectares	72,500 trees	251 species
6 Lambir *Malaysia*	52 hectares	360,000 trees	1,182 species

Sources: Climatic Zones according to Siegmund/Frankenberg; CTFS experience, and the obvious differences between species. For example, an oak tree has different characteristics and different demands on its habitat than a pine tree, so they inhabit different niches. Hubbell does not disagree. He just believes that such differences are irrelevant for the success of a species in a society; that coincidence carries more weight.

The ecologist has condensed his model into a mathematical formula—or 'forest-formula,' if you like. When he examined the plots in Panama and in the Pasoh Forest Reserve in Malaysia, he himself was "surprised how well the calculated number of species and their frequency matched real values." *(See box below.)*

To spread this 'heretical' theory among the forest community was, expectedly, very challenging. Hubbell experienced how difficult it was for unconventional ideas to gain ground in the field of science. The researcher submitted his articles to prominent journals like *Nature*, *Science* and *The American Naturalist*, all to no avail. The typical response—"nothing of particular interest"—was nothing short of a polite refusal. One expert thundered: "Has Hubbell gone crazy? I don't understand the maths, but his conclusions are against intuition and must be wrong."

Perhaps some ideas need the weight of a book to find acceptance—and the Neutral Theory certainly did. Hubbell's book, *The Unified Neutral Theory of Biodiversity and Biogeography*, was published in 2001, creating a huge—and ongoing—controversy among ecologists. He achieved a personal goal: "to shake up the sciences." The book is now a classic in the field, a fixed point around which proponents and opponents continue to circle.

The Neutral Theory is the whetstone against which Peter Ashton sharpens his ideas. Although retired, the 75-year-old scientist cannot stop questioning the origins of biodiversity—much like Dr Hubbell. He, however, thinks more 'niche' than his American colleague and less 'neutral.' But he still believes that Hubbell's construct of ideas is "immensely important."

Ashton, a powerful-looking outdoorsy type, and Hubbell, who is more of an academic, first met in the early 1980s at a conference in Leeds, UK.

Sitting in a conference room in the herbarium of Kew Gardens, London's famous botanical gardens, Ashton recalls, "Hubbell presented his first results, and I was furious! Everything that I had found out pointed in exactly the opposite direction."

After the lecture, they both discussed their controversial views—and eventually agreed to work together to establish a secondary area of investigation. In 1990, they collectively founded the Centre for Tropical Forest Science (CTFS), under the auspices of the STRI, to coordinate the work in a growing number of plots.

Ashton knows the Asiatic forests intimately. He has worked in almost every country in the East, and has traversed the green universes of Brunei, Sarawak, Sabah, Indonesia and Thailand for decades.

His journey in the tropical cosmos began in 1957 in the Sultanate of Brunei, where he documented the mighty 80m-high Dipterocarpaceae, the characteristic trees of the region. From the Iban people of Borneo he learnt to differentiate hundreds of species, and he barely escaped with his life after being bitten by a pit viper on one expedition.

"Come, let me show you a few *Dimeria dipteros*," he says. A narrow, winding staircase takes us to the ground floor, to a cabinet marked 'A46.' Ashton pulls out five A3-size files from its compartments and leafs through them: *Shorea leprosula*, a species of plant from the Dipterocarpaceae family, its leaves brown and eaten by insects, is carefully spread out and fixed with spots of glue. Its thin, faded, flowering stems are placed next to it. The basic facts have been carefully

Liza Comita has been following the fate of tens of thousands of seedlings in the Panama plot. She discovered that the closer the seedlings grow to the mother tree, the smaller its chances of survival. The trees whose trunk circumference can be determined have apparently made it. Processing a 20m^2 plot in Panama takes about 2 days.

Measuring Diversity

The Neutral Theory allows us to calculate tropical diversity with astonishing precision—despite some very simple assumptions.

There is a truism that circulates among authors: a single mathematical formula in a book halves its circulation.

In the case of Stephen Hubbell, it was the other way round. *The Unified Neutral Theory of Biodiversity and Biogeography* gained fame because of its formula, although some biologists have problems understanding the difficult mathematics in detail. But even critics now admit that the American ecologist's short, highly abstract formula can describe the complex diversity of species in nature with great precision.

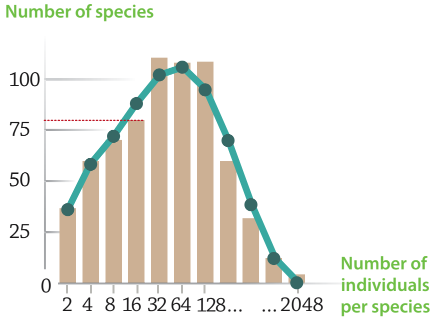
What is Hubbell's chief contribution? He has invented the biodiversity number θ (Theta) and incorporated it into the formula:

$$\theta \propto J_M \bullet \nu$$

The biodiversity number Theta gives information about the wealth of species in a region. It does not calculate the exact number of species, but gives a relative value: Theta varies between zero and infinity. If Theta is 100 for one region and 200 for another, then we can infer that the diversity of species is much greater in the second region, although the exact number cannot be calculated.

How is Theta calculated? It is proportional to (∝) the sum of the total number of individuals of each species in a region (J_M) and the rate (ν) at which new species appear in a region. Both elements can be counted (for example, in a forest census), estimated or calculated from other forumlae.

Hubbell's formula describes the biodiversity in different regions quite precisely. In addition, Theta is an initial value for further calculations—for example, the frequency distribution of species (*see graph*), or for predicting how the composition of the tree community will change over time.



The power of Stephen Hubbell's method can be demonstrated using the example of the Pasoh Forest Reserve in Malaysia. The bars indicate how many species of a particular number grow in a plot. For example, 80 species with 16 individuals each occur here. The points were theoretically calculated with the help of Hubbell's formula.

Ferns of the species *Dipteris lobbiana* line the streams in Borneo. The narrow leaves are an adaptation to their habitat: they offer less resistance to the currents during floods.

Peter Ashton is an expert on Asiatic forests. In 1990, he and Hubbell collectively started the Center for Tropical Forest Science, which coordinates the global forest census.

noted: date of find: 18.03.1949, height: 80ft (24.4m), breadth: 48in (1.22m).

Next to it, four related species, all from the Dipterocarpaceae family, can scarcely be told apart. “They all occur in the Pasoh Forest on the Malaysian peninsula and are totally dependent on each other,” the researcher explains.

The reproductive processes of these five species are as precisely intermeshed as the gears of a Swiss clock. They are all pollinated by tiny insects, thrips, which feed on their petals. As soon as the first species, *Shorea macroptera*, opens its buds, the thrips reproduce en masse. Laden with pollen, these 1mm-long insects fall to the ground in clouds, scatter and deposit their cargo on other plants. The next species starts blossoming right after, benefiting from the services of the multitudes of insects, and offering them new nutrition. This process continues until *Shorea leprosula*, last in line.

Ashton’s interpretation is that the trees compete for the ‘pollinator.’ Over the course of evolution they have coordinated their flowering periods and created different niches. Without this kind of adaptation, one species or another would have fallen by the wayside in the fight for survival. Whereas in this manner, all species can co-exist.

Specialisation works as a driving force for diversity, a phenomenon that Ashton sees everywhere. “As I walked through the forests,” he explains, “I saw certain patterns recurring. The more I studied plants, the more specialised they appeared to me. Each species was ecologically different.” This is wonderful evidence for the importance of niches.

Apart from this specialisation, other signs of order within the thick crush of vegetation became apparent to the scientist. “The variety of species increases if the dry period is shorter and less intense,” he says.

As evidence, he offers figures from the network of research plots. In Thailand’s Huai Kha Khaeng Wildlife Sanctuaries—where there is no rainfall for 6 months at a time—251 species flourish; in Cameroon’s Korup National Park, where the dry period extends to 3 months, there are 494; and in the perenially humid Yasuni National Park in Ecuador, which lies at the foot of the Andes, 1,114 species exist.

It is a convincing correlation. But then there is the plot in the Sinharaja Forest Reserve, which lies at the southern tip of Sri Lanka—and does not fall in line. Despite having a climate similar to Yasuni’s, botanists have counted only 204 species of trees here.

The reason for this difference? “It lies in natural history,” says Ashton. The search for forces that drive the process of biodiversity today can only deliver a part of the truth. It is equally important to look back at earlier periods in earth’s history, and at the evolutionary roots of this tropical wealth. We need to first establish: since when have the regions close to the Equator been so rich in life? Was that always the case?

Ashton’s solution to the Sinharaja puzzle: during the Ice Age in the Pleistocene geological epoch—which ranged from approximately 1.8 million years to 12,000 years ago—there was a weak monsoon several times over, and India and Sri Lanka were rendered dry in this period. The rainforests shrank and several species died out. It was a wide-ranging felling whose consequences can still be seen today.

This, however, means that the roots of diversity do not lie in the recent history of the earth but actually extend way back into the planet’s past. Back, that is, 50–55 million years.

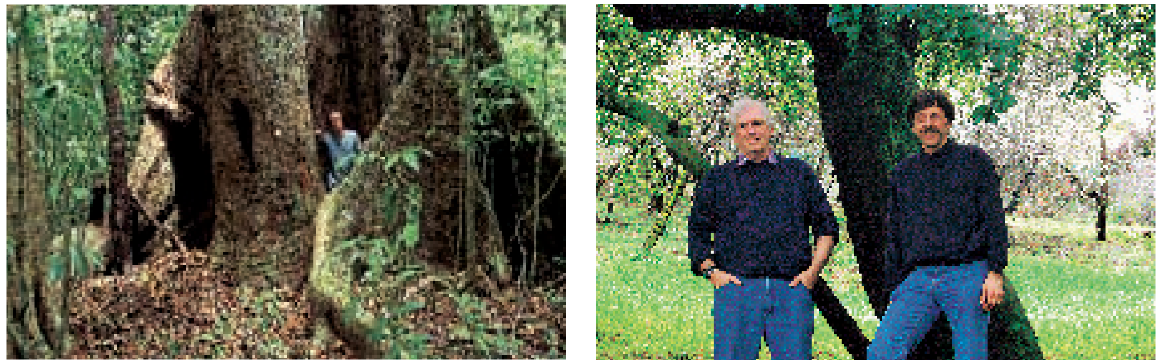
Land-mass and time-frame, coincidence and niche, nutrition and climate—while hunting for the origins of diversity, biologists have formulated a wide range of explanations. With his Neutral Theory, Hubbell has contributed a widely recognised concept. However, it is still uncertain terrain; there are several approximations and many contributing factors. A consensus is not yet in sight. Has the attempt to conquer biology’s Mount Everest been abandoned?

The field of physics once also faced a similar problem: the manifold natural phenomena—electricity, the behaviour of light, the coincidental decay of the atom’s nucleus—were described by varying, disparate theories.

Finally, in the 1960s and 70s, a breakthrough was achieved and standardisation followed. Will biology ever be granted comparable success? Will diversity allow itself to be compressed in a standard ecological theory, in a forest-formula?

Ashton snorts. No, his disbelief suggests; an approximate idea of what is happening is all that we can hope for.

And Dr Hubbell? Despite his belief in simple formulae, he terms the request “an unrealistic expectation.” As far as biodiversity goes, he says, “we are now at the same stage that doctors were during the Renaissance. It is as though we are cutting bodies open, amazed at the organs we find, and then speculating about their function.” ■



■ ■ ■ *Photographer Christian Ziegler, 37 (picture to the left), did not have to search long on Barro Colarado Island to find a giant tree with mighty buttress roots. The biologist has known every inch of the island since he did research for his degree dissertation here. Fascinated by nature in the tropics, he is planning to document the diversity of species in other plots as well. GEO-editor Klaus Bachmann, 51 (on the right, with Dr Hubbell in his garden), was surprised how well the world observation network functioned—despite the cultural differences and financial challenges.*