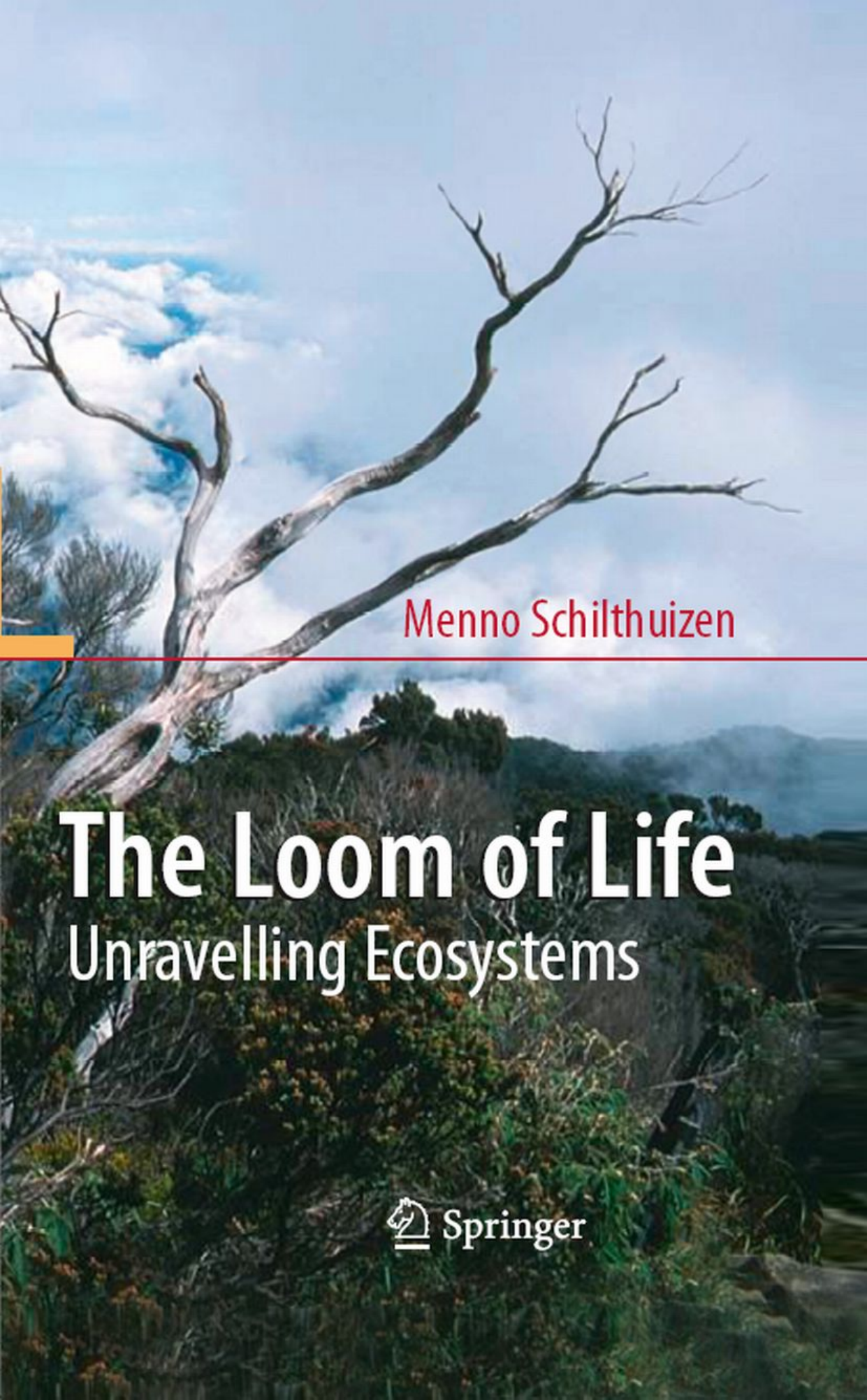
Menno Schilthuizen
The Loom of Life
Unravelling Ecosystems
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When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view this is!

(Charles Darwin, *On the Origin of Species*, p. 74)

The science of biodiversity is not much farther along than medicine was in the Middle Ages. We are still at the stage, as it were, of cutting open bodies to find out what organs are inside.

(Stephen Hubbell,
The Unified Neutral Theory of Biodiversity and Biogeography, p. ix)

To Rachel

Preface

It is a slightly cloudy morning at the end of the rainy season in Kota Kinabalu, a city on the north coast of the island of Borneo. I am writing this on my tiny verandah overlooking the grounds of the house where I have been living for the past five years. Let me describe my garden to you. It is a crescent-shaped plot of land, perhaps 1,000 square metres, at the end of a cul-de-sac appropriately named 'Happy Garden'. The bit that I can see from the verandah is flat, with a grassy lawn and a couple of fruit trees. To my left is a pond and a compost heap where the remains of the banana tree that I sacrificed yesterday are beginning to decay, and behind that a steep retaining wall with drainage pipes sticking out. At the back of the house, the land slopes steeply upward and is covered in my own bit of secondary scrub, which I proudly cultivate to the great bewilderment of my landlord, who keeps offering to have his men cut it down.

On the door of my fridge I keep a list with all the kinds of birds that I have spotted in my garden (and the air space above it). It amounts to a grand total of 47 species, ranging from the noisy flocks of yellow-vented bulbuls that nest in the scrub on the hillslope to the lone chestnut-winged cuckoo that visits each year in October to feast on caterpillars for a few days before heading further south. Other large animals are the huge monitor lizards that sometimes unexpectedly clamber out of the gutter and scare the bejesus out of me, the black cobra that lives in one of the drainage pipes, and the plantain squirrels that frolic in the branches of the *langsat* tree every morning. Including frogs and reptiles, rats and bats, and excluding the fish that was in my pond until my dog ate it last week, there may be several tens of species of vertebrate animals residing in my garden at any one time.

Not bad, but a minuscule diversity compared with the invertebrates, which will take us up about two orders of magnitude. Peek into the water collected in the leaf axils of the 'elephant ear' aroid, and you will find a writhing assembly of mosquito larvae, nematode worms, and euconulid snails. Pore over the debris in the compost heap and many species of fruit flies, ambrosius beetles, dolichopodid flies, and ants stare you in the face. A particularly unlucky plantain squirrel may carry several species of ticks and fleas in its pelt and a mass of nematodes and flatworms in its belly. From the leaves of the fig tree, a whole entomologist's collection of ponerine ants, jewel wasps, jumping spiders, and leaf beetles could be gleaned, and any dusty corner of the garden shed will harbour ensign

wasps, the pumpkin-seed-shaped shelters of tineid caterpillars, and silverfish. I would not be surprised if my garden is home to as many as 2,000 species of insects, worms, snails, and other invertebrate animals.

And it does not stop there. From my perch I can see about 15 different species of tree, ranging from the native and ubiquitous *Dillenia* to the versatile neem tree, native to India, but planted in gardens throughout the Tropics. And I know that round the back there are at least as many more, not to mention all the woody climbers that are constantly trying to smother them. Add to that the bananas, the aroids, the algae in the pond, the grasses, the ferns, the mosses, and the many other herbs, and we can probably append at least 150 species of green plants to the growing list of Happy Garden's biodiversity.

That takes care of most animals and plants that can be seen with the naked eye, but I would not even hazard a guess as to how many species of 'microbes' inhabit this end of the street. During rainy weeks, beautiful veiled stinkhorns pop up in fungal priapism, and when I have been on a trip for a week I find that, as Tom Waits said, 'everything in my refrigerator has turned into a science project.' But the irregular appearance of their fruiting bodies is hardly a proper gauge for the actual diversity of fungi in my garden. Many more kinds are spreading invisibly through the decaying matter in the topsoil, or are living in silent symbiosis in termite nests or, as mycorrhiza, in and around the roots of my plants.

Unicellular organisms abound as well. Diatoms live in the pond, amoebae crawl microscopically in the wet soil, and bacteria are literally everywhere: not just free-living in the soil and the water, but as parasites or symbionts in and on each of the thousands of species of animals, plants, fungi, and protozoa, and many will be specific to their particular host. The velvety-blue *Hypolimnas bolina* butterflies that bask on the leaves of the mango tree, for example, have a *Wolbachia* bacterium in their ovaries that kills male eggs in some parts of the butterfly's range, but here in Borneo appears to be benign. And the banana aphid grows *Buchnera* bacteria in its belly that help it digest its food.

There is no way of telling exactly how many species of organisms share this minute semicircular plot of tropical suburbia, but it will definitely be several thousand. Let us say 10,000 as a very conservative guess. Now if I were to hop over the fence to the garden of the sprightly Indian lady who lives next door, would I find the same 10,000 species? Probably not, as she keeps her garden free of any incipient jungle and thus misses out on a lot of biodiversity. Three thousand species tops, I would say. Still, there may be some species there that are missing from my garden. A paradise tree snake, for example, skulks in her backyard. That is probably accidental. Large predators are rare, and this side of the street may just be able to support one individual, which happens to live next door. But other additional biodiversity comes from habitats in the neighbour's garden that are lacking from mine. There is a coconut palm there, which comes with its own coconut beetles, and also a collection of orchids, which have special mycorrhizal fungi. So between us, our two gardens will have a higher biodiversity than each taken separately. But if I were to keep fence-hopping all the way down the street, continuously adding to my growing species list, how fast would the list grow? And would it keep growing forever or become complete at one point? There's a question.

Returning to the bird list on my refrigerator door, there are some species on that list that are no longer in my garden. A few years ago, startlingly blue collared kingfishers would nest in a dead branch of the mangosteen tree and feed their young with house geckos plucked off my walls. But the kingfishers seem to have disappeared. Conversely, the large-tailed nightjar only last year made its metallic-voiced entry into Happy Garden and seems to be here to stay. Until two years ago, there were huge white-winged tomb bats in my roof that would disperse at dusk with frantic clicking sounds and wildly beating wings. For some reason, the bats have left, but in their stead a yet unidentified species of rat has settled in.

The same thing with the smaller creatures. The ant fauna of my house is in continuous flux. At one point, the tiny Pharaoh ant was everywhere, travelling in six-lane highways along the walls and building their multiqueened nests in the most unlikely places, from piles of laundry to the jewel cases of CDs. But then an army of reduviid bugs and parasitic wasps began to beat them down and they became extinct, only to be replaced by the yellow crazy ant, which experienced a quick cycle of boom and bust, then briefly gave way to its equally nervous cousin, the black crazy ant, but finally retook the house once more. So even though the number of species in Happy Garden seems to remain constant, species become extinct and others establish themselves all the time. Species that were rare become common, and vice versa. Why? Are there imperceptible changes in the garden's microhabitats? Or is it just random turnover, the result of accidental extinctions and immigrations? There's another question.

And let's have another look at that huge tally of 10,000 species in a piece of land barely larger than a tennis court. Does that imply my humble garden is actually an immensely complex ecosystem with that many ecological roles to play? Or not? Take those 150 species

of green plants for example. Throughout the day, a deluge of photons rains down on my garden, the energy of which is tapped by the trees, ferns, herbs, and mosses and used to fuel their carbon-fixation machinery which constantly grabs carbon dioxide from the air and churns out roots, stems, leaves, flowers, and fruits. Each and every one of these plants does this; they all 'eat' carbon dioxide and absorb solar energy. But they may be different in other respects. The elephant ears, for example, grow in the soaking-wet mud beneath the retaining wall, whereas the *Melastoma* herbs prefer dry spots at the top of the wall. The *Macaranga* trees thrive in the blazing midday sun, whereas the gingers grow in the shady places underneath and survive on the flecks of light that make it through the *Macaranga* leaves. Mosses grow on the rocks, but grasses prefer flat patches of loamy soil. There may be one or two more lines by which plants delimit their ecological roles, but the question is whether there are really enough different roles to play for 150 species. If there are fewer, there must be a lot of competition between species – and yet they live happily together in my garden without driving each other to extinction. We may wonder how they do that.

The perceptive reader will already have understood where this exercise in horticultural exhibitionism has been heading. It has served to introduce the subject matter of this book, which can be broadly described as the ecology of diversity, but officially falls into such realms of science as community ecology, system ecology, and macroecology. We will now leave Happy Garden behind us and head for caves, jungles, and coral reefs, and many other natural environments besides that. We will delve into the scientific literature, visit laboratories and field experiments, and meet the brightest ecologists of this and earlier times, trying to find answers to the questions that apply to Happy Garden as much as to the whole wide world. How many species are there and where do they all live? Why are there so many species? How are ecosystems assembled? Does each species have its unique niche or are species interchangeable? Why are some species rare and others common? And we will address a few burning issues as well: How many species are going extinct and how many are newly introduced by people? And how much tampering can our ecosystems tolerate before they embark on a one-way path toward collapse?

Acknowledgements

The famous nineteenth-century American ornithologist Audubon once confided to a friend, 'God save you the trouble of ever publishing books on natural science. I would rather go without a shirt through the whole of the Florida swamps in mosquito time than labor as I have with the pen.' As people close to me can attest, I felt the same way after finishing my book on speciation, *Frogs, Flies and Dandelions*, published in 2001 by Oxford University Press. However, bitter-sweet memories have a habit of fading and transmogrifying, over surprisingly short time, into cherished ones. And it was not before long that I began to feel the urge to start work on another book. Having moved, immediately after finishing *Frogs, Flies and Dandelions*, to Universiti Malaysia Sabah (UMS) in northern Borneo, and suddenly surrounded by members of what ecologists call the 'rainforest mafia', I began to realise that, although I had a fair grasp of the evolution of species diversity, my understanding of its maintenance and its role in ecosystems was limited. So a book project on the *ecology* of species diversity, to serve as a complement to the one on the *evolution* of species diversity, seemed like a good way of (1) teaching myself some ecology and (2) helping others who felt similarly challenged.

In the end, it was another drawn-out struggle to get from a good intention to the book you are now holding. Community ecology turned out to be quite resilient to simplification and popularisation, and I have spent many a day lying on the merbau floor of my house in Kota Kinabalu with papers and books strewn around me, grappling with species abundance curves, species–area equations, and food web stability analyses, thinking of Audubon, especially since on such occasions I was usually without a shirt and in northern Borneo it is always mosquito time. Still, that I could do so was largely thanks to the helpfulness of those around me, who allowed me to take time off, and forgave me for doing so, to write: my employers Maryati Mohamed of UMS and later Ronald van Hengstum and Dirk Houtgraaf of the museum Naturalis in Leiden; and also my children, my partner, my friends, and my colleagues.

For helping me find the relevant literature, I wish to thank the librarians of UMS and of the Danum Valley Field Centre. However, as the older literature was not always available in Borneo, I received a lot of help from trusted friends overseas who gave me access to the libraries of their institutions, and even printed and photocopied piles of obscure papers, in particular Frietson Galis of Leiden University, the Netherlands, Bronwen Scott

of Victoria University, Australia, and Lounès Chikhi of the University of Toulouse, France. The Royal Society and the Sabah Foundation (by way of Glen Reynolds) arranged for me to work in Danum Valley Field Centre for a while, where bearded pigs and bearded British students were the only distractions. Marc and Isabelle Ancrenaz let me stay in their house in Sukau for a week to watch Woody Allen films and work on Chap. 3. My partner Rachel Esner tolerated me in her house in Amsterdam and her apartment in Paris as I worked feverishly on the final chapters in late 2007 and early 2008. And Stephen and Rosalind Sutton of Borneo Books were a great support, especially in the early phase, as were Annadel Cabanban, my agent Lulu Stader, and the people at Springer who made it all possible, in particular Dieter Czeschlik, Anette Lindqvist, and Isabel Ullmann.

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Several friends took the trouble of close-reading large parts of the manuscript and helping me winnow out all inconsistencies, non sequiturs, and unintelligibilities. These were Rachel Esner, Frank van Rooij, Isabel Silva, and Lulu Stader, and I thank them for their dedication.

Contents

Life in Little Worlds 1

1.1 Bottled Biotas

I just bought myself an ecosystem. Even though the promotional babble on the website says it is actually 'a work of art' that is 'carefully crafted to achieve an aesthetic, meditative beauty that can soothe any environment, including home, classroom or office', to me it is primarily an ecosystem. Ecosphere Associates of Tucson, Arizona, USA, specialises in selling little worlds in a bottle. Their Original EcoSphere® comes in various shapes and sizes. Mine is the ISS model: a clear glass sphere the size of a grapefruit, filled two thirds with seawater. Some gravel covers the bottom and a twig of dead coral provides a substrate for green algae. But the star attraction of the crystal ball is a dozen or so tiny red brine shrimp, nervously nibbling away at the algae.

The small sphere and its inhabitants may sound like a meagre sort of fishbowl for a price that could buy me a king-size fishtank with money to spare. But then EcoSphere is no ordinary aquarium. A spin-off from technology developed by NASA, the glass ball is completely isolated from the outside world. There is no way to feed the shrimp, prune the algae, or change the water. It is a self-contained ecosystem, running solely on the sunlight that flies through the glass wall and powers the photosynthesising chloroplasts in the algal cells. These split water into oxygen and hydrogen, sticking the hydrogen onto carbon dioxide molecules to build new algal tissues, and dumping the oxygen in the water. The shrimp breathe in the oxygen and eat the carbohydrates produced by the algae and in the process exhale water and new carbon dioxide for the algae to absorb. The waste products from this cycle, shrimp droppings and dead algal cells, are decomposed by bacteria in the water to provide nitrogen, phosphorus, and other nutrients for the algae. As a result, oxygen, carbon, hydrogen, and a whole bunch of other elements are continually pumped around the food cycles inside the sphere by the power of the sun. The process will not stop until all the shrimp (which do not reproduce) are dead. This, according to Ecosphere Associates, can take more than eight years.

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