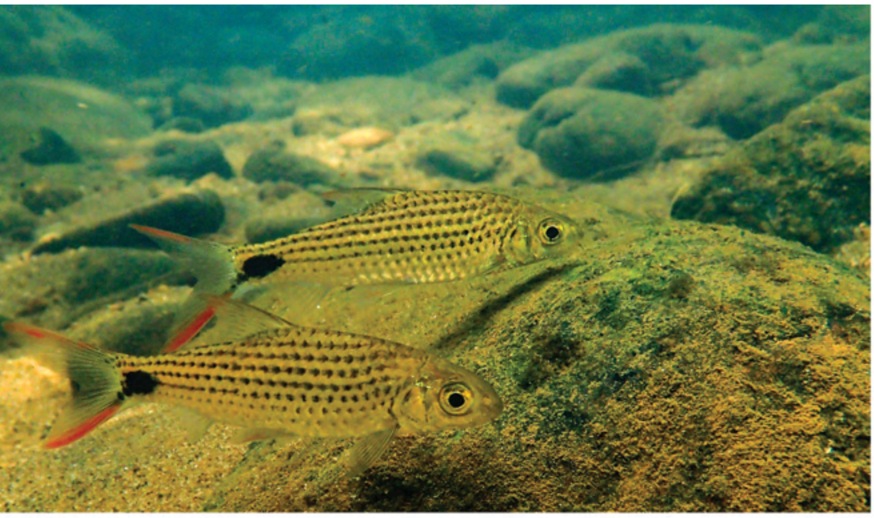
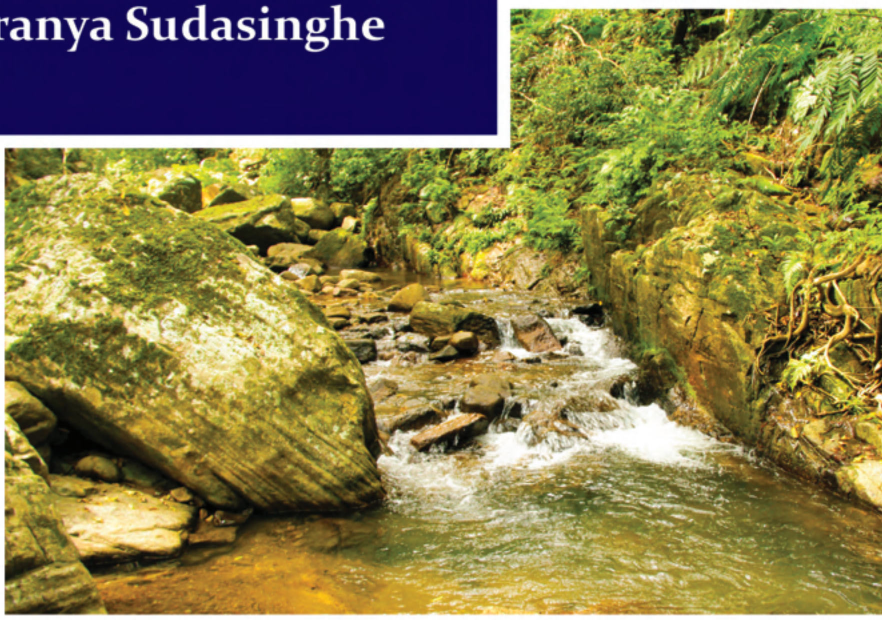


The Ecology and Biogeography of Sri Lanka

A context for freshwater fishes

Rohan Pethiyagoda & Hiranya Sudasinghe



THE ECOLOGY AND BIOGEOGRAPHY OF SRI LANKA

A CONTEXT FOR FRESHWATER FISHES

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A CONTEXT FOR FRESHWATER FISHES

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WHT
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Frontispiece: *Schismatogobius deraniyagalai.*

Contents

Foreword

In 2000 the ecologist Norman Myers and colleagues introduced the concept of biodiversity hotspots for conservation priorities, defining these as biogeographic regions that host exceptional biotic diversity and are under a high threat from anthropogenic activity. At that time, they identified 25 hotspots. Although these encompassed only 1.4% of Earth's land surface, they harboured an astonishing 44% of all vascular plant species as well as 35% of the known amphibians, reptiles, birds and mammals. Today, 35 terrestrial biodiversity hotspots are recognised.

When that paper was published, I was fresh out of graduate school and the idea of biodiversity hotspots struck a chord with me. I find the uneven distribution of biotic diversity both across the globe and across taxonomic groups infinitely captivating, particularly when freshwater fishes—my passion since my early school days—are involved. I started my career as an evolutionary biologist working on the adaptive radiation of cichlids in Lake Tanganyika in Africa, but the hotspot paper opened my eyes to the fascinating biotic diversity of Asia, especially in the Sundaland, Indo-Burma, Himalaya and Western Ghats-Sri Lanka biodiversity hotspots. I was intrigued; but there was also the obvious question: Why were my beloved freshwater fishes excluded from the analyses of biodiversity hotspots? The authors of the paper gave the following reason: "The other vertebrate group, fishes, is excluded because data are generally poor (there could well be at least 5,000 species waiting to be discovered, or more than all mammals)." This was a call for action and an excellent reason to go East, so I took the challenge.

Later on, in 2004, I was working on two groups of Asian freshwater fishes, the fighting-fish genus *Betta* and the Badidae, the chameleon fishes, when I came across a paper titled "Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot" by herpetologist Franky Bossuyt and colleagues. Using molecular phylogenies of several invertebrate and vertebrate groups, they demonstrated that Sri Lanka has a large number of endemic species, often the result of extensive radiation on the island. And yes, the authors of this study did include freshwater fishes: small barbs of the genus *Puntius*, with species now assigned to the genera *Dawkinsia, Pethia* and *Systomus*. Furthermore, this study showed that Sri Lanka harbours a fauna that is notably distinct from that of the Indian mainland.

This result was surprising. Sri Lanka is a continental island separated from the Indian subcontinent by the Palk Strait, a narrow, approximately 10-metre-deep shelf sea. Global sea level reconstructions suggest that during extensive periods in the past, and for almost all of the Pleistocene, Sri Lanka was connected to the Indian mainland through a broad isthmus, called the Palk Isthmus. The expectation was that Sri Lanka's biota would be but a subset of the richness found in the Western Ghats. However, here was a study showing that many sister-group relationships between Indian and Sri Lankan taxa pre-date the Pleistocene and its sea-level fluctuations. Clearly, there was more to Sri Lanka's evolutionary history than had been previously assumed.

How can we explain the unique nature of Sri Lanka's biota? Some of the answers, of course, are hidden in hundreds of scientific articles, old and new, which need to be screened painstakingly. Finding the answers also requires the interested person to become a taxonomic expert for many different groups including plants, invertebrates and vertebrates. One would need to understand the evolutionary history of the biota of Sri Lanka as well as the island's complex geological and climatological history. Better however, would be to start by thoroughly reading *The ecology and biogeography of Sri Lanka – a context for freshwater fishes*, by Rohan Pethiyagoda and Hiranya Sudasinghe.

From this book we learn about the complex interplay between geology and climate in the formation of the Western Ghats-Sri Lanka biodiversity hotspot. The short story is that the break-up of Gondwana and the 70 My-long northward journey of the Indian plate, of which Sri Lanka is a part, ended with the collision with Eurasia around 50 Mya, triggering a major biotic exchange between India and Asia. This exchange, however, was affected by climate changes that caused India to become more arid until rainforests remained confined to south-western Sri Lanka. Thus, climate change modulated biotic interchange between Southeast Asia and India and, more importantly, between southern India and Sri Lanka.

In the Preface, the authors write "Despite this wealth of new knowledge, it is still too early for a synthesis—an overarching narrative that explains how exactly the island's plants and animals came to be as they are." I think this statement is unduly modest. It is true that there are frustrating gaps in our understanding of the biogeographic history of the Western Ghats-Sri Lankan biodiversity hotspot, in particular regarding the exact timing of geological events, the details of past connectivity between different tectonic plates, or tectonic plates and island arcs, or the influence of past climate. But Rohan and Hiranya have succeeded in giving us readers the most complete synthesis possible at this time. And it is not only about freshwater fishes! With *The ecology and biogeography of Sri Lanka…* we, for the first time, have an authoritative overview of Sri Lanka's staggering terrestrial diversity: Roughly 25% of the 3500 vascular plants, over 65% of the 78 species of freshwater fishes, over 60% of the 233 reptiles, over 80% of the roughly 250 species of land snails, and all 51 species of freshwater crabs, are endemic.

As the exploration of Sri Lanka's evolutionary history continues, *The ecology and biogeography of Sri Lanka…* will serve as an essential beacon guiding it. More importantly, the biogeographic connections and disjunctions it reveals will inspire future generations. But aside from its great scientific value, this book is a labour of love and dedication to Sri Lanka's majestic natural beauty. It is beautifully illustrated with maps, figures and wonderful photos of landscapes, animals and plants. A photo says so much more than a thousand words. How wonderful it would be if we had comparable books dedicated to the other biodiversity hotspots in Asia! Sri Lanka is very privileged indeed to have Rohan and Hiranya, two passionate ambassadors of their country's stunning natural heritage.

As I have been working with Asian freshwater fishes for several years, I've had the good fortune to meet both Rohan and Hiranya. Rohan is well known as an ichthyologist and conservationist who in 1991 published the widely acclaimed book *Freshwater Fishes of Sri Lanka*. And yes, he was one of the authors of that important paper on "Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot". As the founder of the Wildlife Heritage Trust of Sri Lanka and as a recipient of the Rolex Award for Enterprise in 2000, he is a relentless champion for Sri Lanka's biodiversity and above all a dedicated mentor who continues to inspire young researchers to get involved with the exploration and conservation of Sri Lanka's natural diversity. Hiranya is one of these, a remarkable, young ichthyologist with expertise in both taxonomy and molecular systematics. Many of the insights we gain from *The ecology and biogeography of Sri Lanka – a context for freshwater fishes* regarding the distribution and phylogeographic patterns of Sri Lanka's ichthyofauna and its historic connections to the Indian mainland are derived from Hiranya's recently published molecular phylogenetic studies on a variety of cyprinid groups including the genera *Dawkinsia, Devario, Garra, Laubuka, Pethia, Rasbora,* and *Systomus*, as well as the snakehead genus *Channa*, amongst others. His research is largely based on his own fieldwork in Sri Lanka, conducted between 2014 and 2019. It is noteworthy that Hiranya is not only an ichthyologist with a strong background in fieldwork, but also an expert naturalist and nature photographer. Many of the photos in this book are his, including all the stunning underwater shots of freshwater fishes, many of them photographed in their natural habitats for the first time.

After reading *The ecology and biogeography of Sri Lanka – a context for freshwater fishes*, Sri Lanka, with its natural beauty and unique freshwater fish diversity, moved to the top of my travel bucket list. I can't wait to embark on a journey of discovery to The Resplendent Isle.

Lukas Rüber, PhD

Natural History Museum Bern, Switzerland, and Aquatic Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Switzerland.

Preface

Why we wrote this book

Despite Sri Lanka being positioned within a Global Biodiversity Hotspot and its fauna and flora being among the best explored in Asia, the island's biogeography has yet to be reviewed in a single work. We discovered this in the course of working on the evolutionary and biogeographic relationships of Sri Lankan freshwater fishes. Chapters 3 and 4 of this book represent a first attempt at joining the dots formed by hundreds of studies of varying scope and focus, and thereby trying to discern the patterns and processes that gave rise to the island's present-day fauna and flora.

Why hasn't this been done before? In a way, it has, in the form of *Ecology and biogeography in Sri Lanka* (1984), edited by Herbert Fernando. The focus of that volume, however, was largely on ecology, with relatively little attention paid to biogeography except in the case of mayflies. This is understandable, given that much of the information needed to construct a narrative of the island's biogeographic story simply did not exist at the time. Although yawning gaps still remain, the past few decades have seen huge advances in key fields associated with biogeographic understanding: tectonics, geology, historical sea levels, past continental connections, climatic history, phylogenetic analyses, molecular clocks, and comprehensive regional species-inventories based on an ever more reliable taxonomy. The rate of progress is evident from the ~800 publications on which the present review is based (listed in References). Almost three-quarters of these were published after 2000, and more than half after 2010.

Despite this wealth of new knowledge, it is still too early for a synthesis—an overarching narrative that explains how exactly the island's plants and animals came to be as they are. There are simply too many gaps. Nevertheless, some patterns are becoming clear, and we draw attention to the ones we have spotted. Yet others present intriguing lines of inquiry: we mention them only as hypotheses. So rapidly is the field evolving that we suspect this book will be out of date almost as soon as it is published.

Why then, do we write it in the first place?

We do so in order to bring together in a single volume the diverse body of evidence there is from multiple disciplines. We needed this to aid our own research. Besides, colleagues who think about similar problems will likely benefit from it, too. Hence this book is written in the hope that it will stimulate more studies of the historical and geographic relationships of Sri Lanka's extraordinary fauna and flora, and the processes that gave rise to these. While most of our current knowledge derives from vertebrate groups, it is clear that the plants and invertebrates too, offer huge opportunities for research. Despite the much greater ease with which plant material can be collected for molecular analysis, DNA-based studies of relationships among vertebrates outnumber those of plants by at least an order of magnitude. This must change, and if this book helps instigate that change, our work will have been done.

We recognize two audiences for a book such as this. A scientific one, which demands a technically coherent text that is extensively referenced so that every datum can be verified; and a general readership composed of those interested in Sri Lankan natural history. We recognize that one size does not fit both. For a fine example of the former approach, see Heads' (2019) review of New Caledonian biogeography. The latter readers, however, arguably prefer a book which presents an illustrated, broad-strokes account of the island's biotic story. We hope that general readers who do not want to be overloaded with technical details can still get an idea of the broad narrative. To make this easier, we provide a non-technical summary in Chapter 1 and conclusions in Chapter 6. In order to make the text more accessible to non-specialist readers, we have also illustrated it extensively. But, most of all, we decided to publish this book because a small number of scientists and students may find the stories we tell and examples we cite inspiring enough to pursue biogeographic inquiries of their own.

Given that our primary interest is in ichthyology, two chapters are devoted to fishes. Chapter 4 reviews the wider relationships of a few groups of fishes for which information is available; Chapter 5 reviews the distribution of fishes within the island and, for the first time for any substantial group of Sri Lankan plants or animals, provides an account of the distribution of genetically distinct populations of several species.

Limitations and significance

Phylogenetic and phylogeographic studies in Sri Lanka

Many new species of freshwater fishes are described from South Asia each year. In most cases, these descriptions are based on samples from only a single locality and based wholly on morphology. Although increasing numbers of taxonomic studies report on the *cox1* barcoding gene, the utility of a single gene marker in illuminating phylogenetic relationships is limited (Mallo & Posada, 2016). Despite these advances, studies of evolutionary relationships between species—and especially diversity within species—are still in their infancy. In the case of Sri Lanka, almost all studies prior to those of Sudasinghe *et al*. (listed in the Literature Cited) were based only on morphology and constrained by limited geographic sampling. In Chapter 5, however, we explore for the first time, across a substantial number of Sri Lankan freshwater fishes, evolutionary relationships derived from the *cytb* and *cox1* mitochondrial markers and the *rag1* and *irbp* nuclear markers. These studies have allowed us to evaluate intraspecific variation, in both morphology and genetics, based on large sample sizes while also helping to delineate the geographic distributions of the various species and lineages.

Mitochondrial markers are maternally inherited and usually not associated with recombination. They also have a higher substitution rate compared with nuclear markers and are hence useful in detecting genetic structure among closely related species and populations. Hence, mitochondrial markers are widely used in phylogeographic studies (Beheregaray, 2008; Hickerson *et al*., 2010). Meanwhile, *rag1* (among many others), a paralog-free gene, is extensively used to elucidate higher level relationships in teleost phylogenetics (Hughes *et al*., 2018, 2021).

While phylogeographic studies have been advancing rapidly in developed countries (Beheregaray, 2008), there is a clear deficiency of such research in most developing countries such as Sri Lanka, particularly given that it lies within a Global Biodiversity Hotspot. Nevertheless, the field of evolutionary biology is advancing rapidly, with genomic data now becoming more and more readily available for comparative population-genomic and phylogenomic studies. Inferences made from genomics data are substantially more informative than those using a few molecular markers, as in our studies. Thus, we are the first to acknowledge the limitations of the results we report in Chapter 5: this is only a starting point.

Despite this, even phylogeographic studies that are thus constrained help us to understand evolutionary patterns and processes, and to test hypotheses on the geographical distribution of lineages of a species by using genetic data (Avise, 2000; Avise *et al*., 1987).

In many cases, we objectively explored species boundaries using a combination of criteria: morphology, genetic data, and geographic distributions following a general lineage concept of species (de Queiroz, 1998). While clarifying the taxonomy of the concerned species—which no one disputes is the starting point for conservation planning and management—these studies are additionally handicapped by limited comparative data from India.

Nevertheless, these studies have, for the first time, detected evolutionary dynamics that have not hitherto been reported: drought refugia in the southern basins, unexpected barriers to dispersal among adjacent river basins, instances of dispersal by river capture, and historical extinction events. We show also that climate has been a major driver in shaping Sri Lanka's biodiversity. This becomes increasingly relevant given the rapid changes to climate that we are now witnessing.

RP & HS, October 2021.

Dawkinsia srilankensis.

Dedications

HS
To my parents, Shantha and Nirmala: for their endless love, and giving me the freedom to explore and discover.

RP
To my mother, Mary, and the memory of my late father, T.B. — for those idyllic early years.

A stream in Kottawa Forest.

Acknowledgements

The idea of this book was first suggested to us by Nimal and Savitri Gunatilleke in 2015. We thank them for commenting on parts of the text and also for several discussions relating to Sri Lankan biogeography over the years. Their work on the community ecology of the rainforest flora of Sri Lanka inspired lines of inquiry we followed in the phylogeographic studies summarized in Chapter 5.

We are grateful to those of our colleagues who commented on various versions of the text and gave us valuable suggestions for its improvement: Lukas Rüber, Madhava Meegaskumbura, Jaap de Vlas, and Michael and Nancy van der Poorten. We alone are responsible for the errors that remain.

This book would not have been possible if not for the many images that illuminate the text. We thank our many colleagues who helped by contributed photographs. They are acknowledged alongside the respective images. In addition to providing us with dozens of images of difficult-to-photograph plants, Himesh Jayasinghe generously shared with us his encyclopaedic knowledge of the Sri Lankan flora.

We are grateful to Lalith Ekanayake and David J. Krishnapillai for advice on improving the quality of print.

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HS thanks (alphabetically) Dhanushka Lakshan, Tharindu Ranasinghe, Charana Widuranga, Kumudu Wijesooriya and many other friends and colleagues who joined and assisted in numerous field expeditions. HS is grateful to the Director General, Department of Wildlife Conservation, Sri Lanka, and the Conservator General, Forest Department, Sri Lanka, for providing all the necessary permits to carry out fieldwork. He also thanks the Director and the Assistant Director of Zoology of the National Museum, Colombo, and their staff for providing access to specimens in their care.

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HS takes pleasure in thanking Madhava Meegaskumbura for his support, guidance and inspiration over the past several years.

Being a review, this book relies heavily on the published literature. Our text distils the discoveries and conclusions made by hundreds of authors over several decades. While they are cited where relevant, we hope we have abstracted their work accurately and in context.

Finally, we thank our wives, Janaki Pethiyagoda and Dayesha Sudasinghe, for allowing us to be distracted from our connubial responsibilities during the writing of this book.

Units, abbreviations, terms, notes

~ approximately.

asl above sea level.

CI confidence interval.

cox1 cytochrome c oxidase subunit 1.

cytb cytochrome b.

DH Deutsche Härte, a unit of water hardness.

Dry zone: Region in which rainfall < 1.8 $m \cdot y^{-1}$ (see Figure 2.6).

Gondwanan: Here applied to taxa whose ancestors inhabited the Sri Lanka-India-Seychelles-Madagascar plate prior to the former rifting from Madagascar *ca* 90 Mya, as well as other elements of the Gondwana supercontinent prior to that.

HPD highest posterior density

Intermediate zone: region in which rainfall is 1.8–2.5 $m \cdot y^{-1}$ (see Figure 2.6).

irbp interphotoreceptor retinoid binding protein

ky thousand years.

kya thousands of years ago.

LGM Last Glacial Maximum.

µm one millionth of a metre

µS micro-Siemens [per cm]: unit of electrical conductivity

My million years.

Mya millions of years ago.

NMSL: National Museum of Sri Lanka, Colombo.

PCA principal component analysis.

Peninsular India: mainland India south of ~21°N.

pH potential of hydrogen: a scale used to indicate the acidity or basicity of an aqueous solution.

Photographs: almost all the photographs of Sri Lankan freshwater fishes in this volume were taken by HS. For consistency, some have been laterally inverted so that the specimen faces left, as is the convention in ichthyology.

rag1 nuclear recombination activating protein 1.

Rain forest: forest occurring in perhumid tropical climates. In Sri Lanka, 'rain forest' includes the Mixed Dipterocarp Forests of the lowland wet zone as well as the tropical montane forests of the highest hills. We recognize such forests primarily on the aseasonality of rainfall rather than floristics.

Rivers: Sri Lankan river names are binomial, the second word of which is of the many local-language words for the different kinds of waterways, such as *ara, aru, ela, ganga* and *oya*. For the convenience of non-native readers, we translate all these as 'River'.

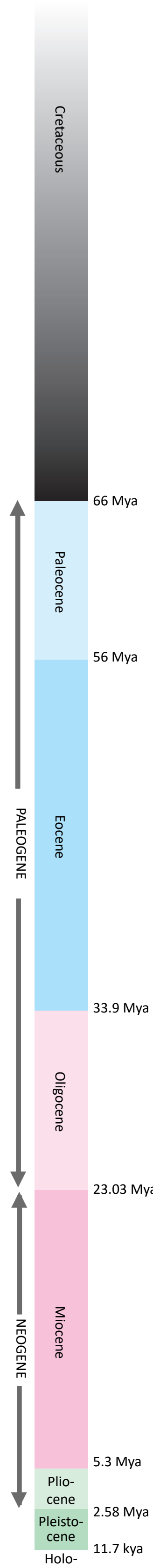
Species: species names change over time, as taxonomy is revised. When referencing the earlier literature, we have updated species names to those currently in use, noting where the identity of a species cannot be inferred with certainty.

sp. abbreviation of 'species', singular. Plural: spp.

Wet zone: region in which rainfall is >2.5 $m \cdot y^{-1}$ (see Figure 2.6).

y year.

ya years ago.



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