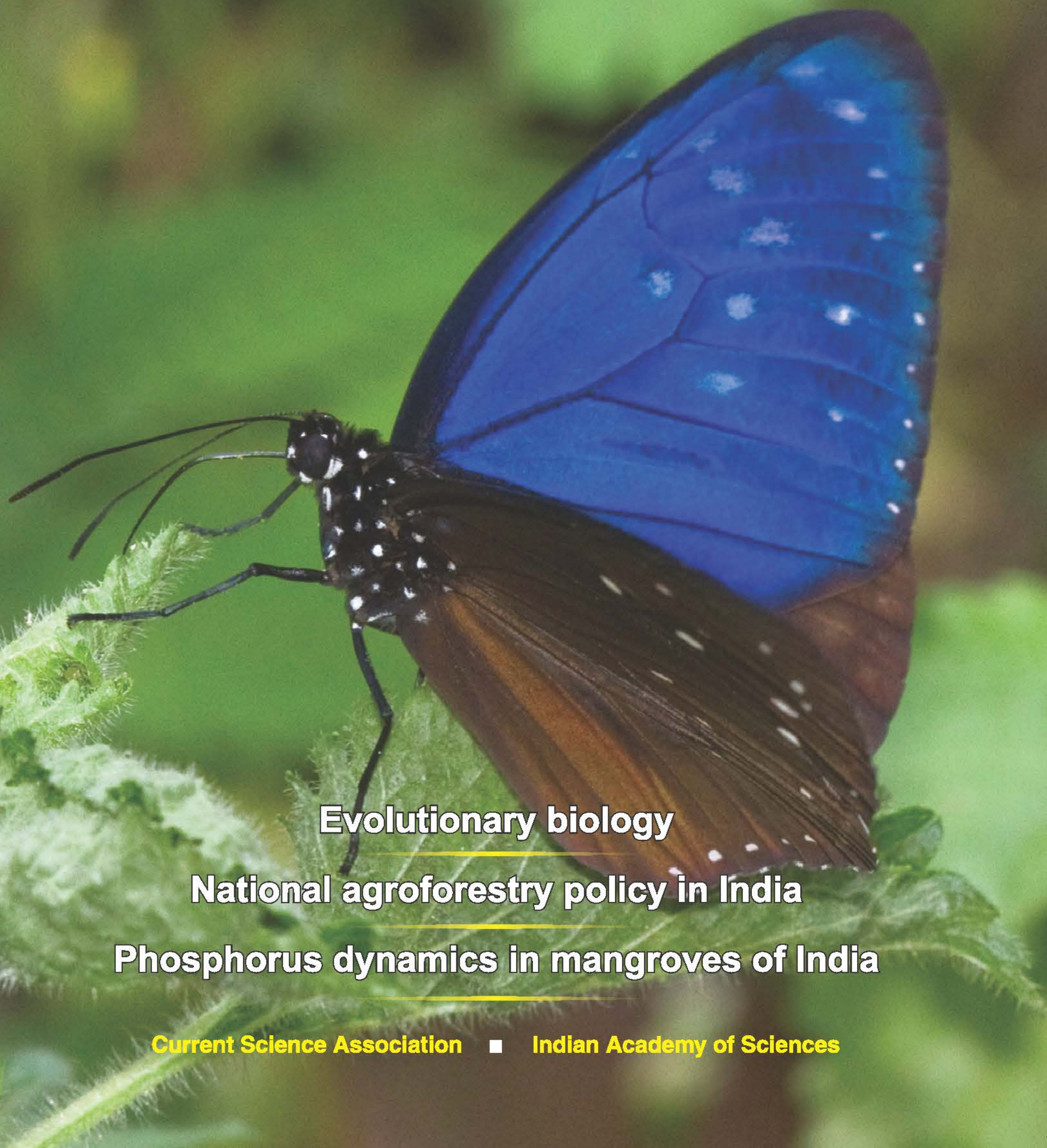
₹ 50

CURRENT SCIENCE

Volume 108 Number 10 25 May 2015



Evolutionary biology

National agroforestry policy in India

Phosphorus dynamics in mangroves of India

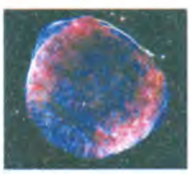
Current Science Association ■ Indian Academy of Sciences

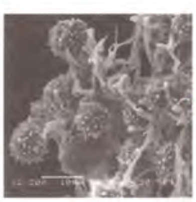
Founded: 1932

ISSN: 0011–3891

CURRENT SCIENCE

Volume 108 Number 10 **25 May 2015**



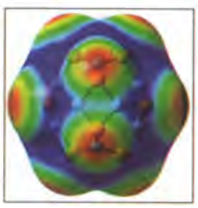


SPECIAL SECTION: EVOLUTIONARY BIOLOGY

REVIEW ARTICLE

RESEARCH ARTICLES

RESEARCH COMMUNICATIONS



COVER. The cover picture shows male *Euploea midamus*, a toxic butterfly that other palatable butterflies mimic. A. R. Wallace, who proposed the theory of evolution by natural selection, wrote about the superabundance of *Euploea* and related danaine butterflies in relation to their mimics while developing the idea of frequency-dependent natural selection. The special section on evolutionary biology explores Wallace's contributions to the field, and presents a selection of current topics in evolution. (Photo credit: Krushnamegh Kunte).

The editor thanks Dr Krushnamegh Kunte and Dr Deepa Agashe, National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bengaluru 560 065, India for agreeing to be guest editors for the special section.

Indexed in CURRENT CONTENTS/GEOBASE/CHEMICAL ABSTRACTS/IndMED/SCOPUS/
WEB OF SCIENCE

Preface

It is a pleasure to present the readers of *Current Science* with a special section on evolutionary biology. This section is an outcome of a symposium, 'Evolution Symposium: Celebrating Wallace', organized in honour of Alfred Russel Wallace on his death centenary, 7 November 2013. The National Centre for Biological Sciences, Bengaluru, generously hosted the day-long symposium, which saw a considerable gathering of not only leading evolutionary biologists, but also students and other young professionals. It was a privilege to celebrate the life and work of Wallace, the brilliant naturalist and scientist who independently discovered the principle of evolution by natural selection. Very few scientific, philosophical or theological ideas have percolated as deeply into society and in modern psyche, and evolutionary biology continues to play a major role in our understanding of the world. This special section brings together the work and ideas of some of the prominent and promising Indian evolutionary biologists at various career stages. The compilation of this work is itself a celebration of the small but vibrant and growing community of evolutionary biologists in India, and their contributions to this key scientific discipline.

Wallace was a peerless naturalist who amassed immense information on the morphological variation and geographical distribution of animals, and conceptualized his observations into a coherent theory of evolution by natural selection. Although Charles Darwin is more famously credited for the idea of natural selection, Wallace has an equal claim to the theory that not only revolutionized biology, but also influenced the thinking of lay people. In fact, in some areas, Wallace's contribution to the theory surpassed Darwin's insights. Wallace spent four years in the Amazon and eight years in the Malay Archipelago collecting specimens for collectors and museums in England as well as for his own studies. Perhaps because his livelihood depended on finding variations and new species, Wallace cared much more about variation in nature, and maintained meticulous notes on species distributions like few of his contemporaries. While Darwin's writings drew heavily on variation and artificial selection in domesticated plants and animals, Wallace drove home the point with lucid descriptions of geographically structured variations that he had seen in nature, and their significance for natural selection and speciation. Wallace elucidated the geographical aspects of reproductive isolation, divergence and allopatric speciation much better than Darwin, and his conceptualization of speciation is closer to modern evolutionary understanding of the process. Wallace also introduced the concept of reinforcement (sometimes called the 'Wallace effect'): the evolution of behavioural isolation when newly diverged species come into secondary contact. This is now believed to be a critical step in completing the speciation process. Besides the independent development of the natural selection theory, Wallace is recognized as the father of biogeography, which deals with the patterns and processes of the geographical distribution of species. Two important biogeographic features in the Indo-Australian Region have been named the Wallace Line and Wallacea in his honour. In addition to his splendid scientific successes, Wallace enjoyed popularity and social influence from the 1860s until his death in 1913. His beautifully written books and travelogues helped to popularize his science, and many of his books are still in print today (we particularly recommend his delightful best-seller, *The Malay Archipelago*). He was also an activist, who campaigned for land nationalization, nature conservation, women's suffrage, and what can be recognized as modern concepts of human rights; causes that resonate with us today. Wallace's achievements are especially impressive in light of his modest family background: Victorian society was notoriously difficult to navigate without political, societal and economic connections. Thus, Wallace was perhaps the first prominent example of a socially responsible and highly engaged scientist.

In the 157 years since Wallace and Darwin first elucidated their ideas, modern evolutionary theory and its applications have become tremendously relevant to other fields of biology as well as to society at large. Why are some populations more susceptible to specific diseases while others are far more robust? Can we predict the future of endangered species, and what are the best ways to ensure their long-term survival? (How) did our evolution as a social species affect our development and life history? A deep understanding of ecological and evolutionary processes is also important to tackle the most pressing problems that we face as a species: ensuring robust global food and energy supplies, reducing disease burden, and mitigating climate change. Evolutionary theory shows that it is not possible to select indefinitely for crops with higher yield and greater disease resistance with minimum nutrient inputs, because physiological trade-offs impose diminishing returns. The problem is exacerbated by climate change, since the expected increase in climatic fluctuations will impose yet another selective pressure on growing crops. An understanding of human ecological and evolutionary history is also critical to predict disease epidemiology and progression. As we all know, rapid evolution of antibiotic resistance severely limits our ability to contain and eradicate major human pathogens. Infectious diseases are also increasingly threatening wildlife, as evidenced by the lethal fungal infections decimating amphibian populations globally. An understanding of evolutionary biology and ecology may ultimately help us find solutions to these environmental, ecological and social problems; for instance, in designing robust antibiotics, devising alternative microbial fuel sources, arresting pathogen evolution and dispersal, and managing endangered wildlife to minimize the risk of zoonoses as well as their own extinction.

In India, evolutionary biology has had a long presence. Beginning in the 1880s, British ornithologists, entomologists and botanists based in India wrote extensively about the natural history of Indian flora and fauna, frequently relating their observations to evolutionary theories of the time. One could argue that modern evolutionary biology took root in India in the 1950s when P. C. Mahalanobis of the Indian Statistical Institute invited J. B. S. Haldane – one of the architects of the Modern Synthesis that combined evolutionary theory with genetics and mathematics – to India. Shortly thereafter, Haldane and his wife and fellow evolutionist Helen Spurway moved from London to Kolkata (formerly Calcutta). Haldane spent the last eight years of his life in India until his death in Bhubaneshwar in 1964, while Spurway continued to work in Bhubaneshwar and then in Hyderabad until she died in 1977. During these years they carried out evolutionary research and writing from India, while also training a generation of Indian evolutionary geneticists, most notably Suresh D. Jayakar and Krishna R. Dronamraju. Jayakar made key contributions with theoretical work on the evolution of sex-determining mechanisms and trait polymorphism, and empirical work on animal behaviour. He also developed statistical methods for population genetics and biometry. Dronamraju has worked on human genetics, and also written extensively about Haldane's life and work, especially his later years in India. Haldane and Spurway's intellectual heritage in India was broken, however, when Jayakar moved to the University of Pavia in Italy, and Dronamraju to the United States of America. The number of students that they trained during their short careers in India was small. Also, in line with the professional trend of the time, many Indian biologists were turning to molecular and cell biology. We remember the story of an Indian expatriate who met Haldane as a young student. When asked for ideas for a research project, Haldane advised him to measure the feathers in a peacock's tail. Naïve to the evolutionary significance of such a study, the student moved abroad to study molecular biology. By the early 2000s – way past the stage to switchfields – the grown scientist regretted having passed up such a golden opportunity and a study system. In the 1970s, sexual selection exploded as a research field and captured scientific as well as public imagination. Exaggerated secondary sexual traits have come to present key adaptations to study a range of phenomena, from the evolution of sexual dimorphism to speciation. The evolution of the peacock's tail is one of the most striking examples of sexual selection as well as the limits of selection, and several notable research papers have been written on the topic recently. One wonders how many such seeds of evolutionary ideas Haldane and Spurway tried to sow in India.

In any case, the growth of the evolutionary biology community in India had to await another spore that grew into a full-blown colony. Having written seminal papers in population ecology and life history evolution, Madhav Gadgil returned to India in the early 1970s with a Ph D from Harvard University. Subsequently, he established the Centre for Ecological Sciences at the Indian Institute of Science (IISc, Bengaluru), and nurtured the next generation of evolutionary biologists such as Raghavendra Gadagkar and Raman Sukumar. They, in turn, have spawned an even more impressive range of evolutionary biologists, many of whom now serve as faculty at leading research institutes such as the Indian Institutes of Science Education and Research (IISERs), IISc and the National Centre for Biological Sciences (NCBS), among many others. At the same time, a steady stream of promising evolutionary biologists trained in some of the best universities and laboratories abroad continue to return to India to set up their labs here. Together, this community already has a considerable presence through their contributions to leading evolutionary journals and international meetings on evolution, genetics and biogeography.

With this historical background and current promise of evolutionary biology, it is surprising that evolution does not feature as a major topic in biology classes in schools and colleges. This may be a key reason why very few Indian students are attracted to evolutionary biology as a career. In recent decades, there have been commendable efforts to include evolutionary biology and its applications in school textbooks. However, evolutionary theory is rarely introduced as the fundamental basis of understanding biological phenomena, and an area of rigorous and current scientific research. Instead, evolution follows large chapters on major features of organisms and is introduced as 'the story of life on earth' that seemingly began and ended with Darwin and Wallace. There is little room for active areas of inquiry that bridge across the content of various chapters, such as evolutionary ecology, population genetics, molecular evolution, and neuroethology. Students learn about biological organization, form and function without any inkling of evolutionary concepts such as homology and convergence that provide the logical framework for this information. Without this context, the vast diversity and intricate functioning of organisms are reduced to dry facts requiring memorization. This is unfortunate because evolutionary biology and ecology are conceptually rich fields of research, with first principles with which students can engage easily. By excluding detailed discussion and instruction in these subjects, we might be squandering opportunities to teach students to think logically and creatively about fundamental problems in biology. With a foundation of critical thinking and basic concepts, students can get interested not only in current problems in evolution, but also in related problems in molecular genetics, conservation, agriculture, epidemiology, medicine and social sciences. This may clearly be remedied with greater engagement of practising evolutionary biologists with schools, colleges and governing bodies. It may also be useful to engage students in scientific research in the field through summer schools and other training/teaching programmes, the likes of which have created leaders in research on evolution and ecology in North America and Europe in the past few decades.

Indian evolutionary biologists have plenty of opportunities for research in this region. The Indian subcontinent has had an interesting geological, plate-tectonic and biogeographic history. The long periods of geographical isolation, colonization after collision with Asia, and geoclimatic events created complex landscapes that gave rise to extraordinary levels of species diversity and endemism in India's four globally recognized biodiversity hotspots. The diverse ecological regimes structured by major mountain ranges and large rivers are responsible for isolation, population divergence, and intense selection pressures in this region. The result is a breathtaking diversity of adaptations exhibited by a wide array of organisms, from single-celled soil microbes and planktonic algae to behemoths such as elephants and whales. These species occupy habitats ranging from small ponds and woodlands to the highest mountains and a diverse range of grasslands and forests. It is remarkable that most colleges, universities and research institutes in India have unparalleled access to such rich biological material, and hardly use it for research or teaching. We believe that the academic promise of evolutionary study systems that are waiting to be tapped in India is tremendous. We will benefit by recognizing and utilizing this academic resource sooner rather than later. Unlike many other modern areas of research, evolutionary studies may be done with small budgets and modest labs on an ordinary college or university campus. With the incredible biological diversity at hand and the size of the potential academic community in India (one of the very few benefits of an excessively populated country), there is reason to believe that India can become a prominent place for evolutionary biology.

This special section presents two 'In Conversation' articles and five reviews on various concepts in evolutionary biology. The two conversations feature evolutionary biologists who have led enviable careers and trained generations of young evolutionists. Amitabh Joshi (Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru) studies the evolution of life history traits in experimental populations of fruit flies. Milind Watve (IISER Pune) has tackled an eclectic selection of topics in evolutionary biology, including host–parasite dynamics, the theory of mind, and the evolution of physiological disorders such as diabetes. In the interviews they share their experiences in research, mentoring and higher education. They demonstrate that internationally cutting-edge evolutionary research can be done in modest lab spaces and infrastructure as long as one possesses a razor-sharp intellect, conceptual clarity, and an ability to design key experiments. As Joshi points out, perhaps the largest capital required for evolutionary research even in modern times is intellectual.

The first two review articles relate to the processes of diversification and speciation, around which much of modern evolutionary research revolves. Rhitoban Raychoudhury (IISER Mohali) reviews (**page 1842**) the genetics of behavioural isolation, which may be an important early stage in the speciation process. Behavioural isolation has been poorly studied at a mechanistic level, but modern genomic tools may help us make much-needed progress in understanding this phenomenon in coming years. This understanding may also advance work on reinforcement, which was among Wallace's special contributions to the concept of speciation. In the second article, Praveen Karanth (IISc) reviews (**page 1847**) recent work on endemic radiations in peninsular India, and shows how patterns of species diversification on the ancient Indian plate relate to radiations in other parts of the Indian subcontinent and neighbouring zoogeographic subregions. Work in this area is uncovering evolutionary and biogeographic patterns and processes that have given rise to the spectacular biodiversity and endemism in the vital Sri Lanka–Western Ghats biodiversity hotspot. One would imagine that Wallace would have been happy to see this work, biogeography and speciation in the Oriental Region being two of his favourite subjects.

The next two articles focus on plant–insect interactions. Hema Somanathan and others (IISER Thiruvananthapuram) review (**page 1852**) the sensory ecology of floral signals, pollinator sensory systems and the structure of plant–pollinator interactions. They emphasize the recent view of co-evolutionary dynamics between plants and pollinators as diffuse species interactions rather than strict two-species co-evolutionary dynamics. Thus, pollination networks may have an important role to play in a changing climate, especially in forested and mountainous landscapes of the Oriental Region. Renee Borges (IISc) discusses (**page 1862**) policing of cheaters in mutualistic interactions such as those observed in figs and fig wasps, through host sanctions, partner fidelity feedback and punishment. This line of investigation is especially productive in rich tropical forest ecosystems, such as those in India.

Finally, Raghavendra Gadagkar (IISc) weighs (**page 1869**) in on a broad range of topics that are relevant to modern biologists, from reconciling mathematical models and empirical data to dealing with hot controversies stemming from contrasting mathematical formulations of biological problems. He specifically applies this to the ongoing controversy about the utility of the concepts of kin selection and inclusive fitness that have been key to understanding the evolution of sociality in eusocial organisms. When faced with scientific controversies, he advises biologists to stay bipartisan and vigilant, and to make biology larger than the mathematics.

We hope that readers will enjoy these articles. Although we could only present a sample of evolutionary work in the country, we hope that it will motivate readers to seek out the larger diversity of Indian labs addressing various problems in evolutionary biology. We also hope that this special section will introduce students and other young researchers to the fascinating world of evolution, and encourage them to consider evolutionary biology as a career. Given the wonderful natural settings, the growing strength of the community, a relatively robust economy, and increased investment in scientific research, evolutionary biology in India appears to have a strong future. The opportunities in India are exciting, and we look forward to seeing an even more vibrant and larger community of evolutionary biologists around us.

Krushnamegh Kunte
Deepa Agashe
Guest Editors – Evolutionary Biology

National Centre for Biological Sciences,
Tata Institute of Fundamental Research,
GKVK, Bellary Road,
Bengaluru 560 065, India
e-mail: krushnamegh@ncbs.res.in, dagashe@ncbs.res.in