More Fun Than Fun: Evolution on Islands in Water, in the Sky and Elsewhere

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The cloud forests of the Western Ghats are a matrix of natural habitats – forests and grasslands (background and in the distance), along with human-modified plantations such as the tea plantations (foreground). These habitats occur on isolated mountain-tops forming habitat islands called sky islands. Photo: Prasenjeet Yadav, Munnar

RAGHAVENDRA GADAKAR

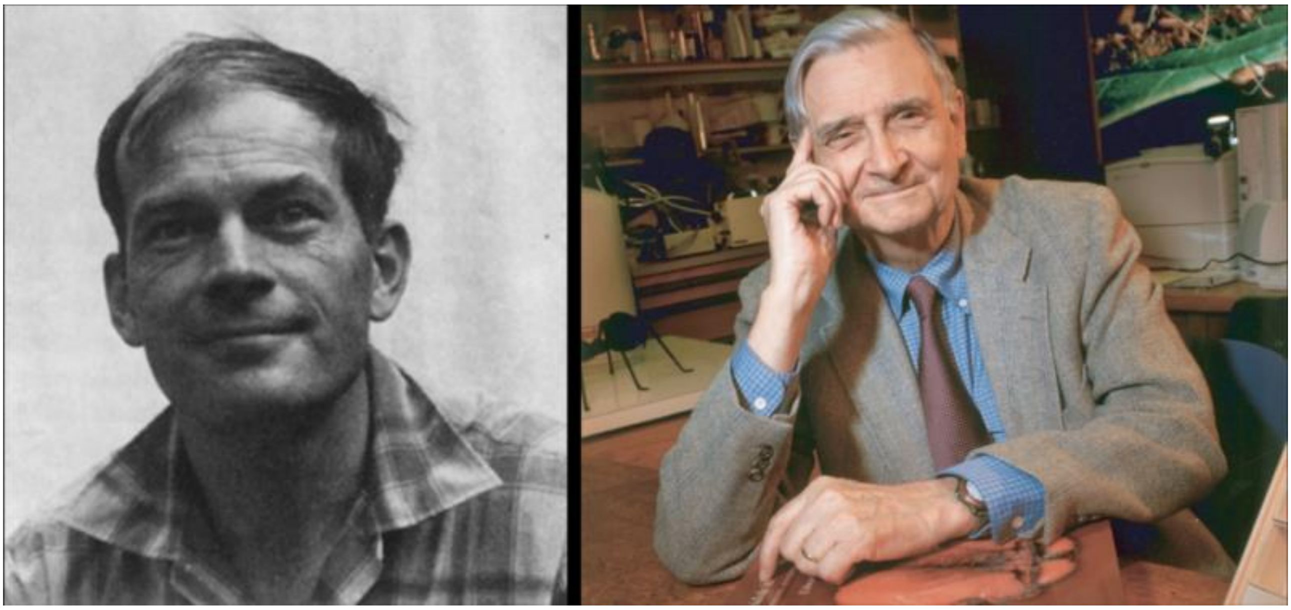
This article is part of the 'More Fun Than Fun' column by Prof Raghavendra Gadagkar. He will explore interesting research papers or books and, while placing them in context, make them accessible to a wide readership.

Islands, both in the literary sense of land surrounded by water and the metaphorical sense of anything being isolated and surrounded by something else, have played an important role in the process of evolution and for our study of it. By the very fact of their isolation, islands permit rapid evolutionary changes and the formation of new species, allowing evolution to perform 'pilot' experiments not easily possible on the mainland. And it is their relatively small size that makes it easier for us to uncover the processes and document the products of evolution. Hence the pride of place for the sub-discipline of island biogeography in the study of evolution.

Not surprisingly, both the co-discoverers of the principle of evolution by natural selection, Charles Darwin and Alfred Russell Wallace, were island biogeographers before they became evolutionary biologists, deriving key insights from their expeditions to the Galapagos Islands and the Malay Archipelago, respectively.

The theory of island biogeography

The study of island biogeography came of age when Robert H. MacArthur, a pioneering theoretical ecologist, and Edward O. Wilson, a naturalist par excellence, joined forces in the 1960s and produced the famed theory of island biogeography. Enduring as their theory is, the inspirational legacy of both MacArthur and Wilson go well beyond.


Left: Robert H. MacArthur (1930-1972). Photo: Wikipedia Commons, fair use. Right: Edward O. Wilson (1929-). Photo: Jim Harrison/PLoS, CC BY 2.5.

MacArthur wrote his *magnum opus*, *Geographical Ecology* (1972), "while convalescing in Vermont with no access to libraries, entirely from memory," just before he died at the age of 42. Some words from his introduction have remained etched in my memory.

"Doing science is not such a barrier to feeling or such a dehumanising influence as is often made out. It does not take the beauty from nature. The only rules of scientific method are honest observations and accurate logic. To be great science it must also be guided by a judgment, almost an instinct, for what is worth studying. No one should feel that honesty and accuracy guided by imagination have any power to take away nature's beauty."

When asked to identify the most important problems facing the world, E.O Wilson said:

> "The worst thing that can happen, will happen, is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process ongoing in the 1980s that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us."

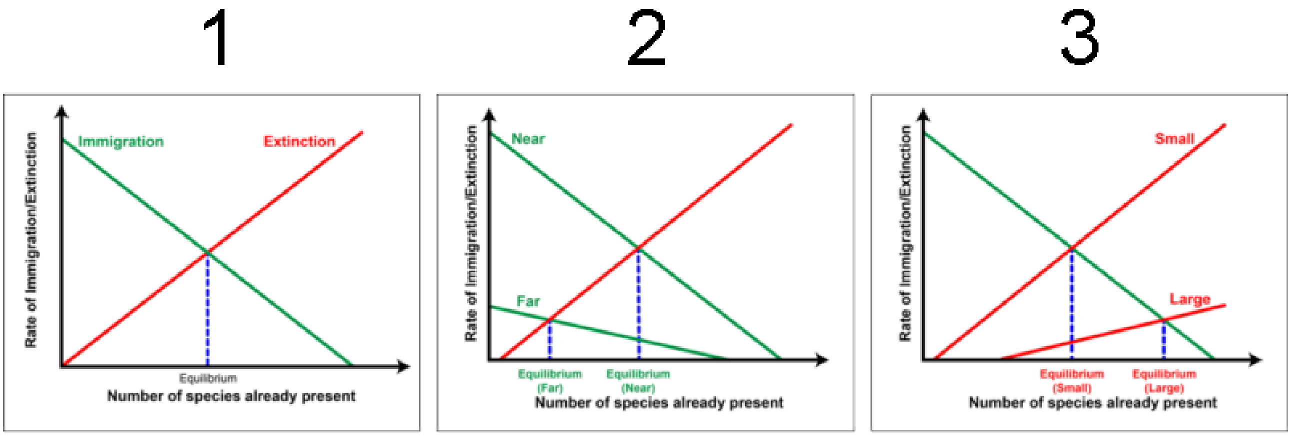
The coming together of MacArthur and Wilson was propitious. They produced a simple and elegant theory, first in a landmark paper in 1963 and then in an influential monograph in 1967.

Combining knowledge of observed patterns, some simplifying assumptions and the results of a mathematical model, MacArthur and Wilson argued that the number of species on an island would be a compromise between two opposing forces. The more species already present on the island, the fewer new species would arrive by immigration from the nearest mainland. Conversely, the more species there are on the island, the more species that would go extinct. The balance between immigration and extinction would predict the equilibrium number of species seen on the island (graph 1, below). This has therefore come to be known as the equilibrium model of island biogeography.

Simple extensions of the basic idea predict that the farther the island is from the mainland, the slower the rate of immigration will be. But the rates of extinction would be unaffected by distance from the mainland. Thus, islands closer to the mainland would have more species than islands farther away (graph 2, below).

By similar logic, the smaller the island, the greater the rates of extinction would be. But the rates of immigration would not be affected by the size of the island. Consequently, larger islands would have more species than smaller islands (graph 3, below).

The accompanying simple graphs illustrate these principles; more realistic graphs are available in their paper and book mentioned above.



MacArthur and Wilson's equilibrium model of island biogeography. (1) The equilibrium number of species is a compromise between rates of immigration and extinction. (2) Two different equilibria for far and near islands due to different rates of immigration depending on the distance from the mainland. (3) Two different equilibria for small and large islands, depending on different rates of extinction based on the size of the island. Source: Author provided

An experimental test of the theory

In 1969, E.O. Wilson and his PhD student Daniel Simberloff published a paper describing the first field-experimental test of the equilibrium theory of island biogeography. Wilson says, "I hesitate to use the usual expression 'studied under me,' because in the years to follow, I learned as much from [Simberloff] as he did from me. We soon became partners."

Wilson and Simberloff conducted their experiment on six small mangrove islands measuring 11 to 19 meters in diameter, in the Florida keys, a set of islands located off the southern tip of Florida, between the Atlantic Ocean and the Gulf of Mexico. First, they painstakingly made a complete inventory of all arthropod species (there was nothing else on these islands), including insects, spiders, isopods, scorpions and a few others. Then they fumigated these islands to exterminate all arthropod species. Finally, they monitored the natural process of recolonisation of the islands by immigration from the neighbouring islands for a year.

The new fauna approximately resembled the pre-fumigation numbers and composition on five out of the six islands, broadly supporting the equilibrium theory.

Trees as islands

One reason for the broad applicability of the MacArthur-Wilson theory of island biogeography is that it applies just as well to metaphorical islands, as long as they harbour life forms and are surrounded by space that is inhospitable for the same forms of life. Within a year of the publication of the MacArthur-Wilson monograph, Daniel H. Janzen suggested that plants in general and trees, in particular, can serve as islands for insects and that the theory of island biogeography can therefore be used to study the colonisation of trees by insects.

Janzen (1939-) is one of the best-known ecologists and conservation biologists alive today. A professor at the University of Pennsylvania, he helped establish one of the most successful ecological restoration projects in Costa Rica.

Later, researchers pointed out that insects on trees often violate the predictions of the theory of island biogeography. It is the mark of a good theory that we learn as much from its failure or inability to explain observed patterns. Insects colonising trees often violate the assumption of a passive trade-off between immigration and extinction and the dependence of these processes on simple factors such as distance and size.

Many insects are host-specific, meaning that they can only live on a particular tree species. Rates of colonisation will therefore depend much more on the suitability of the tree for the survival of the insect species. Moreover, insects and their host trees co-evolve and thus modify future rates of immigration and extinction, and free them from the simple influence of size and distance.

Considering the theory of island biogeography is based on rates of immigration and extinction and the sizes of islands and distance from sources of colonisation, it is not surprising that it has been a significant driver in the rational design of nature reserves. With relentless habitat fragmentation and competing claims for land use, the design of nature reserves is no more than doing the best of a bad job and one that needs all the help it can get from theoretical principles.

Remarkably, the theory of island biogeography endured and continued to inspire research for almost half a century. Its simplicity has been crucial for it isn't just easy to understand and apply but also to understand why it fails when it does. That ecologists to this day are writing papers, like "A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography" and "A call for a new paradigm of island biogeography", is testimony to the power of the MacArthur-Wilson theory to inspire ecological research.

If it fails in the end, it will simply have burned itself out in the service of new theories and empirical research.

Sky islands

In the metaphorical sense of an isolated habitat surrounded by inhospitable nothingness, certain mountain tops represent islands in the sky. A steep temperature or other environmental gradient or deep insurmountable valleys between mountain peaks can make mountain tops uniquely suitable habitats for some species that cannot thrive in the intervening areas. These 'sky islands' can thus provide opportunities for evolution to experiment with rapid change and speciation in much the same way as literal islands of land separated by water.

The best-studied examples of sky islands are the so-called Madrean sky islands found in Arizona and New Mexico and Chihuahua and Sonora in Mexico.

The Western Ghats in India, famed for being a biodiversity hotspot, contain some of the world's most magnificent sky islands, breathtaking in their beauty and unique in their biogeography. The sky islands of the Western Ghats of India spread over a range of 700 km with a variety of different habitats and microhabitats – perhaps the most spectacular of which are the montane cloud forests, also known as Shola.

These sky islands have hitherto remained poorly studied, but now that is changing thanks to some remarkable work by V.V. Robin and his students and collaborators.

Robin is now an assistant professor at the Indian Institute of Science Education and Research in the temple town of Tirupati, Andhra Pradesh. He heads a bird lab with a lively group of bright, young students and postdocs. Robin is a second-generation ecologist, and that's still unusual in India – both his parents are distinguished ecologists and long-standing friends of mine. Having watched Robin since he was a little boy, it gives me great pleasure to study his fascinating work and write about it.

V.V. Robin, with a black-and-orange flycatcher (*Ficedula nigrorufa*), endemic to the Shola sky islands. Photo: Prasenjeet Yadav

In a study published in 2015, Robin, C.K. Vishnudas, Pooja Gupta and Uma Ramakrishnan presented a comprehensive analysis of the bird community of the sky islands in the Western Ghats. Vishnudas, a collaborator on Robin's National Geographic project, is an avid naturalist and ornithologist who has conducted detailed surveys of birds in the Western Ghats. One of Vishnudas's imaginative projects was to revisit the trails previously visited by India's most famous ornithologist, Salim Ali, at the same times of the year and re-survey the bird fauna recorded by the master.

Pooja Gupta was a project student at the time of the study, doing the molecular work. She has since gone on to do a PhD at the University of Georgia, working on avian malaria on the sky island system. Uma Ramakrishnan is a highly accomplished, trail-blazing young researcher in the field of molecular ecology at the National Centre for Biological Sciences (NCBS), Bengaluru, which hosted all the scientists of this study.

Prasenjeet Yadav, whose beautiful photographs adorn this article, combines science and photography. Inspired by Robin, he applied for and won a Young Explorer Grant from the National Geographic Society to document the Shola sky islands and Robin's work. His work has been recognized internationally, and he has won many awards, including the Banff Film Festival. Yadav is now an official photographer for *National Geographic*, with several stories around the world.

Robin is also collaborating with Prasenjeet Yadav and a beatbox musician from New York to create 'Sky Island Beatbox', making music with bird songs. He and his team visit schools and enthuse children with the joy of studying ecology and natural history.

Left: V.V. Robin and C.K. Vishnudas examining museum specimens at the Bombay Natural History Society. Right: C.K. Vishnudas and Uma Ramakrishnan collecting samples in the field for later DNA analysis in the lab. Photos: Prasenjeet Yadav

Robin and his team extensively surveyed the Shola habitats in the sky islands of the Western Ghats and studied almost the entire community of songbirds, the so-called Oscines. Songbirds belong to the order *Passeriformes*, commonly called the passerine, or perching, birds. Using mist-nets, they captured representatives of 23 out of the 25 species that constitute this community. They also collected blood samples from 356 birds, sequenced parts of two nuclear and two mitochondrial genes, and constructed phylogenetic trees of the bird community.

Their study aimed to understand how the sky islands – being potential physical barriers to gene flow – have affected the distribution of birds through colonisation, extinction and interbreeding (or its absence). Deep valleys can be barriers to movement for some species at all times. But the valleys' effectiveness as barriers may vary with climate change. For other species, the valleys may not be barriers at all.

There are three major valleys in their study area: the Chaliyar valley separating Wayanad and the Nilgiri hills; the Palghat gap separating the Nilgiri hills and the Anaimalai hills; and the Shencottah Gap separating the Anaimalai hills and Agasthyamalai.

Thirteen of the 23 species studied were unaffected by the valleys and appeared capable of crossing them. More likely, they had crossed the barriers in the past when the climate permitted. However, 10 species showed genetic divergence at locations, which would be expected if the valleys acted as barriers to gene flow. All the 10 were affected only by the deepest valley, namely the Palghat gap.

Some species, such as the laughing thrush, were affected by all three valleys. Some other species were affected by the Palghat Gap and the next deepest valley, the Shencottah Gap, but not by the Cheliyar valley, the shallowest of the three.

Two of the 23 bird species studied by Robin and his colleagues on the sky islands of Western Ghats – left: grey-breasted Chilappan (Kerala laughing-thrush); right: Nilgiri Sholakilli (shortwing). Photos: Prasenjeet Yadav

The power of this rich study comes from many sources.

First, the researchers combined extensive fieldwork with state-of-the-art molecular analysis.

Second, it was a very ambitious study, for it included nearly all members of the songbird community of these sky islands.

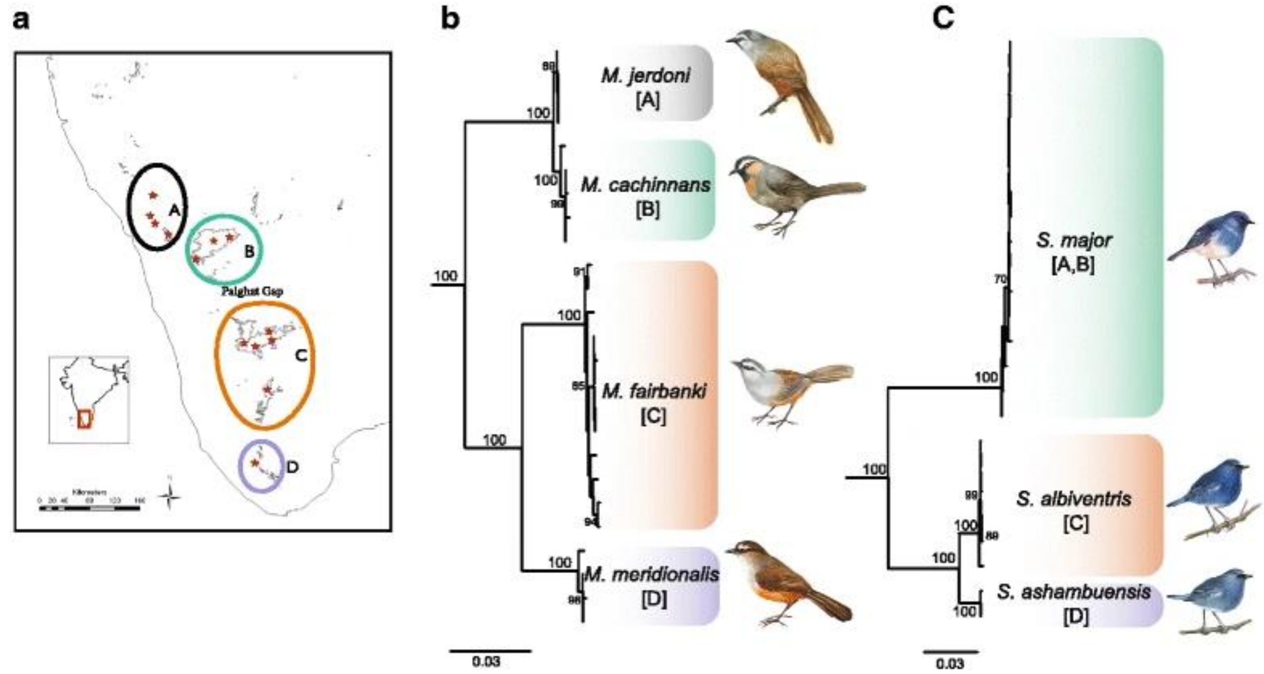
Third, it was the culmination of some two decades of Robin's obsession with birds of the montane forests. While visiting my colleague Raman Sukumar at the Centre for Ecological Sciences, Indian Institute of Science, in 2002, Robin undertook a major survey to assess the habitat preferences of one of these birds, the white-bellied shortwing, along the mountains of Tamil Nadu and Kerala.

Fourth, the 2015 study was preceded by a pilot study in 2010. During his PhD under the mentorship of Anindya Sinha at the National Institute for Advanced Study, Bengaluru, Robin worked with Uma Ramakrishnan of NCBS to examine the effect of valleys and climate on the distribution of one bird species. Together, they established that the Palghat Gap had managed to split the white-bellied shortwing into two different species; they even sang different songs. This study established the proof of principle that allowed Robin to embark on the more ambitious 2015 study.

Fifth and finally, the 2015 study has begun to spawn even bolder new research. In 2017, Robin and his colleagues, including additional collaborators from Singapore and the US, published a revolutionary new study. Incorporating genetic, morphometric, song and plumage data, they reorganised the songbird taxonomy of the region. The researchers questioned the traditional view that two of the species of birds on the sky islands, the laughingthrushes and the shortwings, are a single species each, related to other similar birds in the Himalaya.

Instead, their data showed that these two 'species' are two different *genera* that evolved and differentiated in the sky islands of the Western Ghats after splitting off from their Himalayan relatives over five million years ago. That both groups did so at about the same time highlighted the potential role of climatic factors superimposed on geographic factors.

The Western Ghats laughingthrushes now proudly occupy their own new genus *Montecincla*, with four species. Similarly, the Western Ghats shortwings now occupy their own new genus *Sholicola*, with three species.



Two newly minted genera of songbirds of the Western Ghats Sky Islands. Ranges (a) and phylogenetic relationships of Montecincla (b) and Sholicola (c) species. Inset: map of the Western Ghats shows sampling localities (stars) and divisions of the sky islands based on differentiated taxa. b & c ML bootstrap values are shown at nodes. Bird illustrations by Maya Ramaswamy. Reprinted from Robin et al. 2017, BMC Evolutionary Biology, CC BY 4.0

Robin told me in an email:

> "This finding was a significant step for two reasons. Firstly, Western Ghats were the best described and explored habitats in India, and that the first new genera descriptions for the century were coming from here implied there was much unknown. Secondly (and perhaps more importantly for me), this study revealed that these isolated habitat 'islands' indeed resembled oceanic islands for some species, causing radiations in even vagile taxa like birds."

There is much unknown indeed. But with passionate and committed young researchers like Robin and his colleagues on the scene, I see great hope.

However, we must take note that this kind of research requires significant long-term institutional and financial support. Here is a rare opportunity for scientists in India to cease to be mere followers and become world leaders and rewrite the textbooks of the history of life. I know that young researchers are up to the challenge. But will the slow-moving, conservative state machinery rise to the challenge?

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