

## Biogeography of Sri Lanka

Biogeography is the study of the distribution of biological diversity in geographic space through geological time. The composition of organisms and biological communities often vary along gradients of latitude, elevation, climate as well as isolation and distributional range. Biogeography is an integrative field of inquiry that combines concepts and evidence from ecology, population and evolutionary biology, geology, paleontology, and physical geography. The patterns of species distribution across different geographical regions are elucidated in biogeographic analyses through a combination of historical factors such as continental drift, glaciation, speciation, extinction, dispersal, and vicariance.

### THEORY OF ISLAND BIOGEOGRAPHY, FIFTY YEARS ON

Islands and archipelagoes are among the most intensely studied habitats as model systems in biogeographic research because these island habitats are more condensed and hence are manageable areas of study compared to larger complex ecosystems on the mainland. Therefore, in many respects, islands and archipelagoes are microcosms of the rest of the world. Since Darwin's time islands have provided natural laboratories for the study of evolution and the role of speciation in fashioning diversity. Exactly fifty years ago Robert MacArthur and Edward O. Wilson, in their seminal publication titled 'The Theory of Island Biogeography' (1967), introduced a general mathematical theory to predict the species richness of an island (or an isolated habitat), based on such factors as the rates of immigration and extinction determined by the size of the island and its distance from the mainland. They inferred that the island area and isolation eventually reach a dynamic equilibrium which they referred to as 'the equilibrium model of island biogeography' (MacArthur and Wilson, 1963, 1967; Patino *et al.* 2017). They showed that the extent of decline in bird faunas distributed across the archipelagos of Melanesia, Micronesia and Polynesia, progressively increased from islands near to the mainland of New Guinea to intermediate and far islands (up to distance >3,200 km from the mainland) owing to their increasing geographical isolation, exhibiting typical island syndromes. The study of islands as model systems has played an important role in the development of evolutionary and ecological theory. The Theory of Island Biogeography has made the single most persuasive case for integrating population and evolutionary thinking into biogeographic analyses and interpretation, over the last fifty years.

### PARADIGM SHIFT IN BIOGEOGRAPHY

The pioneering research of MacArthur and Wilson has subsequently undergone a paradigm shift in island biodiversity and biogeography, and promoted the biological exploration of islands as model systems for better understanding of biological communities (Warren *et al.* 2015). The concept and principles of island biogeography has since been applied to deriving principles of protected area design and estimation of species extinctions in fragmented landscapes in the field of conservation science (Diamond 1975). Since of late, this area of research has emerged as a new subfield, *viz.*, conservation biogeography, which provides valuable biogeographic insights into how to conserve diversity, especially in an era of increased anthropogenic degradation of both terrestrial and aquatic ecosystems, coincident with climate change.

Long-term research programs focused on island biota should provide additional insights into, biological invasions and other impacts of human activities, functional diversity and ecosystem functioning, extinction and diversification, and more. Conservation biogeographic research on distributional dynamics of taxa individually and collectively is important for almost every facet of conservation planning and management (Whittaker, 2005, Richardson and Whittaker, 2010). Fifty years on from its publication, MacArthur and Wilson's (1967) book remains one of the most influential texts on ecology and evolution, and continue to be a springboard for research on the origin and maintenance of biological communities. Coinciding with the 50<sup>th</sup> anniversary of the publication of this landmark publication, Patino *et al.* (2017) developed a roadmap for research on island biology. It identifies 50 fundamental questions in four key research foci through a collaborative horizon-scanning approach among the biogeographic community. Addressing these cross-disciplinary set of questions has the potential to stimulate and guide our future research on island biology.

Classical biogeography has been expanded rapidly in recent times by the development of molecular systematics, creating a new discipline known as phylogeography, a relatively young research field integrating ecology and history of organisms (Avies, 2000). Modern phylogenetic data provide unparalleled ability to test biogeographic paradigms, often suggested by differences in species distribution patterns. Another emerging field, community phylogenetics, integrates community ecology (which investigates the nature of physical and biotic interactions, their origins and their ecological consequences) with phylogenetic relationships such as trait evolution, habitat specialization and speciation of organisms. Community phylogenetics focuses on understanding the origins

and histories of species within a community, and offers hypotheses on the influence of historical and ecological factors in structuring communities (Cavender-Bares *et al.* 2009; Graham and Fine, 2008; Webb *et al.* 2002). Both biogeography and ecology are converging at regional spatial scales and broad temporal scales in recent times towards a better understanding of the processes that determine patterns in nature. The integration of ecology and biogeography is a natural undertaking that is based on evolutionary biology and novel research directions are increasingly aimed at the intersection among these disciplines (Jenkins and Ricklefs, 2011).

### **BIOGEOGRAPHIC SIGNIFICANCE OF SRI LANKA-WESTERN GHATS BIODIVERSITY HOTSPOT**

The Sri Lanka-Western Ghats Biodiversity hotspot offers an excellent platform to examine community assembly and phylogenetic relatedness among its constituents incorporating large scale biogeographic patterns of major clades of both plants and animals (Ashton 2014; Meegaskumbura *et al.* 2002). In particular, our hotspot can be considered as an ideal study site in generating broader-scale insights which could be best revealed by incorporating historical biogeography in to community ecology and phylogenetics.

Furthermore, as a continental (land-bridge) island which had intermittent connections with peninsular India, Sri Lanka may have lost species quite rapidly from a stock which was in excess of equilibrium soon after it had detached from connections to the mainland during more recent geological time periods (*e.g.* Pleistocene extinctions; Biswas 2008). Modern biogeographic analyses along these lines could possibly be extended in predicting the number of taxa left in forest island fragments amidst other land uses applying the MacArthur and Wilson's equilibrium theory of island biogeography at entirely different scales of time and space. This would indeed provide, *inter alia*, a resounding affirmation of the basic robustness of the theory.

Phylogeographic and phylogenetic approaches are being increasingly used in evolutionary biology, ecology and biogeography. One of the most common themes of phylogeographic and phylogenetic studies is the search for 'biological refuges' where species survived when the climate was unsuitable in the surrounding matrix and eventually expanded their ranges in favourable climates. Perhumid SW Sri Lanka is one such refugium on account of its extraordinary endemism, and species richness unique for South Asia, reflecting its history with unusually pristine clarity (Ashton 2014). The ever-wet equatorial climate that prevails in the Malesian archipelago from Sumatra to New Guinea in Papuasia survives today in South Asia only in south-western Sri Lanka. It also manifests an extra-ordinary level of local endemism, especially among its mountain ranges compared with those of similar stature in the Far East, thereby again reflecting a truly ancient biological heritage (Gunatilleke and Ashton 1987; Ashton 2014).

Considering the above, the Sri Lanka-Western Ghats

biodiversity hotspot in general, and Southwest Sri Lanka in particular, offer excellent opportunities to both classical and modern biogeographers, to further unravel *inter alia* the unique role of the Indian Plate in geological times in biotic exchanges across the region, using historical, ecological and phylogenetic biogeographical tools.

### **CONTRIBUTION OF THE SPECIAL ISSUE ON SRI LANKA'S BIOGEOGRAPHY**

In this special issue on Sri Lanka's Biogeography, some papers have used these different tools to research on both terrestrial and aquatic systems. The first paper (Pethiyagoda and Sudasinghe) traces the origins and chronological expansion of the recent history of formal biodiversity exploration, inventorying and taxonomic research, which laid the foundation to subsequent analyses of geographic affinities of the Sri Lankan biota. The second (Wickramagamage) elaborates the historical transformation in Sri Lanka's central highland region, so rich in biological diversity, from ancient times to the end of the European colonization. The chronological history of the rapid decline in the island's primeval lower and upper montane rain forest cover for commercial cultivation of coffee and later tea during the 19th century is highlighted herein. The rest of the contributions in this issue review the current status of biogeography (and ecology) of different taxa and their ecosystems within Sri Lanka and one (*e.g.* sea snakes) in the Indian Ocean, using either classical or phylogenetic biogeographic methodology.

Most of the papers in this issue emphasize the ominous fate that belies the conservation of the remaining natural vegetation distributed in different climatic regions of the island. Some authors also reiterate the urgent need to close our knowledge gaps/shortfalls, such as the 'Linnaean Shortfall' (taxa inadequately collected and taxonomically described, *e.g.* bryophytes), as well as 'Wallacean Shortfall' (poorly understood geographical distributions of most species). Both these lead to a third critical gap in our knowledge, the 'Darwinian Shortfall' (lack of information on phylogenetic relationships and thus the evolutionary history) of many organisms (Hortal *et al.* 2015). It is our sincere wish that this special issue of the Sri Lanka Journal of Science would motivate the new generation of biologists to address these knowledge gaps or shortfalls in history, geography, ecology and phylogeny of Sri Lanka's rich biological diversity, in relation to those of South and South-east Asian regions. Furthermore, it is also hoped that a renewed interest in biogeography of Sri Lanka as well that of South Asia would stimulate new, insightful hypotheses, revisit older ones and test them rigorously to enrich our understanding of the processes influencing diversification in our region (Biswas 2008).

However, it is ironic that we are in an era where our ability to study biological systems is developing at an unprecedented pace, yet the natural ecosystems that harbor the vital clues of past biogeographic patterns are being destroyed indiscriminately (*e.g.* SW Sri Lanka) without any ecological responsibility, even before they are scientifically documented (Slik 2013). All contributors

to this special issue make a persuasive appeal in unison that what remains of the exceptional diversity and the vital biogeographic signatures of Sri Lanka's biota be conserved as one of our greatest biological heritages contributing to a sustainable future for the wellbeing of generations to come.

Most papers in this special issue are based on presentations made at a National Symposium on 'Biogeography and Biodiversity Conservation in Sri Lanka in a Changing Climate' organized by the National Science Foundation of Sri Lanka in 2015.

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