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RESEARCH ARTICLE

Biogeography of Sri Lankan bryophytes: the present status

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Abstract: Bryophytes (liverworts, mosses and hornworts) are the closest living relatives of the first group of plants that successfully colonized land. This small but well-established group of plants is unique among other land plants in having a dominant gametophyte phase in their life cycle and a single unbranched sporophyte that depends on the dominant gametophyte plant. Bryophytes occur throughout the world in all continents, occupying an assortment of habitats, especially in moist shady places. Many species have broad geographic ranges that may span two or more continents. Dispersal of bryophytes is brought about by spores, vegetative propagules or by unspecialized fragments of the gametophyte.

The bryophyte flora of Sri Lanka remains relatively poorly researched. According to checklists available, the Island harbours 560 mosses, 327 liverworts and five hornworts. Most of the collecting has been in the southern half of the country, especially in the Central Highlands. Exact locality details are missing for most of these specimens. There is no documentation for moss or liverwort Flora of Sri Lanka. Lack of a thorough taxonomic foundation is a major impediment to study the biogeography of Sri Lankan bryophytes. O'Shea (2003) presented a summary of current knowledge of biogeography of Sri Lankan mosses. According to his statistical analysis based on existing records Sri Lankan mosses show strong relationships with India, Indochina, and Malaysia but a much lower affinity with Africa.

Here we conducted a similar study for liverworts and hornworts using Kroeber's percentage of similarity, which suggests that Sri Lankan liverworts and hornworts show a considerable similarity with those of Java, Malaysia, Thailand, and India. However, more and wider systematic field explorations and taxonomic studies are needed to understand the biogeography of Sri Lankan bryophytes. To address this, field explorations and phylogenetic studies are being carried out, and the results will contribute to elucidate the biogeographic affinities of Sri Lanka's bryophyte flora.

Keywords: liverworts, mosses, hornworts, Kroeber's percentage of similarity.

INTRODUCTION

Bryophytes comprise the progeny of the first plants that successfully colonized terrestrial habitats. The origin of these first divergences in the extant embryophyte phylogeny dates back to the Ordovician period about 475 MYA. Bryophytes include three distinct morphological groups (liverworts, mosses, hornworts) forming three major lineages of land plants; Phylum Marchantiophyta (liverworts), Phylum Bryophyta (mosses) and Phylum Anthocerotophyta (hornworts). These three lineages share a life cycle in which the haploid gametophyte is the dominant and photosynthetically active generation and is therefore unique among all other embryophytes (Heinrichs *et al*., 2009). However, evolutionary patterns of bryophytes is still poorly known.

Dispersal of bryophytes occurs by spores, which are usually very small, commonly wind-dispersed, and by unspecialised asexual propagules originating from the gametophyte with a high potential for regeneration (Heinrichs *et al*., 2009). Bryophytes, unlike other land plants, lack a proper cuticle and their water content is directly regulated by the ambient humidity (poikilohydric). Also, bryophytes lack an advanced vascular system with xylem and phloem and therefore are called non-vascular land plants. Most species take up water through the whole surface of the plant (ectohydric). They also, require external water for their swimming sperms to bring about fertilization. However, despite these primitive characteristics, bryophytes show a variety of adaptations to thrive in extreme environmental conditions: there are many desiccation-tolerant species and some with efficient though simple systems to conduct water and food (Vitt, 1981; Ligrone *et al*., 2000). Due to their small size and efficient dispersal and survival mechanisms, bryophytes frequently have much wider distributions than higher plants. Nonetheless, bryophytes show a wide variety of distribution patterns ranging from very broad to highly disjunct and often localized in isolated parts of the world (Shaw, 2001). These spectacular distribution patterns have traditionally been explained by either continental drift, which found support from the ancient history of the Gondwana breakup or long distance dispersal (Shaw and Goffinet, 2000; Devos and Vanderpoorten, 2009). Among these striking distribution patterns of bryophytes, the Eastern American-Eastern Asian and Western American-Mediterranean disjunctions have been especially well-documented and studied (Schuster, 1983; Devos and Vanderpoorten, 2009).

Bryophytes exhibit a high level of diversity and often form a conspicuous and important component in many terrestrial ecosystems throughout the world (Longton, 1984). Following angiosperms, they are the most diverse group of plants in the world: ~ 5,000 species of liverworts, 13,000 species of mosses and 150 species of hornworts

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(Crandall-Stotler *et al*., 2009; Goffinet *et al*., 2009; Renzaglia *et al*., 2009). The variations of global species richness of liverworts, mosses and hornworts are discussed by von Konrat *et al*., (2007), Geffert *et al*., (2013) and Villarreal *et al*., (2010).

Phylum Marchantiophyta (liverworts) is the earliest diverged lineage of land plants, where their origin dates back to Silurian Period (Kenrick and Crane, 1997; Wellman *et al*., 2003; Heinrichs *et al*., 2006). The scarcity of the fossil records and the poor state of preservation of older fossils, are major impediments to inferring the age of the liverwort lineage (Mishler and Churchill, 1984; Heinrichs *et al*., 2006; Frahm, 2012). The oldest fossil record of embryophytes is thought to be of a liverwort that existed about 475 million years ago during the middle Ordovician Period of the Palaeozoic Era. Most biogeographic studies on liverworts are based on molecular phylogenetic studies; Heinrichs *et al*., 2006, 2007, 2009, 2013; Feldberg *et al*., 2007. Although phylogeny and taxonomy of thalloid liverworts are thoroughly studied for individual lineages in the group, their biogeography is less well understood than that of leafy liverworts (Feldberg *et al*., 2007; Heinrichs *et al*., 2007, 2009, 2013).

Current distribution patterns of the mosses in the world are explained by vicariance and long distance dispersal and the latter is the most prominent (Buck, 1998). Few studies have been carried out to give possible explanations for the biogeography of regional moss flora (*e.g.* Tan, 1996; Buck, 1998). Some studies have used a phylogenetic approach to make inferences about the biogeography of different moss families (e.g. Shaw *et al*., 2008).

The precise phylogenetic position of hornworts remains unclear. As used in the studies regarding liverworts mentioned above, few studies have used molecular dating to study the geographic distribution of modern hornworts and their patterns of species accumulation (Villarreal *et al*., 2015).

Zhang and Corlett (2003) analyzed the phytogeography of bryophytes in Hong Kong; a biogeographically interesting location on the northern margins of the Asian tropics. In this study each taxon of bryophytes in Hong Kong has been assigned to a phytogeographical pattern on the basis of its present worldwide distribution. Kroeber's percentage similarity is used to evaluate the floristic affinities between different regions. They have identified fourteen phytogeographical patterns of Hong Kong bryophytes through the study where the East Asian pattern is the most frequent.

However, none of the studies carried out on global biogeography of bryophytes included Sri Lankan bryophyte (liverwort, moss and hornwort) taxa (von Konrat *et al*., 2007; Villarreal *et al*., 2010; Geffert *et al*., 2013).

BIOGEOGRAPHY OF SRI LANKAN BRYOPHYTES

Sri Lanka is a tropical island of Gondwanan origin located in the Indian Ocean. During the Pleistocene ice ages, land bridges formed between Sri Lanka and mainland India until the glaciers melted and caused the rising of sea level to result in the present separation. Geographical position, topography, modulation of climate, and geological history has mainly contributed to Sri Lankan bryophyte biogeography. The island consists of an outstanding and unique diversity of both flora and fauna distributed through its major climatic zones: arid, dry, intermediate and wet zones (Gunawardene *et al.*, 2007; Bossuyt *et al*., 2004; Pethiyagoda, 2005). Sri Lanka is also endowed with enormous ecosystem diversity that diverges across its main topographical regions; central highlands (montane region), the plains and coastal belt (Gunatilleke *et al*., 2008). Sri Lanka is considered a biodiversity hot-spot together with the Western Ghats of India with a high level of endemism in both flora and fauna (Bossuyt *et al*., 2004; Gunawardene *et al.*, 2007).The Island has been an ideal location for floral and faunal explorations for both local and foreign scientists since ancient times (O'Shea, 2003; Rubasinghe and Long, 2014). Bryological exploration of Sri Lanka was initiated during the British colonial period. George Gardner (1810-1849) and George Thwaites (1820-1882) were the pioneers who also developed the National Botanic Garden and the National Herbarium, Peradeniya. By the mid-nineteenth century, not only the British explorers but also botanists from Germany e.g. Max Ernst Wichura (1817–1866),M. Fleischer (1861–1930), Theodor Herzog (1880–1961) and Italy *e.g.* Odoardo Beccari (1843–1920) had taken a lead. A review of past taxonomic explorations of Sri Lankan bryophytes is presented in Rubasinghe and Long (2014). The collections made by these past explorers were reported by mostly foreign taxonomists (details in Rubasinghe and Long, 2014). Based on these publications, Prof. B. A. Abeywickrama produced a literature-based guide to the genera of Sri Lankan mosses (1960) and checklists of liverworts (Abeywickrama and Jansen, 1978a) and mosses (Abeywickrama and Jansen, 1978b). Since then, Sri Lankan bryophytes were overlooked for several decades. In 2002, Brian J. O'Shea updated the checklist of Sri Lankan mosses, which was also based on a literature compilation. Many Sri Lankan bryophytes collected in the past remain in The Natural History Museum, London (BMNH), most of which remain unpublished. Manuscripts prepared by A. H. G. Alston containing specimen-based checklists of mosses and liverworts of Sri Lanka also remain unpublished in BMNH. The checklist of liverworts and hornworts was updated by Long and Rubasinghe (2014) by compilation and critical review of all the published records of liverwort specimens collected in Sri Lanka. Currently there are preliminary taxonomic surveys on-going on the bryophytes in Sri Lanka, but there have been no comprehensive studies carried out regarding the biogeography of this evolutionarily important plant group.

O'Shea (2003) briefly discussed the biogeographic relationships and the endemism of Sri Lankan mosses. He evaluated the ranges of Sri Lankan moss taxa with those of selected geographic ranges; India, Indo-China, Malaysia and Sub-Saharan Africa. In his analysis, the checklists of mosses in these regions were compared with the checklist of Sri Lankan mosses. The number of shared taxa between geographic units was expressed as a percentage of the flora

of each country. In this study, the number of taxa shared between geographic units has been analysed, and expressed as a percentage of the flora of each country. Kroeber's percentage of similarity is used to calculate the percentages that allow the commonality of floras to be expressed in a standard way.

According to these results, Sri Lanka shows the highest similarity in its moss flora with India (46.7), Indo-China (45.2) and Malaysia (42.0); attributed to its geological history and current geography. Sri Lanka shows a much lower affinity with Africa.

Among the three groups of bryophytes, liverworts and hornworts are the least studied groups in Sri Lanka. According to the recent checklist by Long and Rubasinghe (2014), there are 82 genera with 327 species of liverworts and 4 genera with 5 species of hornworts recorded in Sri Lanka (Long & Rubasinghe, 2014). Sri Lankan liverworts (leafy, complex and simple thalloids) have not been analysed for biogeographic relationships to-date. Therefore, as a preliminary survey, we analysed the biogeographic affinities of Sri Lankan liverworts and hornworts.

EXPERIMENTAL

Based on the most recent checklist of Sri Lankan liverworts and hornworts by Long and Rubasinghe (2014), the recorded species were compared with the available checklists of India, Java, Thailand, Malaysia, Australia, Northern Africa and Madagascar (Table 1) implementing Kroeber's percentage of similarity (van Balgooy, 1971). Authors have standardized all the names of taxa given in checklists on the most recent updates by Crandall-Stotler *et al*. (2009) and Renzaglia *et al*. (2009) before calculations. Kroeber's percentage of similarity is expressed by the formula 50C(A + B)/AB, where A is the number of taxa occurring in the first region; B, the number of taxa occurring in the second region; C, the number of taxa shared by both regions (van Balgooy, 1971). O'Shea (2003) carried out a similar comparison for Sri Lankan mosses and the conclusions are discussed during the present study.

RESULTS AND DISCUSSION

The number of taxa shared between each geographic unit was calculated, and expressed as a percentage of the total number of liverworts and hornworts in Sri Lanka (Table 2).

According to the results of Kroeber's percentage of similarity, Sri Lanka shows a considerable similarity in its liverwort and hornwort flora with Java, Malaysia and Thailand and India, however, the similarity is much less with, Northern Africa and Madagascar (Table 3). The main advantage of using Kroeber's formula is that it minimizes the effect of the size difference between the two regions under comparison (Tan, 1984; Zhang *and* Corlett, R.T., 2003). The prevalent winds from the east could have allowed a steady stream of spores and propagules to be blown towards the Indian subcontinent, thereby establishing a high similarity of liverworts between Sri Lanka and Java. The liverwort genera *Riccardia, Metzgeria, Plagiochila, Porella, Radula, Frullania, Lejeunea* and *Marchantia* are globallybest represented in the tropics, including Sri Lanka (Schofield, 1985; Ruklani and Rubasinghe, 2013; Long and Rubasinghe, 2014). Among the hornworts *Megaceros* and *Dendroceros* are predominantly tropical and Sri Lanka has records of only one species under the genus *Dendroceros* (Schofield, 1985; Long and Rubasinghe, 2014). According to O'Shea (2003) Sri Lanka shows the highest similarity in its moss flora with India (46.7), Indo-China (45.2) and Malaysia (42.0) and a lower similarity with Africa (14.9%).

Quality of data is clearly a significant factor in influencing these results. We agree with O'Shea's (2003) statement 'The results of course depend on the quality of the data, and not all published data is of good quality, and some data derived from older papers will contain large numbers of taxa no longer accepted, other than as synonyms. Lists produced from such a database thus need a great deal of checking'. Therefore, comprehensive and accurate species lists of all existing species of bryophytes in Sri Lanka are a fundamental requirement for any detailed bryogeographic analysis. Without such information, a sound basis for any bryogeographical hypotheses cannot be achieved. Many areas of Sri Lanka remain largely unexplored from a bryological point of view. The limited data sets and the poor state of taxonomy of the group within the island may lead to misleading ideas about the distribution of species and also unsupported speculations of their biogeographic affinities. Clearly, the poor state of taxonomy of bryophytes in Sri Lanka may significantly affect the results.

Currently, field explorations and phylogenetic studies are being carried on the Sri Lankan bryophyte flora, and the results of these studies may modify and improve the data available for analysis. Recent field explorations and taxonomic studies have identified a few new records to the island: Tan (2005) – five new species records of mosses; Ruklani and Rubasinghe (2013) – 10 new records of mosses and liverworts. Also, studies are being carried out to investigate the bryoflora of different ecosystems of the country (Ruklani and Rubasinghe, 2015). These studies will contribute to elucidating the biogeographic affinities of Sri Lanka. Accurate taxonomic identification and elucidating their biogeographic affinities will guide the conservation process of this important group of plants. Further, to ensure their survival conserving the micro-habitats of bryophytes is also essential.

CONCLUSION

A literature based survey of biogeography of the Sri Lankan bryophytes was carried out. A summary of current knowledge of biogeography of Sri Lankan mosses, liverworts and hornworts is presented. Sri Lankan liverworts and hornworts show a considerable similarity with Java (44.9), Malaysia (34.1) and Thailand (35.2) and India (19.0). However the similarity is much less with Africa (6.2) and Madagascar (11.8). A similar pattern of similarity is exhibited by hornworts.

Lack of floristic knowledge and proper taxonomic studies is a major barrier to deduce the species richness, species area-relationships, endemism and the taxonomic status of endemic taxa of Sri Lankan bryophytes.

Table 1: Published checklist sources used in the analysis.

Region/Country	Reference
Sri Lanka	Long and Rubasinghe, 2014
India	Dandotiya *et al.,* 2011
Java	Söderström *et al*., 2014
Thailand	Lai *et al*., 2008
Malaysia	Chuah-Petiot, 2011
Australia	McCarthy, 2003
Northern Africa	Ros *et al*., 1999
Madagascar	Marline *et al*., 2012

Table 2: Shared taxa of liverworts and hornworts as a percentage.

Region	Shared taxa as a percentage of total liverwort flora	Shared taxa as a percentage of total hornwort flora
India	26%	40%
Java	56%	40%
Thailand	38%	40%
Malaysia	48%	20%
Australia	27%	20%
Northern Africa	4%	20%
Madagascar	13%	20%

Table 3: Shared taxa of liverworts and hornworts based on Kroeber's percentage of specific similarity.

Region	Kroeber's percentage of specific similarity	
	Liverworts	Hornworts
India	19.0	24.0
Java	44.9	23.6
Thailand	35.2	29.1
Malaysia	34.1	18.3
Australia	18.8	11.6
Northern Africa	6.2	20.0
Madagascar	11.8	26.6

Extensive field collections of bryophytes from throughout the country and detailed taxonomic studies based on specimens will undoubtedly add to the biodiversity figures of the country. Detailed ecological studies should be carried tracing the collection sites of the past collectors, together with new sites to unveil their distribution patterns and to uncover the species area relationships. Phylogenetic studies are greatly important and will reflect the evolutionary history to infer the dispersal and colonization histories at various taxonomic levels (Phylogeographic approach).

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