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RESEARCH ARTICLE

Historical biogeography of Sri Lankan mangroves

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Abstract: Mangroves are a group of genetically unrelated plant taxa of angiosperms that occur in inter-tidal habitats in sheltered tropical coastlines. Biogeographically, mangrove areas are categorized into two regions: Sri Lanka is situated in the Indo-West Pacific (IWP) region where the plant diversity is significantly greater than in the Caribbean, West Pacific and Atlantic regions (CWPA). More than half the number of mangrove plant species that are exclusive to mangrove areas in the IWP region occur in the Sri Lankan mangrove areas that cover only about 16,000 ha. Being located in the land-sea interface, identification of mangrove areas and plant taxa endemic to mangrove ecosystems is ambiguous as plants that occur in non-mangrove areas too occur in mangrove habitats. This paper presents an insight into aspects relevant to resolving this ambiguity. Accordingly, 24 true mangrove species and a hybrid have hitherto been reported from Sri Lanka, out of which two are reported only once by a single researcher. Processes pertinent to historical biogeography of mangroves in Sri Lanka are discussed in the light of current hypotheses and knowledge base.

Keywords: mangrove biogeography, Sri Lanka, micro-tidal habitats, true mangroves, mangrove associates.

INTRODUCTION

Mangroves comprise trees or shrubs, exceeding 0.5m in height, growing above mean sea level on unconsolidated sediments of the intertidal zone in tropical and sub-tropical sheltered coastal environments, particularly associated with estuaries and lagoons. They are extraordinarily adapted to the intertidal conditions characterized by salinity and hypoxia caused by tides (Tomlinson, 1986). Mangroves are an ecological entity, composed of several genetically unrelated taxa both plants and animals and thus appear to have evolved independently from a diverse assemblage of higher taxa. Although more than 100 plant species are associated with mangrove vegetation, only about 80 that belong to 18 angiosperm families are considered as mangroves or true/ exclusive mangrove plant species (Schmitt and Duke, 2015). As their occurrence is restricted to mangrove environments, i.e. the coastal areas between mean sea level and the highest tide elevation or the inter-tidal zone, they can be considered as plants endemic to inter-tidal zones. Their unique presence in the inter-tidal zone is possible due to a number of adaptations that these plants have developed to cope with high soil salinity, hypoxia, unfavourable conditions for reproduction and dispersal (Lo, 2010). Besides, there are other species that occur in the inter-tidal zone, particularly in the landward fringe of it and also in other freshwater, amphibious or terrestrial habitats and thus are considered as mangrove associates.

EVOLUTION AND DISTRIBUTION OF MANGROVE PLANT SPECIES IN THE TROPICS AND SUB-TROPICS

Fossil pollen discovered of *Nypa* are the evidence exists on earliest occurrence of mangroves, which dates back to the late Cretaceous, however, subsequent to the first appearance of flowering plants (Germeraad *et al.*, 1968). Evolution and differentiation of mangrove plants are believed to have taken place around the Tethys Sea with a number of taxa that are now extinct (Graham, 1995; Saenger, 1998). Events that have taken place during the Pleistocene that affected global climate and sea levels would have had a significant influence on the present distribution of mangrove plants in different parts of the world. During prolonged dry periods in the Pleistocene, mangrove species may have got more confined to the hot and wet climate at the equator than they are today (Woodroffe and Grindrod, 1991). Moreover, declining sea levels due to glacial events in the Pleistocene that resulted in lowering sea levels would have created land connections between the present day land masses in South East Asia, which in turn made available large extents of potential mangrove habitats (inter-tidal areas) that could successfully be colonized and specialized by plants (Clark and Guppy, 1988; Woodroffe *et al.*, 1985; Woodroffe and Grindrod, 1991). Wet and arid climates that prevailed in different parts of the tropics during Pleistocene would have contributed to the mangrove distribution now observed in the New and Old World mangrove areas.

DEFINITION OF MANGROVE PLANTS AND HABITATS

Identification of mangrove areas or habitats is primarily based on the natural presence of mangrove plants in the inter-tidal zone of sheltered coasts. Since soils in inter-tidal zones are saline, plants that occur in them should essentially be halophytes which have the ability to tolerate high soil salinities and grow optimally under moderate soil salinities (Parida and Das, 2005). Mangrove species therefore are halophytes with varying capacities to tolerate salinity and grow optimally under saline conditions.

The word "mangrove" therefore is used not only to

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denote the plants in a mangrove environment, but also the area covered by mangrove plants or the mangrove habitat. In some literature published in the eighties, the word "mangal" was used to distinguish habitat from mangrove plants (Tomlinson, 1986). Use of the word "mangrove" however to signify either the area/habitat or the plant seemingly does not create ambiguity when one considers the context in which it is being used.

Nevertheless, differentiating plant species as exclusive/true mangroves and associates is contentious. Plant species that exclusively occur in inter-tidal habitats which are predominantly occupied by species with morphological as well as physiological adaptations to cope with high soil salinity and hypoxia are considered the true mangroves, while those species that occur not only in saline inter-tidal areas but also in brackish water or freshwater wetlands or in terrestrial habitats (rarely) are reckoned as associates. Accuracy and integrity of this categorization therefore depends largely on the field observations and therefore is subjective. *Pemphis acidula* is considered by most as a true mangrove species, nevertheless, in Sri Lanka, it occurs on the cliff slopes, above the inter-tidal zone at Kudiramalai Point on the north western coast of Sri Lanka which receives sea-spray. *Acrostichum aureum* and *A. speciosum*, the only pteridophyte species in mangrove areas, by this definition, are not true mangroves, but associates as they also occur in brackish water and near-freshwater wetlands which are located away from inter-tidal areas.

Besides *P. acidula* and species of *Acrostichum*, the other species that are often subject to controversy include *Heritiera littoralis*, *Excoecaria agallocha, Xylocarpus granatum*, and *Acanthus ilicifolius.* Based on leaf traits and leaf salt accumulation, Wang *et al*. (2010) classified *A. ilicifolius, X. granatum* and *P. acidula* as true mangroves while *H. littoralis, E. agallocha and Acrostichum* species as associated species. In Sri Lanka, *E. agallocha* is observed in the flood plain riparian forests in the upstream zones of estuaries, among typically freshwater species such as *Terminalia arjuna.* Leaf characteristics of *Clerodendron inerme* often classified as an associate, resemble those of true mangrove species more than those of associates. This species is found not only in the back mangrove areas close to the landward margin but also in the water-front areas among other true mangroves. In the Kala Oya estuary on the north western coast of Sri Lanka, it is found growing luxuriantly among *Rhizophora mucronata* stands at the water-front zone, nevertheless it is an isolated occurrence, as such, *C. inerme* is considered as an associate.

The common true mangrove species are capable of producing mono-specific stands unlike the associates, which show a scattered distribution. True mangrove species that are capable in producing mono-specific stands in the inter-tidal zone or those that dominate mangrove communities are considered as major true mangroves while the others as minor true mangroves (Tomlinson, 1986). Although *E. agallocha* is more appropriate to be considered an associate, it dominates the upstream areas of estuaries, (where the salinity is low) particularly, in Sri Lanka's dry zone and found in abundance among true mangroves in most mangrove areas in Sri Lanka.

In addition to the inter-tidal areas on shoreline of sheltered coasts, mangroves occur in more inland areas that receive tidal water, and mangrove seeds/seedlings, due to the altered local hydrological landscape by anthropogenic activities such as construction of roads and drainage canals.

Exclusivity of mangroves lies with their ability to grow optimally while tolerating salt, lack of freshwater and a stable substratum, and hypoxia when inundated and unfavourable conditions for seed germination and establishment that is commonplace in the inter-tidal zone. Many morphological and physiological adaptations, which vary among taxa, have rendered mangrove species the ability to cope with these harsh conditions (Ball, 1996). Production of a variety of aerial roots that are characteristic to different mangrove plant species is a major adaptation for their survival in periodically hypoxic inter-tidal soils. Some trees of *Bruguiera cylindrica* encountered in mangrove areas on the east coast of the island possessed prop roots in addition to the knee roots, characteristic to this species. Performance of ecological functions of mangrove ecosystems therefore depends on the extent to which individual species are equipped with these adaptations (Ye *et al.*, 2005).

FLORISTICS OF SRI LANKAN MANGROVES

Earliest scientific record on mangroves in Sri Lanka (restricted to the southern coasts) appeared in 1905 by Tansley and Fritsch that followed by Abeywickrema (1960) and Aruchelvam (1968). The occurrence of seven common true mangrove species and two rare true mangrove species have been recorded from the inter-tidal areas of Puttalam lagoon, Dutch bay and Portugal bay on the north-western coast of Sri Lanka (Amarasinghe and Balasubramaniam, 1992; Balasubramaniam and de Silva, 1984; Kanakaratne *et al*., 1983). Jayatissa *et al.* (2002) report the occurrence of 20 true mangrove species and 18 associates in lagoons and estuaries on the south western coast of Sri Lanka. The national Red List 2012 of Sri Lanka (Ministry of Environment, 2012) includes 21 plant species as true mangroves.

Considering the issues related to the ambiguity of grouping plants as true and associate mangrove species, a total 80 mangrove plant species have been reported globally to be endemic to the inter-tidal areas(true mangroves) (Duke, 1995). The true mangrove species of wide distribution in most of the inter-tidal areas of Sri Lanka are *Avicennia marina*, *Rhizophora mucronata*, *R. apiculata* and *Lumnitzera racemosa.* Table 1 includes the mangrove species that match to a large extent with the characteristics of true mangroves. Although *Heritiera littoralis*, occurs in inter-tidal areas of low salinity, it is considered a true mangrove as it has not been observed in freshwater swamps or in terrestrial habitats. Mangrove associated species recorded in Sri Lankan mangrove areas are presented in Table 2. *Terminalia arjuna* and *Diospyros sp.* were encountered only in Kala Oya estuary. *Nymphea nouchali* was observed in estuaries of Kala Oya and Yan Oya.

SRI LANKAN MANGROVES IN THE GLOBAL MANGROVE LANDSCAPE

Mangroves have been estimated to cover 15.6 to 19.8 million hectares in tropical and sub-tropical coastal areas (FAO, 2007). The northern limits of mangrove occurrence is in Japan (31ºN) and Bermuda (32ºN) and the southern limits are in South Australia (38.75ºS) and the east coast of South Africa (32.6ºS) (Tomlinson, 1986). Biogeographic distribution of mangroves is generally confined to the tropical and subtropical regions and the largest percentage of mangroves is found between 5° N and 5° S latitude (Giri *et al*., 2011). Mangroves are distributed pan-tropically and therefore they occur along coastlines of 124 countries and territories in the tropics (Kathiresan and Bingham, 2001).

Diversity of plants and animals in an ecosystem is the cumulative result of numerous physical processes as well as biological interactions that occur in it. It is logical to expect therefore convergent diversity to take place in similar habitats. The mangrove flora however deviates from this, as distinctly different diversities occur in similar inter-tidal habitats in different tropical regions of the world. Biogeographically, mangrove areas are categorized globally into two regions and Sri Lanka is situated in the Indo-West Pacific (IWP) region (Eastern group / Old World). The cold water at the southern tip of Africa and the large distance between Asia and America divide the IWP from the Atlantic-Caribbean and Eastern Pacific (ACEP) region. Although comparable extents are covered by mangroves in these two regions, IWP far outnumbers the tree genera and species (Luther and Greenberg, 2009). ACEP region supports only 15 species of 8 genera while the IWP region harbours 65 species of 23 genera. Among them, 40 species in the IWP are exclusive to mangrove areas (true mangroves) whereas in the ACEP region, only 3 -5 species are restricted to it (Duke, 1992).

The explanation for the above 'anomalous' biogeographic pattern has been related to the 'Centre of origin' hypothesis that proclaims all mangrove taxa originated in the eastern shores of the Tethys sea which is now represented by the IWP region, and later dispersed into other parts of the world. It is suggested that the presence of diverse flora in adjacent terrestrial ecosystems and in relatively seasonal rainfall, that prevailed throughout most of the Tertiary would have been conducive for terrestrial plants to invade mangrove habitats through adaptations to the inter-tidal zone. The restriction of most mangrove taxa to the IWP region may have resulted from poor dispersal with closure of the Tethys connection to the Atlantic Ocean in the middle of the Tertiary period (Latham and Ricklefs, 1993).

Table 1: List of true mangrove species reported from, or observed in Sri Lankan mangrove areas.

1. Abeywickrema, 1960; **2**. Aruchelvam, 1968; **3**. De Silva and Balasubramaniam, 1985; **4**. Nanayakkara, 1986; **5**. Pinto, 1986; **6**. Jayawardena, 1985; **7**. Rao, 1987; **8**. Amarasinghe and Balasubramaniam, 1992; **9**. Jayatissa *et al*., 2002; **10**. Perera , 2014 (Unpublished PhD thesis) **11**. Perera *et al*., 2012; **12**. Personal (Amarasinghe, M.D.) observations; **13**. de Silva and de Silva, 1998; **14** . Setyawan *et al*., 2014, **15.** Tansley and Fritsch, 1905; **16**. Ministry of Environment, 2012.

No	True Mangrove Species	Reference Sources
01	*Acanthus ilicifolius* L.	1, 2, 3, 4, 5, 6, 7, 9, 10,15
02	*Aegiceras corniculatum* (L.) Blanco	1, 2, 3, 4, 5, 6, 7, 8, 9, 10,16
03	*Avicennia alba* Blume*	1, 2, 3, 4, 5, 6, 7, 9
04	*Avicennia marina* (Forsk.) Vierh	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12,13; 16
05	*Avicennia officinalis* L.	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12,15, 16
06	*Bruguiera cylindrica (*L.) Blume	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 16
07	*Bruguiera gymnorriza* (L.) Lamk.	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12,13,15; 16
08	*Bruguiera hainessi* C.G. Rogers*	7
09	*Bruguiera parviflora* Wight & Arnold ex. Griffith	7
10	*Bruguiera sexangula* (Lour.) Poir	1, 3, 4, 5, 6, 7, 9, 10, 12
11	*Ceriops decandra (*Griff.) Ding Hou*	1, 3, 5, 6, 7, 12, 16
12	*Ceriops tagal* (Perr.) C.B. Robinson	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 10, 12,13,16
13	*Cynometra iripa* Kostel*	8, 9, 16
14	*Heritiera littoralis*	2, 12, 16
15	*Lumnitzera littorea* (Jack) Voigt *	1, 3, 7, 9, 12
16	*Lumnitzera racemosa* Willd.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12,16
17	*Nypa fruticans* (Thunb.) Wurmb.	1, 2, 3, 4, 5, 6, 7, 9, 10, 15, 12,16
18	*Rhizophora apiculata* BL.	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 16
19	*Rhizophora mucronata* Lamk.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12,13, 15, 16
20	*Scyphiphora hydrophyllaceae* Gaertn.*	1, 3, 6, 7, 9, 10, 16
21	*Sonneratia alba* J.Smith*	1, 3, 5, 6, 7, 9, 10, 12, 15,16
22	*Sonneratia apetala* Buch.-Ham *	3, 5, 6, 7, 9, 15
23	*Sonneratia caseolaris* (L.) Engler	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 15, 16
24	*Xylocarpus granatum* Konig	2, 3, 4, 5, 6, 7, 9, 12, 16
25	*Rhizophora annamalayana* (hybrid)	14

*Rare mangrove plant species

Table 2: List of mangrove associated species recorded from mangrove areas of Sri Lanka.

	Mangrove Associated Species		Mangrove Associated Species
01	*Acrostichum aureum* L.	18	*Hibiscus tiliaceus* L.
02	*Acrostichum speciosum* Willd.	19	*Manilkara hexandra* (Roxb.) Dubard.
03	*Anona glabra* L.	20	*Nymphaea nouchali* Burm.f.
04	*Ardisia elliptica* Thunb.	21	*Phoenix zeylanica* Trim.
05	*Barringtonia asiatica* (L.) Kurz.	22	*Pongamia piñata* (L.)
06	*Barringtonia racemosa* (L.) Spreng.	23	*Premna integrifolia* Lam.
07	*Calophyllum inophyllum* L.	24	*Salvadora persica* L.
08	*Clerodendron inerme (*L.Gaertn.)	25	*Sphaeranthus amaranthoides* Burm.f.
09	*Caesalpinia crista* L.	26	*Salvinia molesta* D.S.Mitchell
10	*Cerbera manghas* L.	27	*Sesuvium portulacastrum* (L.) L.
11	*Cynodon dactylon* (L.) Pers.	28	*Suaeda nudiflora* Moq.
12	*Derris uliginosa* (Willd.) Benth	29	*Suaeda maritima* (L.) Dumort.
13	*Derris trifoliata* Lour.	30	*Sueda monoica* Forssk. ex J.Gmelin
14	*Dolechandrone spathacea* (L.f.) K.Schumann	31	*Tamarix gallica* L.
15	*Diospyros sp.*	32	*Terminalia arjuna* (Roxb.)Wight & Arn.
16	*Excoecaria agallocha.*L.	33	*Thespesia populnea* (L.) Soland. ex. corr.
17	*Excoecaria indica* (Willd.) Muell.-Arg./	34	*Typha angustifolia* L.

Considering various lines of evidence such as, mangrove fossil records, comparisons between modern and fossil distribution of mangroves and eight gastropod genera that show high affinity to the mangrove environment, species-area relationships of mangroves and associated gastropods in relation to the available habitat area and patterns of individual plants associated with gastropod communities and species, Ellison *et al*., (1999) support the 'vicariance hypothesis'. This hypothesis presumes mangrove taxa evolved around the Tethys Sea during the Late Cretaceous and that regional species diversity has resulted in speciation (allopatric evolution) that has taken place after continental drift which served as a barrier to gene flow. They concluded that the patterns of nestedness at both the community and species level indicate three independent regions of diversification of mangrove ecosystems, i. South-east Asia, ii. Caribbean and Eastern Pacific, and iii. Indian Ocean where Sri Lanka is located.

Biogeographic analysis based on genetic relationships, fossil records and tectonic processes, of the most widespread mangrove genus, *Rhizophora* throws light on the potential role of both vicariance and long-distance dispersal in the development of current biogeographic patterns of mangroves (Lo *et al*., 2014; Duke, 1992). *Rhizophora* is a dominant genus of the pan-tropical mangrove plant family, Rhizophoraceae. Fossil records provide evidence that this genus is in existence since the Pelaeocene about 55.8 - 65.5 Ma and it shows a disjunct species distribution in both IWP and CWPA regions. All *Rhizophora* taxa have the ability to disperse long distances owing to their characteristic large buoyant propagules (viviparous seeds). Of the six *Rhizophora* species described from mangrove areas, three (*R. apiculata, R. mucronata* and *R. stylosa*) are found exclusively in the IWP region while two (*R. mangle* and *R. racemosa*) are restricted to CWPA region. Only one species, *R. samoensis* is common to both regions (Duke, 1992).

Geographical disjunctions of plant and animal lineages can arise through historical long distance dispersal to new areas or through vicariant events that create physical barriers to gene flow and hence facilitate population divergence or allopatric speciation, although the distributional patterns associated with vicariance may not always be distinct from those caused by dispersal (Duke, 1992). For instance, despite the low genetic diversity, significant genetic structuring has been reported to occur among *Rhizophora mucronata* populations in south-east Asia. Contrary to observations made on other mangrove species, genetic differentiation in *R. mucronata* has not been observed between populations on the coasts of the Malay peninsula or shown a correlation with geographical distance (Wee *et al*., 2014). The most distinct genetic discontinuity has been observed at the boundary between the Andaman Sea and the Malacca Strait, and this situation is explained by the prevailing ocean currents in the region. Genetic structure of *R. mucronata* therefore is apparently maintained by ocean-current facilitated propagule dispersal (Wee *et al*., 2014) and thus it is suggested oceanic circulation patterns might have acted as a cryptic barrier to gene flow (Wee *et al*., 2015).

Despite the remarkable differences in life-history traits of mangrove species, which should have had a strong influence on seed dispersal capability and, thus, population connectivity, it is plausible that not only vicariant events, but also climate fluctuations and marine currents would have contributed to distribution of genetic diversity (Cerón-Souza *et al*., 2015). Although adaptation to different habitats govern local distributional patterns, Duke (1995) also suggests that it is likely that the combination of dispersal and historical perturbations has a predominant role in determining the overall distribution patterns (Duke, 1995).

On the contrary, relying on phylogenetic and phylogeographic analyses based on internal transcribed spacer (ITS) sequences, chloroplast DNA (cpDNA), and amplified fragment length polymorphisms (AFLPs) of genomic DNA that demonstrate recent long distance dispersal across the Atlantic ocean, Nettel and Dodd (2007)

Table 3: Distribution of major true mangrove species along the shores of the Indian Ocean Eastwards and westwards to Sri Lanka. (Sources: Spalding *et al.*, 2010; personal (Amarasinghe, M.D.) observations on Sri Lankan mangroves)

True Mangrove Species	East coast of Africa/ Madagascar	Sri Lanka	SE Asia
1. *Acanthus ilicifolius*		√	√
2. *Aegialitis rotundifolia*			√
5. *Aegiceras corniculatum*		√	√
6. *Avicennia alba*			√
7. *Avicennia marina*	√	√	√
8. *Avicennia officinalis*		√	√
9. *Bruguiera cylindrica*		√	√
10. *Bruguiera gymnorrhiza*	√	√	√
11. *Ceriops decandra*		√	√
12. *Ceriops tagal*	√	√	√
13. *Cynometra iripa*		√	√
14. *Heretiera littoralis*	√	√	√
15. *Kandelia candel*			√
16. *Rhizophora apiculata*		√	√
17. *Rhizophora mucronata*		√	√
18. *Rhizophora stylosa*			√
19. *Scyphiphora hydrophyllacea*		√	√
20. *Sonneratia alba*	√	√	√
21. *Sonneratia caseolaris*		√	√
22. *Sonneratia griffithii*			√
23. *Sonneratia ovata*			√

reject the hypothesis of vicariance for the widespread distribution of *Avicennia germinans*. This species however, does not occur in Sri Lankan mangroves.

McCoy and Heck (1976) argue that the 'center of origin' explanation for the distribution and diversity patterns of the organisms comprising the principal shallow-water habitats in the tropics, hermatypic corals, mangroves, and seagrasses, is highly unlikely, based on fossil data and the dispersal capabilities of the organisms. Furthermore, these biogeographic patterns are better explained by the existence of a previously widely-distributed biota which has since been modified by tectonic events, speciation, and extinction.

BIOGEOGRAPHY OF MANGROVE PLANT SPECIES AROUND THE INDIAN OCEAN

Floristic composition of Sri Lankan mangroves, especially on the western coast show more affinity to that of the mangroves on the west coast of Madagascar where mangroves are found exclusively (Rogers and Andrianasaolo, 2003) and the tide reaches up to 4 m during equinox. Nevertheless, the eastern shoreline exposed to the Indian Ocean, is micro-tidal (Gaudian *et al*., 1995), like the coasts of Sri Lanka where the maximum tide has been recorded to be 89 cm. Mangrove species such as *Rhizophora mucronata, Bruguiera gymnorrhiza, Ceriops tagal, Avicennia marina* and *Lumnitzera racemosa* that are common to Madagascar (Rasofolo, 1997) are also common in Sri Lankan mangroves. Although these species are common in mangroves along the Indian coast (Kathiresan and Rajendran, 2005), a noteworthy similarity is observed with respect to occurrence of *Sonneratia alba* in mangroves of Madagascar where it occurs as a common species (Rasofolo,1997) and in Sri Lanka, as a rare species restricted to the north-western coastal areas. *Sonneratia alba* is the dominant species in Malwathu Oya estuary on Sri Lanka's north-western coast and it occupies the water-front zone; this is a very unusual occurrence in Sri Lankan estuaries where the water-front zones most often are dominated by species of *Rhizophora.* In Madagascar, *Sonneratia alba* is a primary colonizer and occupies the water-front zone (Rasofolo, 1997). This similarity may reflect the mangrove distribution in the shores of Tethys sea when the land masses of present day Madagascar and India (including Sri Lanka) were together before their separation 88 million years ago.

Being situated in southern Asia, Sri Lanka's coasts occur between southeast Asian and east African sectors of the Indian Ocean, the presence of mangrove species along Sri Lankan coasts apparently show intriguing affinities to the species distribution along coasts across the Indian Ocean (Table 3). The potential effect of current patterns in their dispersal, in addition to the past vicariant events such as continental drift and separation of land masses during geological time spans would have influenced the current mangrove species distribution in Sri Lanka. Furthermore, occurrence of mangrove species around the Indian Ocean substantiates the conclusion of Ellison *et al*., (1999) that speciation would have taken place independently in regions, for instance, East African (Atlantic and Caribbean areas are also included), South Asian and South East Asian regions.

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