

Local Endemism Within the Western Ghats–Sri Lanka Biodiversity Hotspot

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The apparent biotic affinities between the mainland and the island in the Western Ghats–Sri Lanka biodiversity hotspot have been interpreted as the result of frequent migrations during recent periods of low sea level. We show, using molecular phylogenies of two invertebrate and four vertebrate groups, that biotic interchange between these areas has been much more limited than hitherto assumed. Despite several extended periods of land connection during the past 500,000 years, Sri Lanka has maintained a fauna that is largely distinct from that of the Indian mainland. Future conservation programs for the subcontinent should take into account such patterns of local endemism at the finest scale at which they may occur.

Island biota typically are closely related to the source of colonists when both areas have been in regular contact (1–3). The level of endemism on continental islands is therefore expected to reflect the number and duration of ocean-level lowstands that allowed exchange with the mainland (4). Sri Lanka is a relatively large island (~66,000 km²) in the Indian Ocean and is part of the same shallow continental shelf as India (5). During the Pleistocene ice ages, Sri Lanka was intermittently connected to mainland India (6), until sea level rise created the present disruption ~10,000 years ago (7) (Fig. 1). Classical comparisons of faunal elements from both sides of the Palk Strait indicate a high degree of morphological similarity in several groups, suggesting abundant, recent biotic interchange with southern India (8–12). Similar observations prompted Wallace (13) more

than a century ago to recognize a Ceylonese (or Lankan) biogeographic region, associating Sri Lanka with the southernmost part of the Western Ghats, a hill range along the west coast of India (Fig. 1A). Today, both areas are united in the Western Ghats–Sri Lanka biodiversity hotspot, because they are construed as forming “a community of species that fits together as a biogeographic unit” (14).

Here we explore the evolutionary relationships between the subcontinent’s island and mainland fauna in two invertebrate and four vertebrate groups. The selected taxa are freshwater crabs (Parathelphusidae and Gecarcinucidae), freshwater shrimps (*Caridina*, Atyidae), tree frogs (*Philautus*, Rhacophorinae, Ranidae), caecilian amphibians (Ichthyophiidae and Uraeotyphlidae), shieldtail snakes (Uropeltidae), and freshwater fishes (*Puntius*, Cyprinidae). These animals occupy a diverse range of habitats (terrestrial, subterranean, semiaquatic, and strictly aquatic) (Table 1) and are thus a sample of a broad range of ecologies and life histories. To get unbiased partitions of genetic diversity, individuals were sampled randomly from 125 and 70 different locations (table S1) in Sri Lanka and the Western Ghats of southern India, respectively. We sequenced fragments of mitochondrial DNA for each specimen and then selected one individual per unique haplotype per geographic region for further phylogenetic analysis (15).

Our analyses indicate that the Sri Lankan fauna is derived from an evolutionarily diverse faunal stock on the Indian mainland (16). However, the inferred phylogenetic trees also demonstrate that the overall limited biotic interchange has left both areas with an unexpectedly large number of endemics. For example, the Sri Lankan *Philautus* tree frogs (Fig. 2A) are the result of an extensive radiation on the island (17), and a small clade of deeply nested Indian tree frogs provides evidence for back

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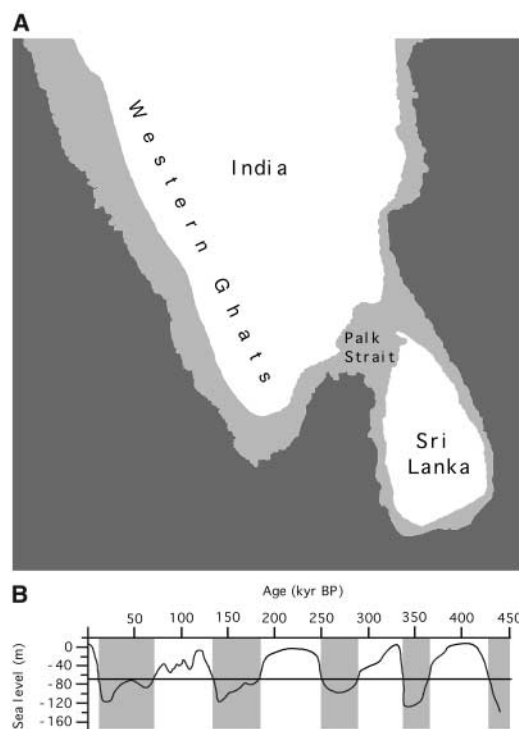


Fig. 1. (A) India and Sri Lanka (current outline in white) are part of the same continental shelf (light gray), which does not exceed 70 m (light gray/dark gray border) in depth. (B) During the past 500,000 years, sea level variations (6) dropping below -70 m (the horizontal line) caused Sri Lanka to be connected to India on several occasions (shaded columns) by a >100 -km-broad land bridge. kyr BP, thousands of years before present.

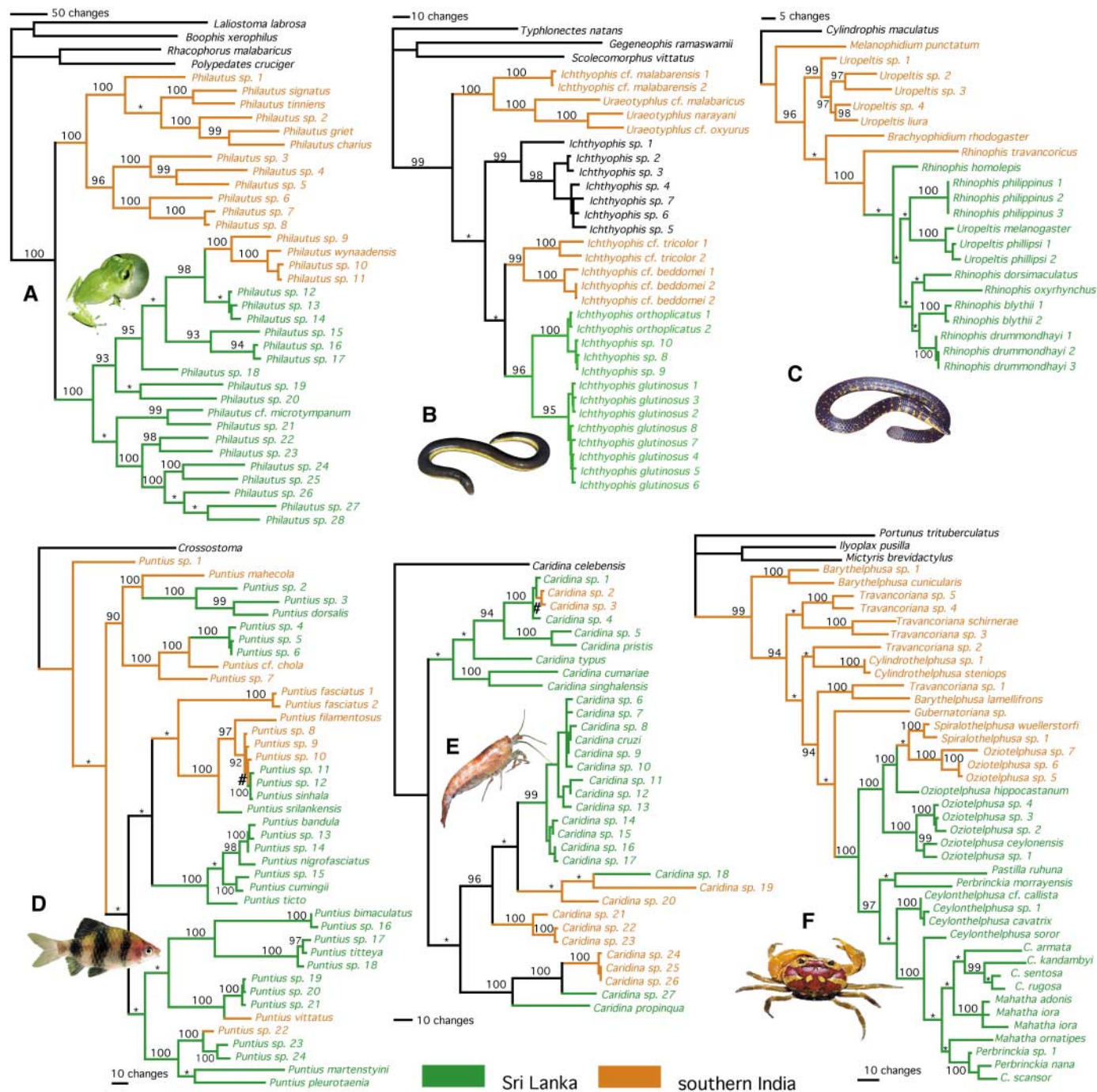


Fig. 2. Phylogenetic relationships among Indian (orange) and Sri Lankan (green) species as revealed by one of the most parsimonious trees for (A) tree frogs, (B) caecilians, (C) uropeltid snakes, (D) freshwater fishes, (E) freshwater shrimps, and (F) freshwater crabs. The strict consensus of equally parsimonious trees for each of these is shown in fig. S1. Black names represent outgroup species, except for *Ichthyophis*, which represents Southeast Asian taxa. Numbers on branches and asterisks in-

dicate metapopulation Genetic Algorithm metaGa branch values of $\geq 90\%$ and $< 90\%$, respectively. Parsimony bootstrap values and Bayesian posterior probabilities are given in figs. S1 and S2, respectively. Numerical designations of operational taxonomic units indicate different haplotypes for mitochondrial DNA, not necessarily different species. Splits indicated with # represent recent exchanges between the mainland and the island.

dispersal of a single lineage to southern India. Similarly, our freshwater crab phylogeny revealed a radiation into several endemic genera of parathelphusids on Sri Lanka, followed by limited dispersal to India in the lowland-associated clade (*Oziotelphusa* and *Spiralothelphusa*) (Fig. 2F). In accord

with morphological studies (18, 19), no gecarcinucids sensu stricto were found on Sri Lanka, leaving no evidence for successful colonization of the island. The uniqueness of both sides of the Palk Strait is most noticeably illustrated by caecilians and shield-tail snakes: In both cases, all sampled island

species represent endemic monophyletic groups (Fig. 2, B and C). Finally, although the pattern of limited biotic exchange is less apparent in strictly aquatic groups (Table 1), part of Sri Lanka's fish and shrimp species nevertheless form distinct clades (Fig. 2, D and E). These observations jointly indicate

Table 1. Taxa included in this study.

Taxon	Total number of specimens	Unique haplotypes	Habitat
Tree frogs	44	34	Terrestrial (including arboreal)
Caecilians	35	28	Subterranean
Uropeltid snakes	33	22	Subterranean
Freshwater fishes	51	41	Strictly aquatic
Freshwater crabs	77	40	Semiaquatic
Freshwater shrimps	44	33	Strictly aquatic

that exchange between the mainland southern Indian and insular Sri Lankan faunas has been severely restricted, despite the recurrent existence of a broad (>100-km) land bridge (5) during several episodes of sea level lowstands (Fig. 1B).

We used the sequence data to estimate the age of biotic exchange events (fig. S2, purple numbers) in each of the six groups. Our calculations (table S4) preclude a late Pleistocene origin for all but two splits and indicate that the corresponding events occurred before the multiple sea level lowstands of the past 500,000 years. These results are reinforced by the fact that our field surveys and phylogenetic analyses did not reveal conspecific populations in India and Sri Lanka in the four terrestrial, subterranean, and semiaquatic groups (Table 1). This was unexpected because, throughout their taxonomic history, there have been many instances in which populations on both sides of the oceanic barrier have been regarded as conspecific (8–10, 12).

Our analyses show that numerous rainforest species form endemic clades, clearly identifying the Western Ghats and Sri Lanka's wet zone as distinct units. There are two possible reasons why biologists may have overlooked the differentiation between Indian and Sri Lankan faunas. First, incorrect systematic affiliations of specimens is understandable a posteriori, because our phylogenies identify homoplasy in coloration and general morphology in all groups. Second, the Sri Lankan fauna comprises a widely distributed, dry low-country element and a more diverse but restricted rainforest component (20). Because the former contains several species common to the dry zones of northern Sri Lanka and southern India that are likely Pleistocene dispersers, it has been assumed that this pattern could be generalized across the whole region.

Exact causes for the restricted dispersal between India and Sri Lanka remain speculative, but our findings highlight the importance of less conspicuous factors as important barriers to terrestrial dispersal. The faunal insularity between the wet zone of Sri Lanka and the moist forests of the Western Ghats likely results from the in-

ability of rainforest organisms to disperse across the intervening dry lowlands. Although the climatic history of South Asia remains poorly understood, our results and the current climatic correlation between the plains of southern India and northern Sri Lanka (21) are possibly indicative of similar conditions during the late Pleistocene, contrary to the idea that rainforest spread onto the land bridge during periods of low sea level (22). Hence, montane areas and their associated climate and vegetation, rather than the present-day coastal outline, may constitute isolated islands in which the rainforest-adapted fauna has been trapped for long periods (23, 24). We therefore expect that similar patterns of restricted dispersal exist elsewhere on the subcontinent, such as between opposite sides of the Palghat gap, a broad valley that traverses the southern Western Ghats. The high degree of endemism in some species of the subcontinent is compatible with this prospect; tree frogs, uropeltids, and freshwater crabs, for example, include point endemics with distributions of often just a few square kilometers (25–27). Thus, treating the Western Ghats and Sri Lanka as a single hotspot carries with it the danger of overlooking strong biogeographic structure within this region (28, 29). Conservation management of the Indian subcontinent will benefit from further characterization of the heterogeneity of biodiversity down to more local scales.

References and Notes

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- Materials and methods are available as supporting material on Science Online.
- The geographic origin and/or direction of dispersal of a clade can only be established if sufficient sampling is available from the whole distribution area. As such, a single mainland origin of Sri Lankan lineages is currently indicated in three of the six examined groups because of their nested position with respect to Indian and/or Asian lineages: caecilians and uropeltid snakes (both indicated by our analyses) and *Phyllautus* tree frogs [not evident from our tree, but shown in (17)]. A mainland origin for Sri Lankan clades is not contradicted in the three other groups, but will only be unambiguously confirmed when more inclusive phylogenies are available for these groups.
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Supporting Online Material
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