

# Did biotic impoverishment facilitate phenomenal diversification in Sri Lanka?

Sayantan Biswas

*Sri Lanka is currently experiencing a tremendous increase in novel descriptions of its endemic diversity. Recent phylogenetic analyses and taxonomic revisions from disparate groups are repeatedly reinforcing this independent nature of the island's diversity compared to Peninsular India. Given Sri Lanka's proximity to the mainland, such in situ speciation calls for an explanation. Here I propose a scenario, which builds upon the earlier observation that lineages on the Indian plate experienced significant turnover during its continental drift and subsequent climate change. I hypothesize that the degree of this past extinction was differential, with Sri Lanka experiencing a higher degree of impoverishment than Peninsular India. This difference created ecological opportunities and facilitated speciation in taxa that survived on the island or later reached the island. Testable predictions under this scenario of impoverishment are discussed and suitable groups for detailed studies in future are also highlighted.*

**Keywords:** Biogeography, dispersal, extinction, island colonization, South Asia.

SRI LANKA, an island of ca. 65,525 km<sup>2</sup>, has been part of the Indian plate through the Gondwanan break-up to form an island only in the Miocene (ca. 23 m.y. BP)<sup>1</sup>. Although uniqueness of its diversity has been previously documented, the overall fauna has been largely considered a subset of the mainland's biota. Only recently, through descriptions of novel taxa<sup>2</sup>, including the discovery of an unprecedented radiation of frogs<sup>3</sup> has the true extent of diversification on this island been revealed. Even though this has further stimulated description of novel endemic taxa<sup>2</sup> and their phylogenetic analyses<sup>4</sup>, hypotheses of what historical events might have triggered such speciation are still poorly addressed<sup>4-6</sup>. Gaining such understanding has, however, both regional and global importance. Regionally, Sri Lanka and the neighbouring Western Ghats of India hold remnants of the Gondwanan elements that influenced diversification in South and Southeast Asia<sup>7</sup>. Globally, endemic diversity of Sri Lanka is impressive for a continental island that was not isolated from the mainland by any formidable barrier<sup>1,2,6,8</sup>. The latter also suggests that studying regions like Sri Lanka may contribute much to the understanding of island diversification in general. Here I propose a new scenario of diversification in Sri Lanka and discuss expectations under this scenario for future testing.

## Earlier proposed scenarios

Major biogeographic hypotheses explaining endemic diversity of Sri Lanka have been succinctly presented by Erdelen<sup>6</sup>. These hypotheses implicated various historical events to explain the unique elements that were disjunctly distributed in Sri Lanka and elsewhere in the mainland. Early explanations ranged from vicariant events such as formation of the Deccan Trap, land masses split by sea to dispersal events via ancient land bridges or islands as stepping stones. Later explanations included elements of vicariance, dispersal, extinction, habitat shrinkage due to Pleistocene glaciations as well as habitat destruction by humans, convergence among species from disjunct areas and competitive exclusion (see Erdelen<sup>6</sup> and Karanth<sup>9</sup> for further details). This focus on explaining disjunct distributions was not surprising, as the disjunct taxa typically represented the uniqueness of the island biota that otherwise appeared largely to be a subset of the mainland's biota. Even though taxonomic revisions are lacking for most groups, recent studies reveal that Sri Lankan diversity is beyond a few unique elements and involves extensive speciation in many taxa<sup>2,10,11</sup>. A correlate of such pattern of diversification has also emerged from a recent phylogenetic study of the island four vertebrate and two arthropod groups<sup>4</sup>. Results suggest that island lineages dispersed from the mainland ancestral taxa mostly before the Pleistocene and underwent *in situ* speciation in Sri Lanka. Subsequently, these insular taxa have rarely or never dispersed back to the mainland<sup>4</sup>. This work seriously challenged the oft-cited explanation of Sri Lankan diversity

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resulting from frequent exchange of lineages between the Indian mainland and Sri Lanka, during periods of sea-level changes in the Pleistocene<sup>12</sup>. Additionally, by reinforcing Sri Lanka's distinctness from mainland South Asia, it provides an opportunity to re-examine the relative influence of these two regions on each other's diversification.

### A new scenario

I hypothesize that a scenario involving biotic impoverishment and/or prior absence followed by colonization and subsequent speciation may provide insights into the origin of the Sri Lankan burgeoning endemic diversity. Such a scenario is based on the following two assumptions: (1) Sri Lanka, along with Peninsular India, not only suffered biotic impoverishment during the continental drift of the Indian plate and subsequent climate change, but the island probably experienced proportionally higher degree of impoverishment (e.g. because of its smaller size) and (2) this impoverishment may have facilitated subsequent *in situ* speciation on the island. This *in situ* speciation, however, may be due to biotic impoverishment or prior absence of the taxa of interest in the island or both. Distinguishing between these two events is contingent on the survival of relict lineages or fossil data. Such data even when unavailable, however, do not in any way affect the testing of the proposed idea, because both impoverishment and prior absence is hypothesized to lead to an increased scope for insular speciation (Figure 1). The proposed scenario builds upon the current consensus that Gondwanan lineages survived on the Indian plate during its continental drift<sup>5,13–16</sup> and draws attention towards potential impact of such plate movement-associated turnover<sup>17</sup> on the nature of subsequent regional diversification.

### Predictions under the new scenario

The proposed scenario and its underlying assumptions in turn generate a number of testable predictions, of which the two salient ones are discussed below.

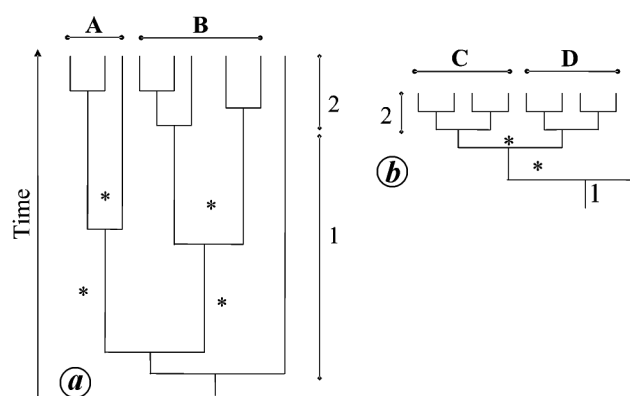
#### Prediction 1 (P1)

The assumption of higher impoverishment of the Sri Lankan biota predicts proportionally greater number of extant ancient lineages on Peninsular India. These lineages would be characterized by long branch lengths on the phylogenetic tree, suggesting their survival through plausible events of impoverishment (Figure 1a). The contrast in proportion of extant ancient lineages between Sri Lanka and Peninsular India would, however, depend on the degree of past impoverishment in the island for any given taxonomic group. Relatively more extensive insular extinction would leave a higher proportion of extant ancient lineages on the mainland, while milder impoverishment would reduce this disparity (Figure 2).

#### Prediction 2 (P2)

Assumption about increased scope of subsequent *in situ* diversification due to biotic impoverishment and/or prior absence predicts that once such an opportunity is available, an ancestral lineage would exploit it and speciate in the process. The consequent phylogenetic pattern would be repeated separation of lineages leading to several species characterized by relatively shorter branch lengths (Figure 1a and b). Two other aspects of this prediction need mention here. First, this prediction represents the phylogenetic pattern once favourable condition for speciation is available to an ancestral lineage. Hence, it can be exhibited by both old extant lineages that survived impoverishment (Figure 1a) and a lineage that did not occur in the island and later dispersed into it (Figure 1b). Second, number of species that would result from such exploitation of an ecological opportunity will be limited by the extent of the favorable condition. P2 would be most pronounced when parallel speciation on the mainland has been limited and has not dampened the higher proportion of faster diverging species on the island (Figure 3; see Jansson and Dynesius<sup>18</sup> for a related discussion).

The proposed scenario and its predictions provide a broad preliminary framework to understand the origin of high endemism in Sri Lanka. Details of this scenario and diversification in Sri Lanka and Peninsular India as a whole need to be addressed before the tenability and generality of this hypothesis can be assessed. First, compre-



**Figure 1.** The proposed scenario to explain high endemic diversity in Sri Lanka can be due to biotic impoverishment (a) or prior absence of the taxa of interest (b) in the island. In (a), hypothetical genera A and B represent old lineages endemic to Sri Lanka that survived plausible impoverishment (time-period 1) and speciated subsequently (time-period 2). In (b), the most recent common ancestor of hypothetical genera C and D dispersed (event marked by 1) into the island where it did not occur before and subsequently speciated into two genera and multiple species (time-period 2). These two possibilities are distinguished by the phylogenetic branch lengths characterizing the extant genera in the island (\*) before period 2. They are longer in (a) and shorter in (b). To what extent (a) and (b) can be discerned from each other, however, also depends on other factors (e.g. response time of lineages to speciation subsequent to impoverishment or dispersal, etc). Nonetheless, the key idea here, common to both of these situations (a and b), is that they have led to increased scope for speciation (time-period 2). Note: Figure not to scale.

hensive phylogenies with molecular dating are required for as many genera as possible that represent the endemic diversity of Sri Lanka and Peninsular India. This will identify potential taxa for testing the scenario and also outline the tempo of regional diversification. The latter is crucial to understand if bulk of the diversification in the island had been continuous through time or occurred during certain phases (consistent with the proposed scenario). Concurrently, information is required on the timing of geological events, impact of climate change and palynological estimates of past vegetation to assess how extents of suitable habitat varied across Sri Lanka and Peninsular India through time<sup>5,17</sup>. This will allow independent testing of the proposed scenario (or any other) deduced from phylogenetic patterns. Ultimate inference of significant support for the proposed scenario would require ingenious application and extension of the currently available methods to study speciation-extinction dynamics<sup>19–22</sup>.

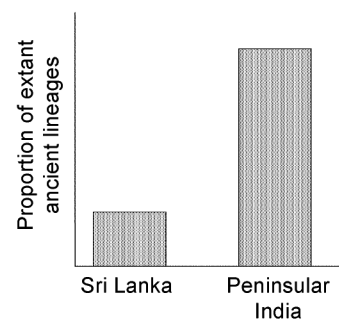
### Phylogenies from the real world

Currently available phylogenies that include regional taxa are not yet amenable to test the proposed scenario (cf. Bossuyt *et al.*<sup>4</sup>), but they provide hints to the scenario and indicate suitable groups for future testing. However, biogeographic and speciation-extinction analyses of comprehensively taxon-sampled phylogenies are required<sup>19–22</sup> to assess if these hints actually corroborate the proposed scenario.

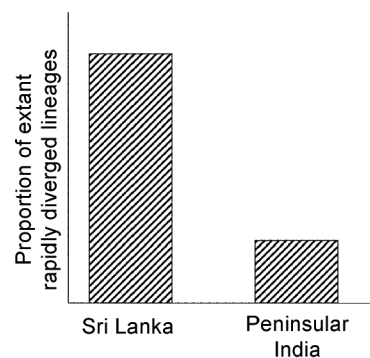
Higher impoverishment in Sri Lanka resulting in proportionally higher number of extant ancient lineages on the mainland (i.e. P1) is difficult to ascertain at this stage due to pending phylogenetic and taxonomic work on most taxa. Preliminary phylogenetic analyses nonetheless indicate old endemic genera of caecilians (*Gegeneophis*, *Uraeotyphlus*)<sup>23</sup> and frogs (*Nasikabatrachus*, *Melanobatrachus*, *Nyctibatrachus*, *Indirana*, *Micrixalus*)<sup>23,24</sup> in Peninsular India, which is consistent with this expectation. Occurrence of endemic frog genera (e.g. *Lankanectes*, *Nannophrys*)<sup>23</sup> in Sri Lanka, however, suggests that any possible impoverishment has been partial in nature (Figure 2). Higher concentration of faster diverging species in Sri Lanka (i.e. P2) seems to hold for a number of vertebrates and arthropods (see phylogenies in Meegaskumbura *et al.*<sup>3</sup> and Bossuyt *et al.*<sup>4</sup>), but require confirmation through more complete taxon sampling of these and other regional taxa. Parallel speciation on the mainland is also apparent for certain groups (e.g. tree frogs)<sup>3,25</sup> and will probably counteract the pattern of higher proportion of fast-diverging taxa in Sri Lanka (cf. Figure 3).

Available phylogenies also provide insights to genera that may be suitable to test the impoverishment scenario. This includes taxonomic groups that exhibit a combination of deeper lineages, suggested by higher-level phylogenies, and medium to high number of island endemics, often indicated to be of recent origin. Potential examples

include freshwater crabs<sup>4,26,27</sup>, uropeltid snakes<sup>4,28</sup>, caecilians<sup>4,23,29</sup> and tree frogs<sup>4,23,24</sup>. With increasing taxonomic revision and phylogenetic analyses, many other genera (e.g. freshwater fishes<sup>4</sup> and freshwater snails<sup>30</sup>) are likely to emerge suitable for testing the proposed scenario. Phylogenies of plant genera may provide additional perspectives compared to animals, and at least one study makes a similar proposition of impoverishment followed by secondary diversification (in *Exacum*, Gentianaceae)<sup>31</sup>. Sri Lankan dipterocarps seem to be highly suited for testing the proposed scenario with distinct monophyletic endemic species groups (e.g. *Shorea*, *Dipterocarpus*, *Hopea*) or genus (e.g. *Stemonoporus*) that are endemic to the island, but the most recent phylogeny unfortunately lacks samples from India and does not infer divergence dates<sup>32,33</sup>. Extant endemism in Sri Lankan and Peninsular Indian vertebrates is dominated by species-poor genera, many of which are relatively more diverse in subtropical or temperate regions, suggesting factors such as isolation by distance or restricted gene flow in differentiation of these island forms. In contrast, genera rich in island endemics (e.g. freshwater crabs, tree frogs, uro-



**Figure 2.** Due to higher degree of faunal impoverishment (i.e. prediction 1), Sri Lanka would harbour lower proportion of extant ancient lineages characterized by long branch lengths on a phylogenetic tree than Peninsular India (see also Figure 1a). More extensive the insular impoverishment, higher would be this difference in proportion between the two regions.



**Figure 3.** Greater insular impoverishment in the past (or prior absence) would provide increased scope for speciation in Sri Lanka (i.e. prediction 2). It would thus harbour a higher proportion of species that diverged within a shorter period of time characterized by long branch lengths on a phylogenetic tree than Peninsular India (also see Figure 1a and b). This difference will be more pronounced when parallel speciation in Peninsular India has been minimal.

peltid snakes, etc.) are predominantly tropical and are more likely to have been influenced by situations under the proposed scenario (i.e. biotic impoverishment and/or prior absence).

### How plausible is this scenario?

The proposed scenario contends that the observed speciation in Sri Lanka has been influenced by the impact of biogeographic events (e.g. extinction) on communities (e.g. leading to their impoverishment). This has subsequently facilitated insular diversification through increased opportunity for speciation in those lineages that survived or later dispersed into the island. But do the correlates of Sri Lankan diversity (i.e. *in situ* speciation, and minimal or no dispersal back to mainland) need such a 'special' explanation? For example, high endemism in Sri Lankan genera may be due to higher rates of net speciation (speciation-extinction) that is unrelated to the community ecological context of lineage survival or colonization. Alternatively, Sri Lankan endemic diversity may be largely due to the age of these clades and hence is an artifact of continued net speciation over time. Likewise, asymmetry in dispersal back to the mainland may be just because of lower population sizes in islands (e.g. due to smaller area). Hence, attending to issues such as rates of net speciation versus ecological opportunity (e.g. due to the extent of rainforest) would be crucial in evaluating the relative role of alternate hypotheses of diversification in the island. Definitive answers are unavailable right away, but current understandings of evolution of rainforests (which harbour majority of the regional endemics) suggest impoverishment and/or prior absence as a plausible hypothesis to explain diversification in the island.

Palynological data suggest that though composition and structure of the rainforest has undergone considerable turnover from late Cretaceous onwards, extensive forest covered most of the Indian plate till the early Eocene (54–49 m.y. BP). This continued into the late Eocene to Oligocene (39–25 m.y. BP), but with increasing regionalization that seemed to have precluded dispersal of rainforest species<sup>17</sup>. Increasing seasonality leading to shrinkage of rainforests continued during most of the Neogene, except during a short phase of rainforest expansion around early mid Miocene (16–10 m.y. BP) that allowed Southeast Asian plant elements (e.g. Dipterocarps like *Hopea*, *Shorea*) to disperse into the Indian plate<sup>17</sup>. This reduction of rainforest was paralleled by establishment of the Indian monsoon due to the uplifting of the Himalaya and the Tibetan plateau that facilitated expansion of seasonal forests<sup>17</sup>. Given this, the proposed impoverishment scenario would suggest initial diversification of rainforest lineages along with extinction of forms due to climate change during continental drift and later, and continued speciation in the lineages that survived or were able to disperse to the island.

Ability of clade age to explain diversity of Sri Lankan endemics would be apparent with more complete phylogenies in the future, but understanding relative habitat availability and ecological opportunity in the island and mainland requires data from various sources (e.g. modelling using climate and palynological data<sup>17,34,35</sup>). The observation of minimal or no dispersal of descendents of island immigrants back to the mainland<sup>4</sup> is not explicitly dealt with above, but is likely to be from adaptation of island forms to local conditions<sup>36</sup> and reduced population size of species in the island. Additionally, assessing historical chances of dispersal will need to factor in both the actual width of the Palk Strait separating Sri Lanka from the Indian mainland that seems negotiable during low sea levels<sup>6</sup>, and seasonality of the habitat on either side of the Strait. Depending on the taxa and their tolerance to seasonality, habitat on either side of the strait may act as a corridor or filter to dispersal<sup>12</sup>.

### Concluding remarks

The proposed idea of ecological opportunity influencing subsequent diversification has been implicated to explain speciation elsewhere in islands (e.g. Hawaii<sup>37</sup>; Caribbean islands<sup>38</sup>) and continental areas (e.g. Cape Province, South Africa)<sup>39</sup>, which provides further credence to it as a legitimate hypothesis for testing. This scenario does not, however, preclude other factors concurrently affecting the diversification process. Once an ancestral population had established on the island, multiple factors (e.g. geomorphology<sup>1,40</sup>, latitude-based climatic conditions<sup>36</sup>, dry zone and sea as barrier to wet zone species<sup>12</sup>, life history strategies, novel traits) and forces (e.g. sexual and natural selection)<sup>37</sup> may have influenced the subsequent nature and extent of speciation. Additionally measures of ecological and phenotypic diversity, currently unavailable, will be required for insular endemics to infer if adaptive speciation has occurred in Sri Lanka<sup>41</sup>.

Finally, decades ago the explanation of Sri Lankan tree diversity by Willis<sup>42</sup> had stimulated Yule<sup>43</sup> to model speciation-extinction dynamics, a topic of central relevance to the proposed scenario. It is hoped that a renewed interest in Sri Lanka as well in South Asian biogeography would again stimulate new, insightful hypotheses, revisit older ones<sup>12,42</sup> and test them rigorously to enrich our understanding of the processes influencing diversification in general.

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