Evolution of disjunct distributions among wet-zone species of the Indian subcontinent: Testing various hypotheses using a phylogenetic approach

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Disjunct distributions among wet-zone taxa of the Indian subcontinent have intrigued biologists for decades. Most authors have invoked variations of either the dispersal or the vicariance model to explain disjunct distribution. However, some have noted that incorrect taxonomy, due to convergence in morphological characters, can erroneously suggest disjunct distribution. An appropriate approach to test these models (vicariance, dispersal and convergence) is to use molecular phylogenetic methods. A survey of recent molecular phylogenetic studies on Indian systems with disjunct distribution suggests that convergence may be quite common. Therefore, I propose that the first step in studying disjunct distributions is to determine if the observed pattern is real (true disjunct) and not due to convergence, i.e. an artifact of incorrect taxonomy (false disjunct).

ONE of the features of South Asian biogeography is the marked discontinuity in the distributions of many wet-zone (areas of over 250 cm rainfall per year) species from India and Sri Lanka (Figure 1). For example, birds of the genus *Batrachostomus* (frogmouths) are found in the wet evergreen forests of southwest India and Sri Lanka, but not in the rest of the Indian subcontinent; they are again found 1500 km away in the wet evergreen forests of northeast India (NEI) and throughout southeast Asia (SEA; Figure 1). Thus, in India, this genus is distributed in two widely separated areas, viz southwest India and NEI. The intervening low rainfall area (50–100 cm per year), referred to as dry zone, consists of seemingly unsuitable habitat. Such discontinuity in the distribution (also called as disjunct distribution) is particularly pronounced in the case of Indo-Chinese elements of the peninsular Indian biota[1]. There are several such cases of disjunct distributions of apparently closely-related taxa in the Indian subcontinent among mammals[2], birds[3–5], freshwater fishes[6], and amphibians and reptiles[7–9]. In addition, there are numerous cases from insects[10] and plants[11].

How could such a geographical discontinuity in the distributions of various wet-zone species be explained? One of the most influential hypotheses put forward to explain disjunct distribution is the Satpura hypothesis[12]

proposed by Hora in 1949. Hora postulated that the wet-zone species colonized southern India by way of once-continuous corridor of tropical evergreen forests from eastern Himalayas across Vindhya–Satpura ranges to the Western Ghats of South India (Figure 2). Other authors
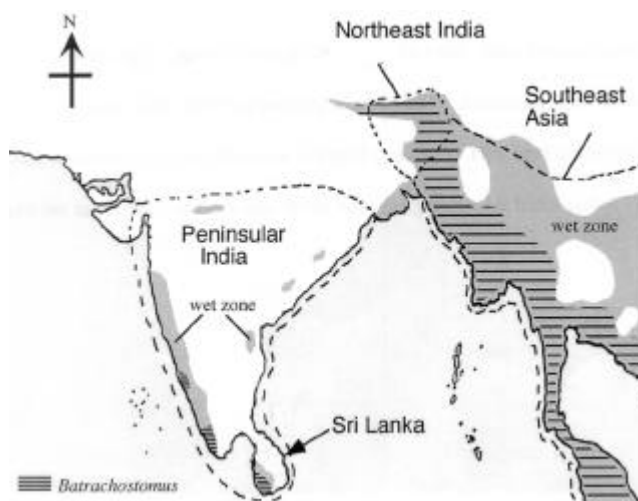

Figure 1. Map of tropical Asia showing various geographical zones. Areas in grey represent the wet-zone (over 250 cm of rainfall). Areas in white correspond to the dry zone (rainfall between 50 and 100 cm). Distribution of frogmouth (genus *Batrachostomus*) is shown by horizontal hatch marks (distribution map modified from ref. 4). Here Sri Lanka is shown as being connected to south India because geologically it is part of the Deccan plate and is separated from India by a shallow strait that might have served as a land bridge during times of lowered sea level. This land bridge might have facilitated the movement of flora and fauna between peninsular India and Sri Lanka.

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have suggested alternative corridors for dispersal, such as the Eastern Ghats[13], the Brij area of northern India[14], and the Aravalli range[1] (Figure 2). Ripley and Beehler[15] pointed out that the Satpura hypothesis is nothing more than a special case of the better-known dispersal model of speciation. Given that there are multiple routes that dispersing wet-zone species could have taken to reach the Western Ghats, I use the approach of Ripley and Beehler[15] and refer to this model as the dispersal model (rather than the Satpura or Brij model).

Numerous authors[1,3,7–9,16] have noted that the current discontinuity of some species might represent a relict of a former continuous distribution. This relict fauna scenario supposes that much of India and SEA was covered with extensive and continuous humid forest that has recently been broken into isolated patches, mainly due to climatic changes (Figure 3). These isolated patches today harbour relict populations of once continuously distributed humid forest species. Therefore, discontinuity must be considered as only faunal impoverishment, but not absolute absence, in the intervening areas[1]. According to Ashton and Gunatilleke[17], fossil flora from the mid-Miocene (18 to 11 m.y. ago) in northwest India contain rainforest taxa. This area is today covered with semi-arid to desert habitat. Fossil evidence also points to a humid climate in the
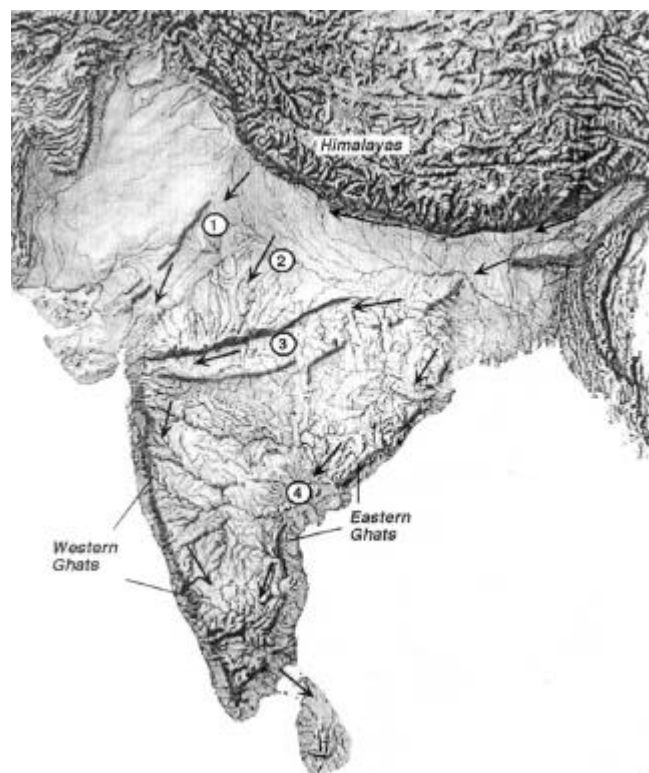
Indian peninsula during most of the Miocene[18,19]. Thus, during the mid-Miocene much of India was probably covered with humid forests. The northward movement of the Indian plate, and the resulting uplifting of the Himalayas and the Western Ghats contributed to the onset of a drier climate and replacement of the tropical evergreen forests by deciduous ones over the majority of the Indian peninsula[19]. By Upper Siwalik times (5.1 to 1.6 m.y. ago), environmental conditions had changed considerably and tropical forests were largely replaced by savannas in the foothills of the Himalayas (p. 103, ref. 20). Interestingly, there is also evidence of a shift from C3 forest plants to C4 grassland plants around this time in the Siwaliks of Pakistan[21,22].

Evidence from different sources also suggests that in more recent times, the subcontinent has experienced multiple cycles of dry and wet periods. According to Gupta et al.[23], throughout the Holocene, cool episodes in the North Atlantic were accompanied by weakening of the Asian southwest monsoon winds. The d^{13}C records from the late Quaternary period in southern India suggest an arid period from 6000 to 3500 years ago, and a short, wet phase about 600 years ago[24]. Randhawa[25], based on evidence from archeology and ancient literature, suggested that around 2000 years ago certain parts of northern India were wetter than today. Indeed, studies done on pollen from Dongar-sarbar swamps in Madhya Pradesh also indicate that in this region a moist and warm climatic condition prevailed around 1800 years ago[26]. Added to all this, forest cover over much of India was also altered by human activity[1,7,27].

Thus due to climatic factors, large tracts of humid forest cover progressively declined and retreated to wetter parts of India (wet-zone) during late Miocene and Pliocene times. This was probably followed by expansion and shrinking of forest cover due to multiple cycles of dry and wet periods during the Quaternary period. Ultimately, anthropogenic factors further reduced forest cover. These lines of evidence suggest that disjunct distribution
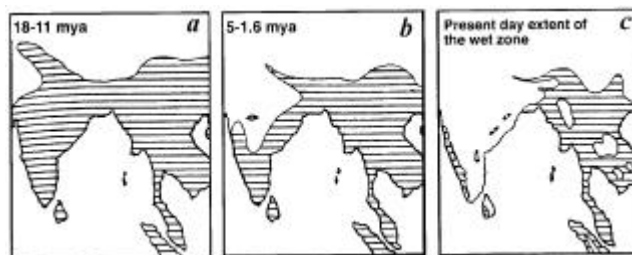

Figure 2. Map showing the major mountain ranges of the Indian subcontinent. Numbers indicate the different dispersal routes that the wet-zone species from NEI could have taken to reach the Western Ghats and Sri Lanka. These routes include the Aravalli range (1), the Brij region (2), the Vindhya–Satpura ranges (3), and the Eastern Ghats (4). Arrows indicate the direction of dispersal.

Figure 3. Recent regression of the wet-zone in the Indian subcontinent (figure modified from ref. 16). *a*, Fossil evidence suggests that during mid-Miocene times, much of India was covered with humid forest that was continuous with the forests of SEA (see text for details). Thus, much of India received high rainfall that could support this humid forest. *b*, Onset of drier climate resulted in regression of the wet-zone. *c*, Human-induced changes resulted in further regression of the wet zone.

for some species might represent relict populations of once widely distributed species. Here, I consider this relict fauna scenario a special case of the more general vicariance model (but see ref. 15). This is because the wet-zone species of peninsular India are cut-off from those in the NEI by the dry zone. The establishment of this dry zone, therefore, is similar to an environmental (vicariance) event, which in turn produced a barrier to gene flow between certain species inhabiting the wet-zones of peninsular India and those in the wet-zone of NEI.

How do we distinguish between the dispersal (Satpura) model and vicariance (relict fauna) model? The relative age of populations versus their barriers needs to be resolved in order to distinguish between these two models[15]. If the wet-zone species arrived in the Indian subcontinent after the establishment of dry zone and used the fragmented wet-zone forests as stepping stones to reach the Western Ghats (southwest India), then this event would qualify as a dispersal event. On the other hand, if the wet-zone species arrived in the Indian subcontinent before the establishment of the dry zone and were isolated from their counterparts in NEI and SEA due to subsequent fragmentation of the wet-zone forests, then this would qualify as a vicariance event. But from current faunal distribution and geological data, it is difficult to determine the relative age of populations versus their barriers. Nevertheless, it must be pointed out that the expanding forest cover during the wet periods of the Quaternary phase might have provided a forest corridor for the dispersal of forest species from NEI to peninsular India at different time periods. According to Daniels[27], the alternating arid–cold and humid–warm climates that the entire tropics experienced during the Pleistocene period is believed to have favoured periodic invasions of both forest and montane birds into southern and western India. One interesting outcome of this argument is that most species that fit the dispersal model might have arrived in peninsular India recently (during Pleistocene times), whereas species that fit the vicariance model might have arrived in peninsular India any time from late Miocene to Holocene (but see ref. 8). Indeed, Daniels[27] points out that montane and grassland birds were isolated in the Western Ghats at a much earlier period than the birds of the lower elevation rainforests and more open habitats.

Roonwal and Nath[28] suggested another different reason for disjunct distribution. According to them, similarity of environments in the two areas in question might be the cause of the independent origin of similar forms from a common ancestral form. Mani[1] developed this idea further when he proposed that discontinuous distribution in a number of species might be the result of local diversification, multiple independent origin, and polyphyletic differentiation, leading to evolutionary convergence and parallelism in the widely separated areas. This apparent disjunction in the distribution of some taxa, therefore might be an artifact of incorrect taxonomy, wherein dis-

tantly-related forms have been placed in the same taxonomic group based on overall morphological similarity. The overall morphological similarity in turn might be a by-product of independent adaptation (convergence) by different species to very similar ecological conditions in widely separated areas. Here I refer to this scenario as the convergence model.

These three models (dispersal, vicariance, and convergence) need to be tested to better-understand the origin of disjunct distributions among certain species of the Indian subcontinent. As mentioned above, it is difficult to distinguish between dispersal and vicariance models based on current faunal distribution and geological data. Therefore, to test these models, it is imperative that we know the precise phylogeny of the species groups in question. Each of the models described above has explicit phylogenetic predictions, which could be used to determine the model that best explains the disjunct distribution. As mentioned earlier, morphological characters can be deceptive in determining the evolutionary relationships (phylogeny) between species due to the problem of convergence. Therefore, an appropriate approach to study this phenomenon would be to determine the molecular phylogeny of species showing disjunct distributions and use the resulting phylogenetic tree to test these models. In the following section I discuss in detail, the predicted tree topology (phylogenetic pattern) for each of these models.

Dispersal model

Here, the wet-zone species of peninsular India and Sri Lanka are predicted to be more closely related to the wet-zone species from NEI and SEA, than they are to the dry-zone species of the Indian subcontinent. Additionally, the topology of the clade constituting the wet-zone species would have a step-like appearance. The southeast Asian wet-zone species would be basal (ancestral) to the rest of the wet-zone species (Figure 4), whereas the wet-zone species from peninsular India and Sri Lanka would be phylogenetically 'derived' from those in NEI and SEA. The phylogeny in Figure 4 would suggest that dispersal occurred from SEA to Sri Lanka in the following sequence: SEA → NEI → (Satpura range) → Western Ghats → Sri Lanka. Here the Satpura range is in parenthesis because there are numerous other possible connections between NEI and the Western Ghats (see above). Moreover, the routes taken by the wet-zone species to the Western Ghats might be different (Satpura, Aravali, Eastern Ghats or Brij) for different species groups. It must also be noted that the Satpura hypothesis has been reviewed by many authors and found to be untenable for different reasons[1,14,29].

Vicariance model

In this model too, the wet-zone species of peninsular India and Sri Lanka are predicted to be more closely

related to the wet-zone species from NEI and SEA, than they are to the dry-zone species of the Indian subcontinent. But the topology of the clade representing the wet-zone species in the phylogenetic tree should mirror the sequence of vicariance events. For example, in Figure 5 the clade representing the wet-zone species from peninsular India and Sri Lanka diverged from the clade-constituting species in NEI and SEA due to the establishment of the dry zone in north India. This was followed by the establishment of the dry zone between peninsular India and Sri Lanka, which resulted in the split between wet-zone forms from these regions.

Convergence model

According to this model, the wet-zone species from peninsular India and Sri Lanka are more closely related to their immediate neighbours in the dry zone, than they are to the wet-zone species from NEI and SEA. Here, the dry-zone species as well as wet-zone species of the Indian subcontinent will be monophyletic to the exclusion of those from NEI and SEA. In addition, the wet-zone species from peninsular India and Sri Lanka might branch with the dry-zone species from these regions (Figure 6). If the wet-zone species from the Indian subcontinent showing the above pattern are currently classified in the

same taxonomic group as the wet-zone species from NEI and SEA, then it is imperative that the taxonomy of the species group in question be revised to reflect their true evolutionary relationship.

Both vicariance and dispersal models would predict that the wet-zone species of the Indian subcontinent are more closely related to the wet-zone species from NEI and SEA, than they are to the dry-zone species of peninsular India. These models also suggest that the wet-zone species of the Indian subcontinent arrived independent of the dry-zone species. Thus, there would have to be two colonization events, one of the wet-zone species and the other of the dry-zone species, to explain current distribution of various species in the Indian subcontinent. Indeed, Ripley[30] has given numerous examples of such 'double invasions' of peninsular India by various bird species. In the hypothetical molecular phylogenies illustrated in Figure 7 *a* and *b*, the dry-zone and wet-zone species fall into two distinct, mutually exclusive groups, suggesting that the wet-zone species are more closely related to each other and that there have been two colonization events. Additionally, in these models the clade constituting the dry-zone species lacks phylogenetic structure due to the absence of any barrier to gene flow. This is because the dry zone is continuous from north India to Sri Lanka, facilitating gene flow. The convergence model, on the other hand, would predict a single faunal colonization of
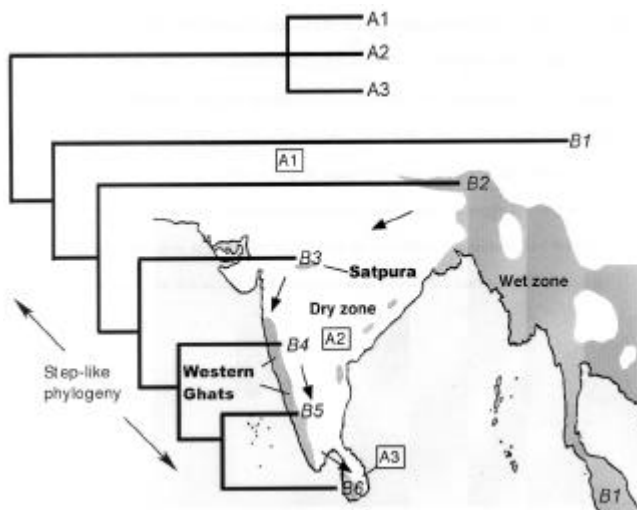

Figure 4. Dispersal model. According to this model, wet-zone species dispersed into southwest India and Sri Lanka through a once-forested corridor connecting the Western Ghats and NEI. This trend is suggested by the step-like pattern of the clade representing the wet-zone species. Wet-zone species B1 (from SEA) is basal to all the other wet-zone species, whereas wet-zone species B3–B6 (of the Indian subcontinent) are derived from B2 and B1 (of NEI and SEA). Thus the sequence of the dispersal event suggested by this phylogeny is: SEA -> NEI -> Satpura range -> Western Ghats -> Sri Lanka. Here A1, A2, and A3 represent the dry-zone species (or populations of a single species) and the squares show their approximate distribution in north India, south India and Sri Lanka, respectively. In this model the dry- and wet-zone species fall into two distinct clades.
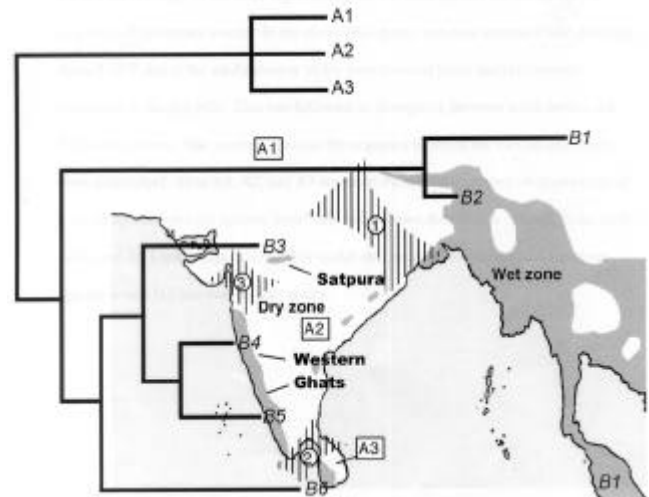
Figure 5. Vicariance model. According to this scenario, wet-zone species of peninsular India represent relict populations of once widely-distributed species that got isolated from northeast Indian populations due to establishment of the dry zone in between. In this model, the topology of the clade representing the wet-zone species should mirror the sequence of vicariance events. In the above phylogeny, wet-zone species B3–B6 diverged from B1 and B2, due to the establishment of the dry zone (vertical hatch marks) between peninsular India and NEI. This was followed by divergence between south Indian and Sri Lankan forms. Numbers indicate the sequence in which the various dry zones were established. Here A1, A2 and A3 represent the dry-zone species (or populations of a single species) and the squares show their approximate distribution in north India, south India and Sri Lanka, respectively. This model also predicts that the dry- and wet-zone species would fall into two distinct clades.

the Indian subcontinent and subsequent divergence into wet-zone and dry-zone forms (Figure 7 *c*). It is apparent from the above discussion that the first step in studying disjunct distributions is to determine if the observed pattern is real (true disjunct) and not due to convergence, i.e. an artifact of incorrect taxonomy (false disjunct). Once 'true disjunct' is ascertained, then one can go on to test if it is due to dispersal or vicariance event (Figure 8).

Examples from literature

Very little molecular phylogenetic work has been done on wet-zone species of the Indian subcontinent. In this section I provide summaries of some studies that are relevant to the question of disjunct distributions. Among the langurs of Asia, the wet-zone species, currently classified in the genus *Trachypithecus*, have a disjunct distribution (see ref. 31 for the current widely accepted classification of langurs). That is, species in this genus are found in the wet-zones of southwest India (Nilgiri langur) and Sri Lanka (purple-faced langur), but are absent in the rest of India (dry zone). They are also distributed in NEI (capped langur, golden langur and Phyare's langur) and throughout SEA (Phyare's langur, silvered langur, dusky langur and Francois' langur). The Hanuman langurs (genus *Semnopithecus*) on the other hand, are widely distributed throughout the Indian subcontinent, predominantly in the dry zone. Interestingly, molecular phylogenetic studies on the langurs suggest that Nilgiri and purple-faced langurs are more closely related to Hanuman langur, than they are to the other species of the genus *Trachypithecus*[32]. Thus, the observed disjunct distribution, in the case of genus *Trachypithecus*, is an artifact of incorrect taxonomy. Here, the overall

Figure 7. Comparison between the three models. B1–B6 represent the wet-zone (WZ) species, whereas A1–A3 represent the dry-zone (DZ) species. SEA, Southeast Asia; NEI, Northeast India; SR, Satpura range; NI, North India; SI, South India; SL, Sri Lanka; WG, Western Ghats. Angled arrows in (*a*) represent direction of dispersal. *a*, Dispersal model DZ and WZ species fall into two distinct groups. Two dispersal events into the Indian subcontinent (indicated by large arrows), one by the common ancestor of the WZ species B3–B6, and the other by the common ancestor of the DZ species A1–A3. Clade representing the WZ species will have step-like topology. Clade representing the DZ species might have shallow branch-length due to ongoing gene flow between populations or due to recent divergence between species. *b*, Vicariance model. DZ and WZ species fall into two distinct groups. Two colonization events of the Indian subcontinent (indicated by large arrows), first by the WZ species followed by the DZ species after establishment of the DZ (indicated by hatch marks). The topology of the clade representing the WZ species should mirror the sequence of vicariance events. Clade representing the DZ species might have shallow branch-length due to ongoing gene flow between populations or due to recent divergence between species. *c*, Convergence model. WZ species from SEA, NEI and peninsular India (B1–B6) are not monophyletic. WZ species of peninsular India (B3–B6) branch with DZ species (A1–A3) of the Indian subcontinent. Single colonization of the Indian subcontinent (indicated by arrow) and subsequent divergence of this population into DZ and WZ species.
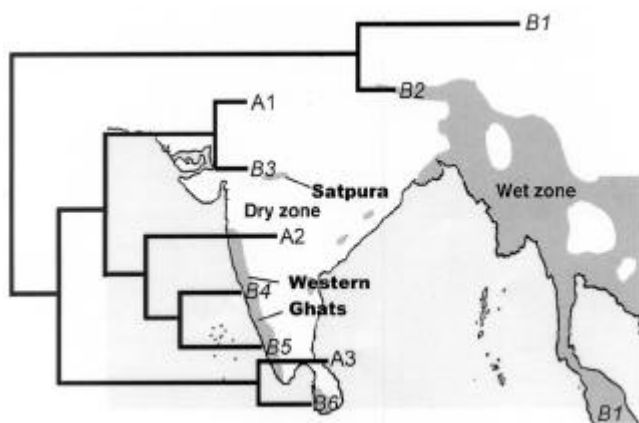

Figure 6. Convergence model. This model would predict that the wet-zone species B3–B6 of peninsular India and Sri Lanka are more closely related to their immediate neighbours in the dry zone (species A1–A3), than they are to the wet-zone species B1 and B2 from NEI and SEA. The overall morphological similarity between B1–B2 and B3–B6 is due to convergence.
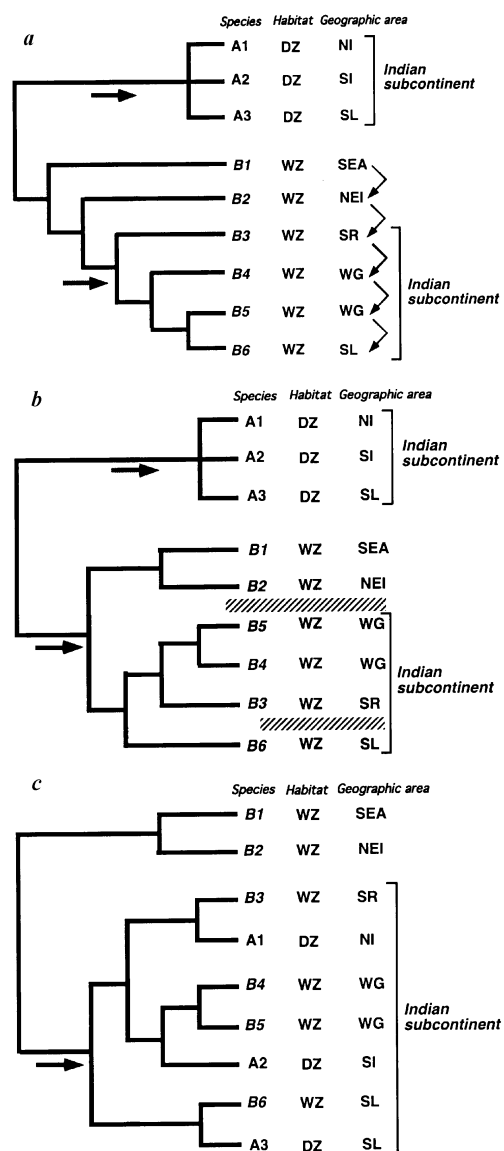
similarity in coat colour of the wet-zone species from peninsular India and Sri Lanka with those from NEI and SEA is due to convergence.

Bossuyt and Milinkovitch[33] performed a phylogenetic analysis of ranid frogs from Madagascar and Asia, using both a nuclear and a mitochondrial marker. Among the ranid frogs, the fanged frogs (genus *Limnonectes*), which have protruding fangs in the lower jaw, show remarkable discontinuous distribution. These species are found from NEI to New Guinea, with a single species known from Sri Lanka; but fanged frogs are absent in the rest of the Indian subcontinent. Surprisingly, the molecular phylogeny of the fanged frogs does not support the monophyly of this group. In fact, the species of fanged frog from Sri Lanka is more closely related to some of the (non-fanged) ranid species endemic to south India, than they are to fanged frogs from SEA[33]. Clearly, in both the above examples, the convergence model explains the so-called disjunct distribution.

Ironically, in the case of the hill-stream fishes from the Western Ghats that were considered by Hora as a model system that supported his Satpura hypothesis, a taxonomic revision has rendered this hypothesis untenable[29]. On the contrary, it appears to be yet another case of convergence.

Figure 8. Systematic study of disjunct distribution. The first step in studying disjunct distribution would be to determine if the observed disjunct is a 'true disjunct' or an artifact of incorrect taxonomy. If it is found to be a 'false disjunct', then one has to revise the taxonomy of the species group in question. On the other hand, if it is a true disjunct then one can proceed to determine the biogeographical mechanisms (dispersal or vicariance) that might have resulted in the observed pattern.

One of the best cases of disjunct distribution supported by molecular data comes from the macaques (*Macaca*) of Asia. Delson[34] classifies the macaques of Asia into four species groups. Among these four species groups, the *silenus* group shows a pronounced disjunct distribution. Species in this group are found in the wet evergreen forests of southwest India (lion-tailed macaque), NEI (pig-tailed macaque) and SEA (pig-tailed and Sulawesi macaques). Interestingly, the intermediate dry zone is inhabited by two macaque species (Bonnet and rhesus macaques) belonging to different species groups. Results from molecular phylogenetic studies[35–37] on the macaques are largely congruent with species groups of Delson[34]. These molecular studies suggest that the lion-tailed macaque is more closely related to pig-tailed macaque from SEA than it is to Bonnet macaque, its immediate neighbour in the dry zone. This scenario is different from that of the langurs of the Indian subcontinent. According to Eudey[38], disjunction in the distribution of the *silenus* group (which we now know is true) was probably initiated by aridity and deforestation, followed by range expansion of the dry-zone species such as Bonnet macaques. These events led to the aggregation of the wet-zone species such as lion-tailed macaque into forest refugium in south India. Thus, in the case of the *silenus* group, disjunct distribution is best explained by vicariance (relic fauna) model. Results from molecular phylogenetic studies on the flying lizards (genus *Draco*) of Asia also support disjunct distribution in this group[39]. Here again, vicariance appears to be the predominant biogeographic process that caused disjunct distribution. From the above molecular phylogenetic studies, it is apparent that convergence is quite common among species with disjunct distribution. These findings reinforce the above mentioned suggestion that the first step in studying disjuct distribution is to determine whether the observed pattern is a true disjunct or a false disjunct.
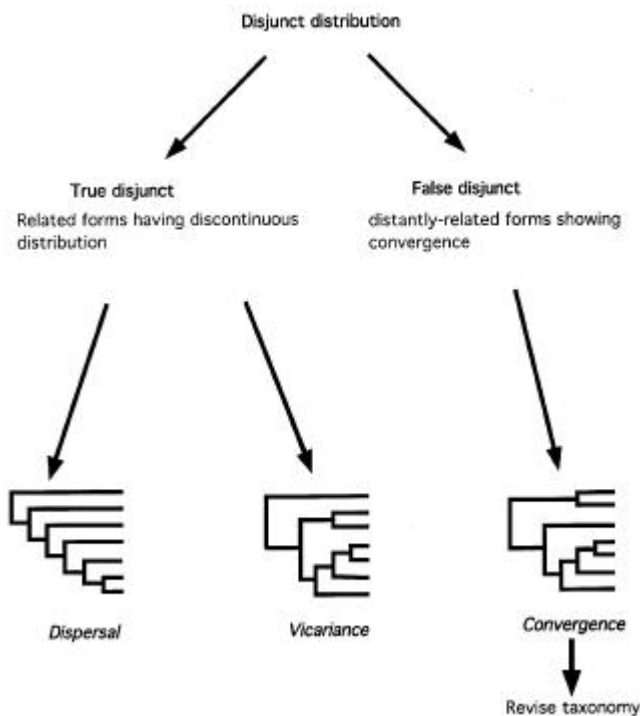
When to use molecular data?

For some species disjunct distributions are obvious, particularly in the case of subfamily or genera that are represented by only one species in peninsular India. For example, the martens (subfamily Martinae, genus *Martes*) that are found in the hills of southwest India at an altitude of over 1250 m, but are totally absent from the dry zone, and are found again in the Himalayas. In this case the convergence model can be ruled out because there are no representatives of this subfamily in the dry zone. Other such clear-cut examples of true disjunct are: Nilgiri tahr among mammals; fairy bluebird and frogmouth among birds. In these cases, molecular phylogenetic approach could be utilized to further understand disjunct distribution (vicariance vs dispersal). The examples discussed above are listed in Table 1.

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Table 1. Examples of species with disjunct distribution discussed in the text

True disjunct
  True disjunct supported by molecular data
    Macaques
      Lion-tailed macaque (*Macaca silenus*), *silenus* group[35–37]
      Bonnet (*M. radiata*)[35,36] and toque (*M. sinica*)[35–37] macaques, *sinica* group
    Reptiles
      Flying lizard (*Draco*)[39]

  True disjunct supported by current distribution
  Birds*
    Fairy blue bird (*Irena puella*)[4,5]
    Frogmouth (*Batrachostomus*)[4,5]
  Mammals
    Nilgiri marten (*Martes gwatkinsi*)[2]
    Nilgiri tahr (*Hemitragus hylocrius*)[2]

False disjunct
  False disjunct revealed by molecular data
    Langurs
    Nilgiri and purple-faced langurs (*Trachypithesus*)[32]
  Frogs
    Fanged frogs (*Limnonectes*) of Sri Lanka[33]

    False disjunct revealed by revised taxonomy
  Fishes
    Hill-stream fishes belonging to eight different genera[29]

*See distribution maps in Grimmett *et al.*[41] for other examples of birds with disjunct distribution.

On the contrary, for numerous other taxonomic groups that have multiple species distributed throughout India in different habitats, convergence might be common. For example, among the flowerpeckers (family Dicaeidae) of peninsular India, the species *Dicaeum concolor* has discontinuous distribution. In India, it is confined to the wet evergreen forests of southwest India and NEI. The intermediate dry zone is inhabited by another species *Dicaeum erythrorhynchos*. It is plausible that *D. concolor* of peninsular India is more closely related to its neighbour in the dry zone, *D. erythrorhynchos* than it is to *D. concolor* of NEI. Thus, here again (like in the case of langurs), convergence might be erroneously suggesting disjunct distribution. It is in such cases that we need to use molecular phylogenetic methods to tease apart true disjunct from convergence.

There are two important points that one should bear in mind before taking up a molecular phylogenetic analysis for the study of disjunct distribution. First, distribution data should be well-documented throughout India, for species selected for such a study. This is because for some species, lack of information from certain regions might erroneously suggest disjunct distribution. Secondly, disjunct distribution in some taxonomic groups (such as birds) is probably due to recent climatic events, while in others (for example, between slender loris and slow loris among primates) is due to geological events that occurred earlier. It is imperative that these two taxonomic groups are studied independently.

Towards a biogeographical synthesis of species showing disjunct distribution

It must be noted that the three models presented here are a simplification of the various biogeographic phenomena underlying these patterns. Moreover, inferring the biogeographic history of a taxon can be challenging, because present-day distributions have often been affected by both vicariance and dispersal, as well as by extinction (see p. 209, ref. 40). Nevertheless, the time is ripe to undertake extensive phylogenetic studies on various taxa of the Indian subcontinent, particularly the ones showing evidence of true disjunct distributions. These phylogenies can be utilized to determine the predominant biogeographic phenomenon (vicariance or dispersal) that explains disjunct distribution across many different taxonomic groups. That is, if multiple taxa show congruent phylogenetic histories, then one can conclude that the same historical events have shaped their current distribution. Such comparative phylogenetic studies will eventually contribute towards a 'biogeographic synthesis' of species displaying disjunct distribution.

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