The Indochinese–Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions

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Abstract

Aim To establish the geographical position of the biogeographical transition between Indochinese and Sundaic faunas using distributional data for the best-documented taxon, the birds.

Methods Distributional data of 544 resident forest and forest edge bird species of Thailand and the Thai–Malay peninsula were examined at 45 sites spanning 15° of latitude from northern-most Thailand to the southern peninsular Malaysia. Sites were grouped into 23 degree or half-degree latitudinal zones and avifaunal similarity coefficients were calculated between each zone.

Results A Mantel test revealed a significant transition between northern Indochinese and southern Sundaic (Indomalay) avifauna assemblages just north of the Isthmus of Kra (10°30′ N). Northern and southern range limits of 152 species (> 269 species and subspecies combined) lie between 11° and 13° N.

Main conclusions This transition between zoogeographical subregions is not coincident with the widely recognized transition between floristic provinces which is traditionally placed 400–500 km further south at the Kangar–Pattani line, but is associated with a change from wet seasonal evergreen dipterocarp rain forest to mixed moist deciduous forest north of the Isthmus of Kra in the northern Thai–Malay peninsula. Climatological and ecological factors associated with the distribution of forest types today are reviewed and it is hypothesized that the avian transition tracks the northern phytogeographical boundary. Palaeogeographical factors, including hypothetical Neogene seaways, which may account for the historical development of both phytogeographical and avifaunal transitions are also described.

Keywords Geographical range limits, biogeographical boundaries, phytogeography, Malaysia, Thailand.

INTRODUCTION

Wallace (1869, p. 158) correctly recognized a ‘time when the whole of the Java sea, the Gulf of Siam, and the Straits of Malacca were dry land, forming, with Borneo, Sumatra, and Java, a vast southern prolongation of the Asiatic continent’. This area is now called Sundaland and recognized as a distinct floristic province and zoogeographical subregion. Although considerable research has focused on Wallace’s line and the eastern limits of this biota (Whitmore, 1981, 1987; Metcalfe et al., 2001), little attention has been paid to the Indochinese–Sundaland transition, which Wallace placed in the Tenasserim region of the northern Thai–Malay peninsula. Finding his dictum (1869, p. 24) that ‘Birds offer us one of the best means of determining the law of distribution’ still holds true today, we base this analysis of the zoogeographical transition on avifaunal records.

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Provincialism remains a central concern of biogeographers (Myers & Giller, 1988; Williams, 1996; Brown & Lomolino, 1998; Cox, 2001) and biogeographical discontinuities and transitions are of interest to both ecologists and paleoecologists. The rapid turnover of taxa at provincial boundaries begs both historical and biological explanation. The position of transitions may be associated with present or former barriers to dispersal, and with the effects of dispersal, competition and invasibility, and obligate co-distribution (Brown & Lomolino, 1998). Here we are interested in the zoogeographical transition between the Indochinese Subregion and the Malayan Subregion (Wallace’s Indo-Malayan Subregion) of the Oriental Region, and the corresponding phytogeographical transition between the Continental SE Asiatic Floristic Province and the Malayan Floristic Province of the Indo-Malayan Subkingdom (Good, 1964). Wikramanayake et al. (2002) recently described this as the transition between the Indochina Bioregion and the Sunda Shelf and Philippines Bioregion. Herein, we will use the terms Indochinese and Sundaeic for the northern and southern biotas, respectively. In describing forest types we follow Ashton (1995) and recognize seasonal evergreen rain forest and mixed moist deciduous forests; other workers call the seasonal rain forest ‘semi-evergreen forest’ and the deciduous forest ‘monsoon forest’.

Kloss (1915), Robinson & Kloss (1921–1924) and Deignan (1963) provided basic information on avifaunal distribution on the Thai–Malay peninsula, and Wells (1976) provided a preliminary analysis of the data as it affects the transition. Wells found that many forest bird species have their distributional range limits at the southern end of the Tenasserim, at the Isthmus of Kra (10°30′ N) where the peninsula is only 45 km wide (Fig. 1). However, he did not conduct a detailed analysis or address the question of whether species assemblages differ significantly above and below the isthmus. Here we report distributional data of resident forest birds of Thailand and assess the statistical significance of a turnover of species along the latitudinal gradient. We discuss ecological and geological evidence that might account for the zoogeographical pattern which, unlike the Central American and Asian-Australian transitions, cannot be explained by plate tectonics. Instead, we will focus on the possible relationship between the avian transition and vegetation, as MacArthur & MacArthur (1961) showed how bird species distributions, and the diversity of bird communities, are highly dependent on vegetation structure. There are two zoogeographical transitions on the peninsula: (1) between perhumid evergreen rain forest and wet seasonal evergreen rain forest, 400–500 km south of the Isthmus of Kra near the Thai–Malay border (Steenis, 1950), and (2) between wet seasonal evergreen rain forest and mixed moist deciduous forests just north of the isthmus (Richards, 1996). Although the avifauna may be co-distributed with the vegetation types today this does not account for the development of either plant or avian biogeographical patterns. Here, and in companion papers (Woodruff, 2003a,b), the evidence for the historical cause of the divergence of Indochinese and Sundaeic biotas will be reviewed.

### MATERIAL AND METHODS

One of us (PDR) has assembled the most detailed set of confirmed bird records available for Thailand. The records used here are reported elsewhere (Round et al., 2003) and are based on personal observations over the period 1979–94, on reliable published records (e.g., Holmes, 1973; Holmes & Wells, 1975), and on bird watcher’s reports reviewed monthly by a committee of the Bird Conservation Society of Thailand (formerly Bangkok Bird Club). The 1990 version of these records formed the basis of the species range maps in the standard field guide to the birds of Thailand (Lekagul & Round, 1991) and, for convenience, we have followed this source for generic and species names. [The new guide by Robson (2002) uses the same maps with minor updating.] Using the 1994 records for the occurrence of birds at forty-six specific sites, we created a data base of the current distributions of 544 bird species and subspecies from fifty-three taxa (families, subfamilies and tribes) (Table 1). Recognizing subspecies in the field is difficult so we were for the most part reliant on older published data to establish subspecific distribution limits. In addition, we added records for Malaysia based on the work of Medway & Wells (1976). We focus primarily on rain forest birds but also include species characteristic of deciduous forests and forest edges. We excluded families of shorebirds, waterbirds, Palaearctic migrants, non-breeding visitors, species known from only a single sighting, and most open country residents from the analyses as their distributions are constrained by different parameters. We also excluded a few species restricted to southeast Thailand whose current ranges are remote to the peninsula. Only families with two or more species found in Thailand were included. The forty-six site survey records were used to establish northern and southern species range limits in twenty-three latitudinal zones (A–W) ranging from Malaysia (lumped as ‘5° N’) and the southern border of Thailand adjacent to Malaysia (6° N) to the northern border with Laos and Myanmar (> 20° N) (Table 2).

Jaccard’s (1908) coefficient of community (S) was used to calculate a matrix of similarities between sites

\[ S = a / (a + b + c) \]

where \( a \) is the number of species present in both sites, and \( b \) and \( c \) are the number of species present at one site and not the other. Double absences are excluded so as not to indicate resemblance.

Similarity values between two sites are negatively related to the distance between those sites (Fig. 2). In the following analysis, we used the residuals of a non-linear regression (\( y = 0.002x^2 - 0.062x + 0.651, r^2 = 0.610 \)) to offset the influence of distance. [Here data from Malaysia (<6° N) and north of the Thailand border (> 20° N) were excluded, because these zones cover > 1° of latitude.]

Multidimensional scaling of the similarity matrix produced a two dimensional plot of the localities, where the distance between the coordinates represents the difference between avifaunas at different sites. We used a cluster analysis to determine the significance of the groupings.
If different assemblages of northern and southern avifauna exist, then the degree of similarity between two localities is dependent upon whether they are in the same region or not. We tested this hypothesis for each latitude. We generated a binary matrix to represent a division of northern and southern regions. Sites which occurred on the same side of the dividing line were assigned a 1, those in opposite regions were assigned a 0. A matrix of the residual similarity values was then compared with the binary matrices using the Mantel test statistic (Z) (Mantel, 1967; Sokal & Thomson, 1987). The Mantel statistic is computed as the sum of the cell-by-cell multiplication of the two matrices. The larger the correspondence between the matrices, the larger the calculated Z statistic. We used a Monte Carlo simulation to generate a distribution of possible values. For each permutation, two random columns and the corresponding rows of the binary matrix were transformed, and a Z value was calculated with a program written by and available from JBH. The statistical significance of the original value of Z was then determined by comparison to this distribution.

The same analysis was repeated including subspecies divisions among the species, increasing the data set to 724 species and subspecies. In cases where subspecies’ geographical ranges are not well defined we set range limits in the middle of the undecided area, usually 1° of latitude or 100 km. The nonlinear regression of the similarity coefficients between localities and their distance apart was calculated (y = 0.004x^2 − 0.1x + 0.652, r^2 = 0.729) and, as in the above case, the residuals of this regression were used to test the statistical significance of a transition between northern and southern avifauna.

RESULTS
The most frequent latitudinal limits of the species examined are between 11° and 13° N, just north of the Isthmus of Kra (Fig. 3–4). Approximately 152 species had northern or southern range limits between these latitudes. This amounts to 28% of the bird species considered and more than half the species occurring in this 200 km wide latitudinal zone.
Table 2 Statistical analyses of avifaunal relationships for species and for subspecies from specific localities grouped into 23 latitudinal zones (A–W). The Mantel probability (P-values) pertain to the transition between the avifauna of a specific zone and the next most southerly zone.

Latitudes are the northernmost limits of the zones

<table>
<thead>
<tr>
<th>Zone</th>
<th>(° N)</th>
<th>Localities</th>
<th>P-value species only</th>
<th>P-value with subspecies</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>&gt; 20°</td>
<td>Doi Pha Hom Pok</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>B</td>
<td>20°</td>
<td>Doi Chiang Dao</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>C</td>
<td>19°</td>
<td>Doi Inthanon; Doi Surhep-Pui</td>
<td>0.99</td>
<td>1.00</td>
</tr>
<tr>
<td>D</td>
<td>18°</td>
<td>Om Koi; Phu Luang; Phu Kradeung</td>
<td>0.97</td>
<td>1.00</td>
</tr>
<tr>
<td>E</td>
<td>17°</td>
<td>Mae Sot; Phu Khieo; Nam Nao; Thung Salaeng Luang</td>
<td>0.99</td>
<td>0.98</td>
</tr>
<tr>
<td>F</td>
<td>16°</td>
<td>Huai Kha Khaeng; Thung Yai; Umphang</td>
<td>0.98</td>
<td>1.00</td>
</tr>
<tr>
<td>G</td>
<td>15°</td>
<td>Bung Kroeng Kavia</td>
<td>0.81</td>
<td>0.97</td>
</tr>
<tr>
<td>H</td>
<td>14°30’</td>
<td>Khao Yai</td>
<td>0.29</td>
<td>0.76</td>
</tr>
<tr>
<td>I</td>
<td>14°</td>
<td>Sai Yok</td>
<td>0.20</td>
<td>0.71</td>
</tr>
<tr>
<td>J</td>
<td>13°30’</td>
<td>Khao Soi Dao</td>
<td>0.03</td>
<td>0.07</td>
</tr>
<tr>
<td>K</td>
<td>13°</td>
<td>Kaeng Krachan</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>L</td>
<td>12°30’</td>
<td>Hua Hin; Khao Sam Roi Yot</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>M</td>
<td>12°</td>
<td>Prachuap; Khao Luang; Khao Nok Wua</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>N</td>
<td>11°</td>
<td>Thasan; Thae Sae</td>
<td>0.22</td>
<td>0.002</td>
</tr>
<tr>
<td>O</td>
<td>10°</td>
<td>Ranong; Tapli</td>
<td>0.26</td>
<td>0.03</td>
</tr>
<tr>
<td>P</td>
<td>9°+9°30’</td>
<td>Khao Sok; Khlong Saeng; Khlong Nakha</td>
<td>0.86</td>
<td>0.61</td>
</tr>
<tr>
<td>Q</td>
<td>8°30’</td>
<td>Khao Phanom Bencha; Khlong Phraya; Krabi; Khao Nong; Khao Luang</td>
<td>0.91</td>
<td>0.74</td>
</tr>
<tr>
<td>R</td>
<td>8°</td>
<td>Khao Nor Chuchi; Khao Pu-Khao Ya</td>
<td>0.93</td>
<td>0.89</td>
</tr>
<tr>
<td>S</td>
<td>7°30’</td>
<td>Trang; Khao Banthad</td>
<td>0.82</td>
<td>0.77</td>
</tr>
<tr>
<td>T</td>
<td>7°</td>
<td>Thale Ban; Ton Nga Chang</td>
<td>0.53</td>
<td>0.65</td>
</tr>
<tr>
<td>U</td>
<td>6°30’</td>
<td>Pattani</td>
<td>0.35</td>
<td>0.44</td>
</tr>
<tr>
<td>V</td>
<td>6°</td>
<td>Yala and Narathiwat provinces</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>W</td>
<td>‘5°</td>
<td>Malaysia</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Within most of the bird families, some species appear to be restricted to either northern Indochinese or the southern Sundaic provinces, while others occur across the whole latitudinal range (Fig. 3). About 190 species are exclusively Indochinese, 150 are Sundaic, and another 147 are widespread; of these latter, eighty-six have both Indochinese and Sundaic subspecies (data in Round et al. (2003). Fifty-six other species are ‘montane island-hoppers’ occurring in the hills of northern Thailand and the hills of peninsular Malaysia but not in the intervening central Thai–Malay peninsula. In Fig. 3 all categories of widespread species are placed arbitrarily below the Sundaic fauna at the base of the figure. Families that best illustrate these patterns of species replacement, with congeneric Indochinese and Sundaic species, include the woodpeckers (Picidae), pheasants (Phasianidae), and bulbuls (Pycnonotidae) (Figs 5–7). In the woodpeckers, for example, there are eleven Indochinese species, sixteen Sundaic species, and eight widespread species of which five show significant range gaps in the northern and central peninsula. There are at least five congeneric biogeographical species replacements involving northern and southern congeneric species with non-overlapping southern and northern range limits. There are also thirteen cases where northern and southern subspecies replace one another along the transect. Only one of eleven Indochinese species show subspecific differentiation, while seven of sixteen Sundaic and five of eight widespread species show such geographical differentiation. In the pheasants, there are eleven Indochinese, seven Sundaic and three widespread species. In the bulbuls, eleven Indochinese species are replaced by seventeen Sundaic species and seven more are widespread. As in the woodpeckers relatively more sub-speciation occurs in the southern than in the northern species.

The multidimensional scaling plot divides the localities into two groups: (1) the localities from 12° N to the northern border of Thailand (latitudinal zones A–M), and (2) the localities from Malaysia to 11° N (zones N–W) (Fig. 8). The Mantel test detected significant transitions of the northern and southern assemblages of bird species between 11° and 13°30′ N (P < 0.001)(Table 2). These results also hold when the range limits of the subspecific taxa are included (n = 269); the Mantel test is highly significant for transitions between 10° and 12°30′ N (P < 0.002) and significant at the 9°30′/10° N boundary (P = 0.032) (Table 2).
Our prime result is therefore that there is a marked avifaunal transition north of the Isthmus of Kra and no detectable cluster of species boundaries further south near the transition between perhumid and wet seasonal evergreen rain forest types (see below) at 7°N.

Figure 4 The number of species taxa reaching their distributional limit at the latitude indicated.

Figure 5 The latitudinal distribution of species and subspecies of the woodpecker family (Picidae). The occurrence/absence of each taxon (species ID #’s from Lekagul & Round, 1991) with sites grouped by latitudinal zone. Column headings are latitudes (° N) with ‘Malay’ being peninsular Malaysia (<6° N). Generic names can be discerned from the species numbers. Different symbols show the ranges of different subspecies; the shaded cell marks an uncertain subspecies break.

The number of species taxa reaching their distributional limit at the latitude indicated.
DISCUSSION

These analyses support the hypothesis that a significant turnover in bird species assemblages occurs between 11° and 13° N on the Thai side of the Thai–Malay peninsula. At the species level the Sundaic avifauna is clearly different from that of the Indochinese subregion. Comparable documentation of the magnitude and geographical position of the zoogeographical transition in other terrestrial animals are still lacking but, as a broad generalization, mammals, reptiles, amphibians and butterflies appear to exhibit similar patterns (Lekagul et al., 1970; Corbet & Pendlebury, 1992; J. Nabhitabhata, pers. comm., 1996). The geographical ranges of mammals described by Lekagul & McNeely (1988) and Corbet & Hill (1992) show that numerous species and subspecies boundaries lie near the Isthmus of Kra. More recently, Chaimanee (1997) has analysed the extant rodent fauna and found that, of sixty-one species, 61% have range limits associated with the Isthmus of Kra. Whitmore (1984), as a result of additional fieldwork on species of dipterocarps, subsequently rotated this boundary between the floral provinces by 90° to a line running west–east between Kangar (Malaysia) and Pattani (Thailand) at c. 7° N latitude along the Thai–Malay border. The position of the Kangar–Pattani line forest transition has been attributed to the increasing seasonality north of this line (Whitmore, 1984; Ashton, 1992). Baker et al. (1998) also put the boundary of the Malesian flora on the Thai–Malay border.

The Kangar–Pattani phytogeographical transition is not well explored ornithologically and additional species and subspecific borders may be discovered in this area. For example, some species (e.g. black-capped babbler, Pellor-neum capistratum) treated as belonging to the same subspecies throughout Malaysia and Thailand, call with different dialects on either side of the Kangar–Pattani transition (PDR, own data). Others like the banded pitta, Pitta guajana are insufficiently known in this area; the extreme southern Thai birds may be referable to the Malaysian subspecies irena rather than the peninsular Thai rileyi. Regardless of such minor revisions, it is clear that most of the birds simply ignore the Kangar–Pattani line.

Whitmore (1984, p. 201) and Richards (1996, p. 403-4) have described this southern transition at Kangar–Pattani.
line as the ‘Kra ecotone’ despite the fact that it lies c. 500 km south of the Isthmus of Kra. Soepadmo (1995) explicitly equates the Isthmus of Kra with Steenis’ turnover of plant genera at the Thai–Malay border and Hirai et al. (2002) similarly misuse the term Isthmus of Kra for sites 400 km further south.

Immediately north of the Isthmus of Kra (at 10°30’N) there is a second less well-known floristical transition. This northern transition, between wet seasonal evergreen dipterocarp rain forest and mixed moist deciduous forest occurs, on the east side of the peninsula, near the town of Chumphon. The mixed moist deciduous forest differs profoundly from the rain forest in stature, absence of emergents, deciduousness (essentially 100%), soil surface environment, and generic composition (Ashton, in litt. 1999). This northern phytogeographical transition is described by Richards (1996, p. 162) as a transition between semi-evergreen rain forest and monsoon forest. On the wetter west coast of the peninsula, in lower Burma (Tenasserim), the transition is broader and extends north to Tavoy (14° N).

Thus both Whitmore and Ashton view the avifaunal transition as coincident with the northern phytogeographical transition between rain forest and mixed deciduous forest and neither are surprised that we found no ornithological boundary at the southern transition as the forest there shows only minor change in structure (Whitmore, in litt. 1995; Ashton, in litt. 1999). Unfortunately, the distributional records of the Malesian and Indochinese plant genera and species upon which their insights are based have never been published. Our current understanding rests on their extensive personal fieldwork and the scattered herbarium sheets known to only a few botanists. Until the range limits of plant species and genera are collected into one database and plotted out against the geography of the peninsula it is difficult to compare the avifaunal and phytogeographical transitions.

We provide a detailed analysis of the underlying bird distributional data elsewhere (Round et al., 2003). A more definitive analysis of the northern and southern range limits can be prepared when the revised distribution data for

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**Figure 7** The latitudinal distribution of species and subspecies of the bulbul family (Pycnonotidae). See Fig. 5 for details.
Malaysian passerines are available (Wells, 1999, unpubl. data) and when current data become available for the Tenasserim (now Thanintharyi State) and the rest of southern Myanmar. However, before leaving this issue we should point out some readily apparent features of the pattern. First, the overall pattern (Fig. 3) is not simply one of Indochinese species replacing Sundacian species in the transition. Some of the Thai species have southern range limits north of the transition and are montane-adapted species lacking suitable habitat in the peninsula (e.g. stripe-breasted woodpecker, Picoides atratus). Others are more flexible and shift from lowland habitat in Thailand to hill habitat in Malaysia, perhaps in response to competition with Sundacian lowland congeners (e.g. orange-breasted trogon, Harpactes oreskios). Simple species replacement may therefore be rarer than the above discussion suggests. Overall the pattern is of a much richer lowland forest fauna in the Sundacian than the Indochinese province and perhaps this is linked to the greater structural complexity of the less seasonal rain forests. Many Sundacian species have no ecological equivalents in the Indochinese fauna. In other cases, one or two Indochinese generalists are either replaced, or added to, by further congeners in the Sundacian province. Among leafbirds, Chloropsis spp., for example, the golden-fronted leafbird, C. aurifrons, is found exclusively north of the Kra Isthmus within the region covered by our analysis (although it reappears in north Sumatra); the blue-winged leafbird C. cochinchinensis, occurs on both sides of the divide, as does a montane species, orange-bellied leafbird, C. hardwickii. Two other lowland species, the greater green leafbird, C. somerati, and lesser green leafbird, C. cyanopogon, are exclusively Sundacian. Finally, there are a few species that have expanded their ranges during the last century in response to lowland deforestation (e.g. Indochinese black-collared starling, Sturnus nigricollis, has spread into the southern peninsula) and therefore tell us little about the historical pattern.

Although the position of the phytogeographical transitions involving > 500 genera may be determined by climatic factors today and the avifaunal transition may be linked causally (directly or indirectly) to the plants, we still have to explain the origination of the different Indochinese and Sundacian biotas. Unlike the Central American biogeographical transition or that associated with Wallace’s Line, the avifaunal transition near the Isthmus of Kra cannot be attributed to plate tectonics and former open ocean barriers to dispersal. Yet the significant transitions on the Thai–Malay peninsula require that some sort of barrier existed in the past in order to permit the provincial biotas to diverge in allopatry. In a companion paper, Woodruff (2003a) argues that marine transgressions during the Miocene and the Pliocene breached the peninsula and permitted the evolutionary differentiation of some terrestrial animals north and south of the seaways. A consideration of Tertiary eustatic changes (Vail & Hardenbol, 1979; Haq et al., 1987; Hallam, 1992; Abreu & Anderson, 1998) leads to the conclusion that the Thai–Malay peninsula may have been breached by marine seaways for two periods relevant to modern bird distributions: during both a mid-Miocene and an early Pliocene high stand. Sea levels of at least +150 m (+220 m according to Hutchison, 1989) during the middle Miocene probably flooded the isthmus from 24 to 13 Ma and possibly longer. Straits probably formed again during the early Pliocene from 5.5 to 4.5 Ma when sea level rose to +140 m according to Hutchison (1989). Today a sea level at +100 m would flood the peninsula in two places (Woodruff, 2003a): in the north, a strait would open between Surat Thani and Krabi, in the south, a strait would open between Songkhla and Kangar. In both cases the seaways would be oriented roughly north–south and contain a number of prominent islands. The northern strait would be 30–100 km wide and the southern strait would be 40–50 km wide. Between these two straits 80% of southern Thailand would be submerged and forest habitat would remain only on the emergent Nakhon si Thammarat Range (Banthad Range) and western hills.

The Pliocene transgression and hypothetical seaways are more relevant to the differentiation of extant avian species and subspecies than the Miocene events. Contrary to earlier views that avian speciation was closely linked to Pleistocene climatic cycles (and geographical differentiation in forest refugia during glacial periods), recent molecular genetic studies indicate that many north temperate species originated in the Pliocene (Bermingham et al., 1992; Blondel et al., 1996; Blondel & Mourer-Chauviré, 1998; Klicka & Zink, 1997, 1999). Similarly, there is no clear relationship between the inferred positions of the rain forest refugia in southeast Asia and the position(s) of today’s transitions (Morley, 2000; Kershaw et al., 2001; Gathorne-Hardy et al., 2002). This is not to deny that Pleistocene environmental changes leave recognizable imprints on modern phylogeography (Avise,
but rather to recognize that the majority of speciation events are older. Hewitt (1996, 2000) and others have argued that Early Pliocene climatic events were a major impetus to speciation, and that cyclical Pleistocene changes have had more impact on subspecific patterning and extinctions.

If a seaway created a barrier to the dispersal of forest plants and birds along the Thai–Malay peninsula, the study of phylogenetic relationships within the genera involved should reveal evidence of genetic differentiation associated with the time of the barrier’s existence. For species-pairs that originated by allopatric divergence on either side of the hypothetical Pliocene straits some predictions can be made. If the resulting species were poorly differentiated after the seaway disappeared, then they are likely to have come back into contact with insufficient niche divergence to live in broad sympatry, and instead may show competitive replacement. Alternatively, we may see hybridization between imperfectly isolated semispecies, although hybrid zones are not known to persist for 4 Myr. The avifaunal records have not yet been formally examined for evidence of competitive replacement, but there is little evidence for multiple zones of interspecific hybridization so the transition is probably ancient rather than recent. In contrast, younger species that originated elsewhere and have entered the region since the barrier disappeared, may have distributions unaffected by such historical features.

The degree to which these hypothetical seaways functioned as barriers to dispersal of individual species would vary tremendously across avian taxa. Some birds, including most raptors and migratory birds, would not recognize a 30 km wide marine strait as an obstacle, while to others a 1-km water gap constitutes a near absolute barrier (e.g. some babblers, Sylvinae, barbets, Megalaimidae, and the honeyguide, Indicator archipelagius, Wells, 1976, 1988). Among the resident forest birds we have to expect a great diversity of responses to water gaps and it would be informative therefore to further examine the present distribution of species on the 300 sea islands around the peninsula (see brief review by Wells, 1999). Such an analysis may suggest both assembly rules for these bird communities and limits on the size and duration of hypothetical barriers.

In conclusion, historical and ecological hypotheses to explain the origin and current position of the transition between Indochinese and Sundaic avifaunas of the Isthmus of Kra have been developed involving Neogene seaways, and seasonality as it affects forest type. Testing these hypotheses can now begin but will be difficult for, as Wells (1999) and others have pointed out, there is still no clear understanding of the linkage between climatological factors, forest phenology, floristic diversity, and bird distribution. Answers to these complex issues may come from the resolution of a host of smaller questions including the following. Are Indochinese species (both birds and plants) more successful in invading Sundaland than Sundaic species are in invading the Indochinese province? What do comparative penetration and invasibility tell us about the history of the interaction? Have repeated major changes in lowland forest area during the Pleistocene favoured Sundaic over Indochinese species? How have Neogene palaeogeographical changes altered the position of the transition? Are today’s plant distributions better indicators of palaeogeographical history than the birds? In contrast, do birds track recent habitat changes more rapidly than plants? Further study of the Neogene history of the region and the behavioural ecology and phylogeography of the species associated with the transition will permit exploration of these questions and tests of these and other hypotheses.

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REFERENCES


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