THE LOCATION OF THE INDOCHINESE-SUNDAIC BIOGEOGRAPHIC TRANSITION IN PLANTS AND BIRDS

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ABSTRACT

The biogeographic transition between the Indochinese and Sundaic (Indomalay) biotas lies today on the Thai–Malay peninsula. A literature review suggests that there may actually be two major phytogeographic transitions about 500 km apart. Most botanists follow VAN STEENIS and GOOD and place the transition at the Kangar–Pattani line near the Thai–Malay border. Others place more importance on the transition between seasonal evergreen and mixed moist deciduous forests that occurs near the Isthmus of Kra, between Chumpon on the east coast and Tavoy on the west coast. A recent review of bird species distributions shows that a highly significant number of their species and subspecies range limits occur just north of the Isthmus of Kra and are associated with the northern phytogeographic transition but not the southern one. The transitions in other groups of animals are less well documented but generally lie north of Kra in the northern peninsula. A review of the climatological and paleogeographic factors alleged to control these transitions shows that we cannot adequately account for their current positions. The possible role of trans-peninsular seaways as barriers permitting the divergence of the Indochinese and Sundaic biotas is discussed and the directions for future research to test various hypotheses are outlined.

Keywords: zoogeography, phytogeography, paleogeography, Tertiary seaways, Thailand, Malaysia, Isthmus of Kra, Sundaland

INTRODUCTION

The biotas of two different zoogeographic subregions and phytogeographic provinces meet in Thailand and this biogeographic provincial boundary begs both historical and biological explanation. ALFRED RUSSEL WALLACE (1876), the founder of zoogeography, recognized a major faunal transition in Thailand but the phenomenon has received little scientific attention since then. He put the boundary between the northern Indochinese Subregion and the southern Indo-Malayan Subregion in the Tenasserim Range at the northern end of the Thai-Malay peninsula. The corresponding phytogeographic transition separates the Continental SE Asiatic Floristic Province and the Malayan Floristic Province of the Indo–Malayan Subkingdom (GOOD, 1964). This transition is typically shown near the Thai–Malay border 900 km further south.
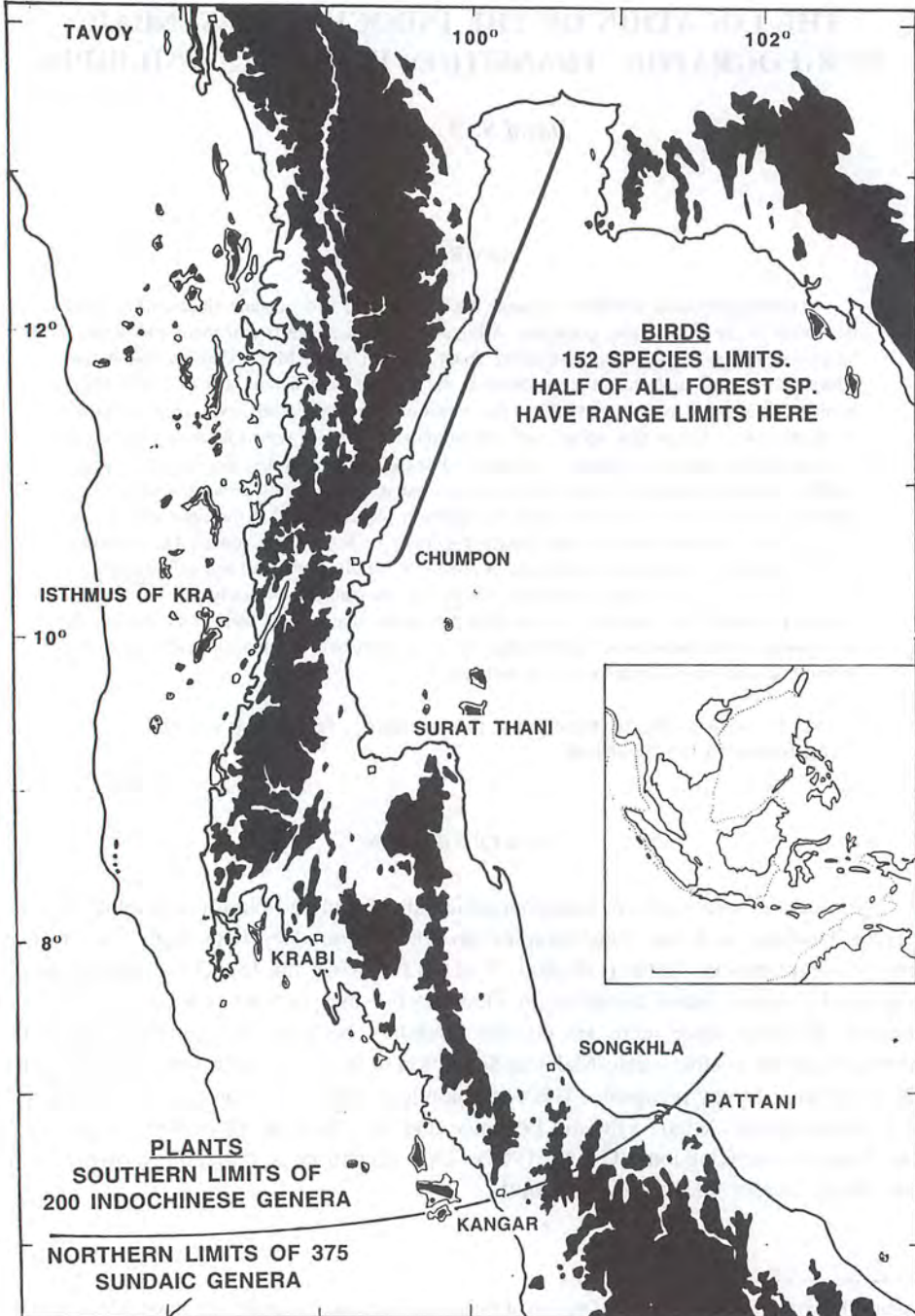
Figure 1. Map of the Thai-Malay peninsula showing the biogeographic features discussed in the text. The phytogeographic data are from VAN STEENIS (1950), the bird species range limit data are from HUGHES, ROUND & WOODRUFF (2003) and ROUND, HUGHES & WOODRUFF (2003). The -100 m isobath is shown in the Andaman Sea and on the inset regional map. Hills above 100 m are shaded.

POSITION OF THE BIOGEOGRAPHIC TRANSITION

Although there is general agreement that a major biogeographic transition occurs on the Thai–Malay peninsula there are diverse opinions as to its location and breadth. The position of biotic transitions may be associated with present or former physical and environmental barriers to dispersal, and with the effects of dispersal, competition and invasibility, and obligate co-distribution (BROWN & LOMOLINO, 1998). The purpose of this review is to draw attention to the problems associated with this particular biogeographic transition and to thus contribute to their solution.

Although Thailand sits centrally in the Oriental Zoogeographic Region the faunas of northern and southern Thailand are clearly different at the species level. Herein, I will use the terms Indochinese and Sundaic for the northern and southern biotas, respectively. The zoogeographic transition was placed at the northern end of the peninsula, at about 14°N by WALLACE (1876). One hundred years later WELLS (1976) provided the first species level analysis of the transition and, based primarily on the distributions of Sundaic birds, he concluded that the transition lay just north of the Isthmus of Kra at 10°30'N. More recently, using bird distributional records extending from Chang Rai to Singapore, my colleagues and I have refined this result (HUGHES ET AL., 2003; ROUND ET AL., 2003). Our statistical analyses revealed a significant turnover in bird species assemblages between 11° and 13°N on the northern Thai–Malay peninsula. We found that 152 species, or half the forest-associated species, have range limits in this area (Fig. 1). Our finding that the avian transition lies a little further north of the latitude described by WELLS in 1976 is, in fact, what he would have predicted and has subsequently found (WELLS, 1999: xxi).

Comparable documentation of the magnitude and location of the zoogeographic transition in other phyla are still lacking but, as a broad generalization, mammals, amphibians and butterflies appear to exhibit similar patterns (LEKAGUL ET AL., 1970; CORBET & PENDLEBURY, 1992; INGER, 1999). PAUWELS ET AL. (2002, 2003) have surveyed reptiles in two provinces 200 km north and south of the Isthmus of Kra, respectively. They found 108 of 152 snake species may have range limits in the northern peninsula but estimate that their species lists are only 55–65% complete and think the Indochinese-Sundaic transition lies further north near Kanchanaburi at about 14°N. The geographic 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. CHAIMANEE (1997) has analyzed the extant rodent fauna and found that, of 35 species of murines, 16 species are restricted to the north and 5 species to the south of the Isthmus; the remaining 14 species occur in both Indochinese and Sundaic subregions. For 16 species of sciurines and 10 species of petauristines, the counts are 2:8:6, and 4:2:4, respectively. Of these 61 species of rodents, 61% have range limits associated with the Isthmus of Kra. Pleistocene fossils, on the other hand, show that individual species shifted their ranges 400–500 km north and south of today's and that the early Pleistocene transition lay 500 km south of Kra. TOUGARD (2001) reviewed the Pleistocene and recent distribution records of large mammals (129 extant species of primates, carnivores, proboscidians, perissodactyls and artiodactyls) in southeast Asia and also concluded that, although today's provincial boundary lies at the Isthmus of Kra, the transition shifted further south to northern peninsular Malaysia during Pleistocene hypothermals. Amphibian and butterfly species also show turnover at the isthmus; in amphibians more Indochinese species extend south than Sundaic species extend north of

the transition (INGER, 1966), and the reverse is reported in butterflies (CORBET & PENDLEBURY, 1992).

There are apparently two phytogeographic transitions on the peninsula of which the best known lies near the Thai–Malay border, 500 km south of the Isthmus of Kra. This southern transition, between perhumid evergreen rainforest and wet seasonal evergreen rainforest, is widely portrayed as the major Indochinese-Sundaic plant boundary (VAN STEENIS, 1950; GOOD, 1964; KENG, 1970; WHITMORE, 1984; UDVARDY, 1969; ASHTON, 1992; RICHARDS, 1996; MORLEY, 2000). WIKRAMANAYAKE ET AL. (2002) also followed VAN STEENIS (1950) in their regional conservation habitat-mapping project and put the boundary between the Indochina Bioregion and the Sunda Shelf and Philippines Bioregion near the Thai–Malay border. There is also a second transition, between seasonal evergreen rainforest and mixed moist deciduous forest, north of the Isthmus of Kra. This northern transition is widely shown on large-scale vegetation maps but not formally documented in the literature. TAKHTAANJAN (1986) and COLLINS ET AL. (1991) placed the boundary between the Indo-Chinese and Malesian floristic regions at the Kra isthmus. As birds are typically co-distributed with plant communities (MACARTHUR & MACARTHUR, 1961) the relationship between the avian transition and the two phytogeographic transitions is puzzling. The birds appear to ignore the southern transition and their relationship with the northern transition is recognized but not yet well documented (HUGHES ET AL., 2003; ROUND ET AL., 2003).

Our understanding of the position of the southern transition has been modified several times during the last century. RIDLEY (1911a, b) was among the first to note that, on the west coast, the flora of what was then called Lower Siam was quite different from that of Malaya. He contrasted the heath floras of Satun (Thailand) and nearby Pahang (Malaysia) and listed many Malay genera that are not found north of Alor Setar (Malaysia). Alor Setar is a town 16 km SSE of Kangar (see Figure 1). He placed the floral boundary between the northern sandstone and limestone hills of Perlis and the granite hills that begin south of Alor Setar. On a foldout map he drew a straight line separating the two floras from just south of Alor Setar in the west to just south of Sai Buri (Thailand) on the gulf coast, 20 km ESE of Pattani. KLOSS (1922) changed the orientation of the line from SW-NE to N-S and mapped the transition to a line between Alor Setar and Songkhla. VAN STEENIS (1950: lxxi-lxxii) affirmed this location and provided more details on this transition based on distribution maps he prepared for 1,200 *genera* of plants. He found that 375 genera of Sundaic plants reach their northern limits, and 200 genera of Indochinese plants reach their southern limits, at this line. WYATT-SMITH (1964) and KENG (1970) supported this placement of the transition. Then, as a result of additional fieldwork on *species* of dipterocarps WHITMORE (1984) rotated this boundary to a line like Ridley's, running west-east between Kangar (Malaysia) and Pattani (Thailand) at about 7°N. BAKER ET AL. (1998) also put the boundary of the Malesian flora on the Thai–Malay border and presented new data on the ranges of selected palms (including rattans), bamboos, euphorbs (understorey shrubs), elaeocarps (trees), and a genus of ferns. This Kangar–Pattani line remains the widely accepted position of the Indochinese-Sundaic boundary.

WHITMORE (1984) reviewed the many changes that occur across the Kangar–Pattani line in the composition and function of the forests. To the north, there is a massive drop in species richness, associated with the disappearance of the remarkable series of ecologically sympatric congeneric species so characteristic of great western Malesian rainforests. Also to the north there is more frequent annual flowering of canopy trees and a dampening or

absence of synchronous mass (sometimes called *mast*) fruiting. He attributed the position of the forest transition to the increasing seasonality and noted that north of this line nearly all seedlings of climax species die during their first dry season, within 12 months of germination in most years. ASHTON (1992, 1995) agreed with these generalizations and concluded that although we do not have statistics to demonstrate it, there is a massive decrease in species north of the Kangar–Pattani line. More than twice as many plant genera reach their northern range limits here as those that reach their southern, and there is no doubt that this difference is greater still at the species level.

In addition to the need for formal mapping there are two other aspects of the Kangar–Pattani transition that should be noted here. First, climatological records do not support the alleged association of the transition between forest types and the southernmost position on the peninsula where a dry season of one month's duration occurs. WELLS (1999: xix, Map 2) shows that the east side of the central peninsula does not experience a dependable month's drought below the latitude of Surat Thani. Thus, on the east side of the peninsula one would expect the transition to be 300 km further north if seasonal drought was the controlling factor. Second, some writers have described the geographic location of this transition incorrectly. The transition at the Kangar–Pattani line lies about 500 km south of the Isthmus of Kra but despite their geographic separation both WHITMORE (1984: 201) and RICHARDS (1996: 403–4) have described this southern transition somewhat ambiguously as the "Kra ecotone". SOEPADMO (1995), discussing plants, explicitly equates the Isthmus of Kra with VAN STEENIS' turnover of plant genera at the Thai–Malay border. HIRAI *ET AL.* (2002) entitled their paper on tree shrews "found in the southern part of the Isthmus of Kra" even though their study site was 400 km further south. Similarly, others (e.g.: TOSI *ET AL*, 2002) have claimed evidence for a biogeographic barrier at the Isthmus of Kra when their only evidence has been the observation of different animals from sites hundreds of km north and south, respectively, of Kra. The term *Isthmus of Kra* must be used with greater precision and the term *Kra ecotone* should be reserved for the northern transition, which will now be described.

The second, or northern, transition occurs, on the east side of the peninsula, immediately north of the Isthmus of Kra near the town of Chumphon at 10° 3'N. Floristically, this transition is between wet seasonal evergreen dipterocarp rainforest and mixed moist deciduous forest. The mixed moist deciduous forest differs profoundly from the rainforest in stature, absence of emergents, deciduousness (nearly 100%), soil surface environment, and generic composition (ASHTON, *in litt.*, 1999). This northern phytogeographic transition is not well documented in the literature. RICHARDS (1996: 162) describes it as a transition between semi-evergreen rainforest and monsoon forest. According to WHITMORE (*in litt.*, 1995) evergreen rainforest is replaced by deciduous "monsoon" forest at Chumpon. There is a total floristic change involving the whole flora including many *genera*. In contrast to the impression given by VAN STEENIS (1950), WHITMORE views the Kangar–Pattani transition as involving *species* but not genera and the Kra ecotone as involving a more significant taxonomic turnover. ASHTON (*in litt.*, 1999) concurs, and notes that despite what VAN STEENIS wrote in 1950 he really envisioned a broad ecotone extending from the Kangar–Pattani line north for 500 km on the east coast and for 800–1000 km on the west side of the peninsula, as far north as the wet seasonal evergreen forest extends on the Burmese side, in the Dawna Range at 17°30'N where such rainforest genera as *Durio* finally peter out. On the Thai side alone, a big change takes place at quite a sharp boundary just north

of Chumpon. In a companion paper, ROUND *ET AL*. (2003: Fig. 1) show a further northward distribution of the Sundaic birds on the moister (Burmese) than on the drier Thai side. This supports WELLS' (1999) argument that vegetation type is the major constraint on bird distribution.

Both Whitmore and Ashton reviewed a preprint of HUGHES *ET AL'S* (2003) report showing the avifaunal transition to be coincident with the northern phytogeographic transition and neither were surprised that no ornithological boundary occurs at the southern transition as, in their opinions, the forest there shows only minor change in structure and appearance. Unfortunately, the distributional records of the Malesian and Indochinese plant genera and species upon which their insights are based have never been published and the differences may be more than minor. Their knowledge rests on 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 (see PARNELL *ET AL*., 2003) and plotted out against the geography of the peninsula it is difficult to compare the avifuanal and phytogeographic transitions. If the plant *generic* limits and the bulk of the *species* limits actually lie between 11° and 13°N, and not at 7°N, as depicted by VAN STEENIS (1950) and those who copied his figure, then the plant and bird patterns may be coincident and causally related. Further, the width of the avian transition may be related to the differences in the plant community distributions on either side of the peninsula.

The wet seasonal evergreen rainforest, which historically covered both lowland and hills of the central and northern peninsula, has been largely replaced in the lowlands in the last hundred years by farms and forestry plantations. Remaining deciduous forest usually predominates in the lowlands, and evergreen rainforest is restricted to the hills, especially in the northern peninsula. The apparently sharp east side avifaunal transition may reflect interspecific competition among close congeners, with the Sundaic taxa being at a competitive advantage in moister hillside vegetation and the Indochinese taxa in drier lowland vegetation. This is what happens in the transition zone between, for example, the Sundaic red-bearded bee-eater, *Nyctyornis amictus*, and the Indochinese blue-bearded bee-eater, *N. athertoni*, with the former occurring in the moister evergreen forest of the middle hill slopes and the latter in the drier foothills habitat (LEKAGUL & ROUND, 1991). Other cases of apparent competitive displacement probably exist.

HENGEVELD (1990), ERDELEN (2001), TURNER *ET AL*. (2001) and WELZEN *ET AL*. (2003) discuss the problems that arise from defining biogeographic boundaries based on different data sets. In this case, we must recognize both variability in the quality of the underlying distributional records and real biological variation in the range limits of different groups of plants and animals. The latter phenomenon characterizes the better documented faunal transition in Central America where mammals show a clear species turnover and a strong southerly transgression, while birds, reptiles and amphibians provide little evidence for a faunal transition and the opposite dispersal bias (STEHLI & WEBB, 1985; WEBB, 1991). Further analysis of the biogeographic transition between Indochinese and Sundaic taxa should include the formal documentation of the distribution patterns of individual species in different phyla. Only then can we begin to investigate the ecological determinants of their range limits and seek to account for the current position of the transition. Until comparable analyses of the roles of local physiological adaptation, behavioral ecology as it affects competition among congeners, and community invasibility are undertaken, the determinants of the position of each species boundary cannot be established. This is, of

course, not a problem peculiar to southeast Asia; there are remarkably few studies of the determinants of species ranges in birds (TERBORGH, 1977) or other organisms (HOFFMAN & BLOWS, 1994). That such investigations are worth pursuing is well illustrated by a recent report comparing tenebrionid beetle, lizard and rodent communities along an aridity gradient that determines the position of a phytogeographic province boundary in the Negev desert (KRASNOV & SHENBROT, 1998).

ORIGIN OF THE BIOGEOGRAPHIC TRANSITION

Although the locations of today's biogeographic transitions may be controlled by climatic factors they cannot explain the origination of the different Indochinese and Sundaic biotas. At some time in the past these two biotas must have been, or were most probably, separated for long enough for their differences to evolve. Recent studies of speciation in diverse taxa suggest that divergence of this magnitude probably required one or more periods of allopatry of on the order of 10^5 to 10^6 years (AVISE, 2000). Unlike the major biogeographic transition associated with Wallace's Line and the eastern edge of the Sundaic biota (WHITMORE, 1987; METCALFE ET AL., 2001), no simple physical barriers are clearly associated with the transitions on the Thai–Malay peninsula. The peninsula has existed in approximately its present form for all of the Tertiary (HALL, 2002), far longer than the species that characterize the two provincial biotas. Similarly, distributional changes associated with multiple Pleistocene glacial phases and isolation in glacial forest refugia (HEANEY, 1991; MORLEY, 2000; VORIS, 2000; GATHORNE-HARDY ET AL., 2002) are unlikely to have resulted in this level of biotic divergence. What circumstances, then, have promoted the observed development of provincialism? In a companion paper (WOODRUFF, 2003), I hypothesize that previously unappreciated marine transgressions during the Miocene and the Pliocene breached the central peninsula and permitted the evolutionary differentiation of some congeners north and south of the seaways. The older of these transgressions apparently flooded the isthmus for about 10 million years from 24 to 13 million years ago (middle Miocene). More recently, shallow marine straits probably formed again for about 1 million years during the early Pliocene from 5.5 to 4.5 million years ago. Today a sea level at +100 m would flood the peninsula in two places (WOODRUFF, 2003); in the north a strait would open between Surat Thani and Krabi and, in the south, a strait would open between Songkhla and Kangar (Fig. 1). Transgressions in the Miocene and Pliocene were probably in the range of +140 to +150 m above today's sea level, although HUTCHISON (1989) estimated the Miocene transgression was +220 m. The northern and southern straits were probably 30–100 km wide and 40–50 km wide, respectively. Both were oriented roughly north–south and contained a number of prominent islands. 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.

These hypothetical seaways are the only barriers proposed so far to account for the origin and differentiation of the Indochinese and Sundaic biotas. Although such seaways have not featured in most recent biogeographic reconstructions, some earlier workers were aware of their possible existence (e.g. PARNELL, 2000). GERINI (1909) cited geological and historical evidence to show that the land between Kedah and Songkhla is an old seabed and argued that boats crossed the peninsula here until a thousand years ago. RIDLEY (1911b: 59) was explicit: 'One can gather from the flora that at no great length of time ago the

Malay Peninsula was cut off from Burmah south of Kedah, by the sea'. CORBET (1941:116) accepted Ridley's argument for a sea channel but argued that it lay further north: 'that while the present Malay Peninsula has undoubtedly been separated from the Asiatic mainland since the advent of the present species of butterflies, this separation occurred north of Kedah and the southward spread of insects and plants has been obstructed by a barrier which is largely climatic'. Any relationship between this historical seaway and an earlier prehistoric flooding associated with the +5 m hypsithermal high stand (7,000 yr BP) and the current biogeography has yet to be established. Clearly, the physical or environmental barriers that permitted the evolutionary divergence of the Indochinese and Sundaic biotas need further investigation. There is currently no evidence for a seaway at the Isthmus of Kra in the past 25 million years.

These observations raise the question of whether the palynological record (fossil pollen grains) allows us to reconstruct the history of this transition. MORLEY (2000) reviews the still limited record and provides the most complete synthesis available on the history of rainforests in southeast Asia since the Cretaceous. Today's forests trace their origins back to the early Tertiary when the southeast Asian peninsula was vegetated by conifers and temperate angiosperms of Laurasian origin. Since then the original flora has been invaded by Gondwanan species first from India and later from Australia. Today's very diverse flora (perhaps 8000 species and 1400 genera on the Thai–Malay peninsula) is a product of this double invasion history. India collided into Asia about 45 Ma and introduced such Gondwanan elements as the dipterocarps to southeast Asia. Australia collided with the Asian plate around 22 Ma and introduced various elements of the current flora including the Myrtaceae (17 Ma), the fern *Stenochleaena* (9.5 Ma), and gymnosperm *Podocarpus* (3.5 Ma). Throughout the Eocene the vegetation would be described as tropical evergreen forest but in the Oligocene and early Miocene the lowland rainforest was replaced in many areas by monsoon (seasonal) forest associations. The dipterocarps diversified during the Miocene and have dominated the Sundaic forests since then. According to MORLEY the vegetation throughout the Neogene has involved a shifting balance between four dominant associations: rainforest, seasonal monsoon forest, deciduous forest and savanna.

The evidence suggests that in Sundaland the rainforest doubled in area in the Late Miocene but gave way to savanna in the drier Pliocene and cooler Pleistocene. The savanna occupied both current continental areas and the exposed continental shelves according to traditional opinion, although KERSHAW *ET AL.* (2001) and some others disagree. Most botanists have held that savanna with abundant grasses extended from continental Thailand to Java and beyond during hypothermal periods in the Pleistocene. During such cool periods the rainforest may have contracted into refugia in western Sumatra and the Mentawi islands, and in northern Borneo and possibly western Java. It is unclear whether rainforest persisted on the exposed continental shelf other than as riverine gallery forest; KERSHAW *ET AL.*, 2001 believe that rainforest remained extensive and doubt the occurrence of the "dry corridor" described above. Although MORLEY'S (2000) palynological history has been useful in testing and discrediting such hypotheses as the durian theory [durians as a model of the most primitive rainforest trees], and the notion that southeast Asian rain forests were the world's oldest, it does not explain the position of the current biogeographic transition. There is nothing in MORLEY'S account that speaks to the occurrence of a present day transition at either the Kangar–Pattani line or at the Isthmus of Kra. He does, however, recognize that a transition occurs at the Isthmus of Kra, between southern rainforest and what he calls northern monsoon forest with tropical rain forest patches.

RECOMMENDATIONS FOR FUTURE RESEARCH

In conclusion, it is not yet clear when or how the differences between the Indochinese and Sundaic biotas developed. Although they have not yet been applied to the southeast Asian region, current hypotheses of diversification invoked elsewhere in the tropics include the refugia model, the riverine model, the vanishing refuges model, the disturbance model and the gradient model (MORITZ *ET AL.*, 2000). The last mentioned can occur between parapatric populations and without physical barriers to gene flow, while the other models of diversification all require barrier-supported speciation in allopatry. Similarly, we cannot explain the current position(s) of the transitions between various groups of fauna and flora and we have to allow that the position(s) have changed in the past, as suggested by the ranges of individual mammal species during the Pleistocene (CHAIMANEE, 1997; TOURGARD, 2001). To test the various physical and environmental hypotheses, a five-part multi-faceted research program should be initiated. First, it is essential to survey existing distribution patterns and compile reliable databases of locality records. This has been undertaken with birds to good effect (HUGHES *ET AL.*, 2003; ROUND *ET AL.*, 2003), but other phyla appear well-enough known taxonomically to permit preliminary analysis, including mammals, reptiles, amphibians, butterflies and flowering plants. Perhaps detailed studies of today's plant species distributions will provide us with insights that are not in the fossil record. Second, for those taxa represented in the fossil record, effort should be made to reconstruct their paleo-distributions. Third, alleged climatic control of the position of the northern and southern phytogeographic transitions needs to be verified. Accurate, current meteorological maps are a prerequisite for testing the alleged associations involving duration of the dry season and soil moisture availability on both a regional and a microgeographic scale. Fourth, estimates of the age of the transitions can now be obtained using phylogeographic methods. One recent report on the diversification of tree-squirrels (Sciuridae) in Sundaland traces a burst of speciation to the lowest pre-Pleistocene Cenozoic sea-level stand, 11.4 to 10.5 million years ago (MERCER & ROTH, 2003). The molecular genetic comparison of Indochinese and Sundaic sister-species with appropriate molecular clock calibrations may reveal the approximate age of the development of the transitions. Genealogical concordance across multiple co-distributed species implies shared historical biogeographic factors shaping their distributions. Phylogeographic comparisons may, for example, indicate that many species-pairs originated at the same time or times (e.g., 1, 2, 5, 10 or 15 million years ago) and thus help focus further research. Highly informative regional phylogeographic analyses involving vertebrates in the southeastern U.S.A., in lowland Amazonia, in Queensland rainforest fragments, and in glaciated Europe are reviewed by AVISE (2000), HEWITT (2000) and MORITZ *ET AL.* (2000). Finally, the geology, geomorphology and paleoclimatology of the Thai–Malay peninsula needs re-examining for evidence of the type of former physical or environmental barriers sought. The ultimate goal of this report is thus to stimulate such research, for as WALLACE (1869: 154) pointed out 'a knowledge of the distribution of animals may reveal unsuspected facts in the past history of the earth'.

ACKNOWLEDGMENTS

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