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Chapter Thirty

BIODIVERSITY AND ZOOGEOGRAPHY OF NON-MARINE TURTLES IN SOUTHEAST ASIA

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INTRODUCTION

Analysis of patterns of global and regional biodiversity is an important part of modern conservation programs. Identification of centers of high diversity or endemism provides information for reserve design and location, and targets high priority areas for focused conservation efforts. Additionally, analysis of species richness and distribution provides an important zoogeographic perspective for elucidating the evolutionary history of species groups of interest as well as the geological histories of the land-masses they occupy (Cox et al., 1976).

Several world regions have recently been identified as having exceptional endemism or biodiversity. Using plants as indicators, Myers (1988) identified 10 areas that occupy only 0.2% of the earth's land surface yet contain 34,000 endemic plant species, or about 27% of all tropical plant species. When non-endemics are added to the figure, approximately 35-40% of all plant species are found in these "threatened hotspots." Mittermeier et al. (1992) noted that at least 19% of the world's amphibians and reptiles are also found in the "hotspots" identified by Myers.

Conservation priorities are, by necessity, shaped largely by politics and geo-political boundaries, stressing the need to develop programs on a country-by-country basis. Seven "megadiversity" countries, Mexico, Columbia, Brazil, Zaire, Madagascar, Australia, and Indonesia, contain more than 54% of the world's plant and animal species (Mittermeier, quoted in Anon., 1988; Mittermeier, 1988; McNeely et al., 1990). Several other countries have since been added to the megadiversity list based on high endemism or species richness including Peru, Ecuador, Venezuela, China, India, and Malaysia (Mittermeier et al., 1992). These countries are important targets for focused conservation efforts.

Turtles, as an order of approximately 257 species (Ernst and Barbour, 1989), have received limited attention from the standpoint of regional or global biodiversity conservation, although some groups such as sea turtles (Bjorndal, 1981) and tortoises (Swingland and Klemens, 1989) have been subjects of considerable conservation effort. Iverson and Etchberger (1989) reviewed patterns of distribution of turtles in Florida, USA, and Beaman et al. (1990) discussed conservation issues for selected turtle species. The general lack of interest in turtle biodiversity is surprising for several reasons. First, turtles are an important component of many ecosystems, often contributing significant biomass (Iverson, 1982; Congdon et al., 1986; Congdon and Gibbons, 1989). Second, many turtle species have been exploited as a source of human food for centuries (Clark and Southall, 1920; Carr, 1952; Moll, 1976; Taylor, 1982). Third, turtles form important linkages in ecosystems, providing dispersal mechanisms for plants (Braun and Brooks, 1987; Iverson, 1987; Kaczor and Hartnett, 1990), contributing to environmental heterogeneity (Kaczor and Hartnett, 1990), and fostering important symbiotic associations with a diverse array of organisms (Lago, 1991; Witz et al., 1991).

Two previous studies examined global patterns of turtle distribution and biodiversity. A compendium of species richness maps was generated by Iverson (1992a). His survey identified several world regions as having high turtle diversity, including the southeastern United States (see also Iverson and Etchberger, 1989), and Southeast Asia. Iverson (1992b) examined the relationship between turtle species richness and twelve environmental variables in major river drainage systems on five continents. Annual rainfall was the only highly significant correlate.

The primary objective of this study was to analyze the patterns of biodiversity of non-marine turtles in island-rich Southeast Asia, a megadiversity area for turtles and other organisms. Since modern patterns of species richness are the result of adaptation, dispersal, speciation, human transport, extinction and vicariance events, it is important to place biodiversity studies within the context of zoogeography in an attempt to elucidate the processes shaping today's patterns (Cox et al., 1976). The geological history of Southeast Asia and its effect on various groups of plants and animals have been studied intensively (see reviews by Whitten et al., 1987a, 1987b), thus providing an opportunity to test patterns of one group against that of another in an effort to ascertain congruence. Non-marine turtles provide an interesting group to study due to their potentially high dispersal capability in island systems compared to other non-volant vertebrates.

METHODS AND MATERIALS

For the purpose of this analysis, Southeast Asia was considered to be all of the Southeast Asian land mass and associated islands south of 20 degrees North latitude, east of approximately 92 degrees East longitude, and west of 127 degrees East longitude (Figure 1). Most of the land in this area sits on the Sunda Shelf, a shallow continental shelf approximated by the 120 m bathymetric line. With the exception of the Philippines and the island of Sulawesi, this area is generally west of Wallace's Line (Whitten et al., 1987a) demarcating the separation between the Oriental and Australian zoogeographic regions. The area of interest was divided into seven major land masses based primarily on the insular nature of the Indo-Malay Archipelago including Sumatra, Borneo, Java, Sulawesi, and the Philippines. Due to the depauperate turtle fauna of the Philippines, the island nation was treated as a single unit in subsequent analyses even though it is composed of over 7,000 individual islands. Two other land masses were considered. The first is Peninsular Malaysia south of its connection with mainland Asia at the Isthmus of Kra. Although not an island, its peninsular geometry and faunal similarity to the other large islands on the Sunda Shelf give it an insular quality (Heaney, 1991a). The second continental land mass considered, the Indochinese Peninsula (hereafter Indochina), was defined as mainland Southeast Asia north of the Isthmus of Kra, south of 20 degrees North latitude, and west of approximately 92 degrees East longitude. The great diversity of turtles in the region, coupled with its proximity and faunal similarity to the islands to the south, establish the area as an important mainland reference point. Land area of the various regions was obtained from atlases or measured from an Azimuthal projection map with a compensating polar planimeter.

The list of turtle species occupying the seven geographic regions discussed above (Table 1) was generated from the distribution maps of Iverson (1992c). Questionable records, namely those for *Indotestudo forstenii* from Sulawesi (see Hoogmoed and Crumly, 1984) and *Geoemyda spengleri* from Borneo, were not included. Analyses

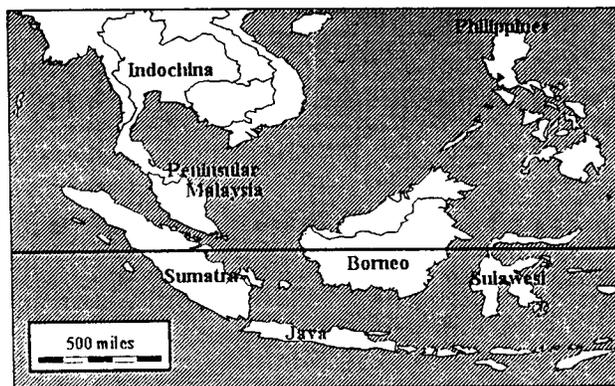


FIGURE 1. Map of the study area defined in the text. The dark horizontal line represents the equator.

were undertaken with full recognition that the ranges of some species are poorly known and that the taxonomy and systematic arrangements of Southeast Asian turtle families, including the Bataguridae (Hirayama, 1984; Sites et al., 1984; Gaffney and Meylan, 1988), Testudinidae (Crumly, 1988), and Trionychidae

TABLE 1
List of Turtle Species Occupying the Geographic Regions Discussed in the Text.
Species Presence is Indicated with an "x".

| Family/Species | Region | | | | | | |
|------------------------------------|-----------|----------|---------|------|--------|----------|-------------|
| | Indochina | Malaysia | Sumatra | Java | Borneo | Sulawesi | Philippines |
| Bataguridae | | | | | | | |
| <i>Annamemys annamensis</i> | x | | | | | | |
| <i>Batagur baska</i> | x | | x | | | | |
| <i>Callagur borneoensis</i> | | x | x | | x | | |
| <i>Cuora amboinensis</i> | x | x | x | x | x | x | x |
| <i>Cuora galbinifrons</i> | x | | | | | | |
| <i>Cyclemys dentata</i> | x | x | x | x | x | | x |
| <i>Cyclemys tcheponensis</i> | x | | | | | | |
| <i>Geoemyda spengleri</i> | x | | | | | | |
| <i>Heosemys grandis</i> | x | x | | | | | |
| <i>Heosemys leytenis</i> | | | | | | | x |
| <i>Heosemys spinosa</i> | | x | x | | x | | |
| <i>Hieremys annandalii</i> | x | x | | | | | |
| <i>Hardella thurji</i> | x | | | | | | |
| <i>Kachuga trivittata</i> | x | | | | | | |
| <i>Malayemys subtrijuga</i> | x | x | x | x | | | |
| <i>Mauremys mutica</i> | x | | | | | | |
| <i>Melanochelys trijuga</i> | x | | | | | | |
| <i>Morenia ocellata</i> | x | x | | | | | |
| <i>Notochelys platynota</i> | x | x | x | x | x | | |
| <i>Ocadia sinensis</i> | x | | | | | | |
| <i>Orlitia borneensis</i> | | x | x | | x | | |
| <i>Pyxidea mouhotii</i> | x | | | | | | |
| <i>Sacalia quadriocellata</i> | x | | | | | | |
| <i>Siebenrockiella crassicolis</i> | x | x | x | x | x | | |
| Platysternidae | | | | | | | |
| <i>Platysternon megacephalum</i> | x | x | | | | | |
| Testudinidae | | | | | | | |
| <i>Geochelone platynota</i> | x | | | | | | |
| <i>Indotestudo elongata</i> | x | x | | | | | |
| <i>Manouria emys</i> | x | x | x | x | | | |
| <i>Manouria impressa</i> | x | x | | | | | |
| Trionychidae | | | | | | | |
| <i>Lissemys scutata</i> | x | | | | | | |
| <i>Amyda cartilaginea</i> | x | x | x | x | x | | |
| <i>Chitra indica</i> | x | | | | | | |
| <i>Dogania subplana</i> | x | x | x | x | x | | |
| <i>Nilssonina formosa</i> | x | | | | | | |
| <i>Palea steindachneri</i> | x | | | | | | |
| <i>Pelochelys bibroni</i> | x | x | x | x | x | | x |
| <i>Pelodiscus sinensis</i> | x | | | | | | |

(Meylan, 1987), will change as new species are described and phylogenies are reconstructed. Nevertheless, enough information has accumulated to allow at least a preliminary analysis.

Pairwise comparisons of geographic regions were made using Jaccard Coefficients (Cheetham and Hazel, 1969). Values range from 0 in cases where no species are shared between regions, to 1 in cases where the same suite of species are found in both regions. Faunal similarities among regions were grouped using cluster analysis with the single linkage method (Wilkinson, 1986). Species area relationships were fitted using least squares regression.

RESULTS

A total of 37 non-marine turtle species, representing 31 genera and four families, are found in the area of interest (Table 1). The greatest number of species occur in Indochina (33) followed in decreasing order by Peninsular Malaysia (19), Sumatra (13), Borneo (11), Java (8), the Philippines (4), and Sulawesi (1). Overall, the regions closest to the Indochinese Peninsula show fairly high similarity (Table 2). The most similar faunas occur between Sumatra and Borneo, Sumatra and Java, and Peninsular Malaysia and Borneo. Slightly less than one-half of the species found in Indochina are found below the Isthmus of Kra in Peninsular Malaysia. Faunal similarity declines precipitously as distance between regions increases along an east-west axis.

Only one species, *Cuora amboinensis*, is found in all seven geographic regions. However, recent taxonomic work with the genus *Cuora* suggests that it is more speciose than previously recognized (Ernst and Lovich, 1990; McCord and Iverson, 1991; Pritchard and McCord, 1991). The wide range of *Cuora amboinensis*, coupled with island specific variation, suggests that it may actually consist of more than one species (Carl Ernst, pers. comm.). *Heosemys leytensis* of the Philippines is the only insular endemic in the region, although several species including *Annamemys annamensis*, *Kachuga trivittata*, and *Geochelone platynota* have relatively restricted geographic distributions.

A dendrogram produced by single linkage clustering of all geographic regions shows that Indochina is distinct from the remaining regions (Figure 2). The next

TABLE 2
Matrix of Jaccard Coefficients for All Pairwise Comparisons of
the Geographic Regions Discussed in the Text.

| | Indochina | Malaysia | Sumatra | Java | Borneo | Sulawesi |
|-------------|-----------|----------|---------|------|--------|----------|
| Malaysia | 0.44 | — | — | — | — | — |
| Sumatra | 0.28 | 0.68 | — | — | — | — |
| Java | 0.24 | 0.42 | 0.62 | — | — | — |
| Borneo | 0.22 | 0.58 | 0.85 | 0.58 | — | — |
| Sulawesi | 0.03 | 0.05 | 0.08 | 0.13 | 0.09 | — |
| Philippines | 0.08 | 0.15 | 0.21 | 0.33 | 0.25 | 0.25 |

branch occurs between the Philippines and Sulawesi combined, and Pensinsular Malaysia, Borneo, Java, and Sumatra. Pensinsular Malaysia then branches from the other three, and within the latter group, Borneo and Sumatra form another cluster.

The relationship between land area and number of species (Figure 3) is significantly positive ($r=0.76$; $P=0.05$). Land area explains 58% of the variance in number of species when fitted with the following model

$$\text{NUMBER OF SPECIES} = 2.488 + [(2.20401 \times 10^{-5}) \times \text{AREA}].$$

The relationship between the two variables is improved ($r=0.89$; $P<0.01$) when Pensinsular Malaysia is removed from the analysis as an outlier. Similarly, the

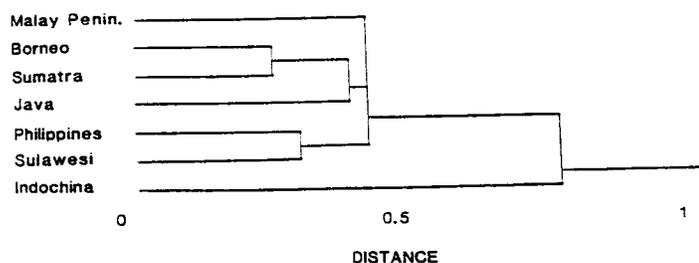


FIGURE 2. Dendrogram of species similarity for the geographic regions discussed in the text. Euclidean distance is shown on the abscissa.

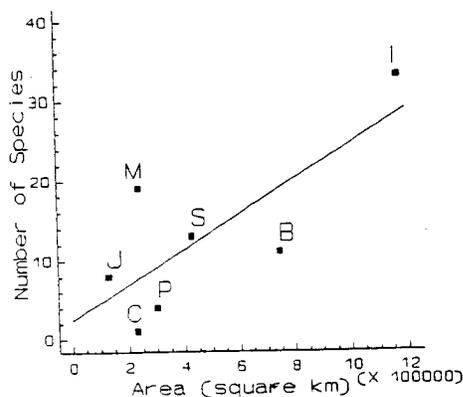


FIGURE 3. Species/area relationship for the geographic regions discussed in the text. Abbreviations are as follows: B = Borneo, C = Sulawesi, I = Indochinese Peninsula, J = Java, M = Peninsular Malaysia, P = Philippines, and S = Sumatra.

relationship between land area and number of genera is significantly positive ($r = 0.77$; $P = 0.04$). Land area explains 60% of the variance in number of genera using the following model (including Peninsular Malaysia)

$$\text{NUMBER OF GENERA} = 2.716 + [(2.00074 \times 10^{-5}) \times \text{AREA}].$$

The relationship between land area and genera is improved ($r = 0.89$; $P < 0.01$) when Peninsular Malaysia is removed from the analysis as an outlier.

DISCUSSION

The modern distribution of the biota of Southeast Asia is shaped largely by the geological history of the area. According to references summarized in BurrIDGE (1992), Peninsular Malaysia, eastern Sumatra, and western Borneo were tectonically stable by the early Tertiary. Some evidence suggests that Sulawesi collided with Borneo in the late Pliocene approximately 3 million years before present (BP), but it is more likely that they have been separated for at least 25 million years (Whitten et al., 1987a), and possibly since the Mesozoic (Inger, 1966). The Philippine Islands originated from the ocean floor during the Miocene and Pliocene (Heaney, 1991a).

During the Pleistocene, most of the islands on the Sunda Shelf were repeatedly connected with and isolated from each other and the mainland due to fluctuating sea levels. In the period of maximum glacial development during the middle Pleistocene, sea levels fell 160 m, and during glacial maxima in the late Pleistocene sea levels fell 120 m (Heaney, 1991b). The most recent exposure of the Sunda Shelf (Sundaland) occurred 11,170-15,000 years BP (BurrIDGE, 1992). The Palawan chain of the Philippines joined Sundaland during the middle Pleistocene, but the other islands of the Philippines remained isolated (Heaney, 1991a). During the last inundation of Sundaland, Sumatra was isolated first from Java, then from Borneo, and finally from Peninsular Malaysia; a sequence mirrored in the degree of similarity between regional biotas (Whitten et al., 1987b).

Most non-marine turtles, or their ancestors, invaded Sundaland from Indochina since none of the modern families of non-marine turtles in Southeast Asia are known from Australia. The Isthmus of Kra was an effective filter to dispersal since less than half of the turtle species found in Indochina today are represented in the fauna south of the Isthmus. The effectiveness of the filter is reflected in the flora of Southeast Asia as 375 plant genera reach the northern limit of distribution at the Isthmus, and 200 genera reach their southern limit at the same point (Whitten et al., 1987b). The Isthmus demarcates relatively dry vegetative communities to the north and relatively wet communities to the south. If other turtle species managed to pass through the filter, they may have become extinct due to rising sea levels in Sundaland and associated changes in the environment.

Non-marine turtle dispersal into Sundaland may have been through large river systems that existed when Sundaland was exposed. For example, the drainage pattern of the North Sunda River once linked the west coast of Sumatra and the east coast of Borneo with west Malaysia, and the East Sunda River linked southern Sumatra with Java and Borneo (BurrIDGE, 1992). As continental glaciers melted

and sea levels rose, colonizing turtle species were isolated in the headwaters of these ancient rivers. Several waves of colonization must have occurred due to repeated exposure of the Sunda Shelf. Extinction and speciation undoubtedly occurred following colonization and isolation, as seen in the case of the endemic species *Heosemys leytenis* in the Philippines.

Some turtles are capable, or potentially capable, of dispersal over land and across saltwater barriers. Several Southeast Asian species including *Batagur baska*, *Callagur borneoensis* (Dunson and Moll, 1980; Davenport and Wong, 1986), and *Pelochelys bibroni* (Ernst and Barbour, 1989) tolerate euryhaline conditions predisposing them for dispersal in marine archipelagos. This capability may explain the wide distribution of *Pelochelys*, but it does not explain the absence of *Batagur* from Java and Borneo, or the absence of *Callagur* from Java. Tortoises (Testudinidae) are well known for their ability to float (Patterson, 1973; Branch, 1991), but this capability does not seem to have fostered wide distribution in Sundaland. The depauperate turtle fauna of Sulawesi, long isolated from Borneo, may be due to the fact that many non-marine turtles, including highly aquatic species, require land connections to facilitate dispersal.

In general, species diversity decreases as distance from mainland Asia increases. The pattern of diversity decreasing with distance from a mainland is often characteristic of peninsulas as demonstrated for turtles on the Florida peninsula by Iverson and Etchberger (1989) (but, see Busack and Hedges, 1984). The connection of modern islands on the Sunda Shelf to mainland Asia would have created a peninsula for colonization during periods of lowered sea level. Apparently, few species of non-marine turtles were able to colonize the eastern end of Sundaland as shown by the depauperate modern fauna. Alternatively, extinction rates may have been higher in eastern Sundaland, but information is currently not available to test this hypothesis.

Patterns of turtle species diversity in Southeast Asia generally parallel those of other biota. For example, Java is more different from Sumatra than are Borneo or Peninsular Malaysia (Whitten et al., 1987b), and the biotas of the Philippines, and particularly Sulawesi, generally share few species with the Asian mainland and the intervening large islands. The pattern of increasing turtle diversity with increasing "island" size is mirrored in numerous other groups including plants, other reptiles, birds, and mammals (Whitten et al., 1987a, 1987b; Heaney, 1991b). Peninsular Malaysia stands out among the geographic regions as having exceptional turtle diversity for its size; a possible consequence of its land connection to species rich Indochina.

The rarity of endemic turtle species on islands in the area contrasts with high insular endemism in other biota. Sixty-one percent of the fruit bats in the Philippines are endemic (Heaney, 1991b) and many species of rats are endemic to Sulawesi (Whitten et al., 1987b). The low degree of island endemism in Southeast Asian turtles may be due to high levels of gene exchange among aquatic turtle populations (Scribner et al., 1984). Alternatively, endemism may be masked by a our current perception of the systematics and taxonomy of Southeast Asian turtles.

Southeast Asia has a "megadiverse" turtle fauna with approximately 14% of the world's species. The factors responsible for such a diverse turtle fauna are unknown,

but Iverson and Etchberger (1989) and Iverson (1992b) suggested that high turtle diversity in a geographic area is correlated with abundant rainfall, an environmental characteristic of Southeast Asia. The overall homogeneity of species richness patterns throughout Sundaland implies a commonality of processes shaping the distribution of a diverse biota (Heaney, 1991b). The similarity of patterns for turtles and other groups is of interest because of the diversity of modes of dispersal available to turtles (floating, swimming, overland travel, or a combination thereof).

Humans are exerting an increasingly devastating effect on Southeast Asian ecosystems (Aiken and Moss, 1975; Mittermeier and Konstant, 1982). As a result, some turtle populations are declining (Moll, 1976). The future of a diverse turtle fauna in Southeast Asia depends on implementation of effective conservation strategies and establishment of functional preserves or preserve systems. Given the great diversity of turtles in Indochina and Peninsular Malaysia, immediate attention should be directed to these areas.

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