# Primate Hotspots on Borneo: Predictive Value for General Biodiversity and the Effects of Taxonomy

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**Abstract:** *The identification of hotspots, or geographic areas that are particularly rich in biodiversity, is increasingly used to set conservation priorities. We investigated the spatial patterns of primate species richness and endemism in Borneo to assess whether primates are good indicators of biodiversity hotspots for other taxa. Based on locality records for the 13 primate species present on the island (*n *= 1414, range 26–273 records/species), we prepared primate distribution maps. By overlaying these distribution maps in a geographic information system, we created maps that revealed the most species-rich area to be a tropical wet evergreen forest in central-eastern East Kalimantan, Indonesia, in which 11 species coexisted. No other studies had so far identified this region as a biodiversity hotspot. Generally, the Malaysian states of Sabah and Sarawak are considered richest in general species diversity. We suggest that the main reason for this is the low number of biodiversity studies that have been conducted in Indonesian Borneo compared with Malaysian Borneo and a focus in biodiversity studies on mountain habitats rather than lowlands. We used two alternative taxonomic classifications of Bornean primates, one based on a biological and the other on a phylogenetic species concept, to determine whether the outcome of hotspot identification depended on taxonomic classification. The location of endemic primate species hotspots depended on the choice of species concept, whereas identification of the hotspots of primate species richness was not affected by choice of species concept. Our results suggest that a hotspot identification based on a relatively small group of taxa can vary with the group of species under investigation and their taxonomic classifications. Because of the lack of congruence between fine-scale hotspots of Bornean primate diversity and other hotspots reported in the literature, Bornean primates appear unsuitable for identifying areas of general species richness. Bornean primates may, however, be useful indicators of lowland diversity on the island.*

Áreas Prioritarias para Primates en Borneo: Valor Predictivo para la Biodiversidad General y los Efectos de la Taxonomía

**Resumen:** *La identificación de áreas prioritarias o geográficas particularmente ricas en biodiversidad se utiliza cada vez más para establecer prioridades de conservación. Investigamos los patrones espaciales de riqueza y endemismo de especies de primates en Borneo para determinar si los primates son buenos indicadores de áreas prioritarias de biodiversidad para otros taxones. Preparamos mapas de distribución de primates basados en localidades de registro para las 13 especies de primates presentes en la isla (*n *= 1414, rango 26–273 registros/especies). Al superponer estos mapas de distribución sobre un sistema de información geográfica, generamos mapas de los que se pudo concluir que el área con mayor riqueza de especies es el bosque tropical húmedo del centro-este de Kalimantan Oriental, Indonesia, en el que coexisten 11 especies. Ningún estudio anterior había identificado esta región como un área prioritaria para la biodiversidad. Por lo general, los estados malayos de Sabah y Sarawak se consideran los más ricos en cuanto a diversidad de especies en general. Postulamos que la razón principal para esto es el número reducido de estudios de biodiversidad en Borneo indonesio comparado con Borneo malayo y el mayor enfoque de los estudios de biodiversidad sobre hábitats montañosos en lugar de tierras bajas. Para determinar si el producto de la iden-*

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*tificación de áreas prioritarias dependía de la clasificación taxonómica utilizamos dos clasificaciones taxonómicas alternativas de primates de Borneo, una basada en un concepto biológico de especie y otra en un concepto filogenético. La ubicación de áreas prioritarias para especies endémicas de primates dependió de la elección del concepto de especie, mientras que las áreas prioritarias en cuanto a la riqueza de especies de primates no fueron afectadas por el concepto de especie. Nuestros resultados sugieren que la identificación de un área prioritaria basada en un grupo de taxones relativamente pequeño puede variar con el grupo de especies a investigar y con sus clasificaciones taxonómicas. Debido a la falta de congruencia entre las áreas prioritarias de diversidad de primates de Borneo a escala detallada y otras citadas en la bibliografia, los primates de Borneo no serían adecuados para identificar áreas de riqueza de especies en general. Los primates de Borneo podrían, sin embargo, ser indicadores útiles de la diversidad en tierras bajas de la isla.*

## Introduction

The purpose of a conservation network is ultimately to ensure the persistence of valued biodiversity (Frankel & Soulé 1981). Persistence is affected by processes depending on intrinsic factors (e.g., ecological, demographic, and genetic) and extrinsic factors (e.g., habitat clearance and degradation, overexploitation, introduced species) (Araújo & Williams 2000). From the early 1980s onward, conservationists have recognized the importance of regional concentrations of species (hotspots) for the identification of sites for biodiversity preservation (e.g., Myers 1988; Prendergast et al. 1993; Dobson et al. 1997; Harcourt 2000; Myers et al. 2000). Definitions of these hotspots vary considerably. Myers et al. (2000) defined them as "areas featuring exceptional concentrations of endemic species and experiencing loss of habitat." They identified 25 global hotspots designated for priority conservation, each of which contained endemic plant species comprising at least 0.5% of all plant species worldwide. Myers et al.'s (2000) specific definition of a hotspot continues to be used today. More generally, however, the term hotspot is now applied to any geographical area that ranks particularly high in species richness, level of endemism, number of rare or threatened species, and intensity of threat (Reid 1998). Examples include the GAP analysis program, which uses hotspots to identify gaps in the existing network of protected areas (Kiester et al. 1996; Jepson et al. 2002), and the mapping of restricted-range bird species (Stattersfield et al. 1998).

In theory, if hotspots coincide for a great many taxa, then less area needs to be conserved to protect biodiversity, and in turn it is more likely that biodiversity will be protected. Unfortunately, the hope that areas of high diversity overlap for different taxa appears in many cases to be in vain (e.g., Prendergast et al. 1993; Howard et al. 1998; Jaarsveld et al. 1998; Harcourt 2000). Still, because species-distribution data for most taxa are limited or unavailable, it is common practice to select a small, relatively well-known group to be predictors of diversity in less-studied groups (Hacker et al. 1998; Stattersfield et al 1998; Sluys 1999). Selection of conservation-priority areas can then be based on the patterns (endemism, species richness) found in well-studied indicator groups.

We investigated two aspects of biodiversity hotspots. First, we investigated whether regional concentrations (hotspots) of species diversity for a well-studied group have any predictive value for those of other taxa. Second, we investigated whether taxon-based hotspots are real or apparent (i.e., whether they depend on any particular taxonomic classification) and whether hotspot identification is more a reflection of where extensive collecting and field work has taken place than where biodiversity resides. We addressed these questions at a finer scale than those of many previous hotspot analyses by restricting our study area to the Southeast Asian island of Borneo and by studying a small group of species, Bornean primates.

In comparison with many other taxa, primates are mostly large, easily observable, diurnal species. They are thus relatively well studied (Rowe 1996). The island of Borneo harbors 13 species of nonhuman primates, 5 of which are endemic (but see Table 1) (Groves 1993). We compiled locality records of all primates on the island and combined them with data on the ecology of the respective species (habitat preference, elevational distribution) to create distribution maps. Based on these maps, we analyzed patterns of endemism and species richness of primates on Borneo.

## Methods

Primate locality records were obtained through direct observations by E.M. from 1994 to 2000 and V.N. in 1996 and 1999–2001, with a total survey effort of more than 400 field days. Surveys covered all major river systems of West, Central, and East Kalimantan and the mountainous areas of Central and East Kalimantan (for geographic names of the states and provinces, see Fig. 1). Several surveys were taken in the Malaysian states of Sabah and Sarawak and in Brunei. We also conducted semi-structured interviews with local people (often hunters) in Bahasa Indonesia, the Indonesian language, which is also understood in the Malaysian states and Brunei. We

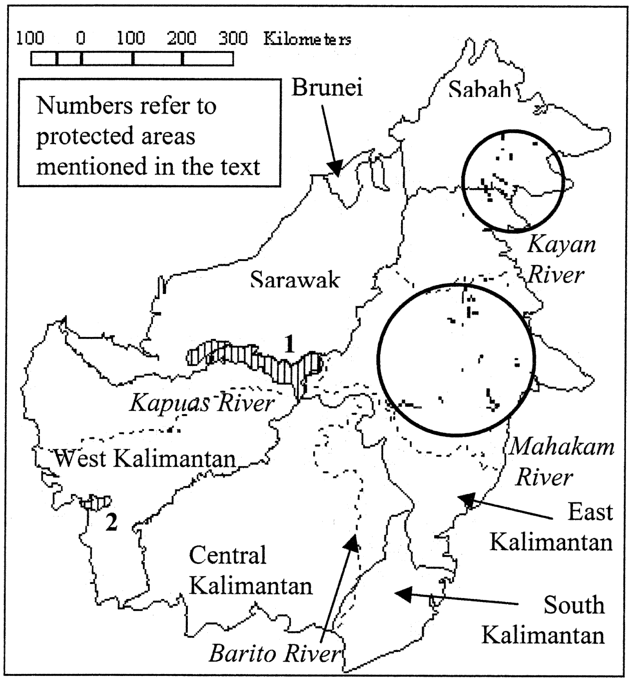


*Figure 1. Grid cells in which the distribution ranges of 10 primate species overlap (small black squares in circled areas): 1, Lanjak-Entimau, Batang Ai, and Bentuang Karimun national parks; 2, Gunung Palung National Park.*

included information from local people only when at least two independent sources indicated the presence of a particular species in an area (for details see Meijaard & Nijman 2000).

Further information on primate distribution was obtained from secondary sources such as the environmental impact assessment reports of Kalimantan's logging concessions. We consulted 153 reports, of which we rejected 38 because the information appeared unreliable. The collections of the zoological museums of Amsterdam, Leiden, Bogor, London, and Singapore were also consulted. We obtained additional information from the literature and from biologists and conservationists working in the area.

We chose geographic information system software, PC ArcView, to enter and analyze our geographically referenced records. Other spatial data layers included the mid-1990s forest-cover types (World Conservation Monitoring Centre [WCMC] database), topography, and established and proposed conservation areas. We divided primate habitat into six classes (Table 1). Riverine forest (RF) is normally included in the tropical wet evergreen forest class, but for species that show a strong association with riverine forest (for instance, the proboscis monkey; Meijaard & Nijman 2000) we created a separate category. (Scientific names of primate species are provided in Table 1.) We defined riverine forest as that within 2 km of a large river and situated below 500 m above sea level. We extracted the map by putting a buffer of 2 km around the rivers provided by the WCMC databases.

We created distribution maps by selecting the species-specific vegetation-class polygons that contained presence records for each of the primate species. We edited these with on-screen digitizing when particular geographical features—mountain ranges or rivers—were known to delimit the distribution range or when it was expected that small forest areas that did not contain a presence record would nevertheless belong to the species' distribution range (e.g., when all forest areas around a forest polygon contained presence records). Thus, we inferred primate distribution using a combination of actual records, potential habitat, vegetation continuity, and our knowledge of the area and species. This may have resulted in an underestimation of the total range, especially in areas where we did not obtain any primate records.

With the spatial analyst function of ArcView, we converted the distribution maps from vector to grid coverage because spatial analysis and overlay is easier in this format. The conversion enabled us to overlay the primate distributions and make comparisons on a cell-by-cell basis. We chose a raster cell size of 0.05° (approximately 5.4 × 5.4 km), which we considered realistic with regard to the species' ranging patterns. We assessed the accuracy of our distribution maps by comparing 113 randomly selected primate species records (which we obtained after completing the mapping) with our model's prediction of primate species presence and absence in the localities of each of these 113 records. These sightings were reported by Duckworth (1997), Yasuma and Abdullah (1997), Hedges and Meijaard (1999), Setyawati (1999), Chong (2001), and William (2001), or made by V.N. during a 2002 survey in East Kalimantan. Finally, to investigate the effect of taxonomic classification on hotspots of endemic species, we mapped the overlapping ranges of endemic species according to two different taxonomic classifications, one based on a biological species concept (BSC) (Mayr 1942) and one on a phylogenetic species concept (PSC) (Cracraft 1983) (Table 1).

## Results

We documented 1414 locality records for the 13 species combined, ranging from 26 locality records for the banded leaf monkey to 273 records for the orangutan. We intend to publish the detailed data elsewhere. Our model correctly predicted the presence of a primate species in 84 of the 113 test records used for the post-

**Table 1. Bornean primate species according to two taxonomic classifications.**

| Letter code | Common and scientific name | Classification[a] 1 | Classification[a] 2 | IUCN[b] | Number of records | Habitat types[c] |
|---|---|---|---|---|---|---|
| A | orangutan *Pongo pygmaeus* | not endemic | endemic | EN | 273 | all, excluding MF |
| B | agile gibbon *Hylobates agilis* | not endemic | endemic | LR/nt | 70 | TWE, PSF, FWS |
| C | Bornean gibbon *Hylobates muelleri* | endemic | endemic | LR/nt | 164 | TWE, PSF, FWS |
| D | banded leaf monkey *Presbytis femoralis* | not endemic | endemic[d] | DD | 26 | TWE |
| E | Bornean leaf monkey *Presbytis hosei* | endemic | endemic | DD | 84 | TWE, TME |
| F | white-fronted leaf monkey *Presbytis frontata* | endemic | endemic | DD | 72 | TWE |
| G | maroon leaf monkey *Presbytis rubicunda* | endemic | endemic | DD | 190 | all, excluding MF, FWS |
| H | proboscis monkey *Nasalis larvatus* | endemic | endemic | EN | 153 | PSF, FWS, MF, RF (2 km) |
| I | silvered langur *Trachypithecus cristatus* | not endemic | not endemic | VU/DD[e] | 100 | PSF, FWS, MF, RF (2 km) |
| J | pig-tailed macaque *Macaca nemestrina* | not endemic | not endemic | VU | 106 | TWE, TME, PSF |
| K | long-tailed macaque *Macaca fascicularis* | not endemic | not endemic | LR/nt | 219 | all, excluding TME |
| L | slow loris *Nycticebus coucang* | not endemic | not endemic | DD | 67 | TWE, PSF, FWS |
| M | western tarsier *Tarsius bancanus* | not endemic | not endemic | DD | 61 | TWE |
| | total endemics | 5 | 8 | | | |

[a]*Classification 1 follows Groves (1993) and classification 2 follows Groves (2001). Taxa labeled endemic are endemic to Borneo.*
[b]*World Conservation Union (IUCN) threatened species categories (Hilton-Taylor 2000): EN, endangered; LR/nt, lower risk/near threatened; DD, data deficient; VU, vulnerable.*
[c]*Habitat types: MF, mangrove forest; FWS, freshwater swamp; PSF, peat swamp forest; TWE, tropical wet evergreen forest; TME, tropical montane evergreen forest; RF, riverine forest.*
[d]*Here named* Presbytis chrysomelas.
[e]*Hilton-Taylor (2000) split this taxon into two new species:* T. auratus *(status VU) and* T. villosus *(status DD). The ranges of both species occur partly on Borneo.*

modeling accuracy assessment; in 29 cases our model did not predict the recorded primate species in that particular location. Most of the mismatched cases (observed, but not predicted by the model) were found in small, isolated forest patches that the software had excluded from the polygon-grid conversion because they were either smaller than 25 $km^2$ or they only partly overlapped with the location of the grid cell. We also found mismatched cases in which the range of a species had been extended considerably by new records—such as for the banded leaf monkey studied by Duckworth (1997) or the white-fronted leaf monkey studied by Setyawati (1999). Finally, our predictions of the distributions of the silvered leaf monkey and long-tailed macaque were poor, with 60% and 63% of the records correctly predicted, respectively. This suggested that these species occur in a wider range of vegetation types—including small forest patches and essentially nonforest habitats—than indicated by Table 1.

Two of the endemic primates deserve special mention. The white-fronted leaf monkey was believed to have a disjunct distribution, with populations in Sarawak separated from those in East and South Kalimantan (Eudey 1987; Oates et al. 1994; Rowe 1996). However, the central part of the island (e.g., the Lanjak-Entimau, Batang Ai, and Bentuang Karimun national parks [no. 1 in Fig. 1] and the confluence of the Kapuas and the Mahakam Rivers) seems to be the only area where the species is common (Blouch 1997; J. K. Gurmaya, personal communication). Furthermore J. M. Lammertink (personal communication) reported a population near Gunung Palung National Park, West Kalimantan (no. 2 in Fig. 1), and Setyawati (1999) reported the species in northern Central Kalimantan. The Bornean leaf monkey was confined to the northern part of Borneo. There did not seem to be a clear geographical barrier to explain the species' distribution, and we digitized the southern and western limit of the species' range along the farthest outlying records.

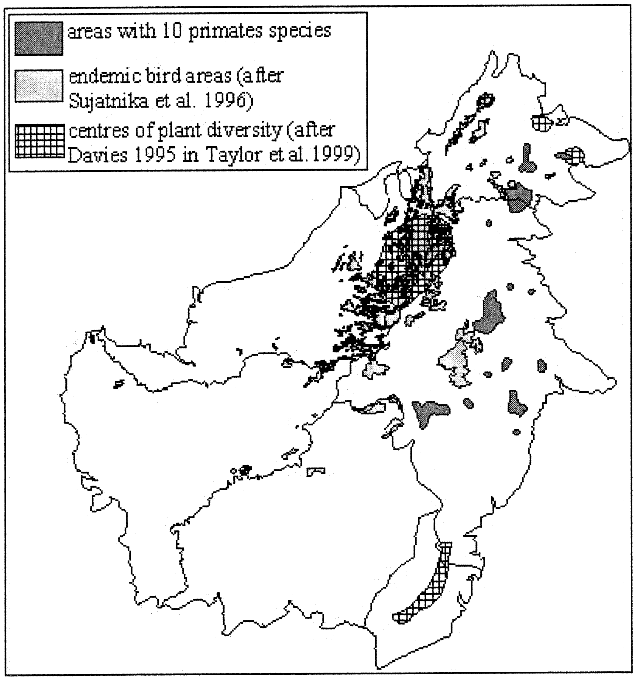


*Figure 2. Diversity hotspots in Borneo according to this research and other sources.*

The maximum number of species that occurred in a single grid cell was 11. The area where these 11 species coexisted consisted of tropical wet evergreen forest near large rivers in central-eastern East Kalimantan. It covered an area of only 410 $km^2$, although the small size of the area is likely to be an artifact of the cell size we used. The area where at least 10 species occurred (Fig. 1) was considerably larger and encompassed, besides central-eastern East Kalimantan (south of the Kayan River), the southeastern part of Sabah and northernmost East Kalimantan. Sarawak and Brunei (Fig. 1) had fewer species; South Kalimantan had the fewest species. The most species-rich areas were situated in the lowlands, below 500 m a.s.l., and the highest species concentrations were in tropical wet evergreen forest. The mountain areas of Borneo had considerably fewer species. The hotspots of 10 co-occurring primate species poorly matched with any previously recorded species richness hotspots (Fig. 2), most of which are located in the mountainous parts of Borneo. The taxonomic classification, either using the BSC (Groves 1993) or the PSC (Groves 2001), had no effect on the hotspots of co-occurring primate species.

The ranges of a maximum of five endemic species overlapped in central-eastern East Kalimantan when we used the BSC (Fig. 3a). Adopting the PSC resulted in several additional areas containing the overlapping ranges of five endemic species, and some contained six endemic species (Fig. 3b). With Groves' (2001) classification five endemic species coexisted in the Gunung Palung area (West Kalimantan), the Bentuang Karimun area (border West Kalimantan and Sarawak), and the southern part of Sabah.

## Discussion

Based on our accuracy assessment, we consider our method reliable enough for assessing overlaps in species distribution, but we recognize that our model excludes primates in small forest patches. In future research we will investigate alternative techniques for achieving more-detailed polygon-to-grid conversion. New primate records will also improve the accuracy of the model's predictions.

Our main finding was that the center of richness for primate species and for primate endemic species is in central East Kalimantan, an area not previously considered a biodiversity hotspot (cf. Sujatnika et al. 1995; Hauser et al. 1997; Taylor et al. 1999; Fig. 2). Restricted parts of northern Borneo have been identified as centers of endemism and as particularly species-rich for a number of taxa, including birds and mammals (e.g., Food and Agriculture Organization 1981; Brandon-Jones 1996; Taylor et al. 1999). For insect groups, such as cicadas (J. P. Duffels, personal communication), moths (Holloway 1978), and dung beetles (Davis 2000), the northern part of Borneo appears to be particularly species-rich. Sites of plant richness and endemism include the Meratus Mountains of South Kalimantan, northeastern Borneo including Sabah and northern East Kalimantan, and the north coast including Brunei and eastern Sarawak (MacKinnon et al. 1996). Other Bornean centers of endemism are associated with particular habitat types (e.g., caves, limestone regions, and heath forest; MacKinnon et al. 1996) or high elevation (Sujatnika et al. 1995; Wikramanayake et al. 2002).

Having established the lack of congruence between primate hotspots and diversity concentrations of other taxa, we investigated whether this is real or apparent. The geographic patterns in the diversity of Bornean nonprimate and endemic species could be a reflection of differences in sampling effort, showing a strong research bias toward the Malaysian states, especially Sabah, and more recently toward Sarawak. There appears to be much more literature on faunal and floral distribution for Malaysian than for Indonesian Borneo. Birds illustrate this research bias. Many species were thought to be confined to Mt. Kinabalu or the northern mountains in Sabah (Smythies 1981; MacKinnon & Phillipps 1993). Fieldwork in mountainous regions in Kalimantan, however, reveals that the "northern mountain endemics" are neither confined to the north nor to the highest mountains (Wilkinson et al. 1991; van Balen 1997, 1999, 2000). In fact, some of these "restricted-range species" have been recorded as far south and west as the Schwaner range

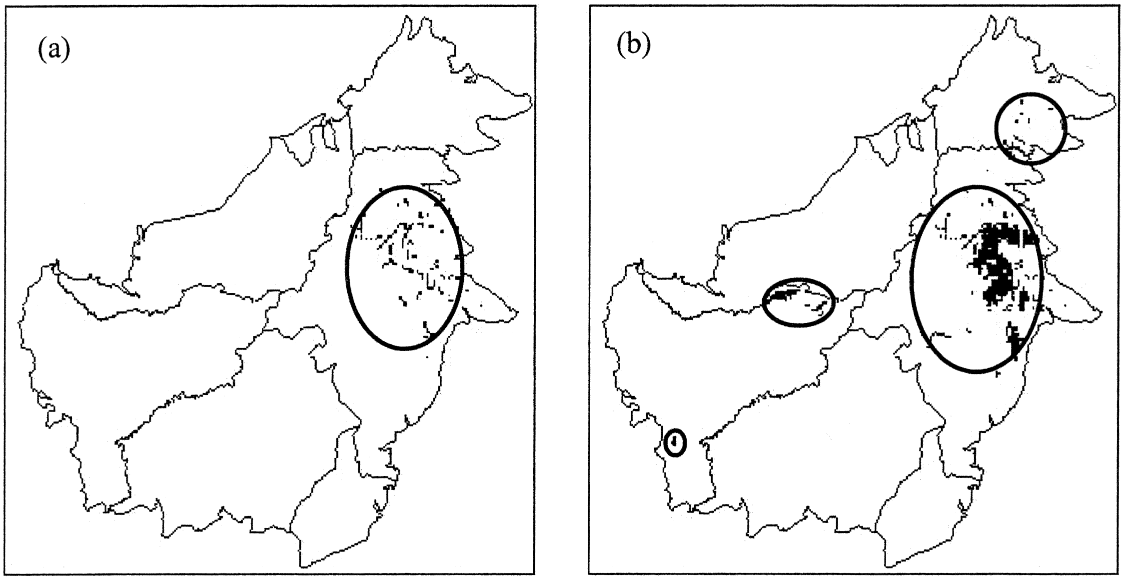


*Figure 3. Areas of five co-occurring endemic primate species: (a) according to the biological-species-concept classification by Groves (1993) and (b) the phylogenetic-species-concept classification by Groves (2001).*

(Rice 1989), Mt. Niut (Prieme & Heeregaard 1988), and the Meratus Mountains (Davison 1997). Similar examples exist for mammals. Based on recent surveys in Indonesian Borneo, Meijaard (1997) suggests that the bay cat (*Catopuma badia*), for which museum specimens suggest a restricted range in Sarawak and northern West Kalimantan (Sunquist et al. 1994), occurred throughout the island. Also, Page et al. (1997) found two "endemic species of northern and eastern Borneo," the black flying squirrel (*Aeromys tephromelas*) and grey tree rat (*Lenothrix canus*), in southern Central Kalimantan. It is therefore conceivable that future surveys in Indonesian Borneo could identify many new records and extend the distribution for the "restricted-range species" of Malaysian Borneo. Further analysis of these data might reveal hotspots in areas other than those identified above.

An alternative explanation for the lack of congruence between primate and diversity hotspots for birds, cicadas, moths, butterflies, and plants is that the speciation of Bornean primates may have been affected by different factors from other taxa. For example, few tropical primates occur exclusively on mountains, and speciation may have occurred during glacial periods when wet, evergreen lowland forest was restricted to refugia (Brandon-Jones 1996). Among birds, small mammals, plants, and many invertebrates, however, there are many mountain endemic species, which explains why diversity hotspots for these taxa are often centered on hills and mountains. If indeed diversity hotspots for primates were fundamentally different from those for other species, primates would be poor predictors of concentrations of general biodiversity. Primates may, however, be important indicators of hotspots for lowland specialists. In the zoological literature on Bornean endemism there appears to be a focus on those species restricted to mountains. More than half the Bornean endemic mammals are not restricted to mountains, however, and 35% could be considered lowland endemics (see Table 1.6 of MacKinnon et al. 1996). For such species, primates could be useful predictors of diversity patterns, although this remains to be tested.

The outcome of our primate hotspot analysis was to some extent related to which taxonomic classification and species concept we applied. Peterson and Navarro-Sigüenza (1998) found a similar effect of species concept on diversity and endemism patterns. They suggest that the BSC leads to a concentration of endemic species in central areas, with faunas increasingly rarefied in peripheral sites. A PSC, in contrast, often identifies species in small, isolated areas along the periphery of the species-distribution complex, making peripheral and particularly isolated areas richer in endemic species. We found a similar pattern with the application of Groves' (2001) PSC, which puts more emphasis on the peripheral areas of West Kalimantan and to a lesser extent northern Sarawak as centers for primate endemism. Full-species status for the Bornean orangutan did not affect patterns of endemism. If Hose's leaf monkey (*P. hosei*) actually consists of two or three—most likely allopatric—species, as suggested by C. P. Groves (personal communication), endemic richness could shift back toward Sabah, but only if we conducted a coarser-scale analysis, at say the full degree-square level or state level. (It is unlikely that the new *P. hosei* species would occur sympatrically within the 5.4 × 5.4 km grid cells we used.)

The dependence of fine-scale hotspots on taxonomy could be a considerable obstruction to accurate definition of hotspots, as long as we cannot agree on how to define species. Because in all kinds of studies species are generally seen as a basic unit, this uncertainty has resulted in a proliferation of species concepts and definitions (Sluys 1999). Two of these, the BSC and PSC are most commonly used in the taxonomy of vertebrates. Cracraft (1997) compared the BSC with the PSC and claimed that PSC species, not polytypic BSC species, are the most appropriate units for conservation. He argued that the PSC leads to a more precise classification of areas of endemism or biological richness than the BSC because the latter tends to underestimate the number of areas of endemism, tends to overestimate their size, and confounds the analysis of their historical relationships. These problems are avoided by the use of the PSC (Cracraft 1997). Sutherland (2000), however, maintains that the use of PSC (which he assumes leads to more species being recognized) can create an imbalance in prioritizing conservation efforts toward areas and species groups that happen to have attracted the attention of an adherer of the PSC. Collar (1996) and Sutherland (2000) furthermore maintain that the BSC tends to focus more on distinctive species than the egalitarian approach of the PSC. A simple solution is not at hand, because the choice of a particular species concept (be it BSC, PSC, or any other) is best determined by that aspect or process that forms the focus of a research agenda (Sluys & Hazevoet 1999). It is important, however, that when comparisons are made—for instance in assessing biodiversity patterns—caution should be employed in taking "species" from published lists or standard works at face value, and researchers should verify the internal structure of named entities whenever possible (Sluys & Hazevoet 1999).

Our results indicate that a thorough taxonomic analysis with an explicit formulation of the species concept adopted and homogeneously distributed species surveys are prerequisites for meaningful identification of biodiversity hotspots. Unfortunately, these prerequisites are rarely included in research efforts in the tropics of Southeast Asia, and the use of species hotspots is presently unlikely to provide a good tool for selecting which areas need to be protected. More research is needed on the reasons why species richness and endemism patterns differ among taxa and whether these distributions are attributable to their ecology and evolution or caused by human factors.

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