

Chapter 3

One Hundred Years of Solitude: Effects of Long-Term Forest Fragmentation on the Primate Community of Java, Indonesia

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Abstract Unlike many other tropical regions where large-scale habitat loss and habitat fragmentation is a recent phenomenon, deforestation on the island of Java, Indonesia, dates back to the first millennium AD. Today forest remains as numerous isolated patches, covering less than 10 % of the island. This makes it an excellent area to study the effect of forest fragmentation in long-lived animals, such as primates. I surveyed 31 forest fragments, ranging from 1 to 1,300 km², to assess the primate community composition. Fragments held between one and five species. Excluding the dry easternmost part of the island, there was a significant relationship between species number and fragments size, with a z -value (slope) of 0.20. A nestedness analysis showed the composition of the different fragments to be highly ordered, with smaller fragments comprising subsets of larger ones. True rainforest species, such as the Javan gibbon (*Hylobates moloch*), are the first species to disappear after isolation. Based on these analyses the minimum fragment size for an area to harbour the entire Javan primate community is between 50 and 400 km². The close relationship between fragment size, primate number, and rainforest dependence may explain the historic extinction of species, such as the siamang *Symphalangus syndactylus* and the orang-utan *Pongo* spp., from Java. With forest disappearing rapidly throughout Southeast Asia the patterns observed on Java allow us one potential view into the future for other regions if forest loss and fragmentation continue along their current trajectory.

It was the last that remained of a past whose annihilation had not taken place because it was still in a process of annihilation, consuming itself from within, ending at every moment but never ending its ending.

Gabriel García Márquez, *One Hundred Years of Solitude*, Harper Perennial, 1998

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Introduction

Due to its dynamic geological past (Holloway and Hall 1998), relatively stable climates (Gathorne-Hardy et al. 2002), and associated rapid speciation processes (Whitmore 1987), the Southeast Asian islands [Malaysia, Indonesia, and the Philippines, known as zoogeographically as Sundaland] are among the richest islands in the world in terms of biodiversity (Myers et al. 2000). A large number of the islands of Sundaland are merely highpoints of an immense shallow continental shelf. During Pleistocene glacial periods the shelf was exposed periodically as dry land allowing species to move through (parts of) the area (Beaufort 1926; Heaney 1985). Given its complex zoogeography (Heaney 1984; Meijaard 2003a, b) the area makes an excellent subject for studying the interrelationships of species richness, island area, and isolation (Harcourt 1999; Harrison et al. 2006; Heaney 1984, 1985; MacArthur and Wilson 1967; Meijaard 2003a, b; Nijman and Nekaris 2010; Nijman and Meijaard 2008; Wallace 1876; Wilcox 1980).

Small areas, be it islands, forest fragments, or sections of larger areas ('samples'), are expected to harbour less species than large areas. There have been many attempts to fit equations to such species–area relationships. The most widely model in use to date is a power-function model, usually expressed as a double-logarithmic transformation, $\log S = z \log A + \log k$, where S represents the number of species, A is the (island) area, and k and z are fitted parameters that describe intercept (the extrapolated fitted line intercepts the species number axis, that is, when area 'is zero' reflects the overall species richness of the study area) and slope (increase in species number as the area increases; Huggett 2004; MacArthur and Wilson 1967; Preston 1960). As a rule of thumb, for islands the values of the exponent z normally ranges from 0.24 to 0.34 (land-bridge islands tend to have smaller values than oceanic islands) and those for mainland samples fall within the range of 0.12–0.17.

Increasingly species–area relationships are used to assess the impacts of forest fragmentation in a biodiversity conservation context (Brooks et al. 1999a, b; Cowlshaw 1999; Kuussaari et al. 2009; van Balen 1999; Wilcox 1980). By comparing small forest fragments with larger ones, and under the assumption that the smaller one once harboured the same species community as the larger one at present, one can estimate extinction rates due to fragmentation (Brook et al. 2003; Diamond et al. 1987). Including a large number of fragments in the comparison allows one to assess minimal fragment sizes for individual species to persist, as well as which species or types of species are most affected by forest fragmentation. Instead of just considering species number in fragmentation studies, it may be worthwhile to consider the community compositions in the different fragments.

Nestedness is a measure of order in an ecological system, referring to the order in which the number of species is related to, for instance, area or degree of isolation. The more a system is 'nested' the more it is organised (Atmar and Patterson 1993). The concept has been frequently applied to questions concerning habitat fragmentation (Michalski and Peres 2005; van Balen 1999). Nestedness analysis gives a good picture of which species are most resilient to fragmentation and which

are not, and which fragments ‘behave’ idiosyncratic in terms of the primate community it has retained after isolation.

Difficulty with these assessments is that the theory behind species–area relationship is based on the explicit assumption of equilibrium (Loreau 2000) and indeed a nestedness analysis becomes less meaningful if species compositions change (rapidly) over time. When fragmentation is a recent event, fragments may contain more, especially long-lived, species than predicted by the species–area relationship, simply because equilibrium has not been reached (Cowlshaw 1999). Even in the absence of any change, over time more species will become extinct. A further problem with assessing the effects of habitat fragmentation in tropical regions is the often recent nature of habitat loss; many not yet reflect the final situation.

The island of Java in Indonesia, situated just south of the equator, is an excellent area to study the effects of long-term forest fragmentation. Densely populated, large-scale deforestation and concomitant forest fragmentation started >1,000 years ago (Whitten et al. 1996) and today little forest remains. Large-scale pattern of deforestation is properly documented, especially for the last 120 years or so. Here I report on the effects of long-term forest fragmentation on Java’s primate community.

Study Area and Its Primate Community

History of Forest Fragmentation on Java

The island of Java, Indonesia’s political and industrial centre, is one of the most densely populated areas in the world. The very fertile soils which lend themselves to terracing for irrigated rice sustain about 121 million inhabitants, at an average population density of 914 people km² (data from 2000: BPS 2004); this is a striking difference to other locations where the effects of fragmentation on primates have been studied (e.g., Amazon; 2 people km²: Chapman and Peres 2001). Java is largely deforested and most of the remaining 10 % forest cover (parts of) the numerous volcanoes on the island. Forest has been replaced by a mosaic of cities and villages, agricultural land, cash-crop plantations (e.g., coffee *Coffea* sp., tea *Camellia sinensis*), and forest plantations (e.g., teak *Tectona grandis*, Sumatran pine *Pinus merkusii*, rubber *Hevea brasiliensis*). Unlike many other tropical regions Java has a long history of cultivation and large-scale deforestation, which had already started in the first millennium AD (possible introduction of teak forest in the second to fifth century, introduction of irrigated rice field system in the eighth to tenth century) (Geertz 1963; Smiet 1990). Deforestation accelerated from the 1830s onwards when the Dutch colonial government imposed the so-called cultuurstelsel which lasted until 1870. To support this agro-economic system, farmers were forced to grow export crops on communal grounds, which were often forest (Whitten et al. 1996). By the end of the nineteenth century the natural forest was severely fragmented, and at the beginning of the last century the remaining forest, especially in the western provinces of Banten, West and Central Java, showed a fragmentation pattern very similar to that seen today.

While the people of Java have a long history of deforestation and intense agriculture, hunting, and in particular hunting of primates, has been, and is, less of an issue. The major religions that have been adopted by the people of Java (Geertz 1960; Ricklefs 2001) either revere primates or consider them unfit for consumption. Some 2,000 years ago two-way contact was established between Java's small coastal kingdoms and India. This ultimately resulted in the arrival of Buddhism and Hinduism to Java, with the former peaking in the seventh and eighth century AD and the latter in the fourteenth and fifteenth century AD (Geertz 1960). While both Buddhist and Hindu kingdoms cleared forest and developed the area for agriculture (Whitten et al. 1996), present-day Buddhist and Hindu attitudes towards primates suggest that hunting of primates may have been less of an issue than in other parts of the tropics. While attitudes towards primates may have changed considerably with the arrival of Islam to the island in the sixteenth century AD (in terms of human consumption, primates are considered *haram*—forbidden—under Islamic tenets), its effect in terms of hunting levels may have remained similar. At present over 90 % of the people on Java consider themselves Muslim, with small Hindu communities scattered around the island and Christian and Buddhist minorities living mainly in urbanised areas. Despite hunting not being a significant issue in studying the effects of forest fragmentation on primate communities in Java, capturing for the pet trade is. Despite legal protection, all species of Javan primates are offered for sale in animal markets, this probably having its greatest effect on Javan gibbons *Hylobates moloch* and Javan slow lorises *Nycticebus javanicus* (Nijman 2004; Thorn et al. 2009).

Java's Primate Community

The distribution pattern of primates on Java is determined by the severe degree of forest fragmentation, as well as by the climate (primarily rainfall, having its effect on forest type). The climate of Java differs greatly over the length of the island. In the central Javan mountains there is up to 9,000 mm of rain annually and not a single month with <200 mm, while in the easternmost corner annual rainfall is typically <1,000 mm annually and there is a pronounced dry season. In general the eastern part and the north coast have a marked dry season, whereas the western half does not. In Java rainforest only occurs in areas where the length of the dry season is short and hence can be mostly found in western Java and the slopes of the higher mountains in eastern Java (van Steenis and Schippers-Lammertse 1965).

The extant primate community of Java comprises five species. Three are endemic to the island, i.e., Javan gibbon found east to 109°49'E (Nijman 2006), the grizzled langur *Presbytis comata* found east to 111°19'E (Nijman 1997), and the Javan slow loris found east to 112°51'E (Thorn et al. 2009). The ebony langur *Trachypithecus auratus*, also occurs on the smaller islands of Bali and Lombok to the east of Java (Nijman 2000); and, the long-tailed macaque *Macaca fascicularis*, has a wider distribution including much of Southeast Asia (Nijman and Meijaard

2008). This sequence also reflects the species' dependence on rainforest, with the Javan gibbon being confined to it, and the long-tailed macaque additionally occurring in drier forest types, including mangrove forests.

Methods

Data Acquisition

Between 1994 and 2005 I surveyed 31 forest areas on Java for a total of ~350 days in the forest. While most national parks and larger nature reserves were included in the surveys over 80 % of the survey effort was outside the established protected area network. Small forest fragments may have visited for 1 or 2 days, often more, however, most large forest areas (>150 km²) were visited typically for some 2 weeks (median 13 days, range 3 days to 6 months). A forest area was considered a fragment if it was isolated from other natural forest areas by >1 km of non-forest land (this included tree plantations) and was judged to be isolated for at least 30 years. The latter was assessed using forestry maps presented by van Steenis and Schippers-Lammerste (1965) [forest cover ~1963], Anonymous [1938], and Hoogerwerf and Rengers Hora Siccama (1938) [forest cover early 1930s] and Koorders (1912) [forest cover ~1891]. Often forest fragments were very isolated with gaps of non-forested land of >10 km and were indeed isolated from other fragments for >100 years.

For each forest fragment I established which of the five species were present. For the nocturnal slow loris I largely relied on data from the literature, through correspondence with other primatologists, and less so on personal observations: in all likelihood this will have led to an under-recording of this species' presence but the pattern that emerged from the surveys is similar to that when using museum specimen data (Thorn et al. 2009).

The gibbons and the langurs are confined to forest (as is the slow loris), but the long-tailed macaque often can be found at the edge of the forest or outside forest areas. When recorded in close vicinity of the forest fragment it was included as being present, and if it was recorded a >0.5 km distance, it was not.

Analysis

The relationship between species-richness and fragment size was calculated using log-transformed data. The analysis was run for the entire dataset and, given that a number of species are confined to rainforest, to a subset of fragments that exclude the areas east of Mt Lawu [111°19E]. The resultant z-values were assessed to see if the fragments act as 'islands' or as 'samples'.

Atmar and Patterson (1993) introduced ‘temperature’ as a measure of nestedness. The calculation of ‘temperature’ is based on the number of unexpected occupied sites in the species–fragment matrix as well as unexpected unoccupied sites (gaps) and outliers. In studies of fragmentation, the temperature expresses the order in which species’ extinctions have occurred (in real island studies it reflects the order of colonisation). The ‘colder’ the system is, the more fixed the order of extinction is (in each fragment species 1 goes extinct first, then species 2, and so on) whereas in warmer systems, extinctions have taken place in a more random order. Temperatures range from 0° , indicating an absolutely fixed extinction pattern, to 100° indicating a total random pattern of extinction.

I used the nestedness temperature calculator (Atmar and Patterson 1995) to calculate the coolest matrix possible (i.e., the matrix with the highest degree of nestedness); significance of the model was tested by running 100 Monte Carlo simulations on the same programme.

Results

Species–Area Curves

When considering all 31 fragments, there is no significant relationship between area and species-richness. The relationship has a z -value of 0.108, with a mere 24 % of the variation in species-richness being explained by the area size. Focussing on fragments in the western three-quarters of the island only (21 fragments), there is a significant relationship between $\log S$ and $\log A$ with a z -value of 0.205, explaining 60 % of the variation (Fig. 3.1). Note that the z -value is what we typically find for real islands as opposed to samples. Hence, for primates the fragments act as islands and are truly isolated from one another.

Nestedness

Of the 31 fragments, six had all six primate species present, i.e., from west to east, Ujung Kulon [750 km²], Halimun [400 km²], Salak [50 km²], Gede Pangrango [150 km²], Telaga Warna [5 km²], and Dieng [255 km²]. These are represented by Dieng in the upper row of Fig. 3.2. The fill was 44.6 %. There was a very high degree of nestedness, expressing itself as a low system temperature of 7.95° . With an average temperature of $46.27^\circ \pm 8.99^\circ$, the Monte Carlo-derived probability that the matrix was randomly generated was extremely low [$T < 7.95^\circ = 1.04 \text{ e}^{-05}$].

As can be seen (Fig. 3.2), the first species to drop out are the Javan slow loris and the Javan gibbon, with the slow loris recorded in 6 of the 31 fragments and the gibbon in 7. The most resilient species appear to be the ebony langur and the long-tailed macaque, with the latter showing the most idiosyncratic pattern. The most

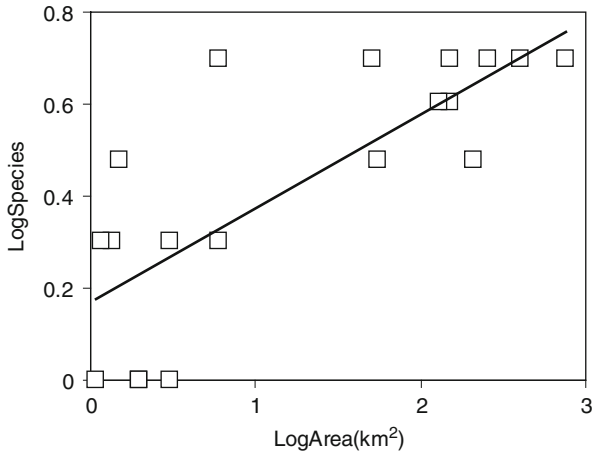
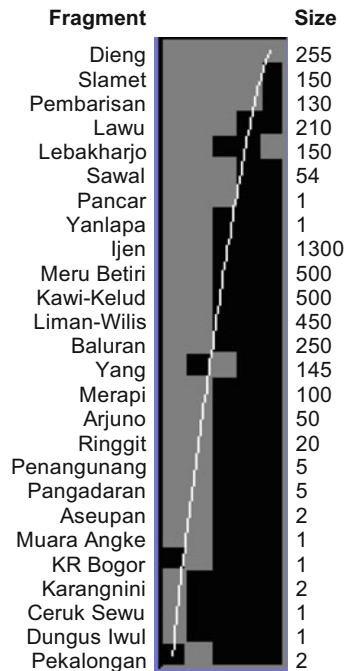


Fig. 3.1 Relationship between the number of primate species and forest areas size in Java, Indonesia, following a double-logarithmic function ($\log S = 0.205 \log A + 0.168$, $R^2 = 0.600$, with A being size of the forest area in km^2 and S being primate species-richness). Included are 21 isolated forests east to Mt. Lawu, excluding forest areas in the drier eastern part of the island

Fig. 3.2 Nestedness of primate communities of 31 forest fragments on Java. Fragments (rows) with similar primate communities are listed from large to small, with the species order (columns) being ebony langur, long-tailed macaque, grizzled langur, Javan gibbon, and Javan slow loris. Note that in addition to Dieng, listed at the top, there are five other fragments that have all five species present, viz., Ujung Kulon [750 km^2], Halimun [400 km^2], Gede Pangrango [150 km^2], Salak [50 km^2], and Telaga Warna [5 km^2]



idiosyncratic fragment in terms of primate community was Lebakharjo in East Java. This coastal lowland forest harbours ebony langurs, long-tailed macaques, and Javan slow loris, but lacks Javan gibbons and grizzled langurs. It seems that the area is too far east for the latter two species to exist as it is situated up to 100 km east of their easternmost (historical) records.

Large areas with a relatively impoverished primate community, such as Ijen [1,300 km²], Meru Beteri [500 km²], and Kawi-Kelud [500 km²], are all situated in the drier easternmost part of the island, which accounts for the absence of rainforest primates. On the other end of the spectrum, Telaga Warna, which is on 5 km², harbours all five species. Situated close to the forest Mt Gede Pangrango it may in fact be less isolated than the other forest fragments included in the analysis.

Discussion

Effects of Fragmentation on Primate Communities

I here show that the primate community in 31 fragments on Java shows a clear pattern, with smaller fragments containing a subset of larger ones. When focussing on the fragments situated in the wetter parts of the island—hence those that can potentially harbour all species of primate, including those that are dependent on rainforest—the size of a fragment is a good predictor for species number. The slope of the regression equation is steep, suggesting that (1) the fragments indeed isolate primate communities with only very limited or no emigration between them, and (2) the fragments have been isolated for long times with (multiple) extinctions having occurred in the smaller fragments.

In highly nested matrices, such as seen in this study, all islands and species contribute rather uniformly to the system temperature of the matrix, regardless of the matrix's temperature. This suggests similar biogeographical histories for these fragments. The single 'outlier' Lebakharjo may result from habitat heterogeneity, or signify a different biogeographical history. Idiosyncratic species (here, albeit only to a minor degree, the long-tailed macaque) might variously recolonise some fragments after they became locally extinct on them or may be affected by competitive exclusion. Recolonisation seems consistent with the species ecology but to what extent long-tailed macaques are affected by competitors remains largely unknown.

The data from the regression and nestedness analysis suggests that for an area to harbour the entire Javan primate community it needs to be some 50–400 km² in size. Below this species drop out. The single exception is the small forest fragment of Telaga Warna that probably until recently was not effectively isolated from nearby larger fragments. While Javan slow loris, Javan gibbon, and grizzled langur generally need areas >50 km², ebony langurs and long-tailed macaques can persist in significantly smaller areas. Note that these values are probably mostly valid for the wetter part of Java only, and extinction patterns in the drier parts of Java may have followed a slightly different pattern.

Extinction Following Fragmentation

An analysis of the primate communities on 25 islands >500 km² in the Sunda Region shows a very strong relationship between the size of the island and number of primate species (Nijman and Meijaard 2008; Nijman, unpubl. data). It also shows that for its size Java has a relatively low number of primate species. Remains of three species of primate currently not found on Java, i.e., pig-tailed macaque *M. nemestrina*, siamang *Symphalangus syndactylus*, and orang-utan *Pongo* sp. dated to ~120 ka, are known from Punung [08°08'S, 111°01'E] on the south coast of East Java (Westaway et al. 2007). At present this part of Java has a prolonged dry season and the nearest rainforest is found >30 km away on the slopes of Mt Lawu. These rainforest primates probably disappeared from Java during the last glacial maximum when drier conditions and increased seasonality reduced the amount of available rainforest (van den Bergh et al. 2001) but one or more species may have persisted much longer in the wetter parts of Java. Further deforestation and resultant fragmentation, exacerbated by the capturing of primates for the pet trade, have led all but the long-tailed macaque to be considered globally threatened.

If data from present-day forest fragments can teach us anything about primates in the past we can infer the minimum sizes of fragments to sustain larger communities. Extrapolating from the regression equations, to sustain a community with two or three additional species (as was the situation in the past) fragments would have to have been some 3,500–13,000 km² in size. Judging from forest maps presented by Koorders (1912) fragments of these sizes must have been very rare even over 120 years ago, especially in the wetter western part of the island where species such as pig-tailed macaque, siamang, and orang-utan could have persisted.

Lessons from Java

While large-scale anthropogenic deforestation on Java dates back hundreds if not thousands of years, one may expect that the primate community has reached the so-called relaxation phase (i.e., the number of species is in equilibrium with the available habitat). Following Brooks et al. (1997) the number of species in the remaining forest can be predicted by $S_{n2} = S_{o2} (F_n/F_o)^z$ where S_{o2} is the number of expected species for an area (here the island of Java) as derived from a species area curve (based on 23–36 primate species on 116 islands in Sundaland: Nijman and Meijaard 2008), S_{n2} is the number of predicted species on the basis of the remaining forest (the number of species we expect to find at present if indeed the number of species is in equilibrium with the available habitat), F_o is the original and F_n is the remaining forest area (136,920 and 12,912 km², respectively: MacKinnon et al. 1982; van Balen 1999), and z is the slope of the regression line (0.13–0.16: Nijman and Meijaard 2008). Filling in the equations it turns out that on the basis of present forest cover Java should have three to four primate species (i.e., one or two less than at present).

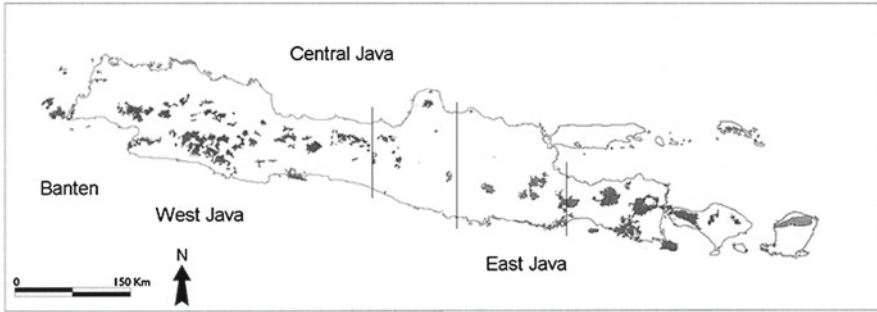


Fig. 3.3 Mid 1980s forest cover on Java, and the islands of Bali and Lombok to the east of Java (after RePPProT 1990), showing the severe degree of forest fragmentation. The *three vertical lines* indicate the geographical boundary of (from west to east) Javan gibbon *Hylobates moloch*, grizzled langur *Presbytis comata*, and Javan slow loris *Nycticebus javanica*; the ebony langur *Trachypithecus auratus* is restricted to the islands of Java, Bali, and Lombok, whereas the long-tailed macaque *Macaca fascicularis* can be found on all three islands, as well as islands to the north, west, and east

The results are only partially dependent on the choice of parameters, i.e., the steeper slope [0.16] gives rise to the higher number of primate species [four as opposed to three], but not on the exact estimation of the amount of remaining forest (note that in the equation it is the ratio that is of relevance, thus replacing all the remaining forest in the equation with lowland forest only, under the correct assumption that some primate species are altitudinally restricted, and do not change the results). These findings are comparable to that which has been found for primate communities in African forest, with typical ‘extinction debts’ of 30 % (i.e., an excess of between four and eight primates in individual fragments) (Cowlshaw 1999). The sobering lesson is that while in Cowlshaw’s dataset the extinction debt was present some 50 years after deforestation commenced, the data from Java suggest that these extinction debts can last for centuries (cf. Vellend et al. 2006).

One major caveat in using species–area curves and nestedness analysis to explain present-day primate community composition and past extinctions is that they are based on the implicit assumption that the primates are evenly distributed over the available forest area, both in the present and in the past. For Java this is not the case (see Fig. 3.3), with more species occurring in the west than in the east. Hence loss or preservation of forest areas in the wetter parts will have a disproportional effect on the number of species that (theoretically) can persist in the remaining forest. Likewise, fragmentation per se has its effect on the composition and number of the remaining species, and we can use this knowledge to guide habitat and species conservation as it allows maximising results with the limited resources available.

In conclusion, despite centuries of deforestation resulting in a close relationship between forest fragment size and primate species number and composition, it appears that, on the basis of habitat availability alone, Java may expect to lose one

or two more species, in addition to the three it has lost already since Pleistocene times. The history of deforestation and forest fragmentation on Java is currently repeated in other parts of Asia (Sodhi et al. 2004, 2010), and hence, we can expect primate extinctions similar as observed in Java to occur elsewhere.

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