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Mainland versus Island Adaptation: Paleobiogeography of Sunda Shelf Primates Revisited

Halmi Insani and Masanaru Takai

Abstract

Southeast Asian primates appear to be one of the most successful mammals in the dynamic paleoclimatic changes since at least 1 mya. Human and non-human primates reflect the complex history of a wide range of ecological and geographic variation, which presents to be the source of different systematics and biogeographic models. The past combinative effects of geographic factors (latitude, bathymetric barrier, and duration of island isolation), periodic sea level changes, and the contribution of human and/or non-human primate interaction are crucial subjects in studying the north-to-south, which is from continental to archipelago of Sunda Shelf, dispersal events and phylogeographic analysis of human and non-human primates. Cranial size and shape difference between *Homo erectus* in mainland and island displays peculiarity on the effect of insularity. Data analyses on cranial landmarks of three non-human primate genera provide more clear resolution to reconstruct the complete scenario, whereby insular primates are dispersed and adapted to their present biogeographical distribution.

Keywords: primate, ecogeographical rule, body size, biodiversity, Sunda shelf

1. Introduction

Mainland and island are two unique bodies of landmasses that hold not only the obvious different area dimension but also a timeline that portrayed dynamic changes on their geographical and ecological features. Southeast Asia that comprises mainland and the patches of island is a home for the primate species diversity with high rate of endemism and provinciality [1]. Since the emergence of primates in the region during Quaternary to recent, 13 genera have been taxonomically recognized: *Homo*, *Pongo*, *Hylobates*, *Symphalangus*, *Nomascus*, *Hoolock*, *Macaca*, *Trachypithecus*, *Presbytis*, *Simias*, *Nasalis*, *Nycticebus*, and *Tarsius* [2]. With the high variability on body mass and body size, Southeast Asian primates, both the mainland and island populations, remain enigmatic when confronted toward ecogeographical “rules,” resulting positive [3], contradictory [4, 5], and inconsistent results [6]. However, given their peculiarity in adaptive functional characters among other mammal taxa and their close evolutionary trajectory to human [7], primates share similarities showing their capability in grasping object [2] for faster food procurement and high occasional flexibility in locomotion (e.g., arboreal quadrupedalism, terrestrial quadrupedalism, and bipedalism) [2, 8]. These functional characters support their high adaptability in predator avoidance and alternate dietary shifts when resources are limited [9].

Lying over a wide range of latitude and various sizes of islands, the Southeast Asian region is frequently subjected for the studies of primate insularity that involved spatial factors (e.g., island size, latitude, and island-mainland distance) [3–5, 10] and temporal factors (e.g., isolation duration and geological chronology) [5]. Insularity on primates is an interesting phenomenon that invites many reports, linking to their ecomorphological complex (body size and body shape) [6] and biodiversity changes [11].

In many ecological aspects, mainland environment differs from island environment. In addition, large-sized island provides different ecological scenarios from small-sized island. Certain duration of isolation on a relatively small island may lead to limited resources, fewer predators, and reduced interspecific competition [12]. Although it is not impacted universally, the combinative geographical effects on island size and island isolation can promote gigantism in smaller insular mammal species and dwarfism in larger mammal species. It is widely known as island rule (=Foster's rule) [6, 13–18]. With the wide span of latitudinal range, primates inhabiting the Sunda Shelf region are also assumed to follow Bergmann's rule, by testing the effect of latitudinal position to body size [3–5]. This study aims to elicit the validity of ecogeographical rules affected body size and biodiversity changes of primates around Sunda Shelf throughout the geological chronology, since their appearance in Quaternary until recent.

2. Mainland vs. island: impacts and consequences

2.1 Body size

Among mammal taxa, the record of body size shift has not been found spectacular in all primate species [19]. Before the Quaternary, the primate fossil records adapted to island rule are found in Madagascar and Caribbean islands. Strepsirrhine primates found in Madagascar (e.g., *Archaeoindris fontoynontii* and *Megaladapis edwardsi*) are known to have become gigantic [20], while an extinct dwarf lemur, *Cheirogaleus* spp., is known to occupy Nosy Hara Island, a small islet off the north-west coast of Madagascar [21]. The specific examples of island gigantism are also found in platyrrhine monkeys, such as *Paralouatta mariane* from Cuba [22] and *Xenothrix mcgregori* from Jamaica [23].

Hominine taxa represented by the *Homo floresiensis* [24] and *Homo luzonensis* (judging from the small-sized molar [25]) have become the object of comparison to their predicted common ancestor, *Homo erectus*, who inhabited a large-sized island (Java) and Asian continent (Zhoukoudian, China) [24–26]. Until recent, there is no evidence of gigantism found on Southeast Asian insular primates. Looking upon their localities, it shows that the island rule on primates likely occurs in a warmer area within the latitudinal span approaching equator. Throughout several reports [6] island rule on insular primates causing body size change is more evident in oceanic islands due to the deep bathymetric barrier from the mainland regardless of their short island-mainland distance (e.g., Madagascar Island and Mentawai Island) [12].

Gained with the fact that three primate genera (*Macaca*, *Presbytis*, and *Hylobates*) stand as the most widely distributed taxa over Sunda Shelf islands, an attempt is conducted to compare the body size profile between living populations in mainland and island, addressing that an island, regardless of their various sizes, bathymetric barrier, and distance to mainland, is assumed to generate body size changes or body shape variation. Three-dimensional measurements were employed on 20 landmark points on lateral crania (**Figure 1**, **Table 1**, **Table 2**) of five species that strictly inhabit mainland and island (*Hylobates lar*, *Hylobates agilis*, *Macaca fascicularis*,

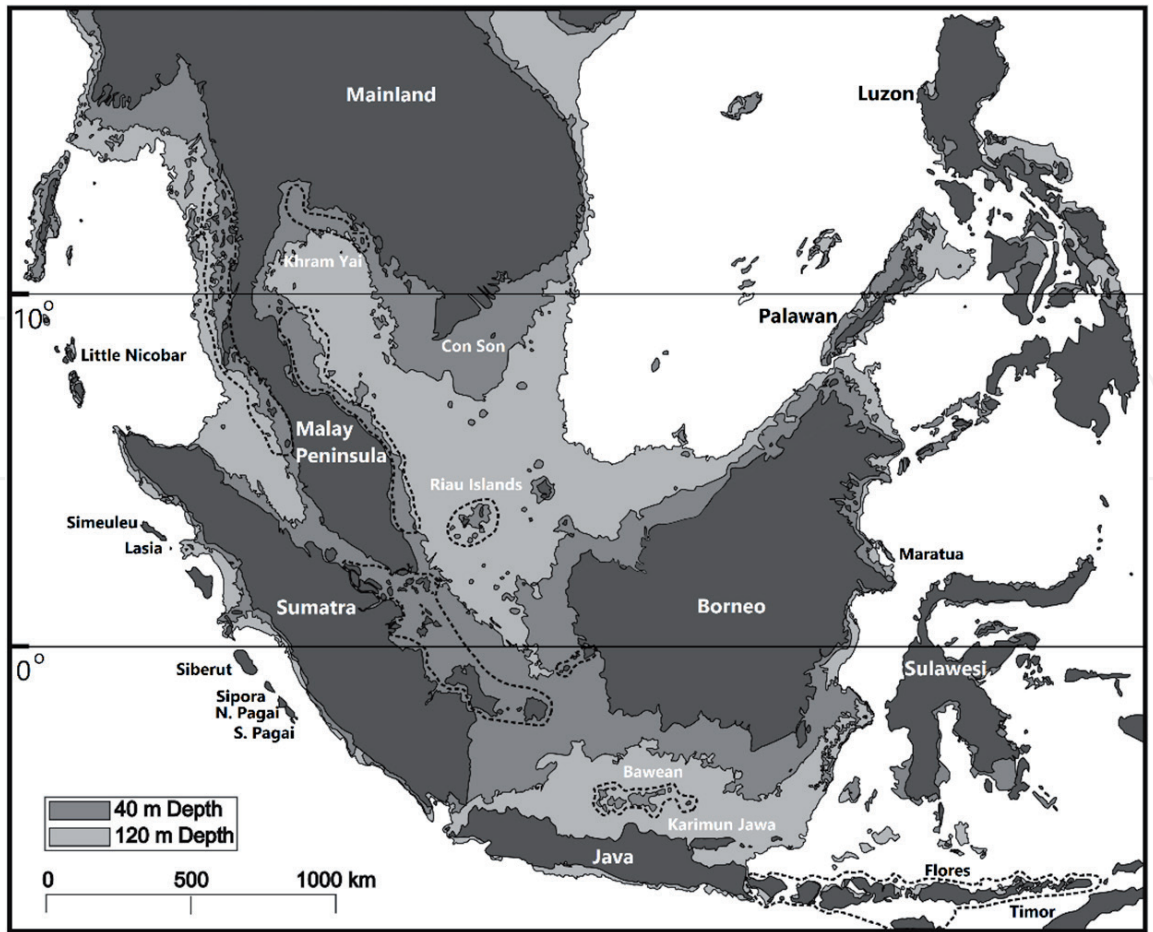


Figure 1. Map showing two different generalized bathymetric levels from 40 and 120 m throughout Sunda shelf. Closed dash lines present the group of islands with relatively equal range of sea depth.

Sex group	Hylobates		Macaca		Presbytis
	<i>H. lar</i>	<i>H. agilis</i>	<i>M. fascicularis</i>	<i>M. nemestrina</i>	<i>P. femoralis</i>
M	31	9	60	20	38
F	22	12	39	8	43

All specimens are housed in Lee Kong Chian Natural History Museum and museum Zoologicum Bogoriense Indonesia.

Table 1. Sample size measured in this study.

Macaca nemestrina, *Presbytis femoralis*). The landmark points were obtained using 3D digitizer (MicroScribe MX; Immersion Corp., San Jose, CA) and translated into centroid size that stands as alternative check to compensate spatial size over two-dimensional size (**Figure 2**).

The box and whisker plot diagrams (**Figure 3**) exhibit two distinction profiles between Hylobatidae and Cercopithecidae. Island populations of *H. lar* and *H. agilis* show smaller craniolateral size to the mainland population. Noting that most island Hylobatidae population inhabits large-sized islands (Sumatra, Borneo, and Java); their comparatively smaller craniolateral size is seemingly hard to be explained by island rule, knowing that they occupy large-sized islands with shallow bathymetric barrier to the mainland. The presence of much higher-canopy rain forest in mainland may contribute to large-sized body proportion of *Hylobates* in mainland. The reversed results profiled in Cercopithecidae (*M. fascicularis*, *M. nemestrina*, and *P. femoralis*) (**Figure 3**). Given that Southeast Asian islands

Abbreviation	Definition
PRS	Prosthion: anteroinferior point on projection of premaxilla between central incisors
PRS2	Prosthion2: anteroinferiormost point on premaxilla, equivalent to prosthion but between central and lateral incisors
PMS	The point where premaxillary suture crosses alveolar margin
MP3	Mesial P3: most mesial point on P3 alveolus, projected labially onto alveolar margin
MM1	Mesial M1: contact points between P4 and M1, projected labially onto alveolar margin
MM3	Mesial M3: contact point between M2 and M3, projected labially onto alveolar margin
DM3	Distal M3: posterior midpoint onto alveolar margin of M3
PMA	Most posterior point of maxillary alveolus on the maxilla palatine
NSP	Nasospinale: inferiormost midline point of piriform aperture
WPA	Point corresponding to largest width of piriform aperture
NPM	Meeting point of nasal and premaxilla on margin of piriform aperture
RHI	Rhinion: most anterior midline point on nasals
PMN	Premaxillary maximum superior PMS where premaxillo-maxillary suture meets nasal bone or aperture
NAS	Nasion: midline point on fronto-nasal suture
GLA	Glabella: most forward projecting midline point of frontals at the level of the supraorbital ridges
BRG	Bregma: junction of coronal and sagittal sutures, on sagittal crest if necessary
INI	Inion: most posterior point of cranium, when viewed in the Frankfurt horizontal, be it on sagittal/nuchal crest or not
OPS	Opisthion: posterior most point of foramen magnum
LOC	Most anterior point on the occipital condyle along the margin of the foramen magnum
AOC	Occipital condyle along the margin of the foramen magnum between POC and AOC

Table 2.
Abbreviation and definition used in this study [27].

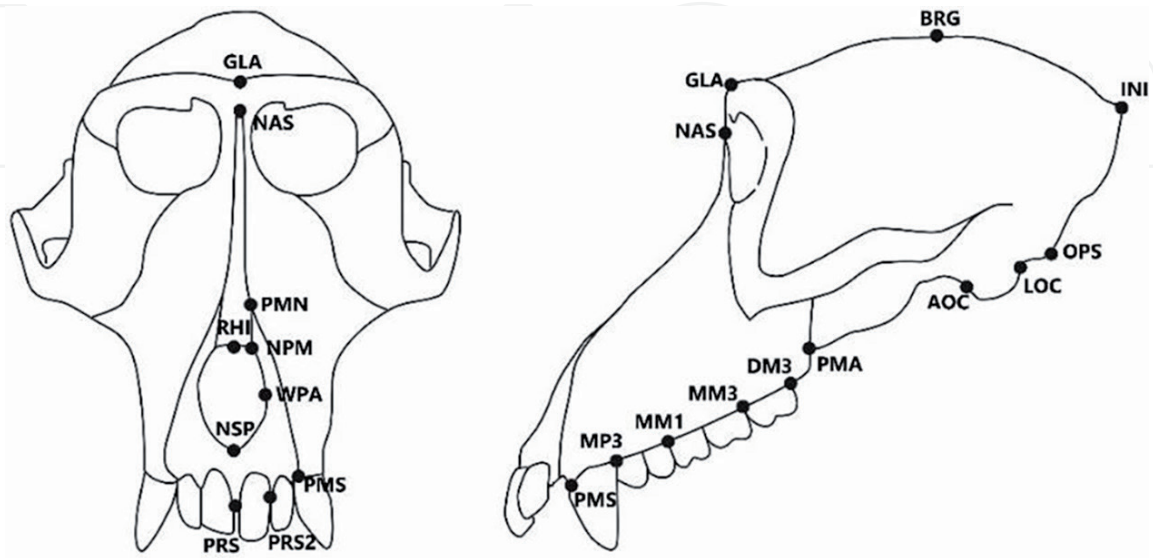


Figure 2.
*Frontal (left) and lateral (right) views of the generalized *M. fascicularis* skull, showing 20 landmark positions used in the analysis. Number and position of landmark points are applied with the same procedure in all species measured.*

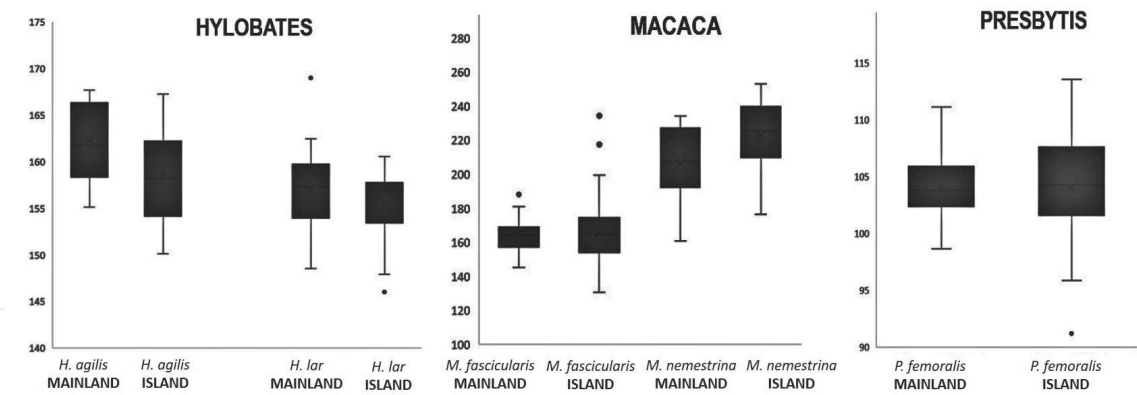


Figure 3. Box and whisker diagram showing the variation of craniolateral centroid size (CS) among five non-human primate species in mainland and island group.

are geographically characterized with various sizes, latitudinal and longitudinal positions, maximum sea depth, and island-mainland distance, this condition arises to a consequence on more diverse insular adaptation that contributes to numerous variations in body size.

2.2 Biodiversity changes and extinction

For the last 30 years, benefited by the advanced methodology of molecular biology, the expansion of studies on primates of Southeast Asia have resulted in the increased number of taxonomic diversification [28–30], which was previously mostly explained by the superficial character (e.g., pelage color, tail length, and behavior) on the living taxa [2, 5]. Mainland and large islands have been claimed to correspond to the higher taxonomic diversity than islands [31]. With the wide span of area, mainland and large islands have a great advantage to develop more topographic diversity, formed as geographic barriers (e.g., peak, valley, river), linking to high possibility to allopatric speciation [32].

Principal component analyses (PCA) on the craniolateral shape of the five species share similarities in the wider shape variance of all three insular species (**Figure 4**). The mixed category between large-sized island and small-sized island in this study (**Table 3**) may strongly correspond to the higher craniolateral morphology, by considering (i) each isolated small island with unique geographical-ecological condition and different degrees of isolation may contribute to the shape modification, furthermore to endemism [12]; (ii) large islands may lead to various shape modifications, generated by various topographic-diversity-derived habitat variations [32]. Reflecting the wide variance morphology on three insular genera of this study, insularity does not gain merely on taxonomic diversity; furthermore strong individual differentiation within population or intraspecific variation could also possibly generated.

The isolation process on an island may lead to enforce the possibility of extinction in certain species [30]. For example, in Java Island, with area span 138,000 km², three primate species (*Homo erectus*, *Pongo pygmaeus*, and *M. nemestrina*) occurred during Middle-Late Pleistocene, but finally disappeared [33] (**Table 4**). Harsh ecological condition (e.g., low carnivore-herbivore ratio and habitat change) on island will contribute to the adaptability of particular species. *M. nemestrina*, which is more terrestrial species than the survived species, *M. fascicularis* [27] (**Table 4**), is assumed to be less adaptive to avoid terrestrial and predators. *Pongo*, which is recently absent in Java Island and

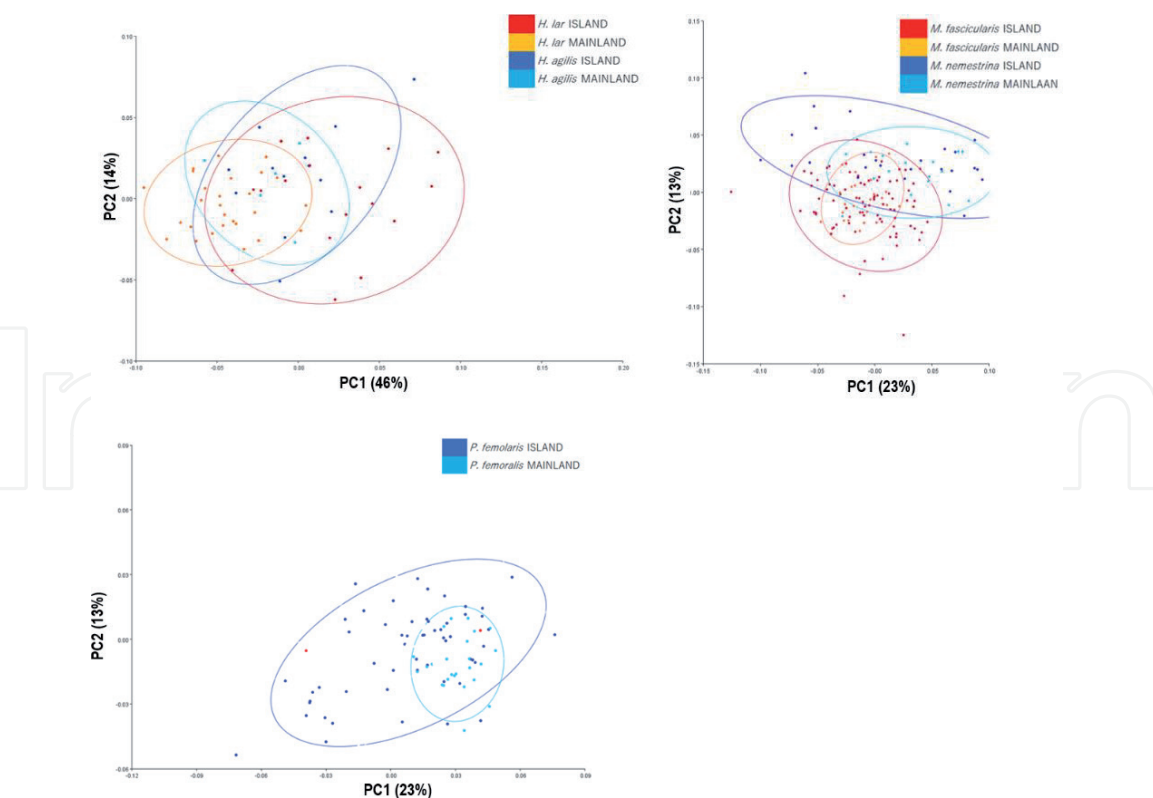


Figure 4. Plots of principal component PC1–PC2 displaying the variance between mainland and island population among five species observed.

Genera	Species/subspecies	Island	Latitude	Island size (km ²)	Island size category [33]	max. elevation (m)
CONTINENTAL ISLAND						
Ponginae	<i>Pongo pygmaeus</i> [2]	Borneo	8°N–2°S	743,330	Large	4095
	<i>Pongo abelii</i> [2]	Sumatra (north)	2°–4°N	473,481	Large	3805
	<i>Pongo tapanuliensis</i> [34]	Sumatra (north)	2°–4°N	473,481	Large	3805
Hylobatidae	<i>Hylobates moloch</i>	Java (west)	8°–10°N	128,300	Large	3676
	<i>H. albibarbis</i> [2]	Borneo (south)	8°N–2°S	743,330	Large	4095
	<i>H. muelleri</i> [2]	Borneo (north)	8°N–2°S	743,330	Large	4095
Cercopithecinae	<i>M. f. atriceps</i> [5]	Khram Yai	12.70°N	20,28	Small	219
	<i>M. f. condorensis</i> [5]	Con Son	8.71°N	51,52	Small	560.8
	<i>M. f. mandibularis</i> [5]	Riau Islands	2.50°–3.13°N	106	Small	959
	<i>M. f. baweana</i> [5]	Bawean	5.80°S	196,27	Small	655
	<i>M. f. karimoendjawae</i> [5]	Karimun Jawa	5.85°S	71,2	Small	506
Colobinae	<i>Presbytis natunae</i> [2]	Natuna Besar	4°N	1720	Small	187
	<i>Presbytis thomasi</i> [2]	Sumatra (north)	2°–4°N	473,481	Large	3805
	<i>Presbytis frontata</i> [2]	Borneo	8°N–2°S	743,330	Large	4095

Genera	Species/subspecies	Island	Latitude	Island size (km ²)	Island size category [33]	max. elevation (m)
	<i>Presbytis chrysomelas</i> [2]	Borneo (north)	8°N–2°S	743,330	Large	4095
	<i>Presbytis hosei</i> [2]	Borneo (northeast)	8°N–2°S	743,330	Large	4095
	<i>Presbytis rubicunda</i> [2]	Borneo (east)	8°N–2°S	743,330	Large	4095
	<i>Trachypithecus auratus</i> [2]	Java	8°–10°N	128,300	Large	3676
	<i>Nasalis larvatus</i> [2]	Borneo	8°N–2°S	743,330	Large	4095
OCEANIC ISLAND						
Hylobatidae	<i>Hylobates klossii</i> [2]	Mentawai Islands	1.2°–3°S	268–4030	Small	384
Cercopithecinae	<i>Macaca maura</i> [2]	Sulawesi (southwest)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca ochreata</i> [2]	Sulawesi (southeast)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca tonkeana</i> [2]	Sulawesi (central)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca hecki</i> [2]	Sulawesi (northwest)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca nigrescens</i> [2]	Sulawesi (north)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca nigra</i> [2]	Sulawesi (northeast)	0.3°N–5.3°S	174,600	Large	3478
	<i>Macaca siberu</i> [2]	Mentawai Islands	1.2°–3°S	268–4030	Small	384
	<i>Macaca pagensis</i> [2]	Mentawai Islands	1.2–3S	268–4030	Small	384
	<i>M. f. umbrosa</i> [5]	Little Nicobar	7.32°N	140	Small	435
	<i>M. f. tua</i> [5]	Maratua	2.25°N	22,8	Small	94.18
Colobinae	<i>M. f. philippinensis</i> [5]	Palawan	9.70°N	14,650	Large	2086
	<i>M. f. philippinensis</i> [5]	Luzon	16.9°N	110,000	Large	2922
	<i>M. f. lasiae</i> [5]	Lasia	2.17°N	15,12	Small	69
	<i>M. f. fusca</i> [5]	Simeulue	2.65°N	2310	Small	567
	<i>Presbytis pagensis</i> [2]	Mentawai Islands	1.2–3°S	268–4030	Small	384
	<i>Presbytis potenziani</i> [2]	Mentawai Islands	1.2–3°S	268–4030	Small	384
	<i>Simias concolor</i> [2]	Mentawai Islands	1.2–3°S	268–4030	Small	384
The category of island refers to the indicator of small island category (<12,000 km ²) [34].						

Table 3.
List of modern non-human primate species/subspecies native to islands with the latitudinal position.

mainland, became extinct probably due to the deterioration of the habitat from tropical forest to more open environment [33] during Late Pleistocene to Holocene.

3. Synthesis and discussion

3.1 Spatial cost: do primates follow ecogeographical rules in mainland and islands?

3.1.1 Bergmann's rule

Southeast Asia with wide span of latitude ranging from 6°N to 14°S is split by the equator line, demanding at least two comprehensive separations that require thermoregulation connection from the equator to southern and northern latitudes. Mammals of mainland Southeast Asia have been subjected to describe body size variation following thermoregulation effect, widely termed as Bergmann's rule [6]. Concluding that Bergmann's rule may occur within a species, it predicts that population in warmer climates (commonly referred to lower latitudes) have smaller mean body size than conspecifics in colder climates (generally marked with higher latitude) [6]. Published accounts applying this ecogeographical rule on non-human primates has been intensively investigated in the widely distributed species in Southeast Asia: *M. fascicularis* [4, 5, 10] and *M. nemestrina* [3]. The Bergmann's rule was positively performed on northern pig-tailed macaques (*M. leonina*) [3, 6] and crab-eating macaques (*M. fascicularis*) [4, 5, 10] in the mainland, demonstrated by the increasing body size toward higher latitude.

Interestingly, anti-Bergmann's rule appears north side of Kra Isthmus (the narrowest area differing Indochinese mainland and Malay Peninsula at 12.2°N) [4, 5]. Explanatory cause for this inversed Bergmann's rule has not been uncovered. In response to this matter, *M. fascicularis* population from the northeastern localities that is bound by the geographic barrier of north-south oriented high topographic range of Tenasserim Hills most likely underwent different and unique ecomorphological adaptations to the rest of the western low land area of Indochinese mainland population. Due to the limitation number on available samples, to date, there is no further study testing this ecogeographical rule in this species or in other non-human primate taxa.

Although serious attempts to test Bergmann's rule on insular non-human primates have increased, the result of the statistical analysis on the cranial size of southern pig-tailed macaque (*M. nemestrina*) surprisingly demonstrates anti-Bergmann's rule [3]. However, insular *M. fascicularis* tested in western Southeast Asian archipelago [4, 5, 10] and large-sized islands of Sunda Shelf still shows constant Bergmann's rule [27]. Taken together from observed results correlating non-human primate body size to thermoregulation mechanism in Southeast Asian archipelago, they frequently came as debatable subjects [6] because (i) most islands are situated in short range of latitudinal position referring to low temperature variation; (ii) the equator line that passes over or nearby most of the islands, both northward and southward, directs to similar typical tropical habitat; and (iii) each island is addressed to various unique insular geographical properties (e.g., island area, max. Depth separating to mainland, and island-island distance), which likely gives the stronger island effect than the latitude effect to the population. This aspect needs a more complicated operation when we apply Bergmann's rule in islands than in mainland.

3.1.2 Foster's rule

In the context of conservative classification on island area, primate insularity has been investigated into categorization of area size, e.g., small and large island, which was directly calculated by metric size of island [31]. This ecogeographical rule implemented exclusively on island, commonly known as Foster's rule, proposes

that population of large-bodied mammals on island tend to have a smaller mean body size than mainland population (dwarfism), while small-bodied mammals become larger (gigantism) [6]. One suggested that, in the scope of insularity on Southeast Asian mammals, the small island criterion is defined by the island size $<12,000 \text{ km}^2$ [34] (**Table 3**). Without providing the specific primate species group, one suggested that primates follow island rule [19]. However, a study tested in body length of *Macaca fascicularis* found that island area and body length shows no significant relationship [10].

The most spectacular evidences of dwarfism on extinct Homininae taxa are *Homo floresiensis* aged 60,000–100,000 years ago in oceanic island of Flores, Indonesia [11, 24], and *Homo luzonensis* (judging from the small molar) aged $66,700 \pm 1000$ years ago discovered in Callao Cave, Luzon Island, Philippines [25]. The consideration of island rule causing diminutive character on *Homo luzonensis* remains enigmatic, since Luzon Island is a large island (**Table 3**). However, the coexisted fossil macaque, *M. f. philippinensis*, which still occurs in modern western, eastern, and northern islands of the Philippines, suggests that it occupied the island since 160,000 years ago [5]. It permits the long duration of isolation that impacted not necessarily on body size reduction, but the possibility of endemism. Furthermore, insular dwarfisms that were reported on *M. fascicularis* in Bintan Island and Singapore are possibly caused by ecological effects, such as food limitation and high population density [6], not geographical effect such as island size.

Among gibbons, diminutive body size has been presented by *Hylobates klossii*, an endemic species of four Mentawai islands (Siberut, Sipora, North Pagai, and South Pagai). There are few gibbons occupying small-sized island in continental Sunda Shelf (only found in Paku Island, collection of Lee Kong Chian Natural History Museum), because the small island usually tends to do not support the development of dense rain forest habitat with high canopy cover where gibbon is dependable to live [34].

Researchers have long endeavored to uncover the Foster's rule in Southeast Asian archipelago [4, 5, 10], but most outcomes show no statistically significant results [11]. On exclusively *M. fascicularis* inhabiting shallow-water fringing islands over Sunda Shelf, small-sized island was found to contribute more to the variation of subspecies [4, 5] (**Table 3**). The implementation only using island size or the distance between island and mainland as a proxy is unlikely relevant to the test of Foster's rule in Southeast Asian archipelago, neither. Deep bathymetric barrier possessed by oceanic islands (**Table 3**) convincingly appears as the main factor of island rule, followed by the unique island ecological condition in the duration of island isolation.

3.1.3 Vicariance biogeography

Mainland Southeast Asia contains the high variation of non-human primate species. Recent molecular biological studies revealed critical systematics of non-human primates (i.e., *Macaca* [28, 29] and *Hylobates* [30]), showing the high intra- and interspecific variation. Topographic diversity in mainland Asia is likely correlated to the speciation process of animals [11, 35], and islands are not exception for this correlation. Historical change of paleobiogeography in large-sized islands (Sumatra, Java, and Borneo) over Sunda Shelf can be explained by Pleistocene volcanic activities caused by the geologic subduction between Sunda and Australian Plates.

In Java, a chain of 38 mountains forming east–west spine with various slopes, illustrated by jagged highlands by alternating peaks and valleys, leads to classes of topographic diversity [35]. This phenomenon led the geographically separated populations to undergo allopatric speciation. According to the modern Javanese mammal fauna, the low topographic diversity in East Java resulted in less

Genera	Specimen	Locality	Pleistocene			Holocene
			Early	Middle	Late	
MAINLAND						
Hominidae	<i>Homo erectus</i> all Zkd (but 5) [25]	Zhoukoudian Caves, China		0.6–0.4		
	<i>Homo erectus</i> Zkd 5 [36]	Zhoukoudian Caves, China		0.4–0.5		
	<i>Homo erectus</i> [37]	Had Pu Dai, Thailand		●		
	<i>Homo erectus</i> [37]	Tham Khuyen, Vietnam		●		
	<i>Homo erectus</i> [37]	Lang Trang, Vietnam		●		
	<i>Homo</i> sp. [37]	Ma U’Oi, Vietnam		●		
	<i>Homo</i> sp. [37]	Thum Wiman Nakin, Thailand		●		
Ponginae	<i>Gigantopithecus blacki</i> [37]	Gigantopithecus Cave, China	●			
	<i>Gigantopithecus blacki</i> [37]	Jianshi, China	●			
	<i>Gigantopithecus</i> sp. [38]	Baikong, China	2.2			
	<i>Gigantopithecus</i> sp. [21]	Juyuan, China	1.8			
	<i>Gigantopithecus</i> sp. [38]	Sanhe, China	1.2–1.6			
	<i>Gigantopithecus</i> sp. [38]	Queque, China	<0.7–1	≤0.7–0.8		
	<i>Gigantopithecus</i> sp. [38]	Yangliang, China	●			
	<i>Gigantopithecus</i> sp. [37]	Had Pu Dai, Thailand		●		
	<i>Gigantopithecus blacki</i> [37]	Daxin, China		●		
	<i>Gigantopithecus blacki</i> [37]	Wuming, China		●		
	<i>Gigantopithecus blacki</i> [37]	Bama, China		●		
	<i>Gigantopithecus blacki</i> [37]	Tham Khuyen, Vietnam		●		
	<i>Gigantopithecus blacki</i> [37]	Tham Hai, Vietnam		●		
	<i>Gigantopithecus</i> sp. [37]	Heijang, China		●		
	<i>Gigantopithecus</i> sp. [37]	Shuangtan, China			●	
	<i>Pongo</i> sp. [37]	Gigantopithecus Cave, China	●			
	<i>Pongo</i> sp. [38]	Baikong, China	>2.2			
	<i>Pongo</i> sp. [38]	Juyuan, China	>1.8			
	<i>Pongo</i> sp. [38]	Sanhe, China	1.2–1.6			

Genera	Specimen	Locality	Pleistocene			Holocene
			Early	Middle	Late	
	<i>Pongo</i> sp. [38]	Queque, China	<0.7–1	≤0.7–0.8		
	<i>Pongo</i> sp. [38]	Yangliang, China	●			
	<i>Pongo</i> sp. [37]	Had Pu Dai, Thailand		●		
	<i>Pongo</i> sp. [37]	Tham Khuyen, Vietnam		●		
	<i>Pongo pygmaeus</i> [37]	Thum Wiman Nakin, Thailand		●		
	<i>Pongo</i> sp. [37]	Daxin, China		●		
	<i>Pongo pygmaeus</i> [37]	Hoshantung, China		●		
	<i>Pongo pygmaeus</i> [37]	Koloshan, China		●		
	<i>Pongo</i> sp. [37]	Bama, China		●		
	<i>Pongo pygmaeus</i> [37]	Tam Hang, Laos		●		
	<i>Pongo pygmaeus</i> [37]	Tham Khuyen, Vietnam		●		
	<i>Pongo pygmaeus</i> [37]	Tham Hai, Vietnam		●		
	<i>Pongo pygmaeus</i> [37]	Phnom Loang, Cambodia		●		
	<i>Pongo pygmaeus</i> [37]	Thum Wiman Nakin, Thailand		●		
	<i>Pongo</i> sp.? [37]	Kao Pah Nam		●		
	<i>Pongo</i> cf. <i>pygmaeus</i> [37]	Thum Wiman Nakin, Thailand		●		
	<i>Pongo</i> sp. [38]	Hei, China		0.3–0.38		
	<i>Pongo</i> sp. [38]	Heijang, China		●		
	<i>Pongo</i> sp. [38]	Tongzi, China			●	
	<i>Pongo pygmaeus</i>	Keo Leng, Vietnam			●	
	<i>Pongo pygmaeus</i>	Hang Hum II, Vietnam			●	
	<i>Pongo</i> sp. [38]	Shuangtan, China			●	
	<i>Pongo</i> sp. [38]	Yixiantian, China			●	
	<i>Pongo</i> sp. [38]	Gonglishan, China			●	
	<i>Pongo</i> sp. [38]	Zhiren, China			●	
	<i>Pongo</i> sp. [38]	Nongbashankou, China			●	
	<i>Pongo</i> sp. [38]	Baxian, China			●	
	<i>Pongo</i> sp. [38]	Loushan, China			●	
Hylobatidae	<i>Hylobates</i> sp. [38]	Baikong, China	2.2			
	<i>Hylobates</i> sp. [38]	Juyuan, China	1.8			
	<i>Hylobates</i> sp. [38]	Sanhe, China	1.2–1.6			
	<i>Hylobates</i> sp. [38]	Queque, China	0.7–1	≤0.7–0.8		
	<i>Hylobates</i> sp. [38]	Hei, China		0.3–0.38		
	<i>Hylobates</i> sp. [38]	Heijang, China		0.4–0.32		
	<i>Hylobates</i> sp. [38]	Yenchinkou, China, China	●	●	●	
	<i>Hylobates</i> sp. [38]	Szechwan, China	●	●	●	

Genera	Specimen	Locality	Pleistocene			Holocene
			Early	Middle	Late	
	<i>Hylobates</i> sp. [38]	Niah Cave, Borneo, China			●	
	<i>Hylobates</i> sp. [38]	Shuangtan, China			●	
	<i>Hylobates</i> sp. [38]	Yixiantian, China			0.1	
	<i>Hylobates</i> sp. [38]	Gonglishan, China			●	
	<i>Hylobates</i> sp. [38]	Zhiren, China			0.11	
	<i>Hylobates</i> sp. [38]	Baxian, China			●	
	<i>Hylobates</i> sp. [38]	Loushan, China				●
Cercopithecinae	<i>Macaca</i> sp. [38]	Baikong, China	2.2			
	<i>Macaca</i> sp. [38]	Juyuan, China	1.8			
	<i>Macaca</i> sp. [38]	Sanhe, China	1.2–1.6			
	<i>Macaca</i> sp. [38]	Queque, China	<0.7–1	≤0.7–0.8		
	<i>Macaca</i> sp. [38]	Yangliang, China	●			
	<i>Macaca</i> sp. [38]	Hei, China		0.3–0.38		
	<i>Macaca</i> sp. [38]	Heijang, China		0.4–0.32		
	<i>Macaca</i> sp. [38]	Shuangtan, China			●	
	<i>Macaca</i> sp. [38]	Yixiantian, China			0.1	
	<i>Macaca</i> sp. [38]	Gonglishan, China			●	
	<i>Macaca</i> sp. [38]	Zhiren, China			0.11	
	<i>Macaca</i> sp. [38]	Nongbashankou, China			●	
	<i>Macaca</i> sp. [38]	Baxian, China			●	
	<i>Macaca</i> sp. [38]	Loushan, China				●
Colobinae	<i>Trachypithecus</i> sp. [38]	Baikong, China	2.2			
	<i>Trachypithecus</i> sp. [38]	Juyuan, China	1.8			
	<i>Trachypithecus</i> sp. [38]	Sanhe, China	1.2–1.6			
	<i>Trachypithecus</i> sp. [38]	Queque, China	<0.7–1	≤0.7–0.8		
	<i>Trachypithecus</i> sp. [38]	Hei, China		0.3–0.38		
	<i>Trachypithecus</i> sp. [38]	Heijang, China		0.4–0.32		
	<i>Trachypithecus</i> sp. [38]	Shuangtan, China			●	
	<i>Trachypithecus</i> sp. [38]	Yixiantian, China			0.1	
	<i>Trachypithecus</i> sp. [38]	Gonglishan, China			●	
	<i>Trachypithecus</i> sp. [38]	Zhiren, China			0.11	
	<i>Trachypithecus</i> sp. [38]	Nongbashankou, China			●	
	<i>Trachypithecus</i> sp. [38]	Baxian, China			●	
	<i>Trachypithecus</i> sp. [38]	Loushan, China				●
CONTINENTAL ISLAND						
Hominidae	<i>Homo erectus</i> S4 [25]	Sangiran, Java	0.99–1.5			
	<i>Homo erectus</i> S17 [25]	Sangiran, Java	0.78–1.3			
	<i>Homo erectus</i> S12 [25]	Sangiran, Java	1.2–0.98			

Genera	Specimen	Locality	Pleistocene			Holocene
			Early	Middle	Late	
	<i>Homo erectus</i> S2 [25]	Sangiran, Java	1.2–0.99			
	<i>Homo erectus</i> Smb [25]	Sambungmacan, Java	≤0.78			
	<i>Homo erectus</i> Ng [25]	Ngawi, Java		●	●	
	<i>Homo erectus</i> Nd [25]	Ngandong, Java		●	0.05–0.032 or 0.1	
	<i>Homo sapiens</i> [25]	Punung, Java			0.0118	●
Pongidae	<i>Gigantopithecus</i> sp. [39]	Semedo, Java	?	?		
	<i>Pongo pygmaeus</i> [33]	Punung, Java			0.125	
	<i>Pongo</i> sp. [40]	Lida Ayer, Sumatra				●
Hylobatidae	Hylobatidae [41]	Trinil, Java		●	●	
	<i>Hylobates syndactylus</i> [33]	Punung, Java			0.0118	●
	<i>Hylobates</i> sp. [40]	Lida Ayer, Sumatra				●
	<i>Hylobates</i> sp. [40]	Niah Cave, Borneo			0.04	
Cercopithecinae	<i>Macaca</i> sp. [38]	Sangiran, Java				
	<i>Macaca</i> sp. [38]	Punung, Java			0.0118	0.008
	<i>Macaca nemestrina</i> [38]	Sangiran, Java	1			
	<i>Macaca fascicularis</i> [38]	Sangiran, Java	1			
	<i>Macaca fascicularis</i> [38]	Callao Cave, Luzon			0.065	
	<i>M. f. philippinensis</i> [38]	Ille Cave, Palawan			●	●
Colobinae	<i>Presbytis comata</i>	Sangiran, Java		●		
	<i>Presbytis</i> sp.	Punung, Java				0.01
	<i>Trachypithecus auratus</i>	Sangiran, Java	1.9			
OCEANIC ISLAND						
Hominidae	<i>Homo cf. floresiensis</i> [42]	Mata Menge, Flores		0.7		
	<i>Homo floresiensis</i> [24]	Liang Bua, Flores		●	0.06–0.1	
	<i>Homo luzonensis</i> [25]	Callao Cave, Luzon			0.06	
Cercopithecidae	<i>M. f. philippinensis</i> [25]	Callao Cave, Luzon			0.065	
	<i>M. f. philippinensis</i> [43]	Ille Cave, Palawan			●	●
	<i>Macaca fascicularis</i> [28]	Timor Island				0.007

Table 4.
List of fossil/subfossils of primate species/subspecies discovered in archeological sites throughout Southeast Asia.

variation in endemic mammals than in the West and Central Java. This topographic profile is supported by the presence of two endemic non-human primate species/subspecies strictly occupying western Java forests; *Hylobates moloch* and *Trachypithecus auratus auratus*. This endemism also shows the high correlation with the number of natural parks in West and Central Java [32], which probably corresponds to the high soil fertility rates gained from the high-contained mineral of the eruption sediments.

Conversely, a higher endemic mammal species diversity was more visible in East Java during the Middle Pleistocene, in the stage of *Stegodon-Homo erectus* [32]. Two Hominoidae taxa, *Gigantopithecus* sp. [39] and *Homo erectus*, co-existed in the eastern part of the island during the Middle Pleistocene (**Table 4**). It is also followed by the known primate fossils, including *Trachypithecus auratus*, *Presbytis comata*, *M. nemestrina*, *M. fascicularis*, *Hylobates* sp., and later *Pongo pygmaeus* in the Late Pleistocene [33, 44]. All cercopithecoid species are comparable to extant species inhabiting Java Island, while Hominoidae taxa are all extinct. *Gigantopithecus* sp., *Homo erectus*, *Pongo pygmaeus*, and *M. nemestrina*, which have disappeared in recent Java Island, are assumed to indicate the incapability to adapt toward paleoclimatic changes resulting in habitat loss or ecological replacement from rain forest to open woodland and possible human intervention such as hunting. Although this result is likely related to excavation bias where most of the archeological localities are located in East Java [32, 37], the possible intraspecific variation is reported in *Homo erectus*, which is commonly discovered in eastern Java localities, specifically as craniodental specimens [25].

With the numerous *Homo erectus* findings in Java Islands, it leads to the high morphological diversity [25] exclusively on cranial morphology. A comprehensive study on comparison of *Homo erectus* cranial morphology between island and mainland population has been investigated showing the peculiar distinction on mainland vs. island population. Zhoukoudian *Homo erectus* represents mainland population (**Table 4**), and the common ancestor of Javan *Homo erectus* demonstrates a less morphological variability to the Early Pleistocene Java *Homo erectus* (that mostly unearthed in Sangiran Dome), while Late-Middle Pleistocene Javan *Homo erectus* are reported to share similarities in cranial shape [25]. It is suggestive that the lower habitat vicariance in mainland during Middle Pleistocene and Java Island during Middle-Late Pleistocene indicates less genetic isolation. Taking this into account, geographic barriers such as volcanic mountains, added with the isolation of Java, might enforce high intraspecific variation during Early-Middle Pleistocene, supported by the extensive paleoclimatic change. Out of Sunda Shelf, the obvious record of this mechanism appears in Wallacea non-human primates inhabiting Sulawesi. High bathymetric boundaries to Sunda Shelf and the islands surrounding, and diversified topographic barrier of Sulawesi contributes to six endemic macaque species; *Macaca nigra*, *Macaca tonkeana*, *Macaca maura*, *Macaca nigrescens*, *Macaca ochreata*, and *Macaca hecki* that some of the species were found in the archeological cave Leang Burung 2 that occupied with the early human occupation on the island in Late Pleistocene.

3.2 Temporal cost: isolation and endemism from Pleistocene to modern

3.2.1 Duration

Time by duration and particular period falls to the temporal scope of inhabitation of certain population on island is pronounced to impact body size evolution [12]. Higher duration of island isolation increases the chance for ecological release to influence functional characters (e.g., diet, locomotion, and bauplan) among species. The report on paleoinsular mammals has claimed that body size shift on island mammal species occurred when residence time reached more than 10,000 years [12]. While the evidences are prominently strong on terrestrial herbivores, including terrestrial primates (e.g., *Homo floresiensis*, 60,000–100,000 years ago [26]), it also evidently impacts the arboreal non-human primate species or subspecies (e.g., *Macaca fascicularis* and endemic primate species on Simeulue, Lasia, Nicobar, Mentawai Islands).

Typically expressed by the estimated dispersal chronology in Southeast Asian Archipelago, duration of island isolation shows the function of maximum sea depth separating island from mainland or neighboring large island, mainly in small-sized island. Some oceanic islands in the region (Simeulue, Lasia, Siberut, Sipora, North Pagai, South Pagai) remarked with bathymetric barrier more than 120 m (**Figure 1**) display clear effect of isolation than the shallow-water fringing island over Sunda Shelf. The shallow depth of Sunda Shelf sea floor (0–40 m) allows the emergence of exposed dry land that permits colonization, reversed colonization, or recolonization of the island which most commonly occur during the sea level drop during the Last Glacial Maximum (LGM), which reduces the optimum genetic isolation.

On the level of subspecies, the long duration of island isolation appears to indicate the development of new intraspecific features in *Macaca fascicularis* inhabiting oceanic islands. Estimated from the last connection with the progenitor mainland species ca. 160 ka (gained from recent bathymetric barrier), some oceanic islands mostly located in western archipelago are interpreted to develop unique *M. fascicularis* subspecies, such as *M. f. umbrosa* in Nicobar Islands, *M. f. fusca* in Simeulue Island, *M. f. lasiae* in Lasia Island, *M. f. tua* in Maratua Island, and *M. f. philippinensis* in western, northern, and eastern islands of the Philippines. The subspecies variation also took place later in continental islands, with shorter island isolation duration started ca. <18 ka such as *M. f. karimoendjawae* in Karimun Jawa Island, *M. f. atriceps* in Khram Yai Island, and *M. f. condorensis* in Con Son Island, marking weak differentiation based on superficial characters [5].

3.2.2 Changes through time

According to the previous paleontological works on mammal evolution of Southeast Asia, there is no fossil evidence of primates before ca. 0.9 Ma in Java Island. The first colonization of primates to Java is estimated to occur at the end of Early Pleistocene, when Sunda Shelf fully emerged and then periodically entered Java via Siva-Malayan corridor route during Middle Pleistocene [33]. Along with the balanced mammal association, including *Homo erectus*, this period seemingly shows the suitable ecological condition for arboreal high-adapted non-human primates (*Macaca*, *Trachypithecus*, and *Presbytis*) to adapt to mainly open woodlands in relatively dry climate condition [33]. The long duration allowing the dry landmass that connected recent mainland and island during this period possibly permits the occupation access for a hominine species (elaborated as *Homo cf. floresiensis* [42]) to inhabit the oceanic island of Flores.

To date, there is no chronological and geographical comparative study demonstrating body size of non-human primates between fossils and recent on Java Island. It rather revealed the similarities on morphological characters in accordance with the attempt in determining species. So, it was difficult to answer whether Middle Pleistocene non-human primates of Java are the continuously highly adapted species until recent or the extinct species that disappeared in the Middle Pleistocene like other mammals (including *Homo erectus*).

Late Pleistocene displays the rise of tropical rain forest non-human primates (*Hylobates* and *Pongo*) to develop in Sunda Shelf where the Chinese origin fauna enter to exhibit similar association to recent fauna [33]. Primate species/subspecies that became native to some oceanic islands (e.g., *M. siberu*, *M. pagensis*, *H. klossii*, *P. potenziani*, *P. pagensis*, and *Simias concolor* in Mentawai islands, *M. f. condorensis* in Nicobar Islands, *M. f. fusca* in Simeulue Island, *M. f. lasiae* in Lasia Island, and *M. f. tua* in Maratua Island). Considering the limitation of swimming ability (max. Swimming distance limit 100 m in *M. fascicularis* [5]) and large island-mainland distance, dispersal route to the oceanic island is most likely through corridor route over dry landmass, furthermore by passive dispersal, such as natural rafting [5]. The dispersal

scenario passing deep sea barrier to reach oceanic islands of Lesser Sunda presumably occurred by human transport during <4.5 ka [5], because swimming is not possible due to the strong sea current in Lombok Strait. This data is supported by the presence of *M. fascicularis* remains in archeological cave aged ca. 7 ka in Timor Island [5, 27].

3.3 Ecological cost: fauna association and vegetation

3.3.1 Fauna association

With limited connection to the diverse mainland fauna, isolated island promotes the poor taxonomic diversity and the imbalanced rate between herbivores and carnivores. Small island has been claimed to reduce the sympatric speciation than large island [31]. This condition drove a disharmonic inter- and intraspecific variation [12]. For instance, in severe ecological condition when food resources are limited in long duration, the large-bodied species tends to expand their territory where small-bodied species fails to compete and being enforced to undergo stronger dietary adaptation. This response to ecological condition led to a radiation into different size classes and morphotypes, which arrives to appear in the form such as anatomical modification (e.g., dental pattern, size, and shape of limb bone) causing genetic radiation [12].

In most case, this disharmonic taxonomic diversity condition dropped the survivability. The heavily impoverished condition leads to some species to extinction, for example, in all Late Pliocene-Early Pleistocene (*Sinomastodon-Megalochelys* stage) species in Java and large- to intermediate-bodied fauna in Flores Island in Late Pleistocene. It is followed by imbalanced condition where the normal ratio between carnivores and herbivores is high. Predator avoidance is suggested to cause the limb bone modification. A species that is not threatened by the carnivores might not often walk and run leading to the less development of limb bones.

3.3.2 Vegetation

The vegetation type of an area derives from mean temperature caused from latitudinal position, geographical topography, seasonality by monsoon, and geological sediments. During Quaternary, the fluctuating temperature prominently contributes to habitat changes. The ecological shift from tropical rainforest to more open environment in Early-Mid Holocene resulted in biodiversity loss in non-human primates; for example, it is shown by the disappearance of *Presbytis comata* (Javan langur) in eastern Java that was previously found in Braholo Cave, East Java (Late Pleistocene to Mid Holocene) [45], and the extinction of Pongo in Java that was formerly discovered in Punung rockshelter, East Java (Late Pleistocene) [46–48]. This open environment niches created the mosaic ecological niche in eastern Java [45, 49] that enforced the early *Homo sapiens* inhabiting Java to hunt the remaining arboreal fauna including non-human primates as food resources. Archeological evidence depicting *Homo sapiens* that consumed monkeys (*Macaca*, *Presbytis*, and *Trachypithecus*) are also discovered in Song Terus cave in the period from 9000 to 5000 years ago [50] and Niah Cave, Borneo [51]. Further ethnographic account resembling this phenomenon is found as butchery marks and burnt bone fragments on cercopithecids assemblage in Punan Vuhang, Sarawak, Borneo [52].

4. Conclusions

1. Prefigured by many geographic properties, bathymetric barrier presents to appear as the strongest casual effect in enforcing island isolation in Southeast

Asian Archipelago, expressed by the high degree of endemism in level of species in oceanic islands (i.e., *Homo floresiensis* in Flores Island and six non-human primates in Mentawai Islands). Vicariance geography in any form of barriers (e.g., mountain and river) could create allopatric speciation or endemism; however bathymetric barrier on island extraordinarily emerged in different process. The higher sea depth caused the higher chance for island population to disconnect more to the original continental population.

2. The duration of island isolation widens to promote the evolutionary results that yield the island ecological mechanism becoming intensified. The higher time cost on ecological factors such as selective pressures and predator avoidance could escalate the chance for anatomical feature to be modified. Although it is hard to know the absolute duration of island isolation, the relative isolation can be seen from the present bathymetry showing the predicted terminal time for body of water to cover the maximum depth that stop the connection from mainland to surrounding islands. Constituted by this concept, oceanic islands with high bathymetric barrier will definitely prolong the disconnection signal from mainland than continental islands.
3. When we control geographical and chronological isolation factors, the two main island ecosystem factors, faunal association and vegetation type, strongly contribute to the change of body size and shape, resulting in a higher island effect. Patterns impacted by this ecosystem factors are not the same in all islands. The imbalanced condition on fauna between the number of herbivores and carnivores and less interspecific faunal diversity could lead to the body size shift and anatomical modification. On primates, oceanic islands located near the equator covered with the densely tropical rain forest gave less likely island effect (e.g., Mentawai Island and Simeulue Island) than in oceanic island with drier and more open environment where resource is less abundantly available (e.g., Flores Island).
4. Latitudinal factor is clear to be seen in the mainland. While each island holds unique geographical properties directing to isolation (e.g., bathymetric barrier and island size), most Southeast Asian islands that are located around the equator with tropical weather resulting in major rain forest cover and short latitudinal range rather rise to contribute to more diverse body size and body shape longitudinally. Thus, Bergmann's rule is seemingly irrelevant to be evaluated in such condition.
5. The primates of Sunda Shelf occupying the great number of islands scattered in large scale area did not perform any pattern in regard to correlation between body size and island size. Potential causal relation to island size is more manifested in the increasing taxonomic diversity. Large-sized islands throughout Sunda Shelf hold higher diversity in anatomical variation than in small-sized island. It is supposedly due to the combination of possible isolation-derived process by geographic or ecological barrier and the resiliency of relict species along many stages of period. This circumstance is conceivably reassured from the Quaternary through recent, for example, the high diversity of calvarium morphology seen in *Homo erectus* of Java Island and the occurrence of four varied living *Presbytis* species in Borneo Island.
6. Endemism featured on non-human primates in continental islands of Sunda Shelf mostly direct to the resilience of relict groups occupying the island, not

necessarily in response to a long-term island isolation process. In the level of species, this premise is endorsed by the existence of a single taxon occupying large islands (e.g., *P. abelii* in Sumatra, *P. pygmaeus* in Borneo, *H. moloch* in Java). Smaller continental islands bordered by relatively higher bathymetric barrier could possibly produce the isolation-derived endemism process in the level of subspecies (e.g., *M. f. baweanus* in Bawean Island and *M. f. karimoend-jawae* in Karimun Jawa Island).

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Conflict of interest


The authors declare no conflict of interest.

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