



Western Eurasian genetic influences in the Indonesian archipelago



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ABSTRACT

Western Eurasia, notably the Near East and South Asia (Indian sub-continent), has interacted with Indonesia through Indian Ocean trade (the Maritime Silk Route) for more than 2000 years. The Indianization, and later Islamization, of Indonesia was enacted largely through trading activities, but also spread with help from the many Indianized and Islamic kingdoms that reigned over parts of the Indonesian archipelago during this time. Western Eurasian interaction left behind not only imported trade goods and cultural features, but also genetic traces. To locate the primary areas of Western Eurasian genetic influence in Indonesia, we have assembled published uniparental genetic data from ~2900 Indonesian individuals. Frequency distributions show that Western Eurasian paternal lineages are found more commonly than Western Eurasian maternal lineages. Furthermore, the origins of these paternal lineages are more diverse than the corresponding maternal lineages, predominantly tracing back to South West and South Asia, and the Indian sub-continent, respectively. Indianized kingdoms in the Indonesian archipelago likely played a major role in dispersing Western Eurasian lineages, as these kingdoms overlap geographically with the current distribution of individuals carrying Western Eurasian genetic markers. Our data highlight the important role of these Western Eurasian migrants in contributing to the complexity of genetic diversity across the Indonesian archipelago today.

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1. Introduction

Western Eurasia (WE), notably the Near East and South Asia, had established very close contact with Island South East Asia, particularly Indonesia, through cultural and trading networks in the Maritime Silk Route as early as the 1st century B.C.E. (Ardika and Bellwood, 1991; Ardika et al., 1997; Calo, 2014; Lawler, 2014). Contacts between the Indian sub-continent and Southeast Asia occurred even earlier (from the late 2nd millennium B.C.E.) if we consider the evidence from transfers of plants (Fuller, 2006; Asouti and Fuller, 2008), and trade networks were well established by the 1st millennium B.C.E. (Bellina and Glover, 2004). Indianization and Islamization in Indonesia led to the development of Hindu, and

later Islamic, kingdoms between the 5th and 15th centuries, which reinforced interactions and influence from WE to all regions of western and central Indonesia (Gonda, 1975; Kanchan, 1990; Beaujard, 2012). These interactions brought not only new ideas and trade goods into the Indonesian archipelago, but were also accompanied to some degree by gene flow, which contributed to a number of modern Indonesian populations. Considering the historical events of the last two millennia, it has been variously postulated that WE genetic influx into Indonesia could have originated from populations in India (via the main Indian kingdoms – Pallava and latter Chola in Southeast India; Gurjara and Rashtrakuta in north and east India; and later Indian sultanates) (Mabbett, 1977; Lansing, 1983; Lukas, 2003; Beaujard, 2012), the Near East (via Persian influence, the Sassanid empire and later the Arab Muslim empire) (Jacobsen, 2009; Beaujard, 2012) or Europe following Portuguese and Dutch colonialism (Taylor, 2009). The genetic evidence so far suggests that the primary contribution came from the Indian subcontinent (Karafet et al., 2005, 2010; The HUGO Pan-Asian SNP Consortium, 2009), but there is still debate regarding

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the importance of Indian gene flow, and its geographic diffusion into and impact on the Indonesian archipelago. Some scholars propose either colonization by Indian exiles (Majumdar, 1963), large-scale migration establishing Indian colonies in South East Asia (Mabbett, 1977), or more punctuated contact by Indian traders (Lansing, 1983; Sandhu and Mani, 1993), but the available data are insufficient to suggest a reliable chronological framework for these gene flow scenarios at the scale of the whole Indonesian archipelago. Historical evidence mentions the "... constant flux of people from Gujarat and neighboring regions [in the Indian sub-continent] ..." to Java early in the 9th century, related to the construction of the Plaosan temple (Beaujard, 2012, pp. 94). Indeed, genetic traces of paternal Indian ancestry have been detected at low frequency in Indonesia (<10%) (Karafet et al., 2005, 2010) across several islands (Sumatra, Java, Borneo and Bali), but in comparison, no Indian maternal lineages have been detected (Tumonggor et al., 2013). The influx of Indian ancestry has also been observed from genome-wide analysis using a limited number of nuclear SNPs (The HUGO Pan-Asian SNP Consortium, 2009) in just a few populations from western Indonesia (Sumatra). However, Indian markers in autosomal data were not detected in large-scale genotyping of eleven populations across Island Southeast Asia (Pugach et al., 2013).

Our study is based on the largest dataset of maternal (mtDNA) and paternal (Y chromosome) lineages assembled for the Indonesian archipelago to date. However we need to bear in mind some limitations of this dataset; namely (1) the resolution of the data (at the haplogroup level), which only allows the tracing of haplogroup origins at a regional scale (the Indian sub-continent, Middle East and Europe), and (2) the source of gene flow, which is inferred from the hypothesized origin of WE haplogroups (which, in turn, is

starting at least from the late 1st millennium B.C.E. with a likely intense phase during the period of the Hindu kingdoms in Indonesia (7th–16th century AD) (Beaujard, 2012; Calo, 2014). These assumptions and approaches are reasonable and standard in the field. Our primary aim is to use a phylogeographic approach (assessing the frequency of WE haplogroups in Indonesia) to (1) map Western Eurasian genetic influences in Indonesia, and to a lesser extent to (2) identify the main regional sources of these influences (the Indian sub-continent, Middle East and Europe). Considering early cultural and trade networks with the Indian sub-continent, we will test the hypothesis that India is the main source of WE influence in Indonesia, and that this WE gene flow is probably sex biased. We propose that genetic contributions from Western Eurasia and the Indian sub-continent are mostly restricted to the areas where Indianized kingdoms were most powerful. We also show that genetic contact with both Indian men and women was involved.

2. Materials and methods

2.1. DNA samples and data sources

Indonesian samples used in this study have been described previously (Karafet et al., 2010; Gunnarsdóttir et al., 2011; Tumonggor et al., 2013; Kusuma et al., 2015). In brief, the mtDNA dataset includes 2841 individuals, and the Y chromosome dataset includes 2095 individuals, from 7 major Indonesian islands, representing 22 and 17 different ethnic groups, respectively (Table 1). These two datasets represent the largest Indonesian genetic assemblage studied to date.

Table 1
List of populations used in this study.

Group	Islands	Population code	Population	N mtDNA	N Y chromosome	Ref.
Western Indonesia	Sumatra	1	Gayo	62	NA ^a	Eijkman Institute archived samples
		2	Batak Toba	42	37	Karafet et al., 2010; Tumonggor et al., 2013
		3	Besemah	36	38	Gunnarsdóttir et al., 2011
		4	Semende	36	37	Gunnarsdóttir et al., 2011
		5	Nias	59	60	Karafet et al., 2010; Tumonggor et al., 2013
		6	Mentawai	128	74	Karafet et al., 2010; Tumonggor et al., 2013
	Borneo	7	Lebbo'	19	15	Kusuma et al., 2015
		8	Ma'anyan	159	90	Kusuma et al., 2015
		9	SK Dayak ^b	64	NA	Eijkman Institute archived samples
		10	EK Dayak ^b	NA	85	Karafet et al., 2010
Eastern Indonesia	Java	11	Java	51	61	Karafet et al., 2010; Tumonggor et al., 2013
	Bali	12	Bali	487	634	Karafet et al., 2010; Tumonggor et al., 2013
	Sulawesi	13	Mandar	54	54	Karafet et al., 2010; Tumonggor et al., 2013
		14	Kajang	46	NA	Tumonggor et al., 2013
		15	Toraja	50	NA	Tumonggor et al., 2013
		16	Bugis	50	NA	Tumonggor et al., 2013
	Lesser Sunda	17	Bajo	27	27	Kusuma et al., 2015
		18	Sumba	634	349	Karafet et al., 2010; Tumonggor et al., 2013
		19	Flores	469	388	Karafet et al., 2010; Tumonggor et al., 2013
		20	Lembata	92	89	Karafet et al., 2010; Tumonggor et al., 2013
21		Pantar	29	NA	Tumonggor et al., 2013	
22		Alor	23	27	Karafet et al., 2010; Tumonggor et al., 2013	
Maluku	23	North Maluku	224	NA	Eijkman Institute archived samples	
	24	Maluku (Hiri and Ternate)	NA	30	Karafet et al., 2010	

^a NA = Not Available for analysis.

^b Samples of SK Dayak were collected from various Dayak ethnics in South Kalimantan, while the EK Dayak were collected from various Dayak ethnics in East Kalimantan.

inferred from where these are found at high frequencies in populations today). In addition, there are chronological limitations caused by (3) the inability of dating the time of WE gene flow to Indonesia from the data used in this study, that lead us (4) to rely on the archaeological and historical chronology (e.g., gene flow

2.2. Haplogroup assignment

Mitochondrial DNA hypervariable region I sequences were compiled from published sources (Table 1) and aligned against the revised Cambridge Reference Sequence (rCRS) (Andrews et al.,

1999) using the MAFFT aligner v.7 (Kato and Standley, 2013). Mitochondrial haplogroups were determined with the Haplogrep program (<http://haplogrep.uibk.ac.at>) based on Phylotree v.16 (Van Oven and Kayser, 2009).

Y chromosome haplogroups were assigned from SNP data based on the updated ISOGG Y-DNA haplogroup tree (International Society of Genetic Genealogy, 2014) and the Y-Phylotree (Van Oven et al., 2014).

2.3. Statistical analyses

Western Eurasian mitochondrial DNA and Y chromosome haplogroup frequencies in Indonesian populations were plotted geographically with Surfer v.12.0 (<http://goldensoftware.com>) using the Kriging method. Mitochondrial DNA and Y chromosome haplogroup diversity was calculated using Nei's method (Nei, 1987) as implemented in Arlequin v.3.5 (Excoffier and Lischer, 2010) with 5040 permutations for statistical testing. To observe Western Eurasian and Asian components in both the paternal and maternal datasets, Principal Component Analysis (PCA) based on mtDNA and Y chromosome haplogroup frequencies (Supplementary Table A1 and A2) was performed on populations grouped by island in R (<http://www.r-project.org>) and visualized with a biplot graph implemented in the ggbiplot package.

3. Results

We observed 13 Western Eurasian mtDNA and 15 Western Eurasian Y chromosome haplogroups in 9 (out of 22) and 7 (out of 17) Indonesian populations, respectively (Supplementary Table A1 and A2). Western Eurasian Y chromosome haplogroups are more frequent (4.49%) and diverse (0.0222–0.439) than Western Eurasian mtDNA haplogroups (1.55% and 0.00320–0.242) (Supplementary Table A3). This is in agreement with the putative geographical origins of the WE haplogroups found in Indonesia. Indeed the source locations of WE mtDNA and Y haplogroups found in Indonesian populations do not overlap perfectly (Supplementary Table A1 and A2). The 13 WE mtDNA haplogroups are primarily derived from South Asia, mainly the Indian sub-continent. Conversely, the 15 WE Y chromosome haplogroups in Indonesia exhibit more diverse origins, yet South Asia remains the most frequent point of origin. The most common Y chromosome haplogroup is R1a1a (M17), which was observed in 5 of the 7 Indonesian populations that carry WE haplogroups, followed by R2a in 4 populations. Outside Indonesia, R1a1a and R2a (M124) have similar distributions with relatively high frequencies in South Asia (Sengupta et al., 2006; Underhill et al., 2010). For mtDNA, M5 is the most frequent haplogroup found in Indonesia, observed in 4 of 9 populations that carry WE haplogroups. Outside Indonesia, M5 is mainly found in India (Sahoo and Kashyap, 2006; Sun et al., 2006; Thangaraj et al., 2006).

The distribution of WE haplogroups across Indonesia is depicted in Fig. 1. Western Eurasian Y haplogroups are clustered in central Indonesia, and geographically restricted to populations to the south of the Celebes Sea, with the exception of one individual in northern Sumatra. WE Y chromosome haplogroups reach highest frequency in Bajo from Sulawesi (25.9%; 7 of 27 individuals), Java (14.7%; 9 of 61 individuals), and Bali (11.0%; 70 of 634 individuals). A broadly similar pattern can be observed from the distribution of WE mtDNA haplogroups, which are also detected in populations south of the Celebes Sea, with the exception of a population from Gayo in north Sumatra. WE mtDNA haplogroups reach highest frequency in Gayo (12.9%; 8 of 62 individuals), followed by Pantar (10.3%; 3 of 29 individuals), and Java (7.8%; 4 of 51 individuals).

A PCA plot of the distribution of Western Eurasian versus Asian lineages among Indonesia populations (grouped by island) also supports these results (Fig. 2). The strongest Western Eurasian influence on the paternal gene pool can be seen in populations from Java, Bali, and Sulawesi. The strongest WE influences on the maternal gene pool are found in Java, Sumatra, and the Lesser Sunda islands. Java is the only population with a high frequency of WE haplogroups for both paternal and maternal lineages (14.8% and 7.84%, respectively).

4. Discussion

New archaeological evidence shows that a network of interactions moved goods and ideas across the Indian Ocean at least 2000 years B.C.E (Lawler, 2014). Island South East Asia, and particularly the Indonesian archipelago, joined this network later in the 1st century B.C.E., with connections at first mostly with India (Ardika and Bellwood, 1991; Ardika et al., 1997; Calo, 2014). This promoted Western Eurasian influences in Indonesia, and Indianized cultures became widespread in Indonesia shortly afterwards. Typical influences included old writings in Sanskrit, shadow puppets (wayang) and dances, sculptures, vast Hindu temples in Java and Bali, and modified socio-cultural structures, such as the caste system in Bali (Mellema, 1954; Pigeaud, 1960; Coedes, 1968; Dumarcay, 1986; Kanchan, 1990; Sumarsam, 1995; Covarrubias and Vickers, 2008; Guy, 2014). Indian influences were accepted and frequently assimilated by Indonesians, and spread through many Hindu and Islamic kingdoms in Indonesia, such as Heluodan (5th century), Tarumanagara (5th century), Walaing (7th–8th centuries), Kahuripan/Kediri (11th century), Singhasari (13th century), and Majapahit (13th–15th centuries) (Beaujard, 2012). In parallel to cultural and trading influences, movements of people from South and Southwest Asia to Indonesia also likely occurred, but their impact on the gene pool of modern Indonesia has been debated and drove this investigation.

Our study shows that a Western Eurasian genetic contribution exists at non-negligible levels. Frequency distributions of Western Eurasian maternal and paternal lineages in Indonesian populations suggest that 1) about the same number of Indonesian populations (~40%) carry WE paternal and/or maternal haplogroups, 2) populations with the highest WE contributions are found in central Indonesia, to the south of the Celebes Sea, 3) WE input is more frequent in the paternal (4.49%) than maternal (1.55%) Indonesian gene pool, and 4) the geographical origin of WE maternal and paternal haplogroups suggests a preponderance of haplogroup sources in South Asia (the Indian sub-continent).

WE paternal lineages seem to be sourced from across a broader geographical area (South West and South Asia) (Supplementary Table A1 and A2) than maternal lineages, which are mainly derived from the Indian sub-continent. This may be due to a male bias in trading activities, and also fits the hypothesis that Indian influence was not restricted only to trading/cultural activities, but involved a substantial movement of men from the Indian sub-continent into Island South East Asia (Mabbett, 1977; Beaujard, 2012).

A recent study based on genome-wide data from eleven populations across Island Southeast Asia (including nine from Indonesia) could not detect Indian markers in any Island Southeast Asian populations, but only in Australo-Melanesian populations (Aboriginal Australians) (Pugach et al., 2013). Our study, by using uniparental markers and a large numbers of populations across the Indonesian archipelago, allows a different perspective on this specific point, showing (1) the presence of WE (including Indian) gene flow into Indonesia, (2) the pattern of its geographic distribution across Indonesia, (3) potential WE sex-biased gene flow, and

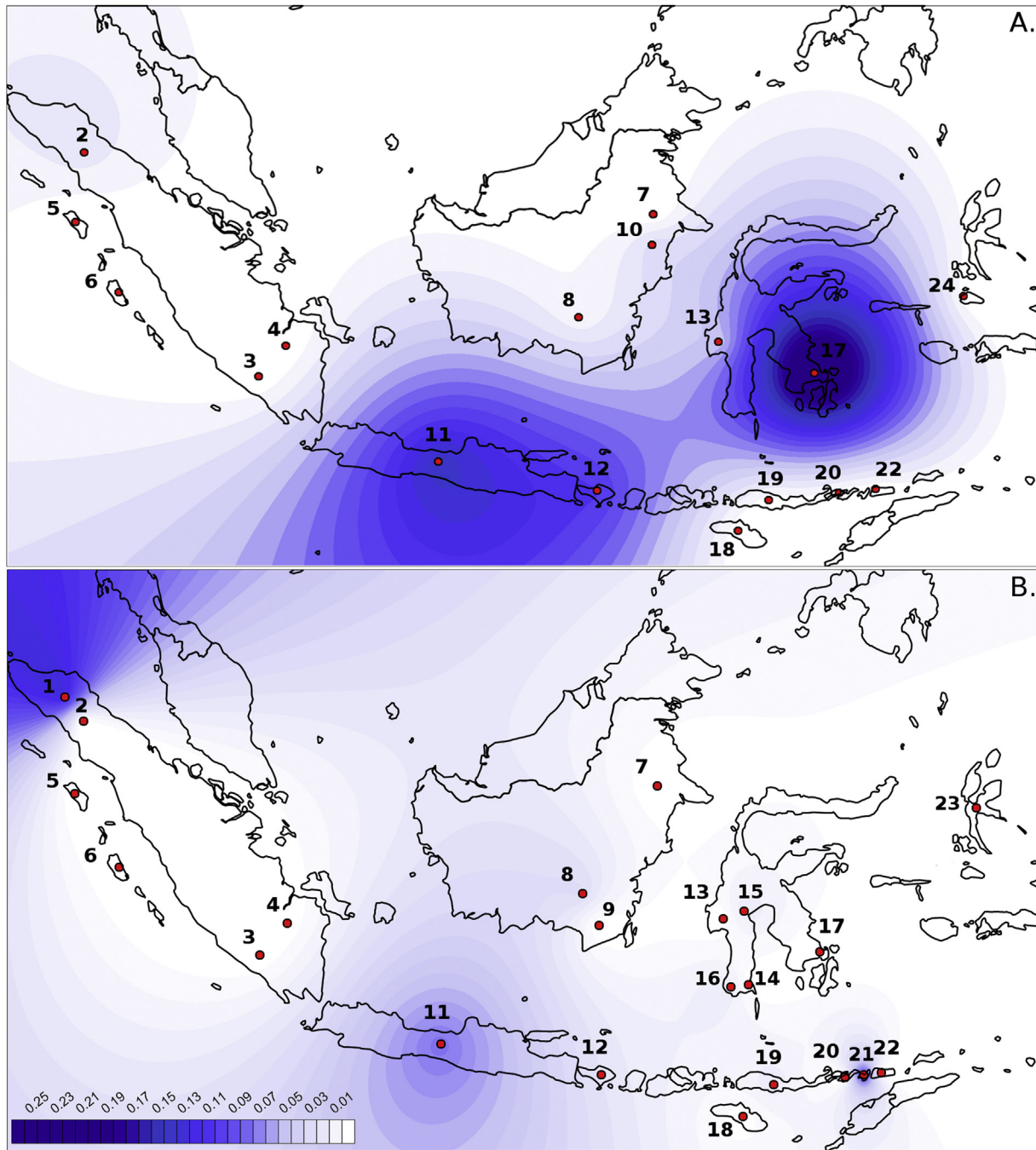


Fig. 1. Frequency of Western Eurasian A) Y chromosome and B) mtDNA haplogroups among Indonesian populations (indicated by red dots). Dark shaded areas have higher frequencies. Data and population details are provided in Tables 1, A1 and A2. Population identifiers: 1. Gayo, 2. Batak Toba, 3. Besemah, 4. Semende, 5. Nias, 6. Mentawai, 7. Lebbo', 8. Ma'anyan, 9. SK Dayak, 10. EK Dayak, 11. Java, 12. Bali, 13. Mandar, 14. Kajang, 15. Toraja, 16. Bugis, 17. Bajo, 18. Sumba, 19. Flores, 20. Lembata, 21. Pantar, 22. Alor, 23. North Maluku, 24. Maluku. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(4) the possibility of tracing WE origins at the regional scale (the Indian sub-continent, Middle East and Europe). However, one main limitation is our inability to date the timing of WE gene flow into Indonesia.

While it is difficult to evaluate whether WE gene flow has been constant since the first contacts and exchanges between the Indian sub-continent and Indonesia in the late 1st millennium B.C.E., it is likely that this gene flow was particularly intense during the period of the Hindu kingdoms in Indonesia (7th–16th century AD). These assumptions, based on archaeological and historical data, are also in broad agreement with dating on unpublished genome-wide SNP

markers from Island Southeast Asia (unpublished data). Gene flow from the late 1st millennium B.C.E. onward still has to be reconciled with the dates from Pugach et al. (2013), who reported South Indian migration into Australasia at least 2000 years earlier. The possibility of two separate migration events (to ISEA and to Australasia) seems unlikely given the archaeological, historical and genetic evidence assembled to date, which supports a more constant level of gene flow from the Indian sub-continent to Island Southeast Asia, via either a land or coastal/maritime route. We therefore hypothesize that the 4000 year estimate may reflect a relatively sparse arrival of Southern Indians into Australasia, which was only a single end-

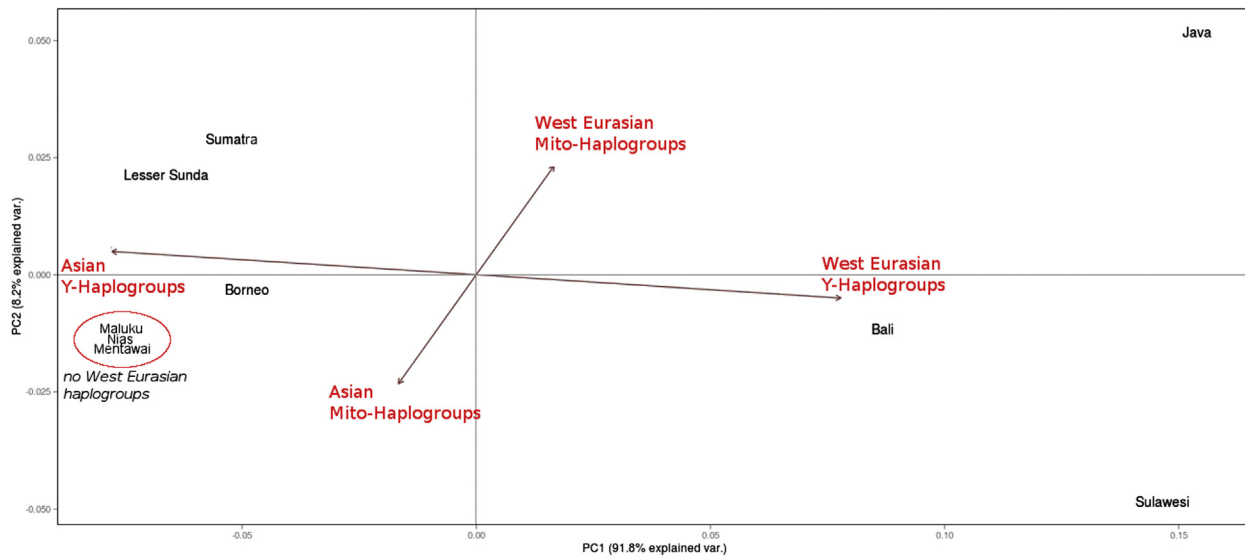


Fig. 2. PCA plot showing the 1st and 2nd principal components computed from Western Eurasian mtDNA and Y chromosome haplogroup frequencies in Indonesia (grouped by island).

point, while Indian-Indonesian contact from the 1st millennium B.C.E. onward should reflect the midpoint of Indian gene flow between 4000 years ago and more recent times. It is likely that contact between the Indian sub-continent and Indonesia started earlier than recorded in the archaeological record, as the Indian Ocean network was active since at least 2000 years B.C.E. (Lawler, 2014). Interestingly, traces of Western Eurasian genetic lineages in Indonesia are mostly observed in regions where ancient Hindu and Islamic kingdoms were located. These kingdoms governed their regions in different, but often overlapping, geographical regions from the 7th to 16th centuries. For example, Srivijaya was based in Sumatra; Majapahit, Singasari and Kahuripan/Kediri in Java; Kutai in Kalimantan and Sulawesi; and Buleleng in Bali and neighboring islands in the Lesser Sunda chain (Pigeaud, 1960; Wolters, 1967; Kanchan, 1990; Beaujard, 2012). Later, Islamic kingdoms arose in northern Sumatra around the 14th century, influenced culturally by Arab (Near East) or Gujarat traders (India) (Ali, 1975; Ricklefs, 1993). In this study, WE traces are found in East Kalimantan, Sulawesi, Java, Bali, and northern Sumatra for both paternal and maternal lineages, and in the Lesser Sunda islands for maternal lineages. This indicates that the influence of Indianized/Islamic kingdoms in Indonesia was not restricted simply to cultural assimilation, trading and economic or political power, but was also associated to some degree with gene flow into Indonesia from cultural and/or trading centers in South and South West Asia.

5. Conclusion

Western Eurasian influences into Island South East Asia helped shape the genetic background of modern Indonesian populations. Despite their relatively small genetic impact (in striking contrast to its huge cultural impact), Western Eurasian lineages are found in both the paternal and maternal Indonesian gene pools, suggesting that contact extended beyond cultural and trading activities to at least some small-scale population movements coupled with long-term settlement. The exact small-scale geographical sources of these Western Eurasian contributions still need to be clarified, but genetic evidence indicates slightly different origins for paternal and maternal Western Eurasian lineages, while emphasizing the major role played by the Indian sub-continent. Further genetic studies will need to be performed using larger sample sizes and a broader

array of genetic markers (including genome-wide genotyping) in order to provide additional information on the exact sources, timing, and modality of the Western Eurasian genetic contribution to Indonesia.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2015.06.048>.

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