International Journal of Advance and Applied Research (IJAAR)
Peer Reviewed Bi-Monthly

ISSN – 2347-7075
Impact Factor –7.328
Vol.8 No.5 May – June 2021

INDIAN GENETIC HERITAGE IN SOUTHEAST ASIAN POPULATIONS

Dr. Ashok Kumar
Magadh University, Bodh Gaya, Bihar

Abstract:

The great ethnolinguistic diversity found today in mainland Southeast Asia (MSEA) reflects multiple migration waves of people in the past. Maritime trading between MSEA and India was established at the latest 300 BCE, and the formation of early states in Southeast Asia during the first millennium CE was strongly influenced by Indian culture, a cultural influence that is still prominent today. Several ancient Indian-influenced states were located in present-day Thailand, and various populations in the country are likely to be descendants of people from those states. To systematically explore Indian genetic heritage in MSEA populations, we generated genome-wide SNP data (using the Affymetrix Human Origins array) for 119 present-day individuals belonging to 10 ethnic groups from Thailand and co-analyzed them with published data using PCA, ADMIXTURE, and methods relying on f-statistics and on autosomal haplotypes. We found low levels of South Asian admixture in various MSEA populations for whom there is evidence of historical connections with the ancient Indian-influenced states but failed to find this genetic component in present-day hunter-gatherer groups and relatively isolated groups from the highlands of Northern Thailand. The results suggest that migration of Indian populations to MSEA may have been responsible for the spread of Indian culture in the region. Our results also support close genetic affinity between Kra-Dai-speaking (also known as Tai-Kadai) and Austronesian-speaking populations, which fits a linguistic hypothesis suggesting cladality of the two language families.

INTRODUCTION:

Mainland Southeast Asia is a region with great ethnolinguistic diversity. We studied genetic population history of present-day mainland Southeast Asian populations using genome-wide SNP data. We generated new data for ten present-day ethnic groups from Thailand, which we further combined with published data from mainland and island Southeast Asians and worldwide populations. We revealed South Asian genetic admixture in various mainland Southeast Asian ethnic groups which are influenced by Indian culture but failed to find it in groups that remained culturally isolated until recently. Our finding suggests that migrations of Indian people in the past may have been responsible for the spread of Indian culture in mainland Southeast Asia. We also found support for a close genetic affinity between Kra-Dai- and Austronesian-speaking populations, which fits a linguistic hypothesis suggesting cladality of the two language families.

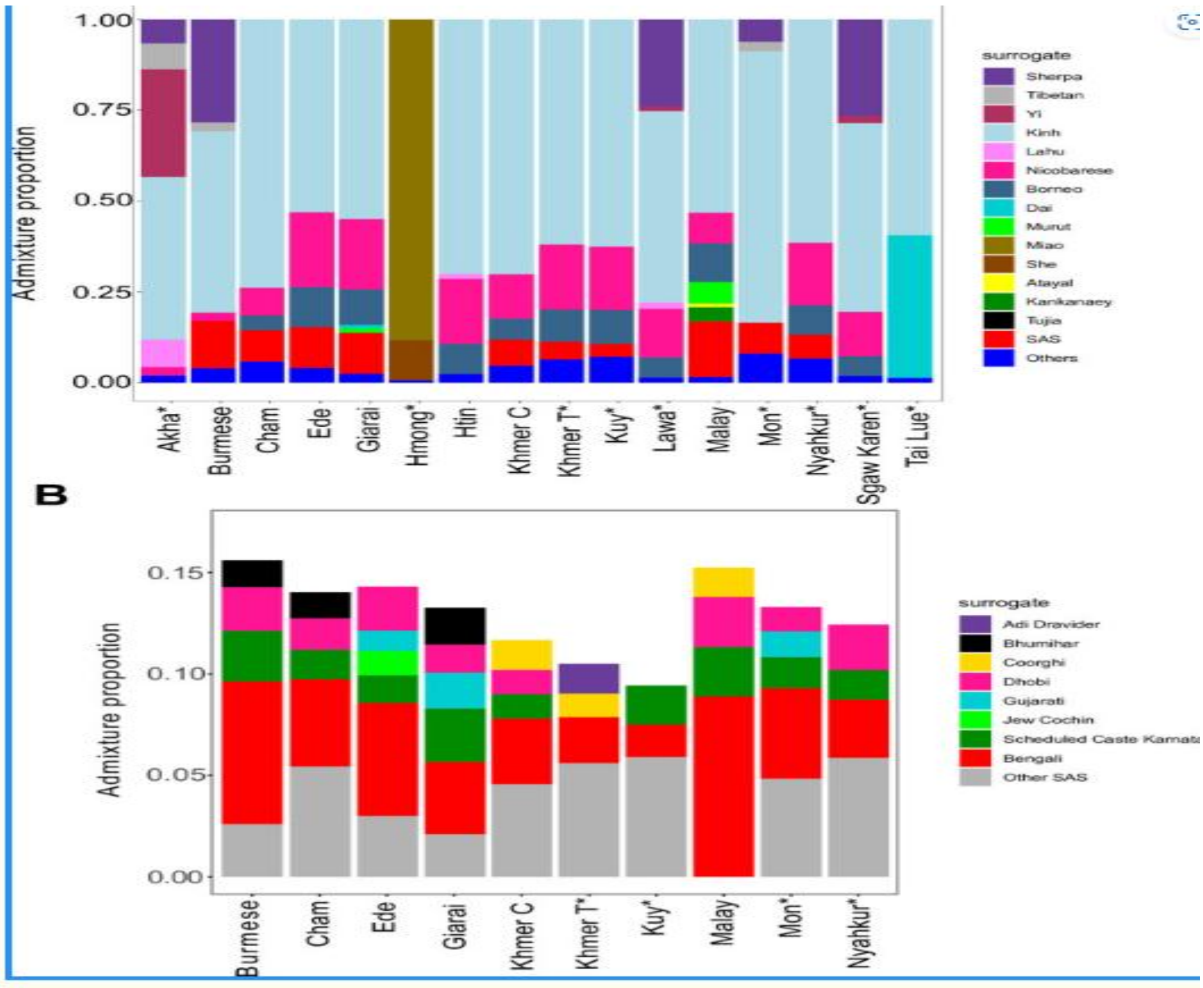
METHOD:

Currently, Indonesia, more than most other countries in Southeast Asia, remains most heavily influenced by aspects of Indian culture. Bahasa Indonesia (the nation's official language) along with "Javanese and Balinese have all absorbed a great deal of Sanskrit vocabulary".27 Hinduism features prominently in day-to-day life, especially in the islands of Java, the most densely populated of Indonesia's islands, and Bali, the most popular tourist destination in the country. The pervasive legacy of Hinduism across Indonesia, not as a widely practiced religion but as a visual presence, is most evident from the 20,000 rupiah currency note of Bank Indonesia which has an inscription of an image of the Hindu God Ganesh. The very inscription of Ganesh on something as ubiquitous and significant as a currency note – an item that is strongly linked to national identity, is more frequently and widely used than almost anything else, and is of both economic and emotional value in people's lives – conveys the impact that Hinduism has managed to retain on the cultural landscape of Muslim-majority Indonesia. Mainland Southeast Asia (MSEA) is a region with high ethnolinguistic diversity and complex population history. Hundreds of indigenous languages belonging to five major language families (Austroasiatic, Austronesian, Hmong-Mien, Kra-Dai, and Sino-Tibetan) are spoken in MSEA [1]. Archaeological evidence shows that anatomically modern humans migrated to MSEA roughly 50000 years ago [2,3]. Previous archaeogenetic studies indicate that the earliest MSEA individuals belong to the deeply diverged East Eurasian hunter-gatherers [4]. Andamanese hunter-gatherers (Onge and Jarawa) and MSEA Negritos are present-day populations with substantial proportions of ancestry from the deeply diverged East Eurasian hunter-gatherer lineage [4,5]. Neolithic populations in MSEA were established by admixture between these local hunter-gatherers and agriculturalists who migrated from South China around 4000 years ago [4,5]. The genetic makeup of MSEA Neolithic individuals is similar to present-day Austroasiatic-speaking populations [4,5]. That pair of studies also detected additional waves of migrations from South China to MSEA during the Bronze and Iron Ages. There is evidence of trading in Indian goods in MSEA and of glass bead manufacturing by MSEA locals using Indian techniques during the Iron Age [2]. Early states in MSEA during the first millennium CE, such as the Pyu city-states, Funan, Dvaravati, Langkasuka, and Champa were established with a substantial influence from Indian culture [6]. A Chinese source described Funan, one of the earliest known states in MSEA, as established by an Indian Brahmin named Kaudinya and a local princess [2,6]. The spread of Indian culture had various impacts on the region, such as state formation, laws, religions, arts, and literature. Ancient Sanskrit inscriptions were found throughout MSEA, and several present-day languages in the region contain numerous Sanskrit loanwords.

DESCRIPTIONS:

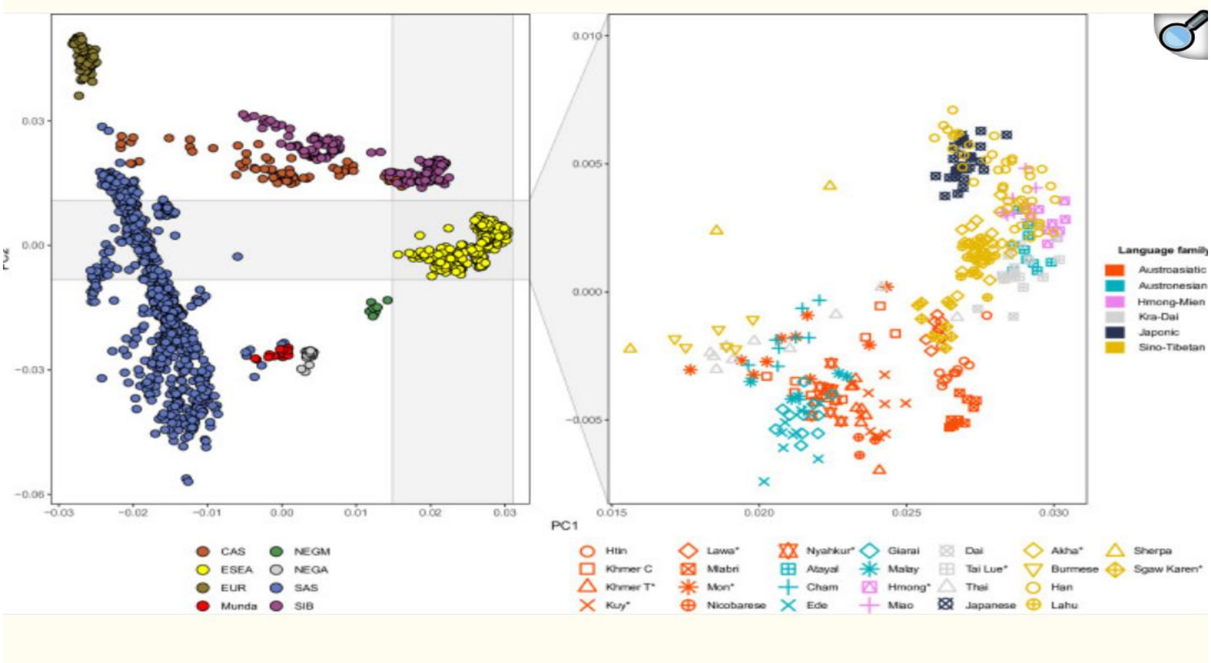
We generated genome-wide SNP genotyping data for ten populations from Thailand: six Austroasiatic-speaking populations (Khmer, Kuy, Lawa, Maniq, Mon, and Nyahkur), one Hmong-Mien-speaking population (Hmong), one Kra-Dai-speaking population (Tai Lue), and two Sino-Tibetan-speaking populations (Akha and Sgaw Karen). Akha, Lawa, Karen, and Hmong are officially recognized as hill tribes (a term commonly used in Thailand for minority ethnic groups residing mainly in the northern and western highland regions of the country) in Thailand [21]. Another group genotyped in this study, Khmer from Thailand, is a Northern Khmer-speaking population which is closely related to Cambodian Khmer (Cambodians), the majority population in Cambodia [1]. Present-day Khmer are likely to be descendants of people from ancient Khmer states in the region [22]. Kuy is a population which has interacted with the Khmer since ancient times [23]. The Mon and Nyahkur languages belong to the Monic branch of the Austroasiatic language family [1]. These populations are probably related to people from ancient Mon states in present-day Thailand and Myanmar [22]. Tai Lue is a Kra-Dai speaking group, which is closely related to Dai from Southern China [1]. Maniq, a MSEA Negrito group, are present-day hunter-gatherers. We combined our data with published MSEA and worldwide data. The aims of our study are: 1) to explore South Asian admixture in MSEA populations to find out if the Indian cultural expansion was driven by cultural diffusion or movement of people from India and subsequent inter-marriage with local MSEA people; 2) to investigate population structure in MSEA groups; and 3) to study the genetic connections between Kra-Dai and Austronesian-speaking populations since a sister-clade relationship between the two languages families was previously suggested.

Admixture proportions inferred using SOURCEFIND.



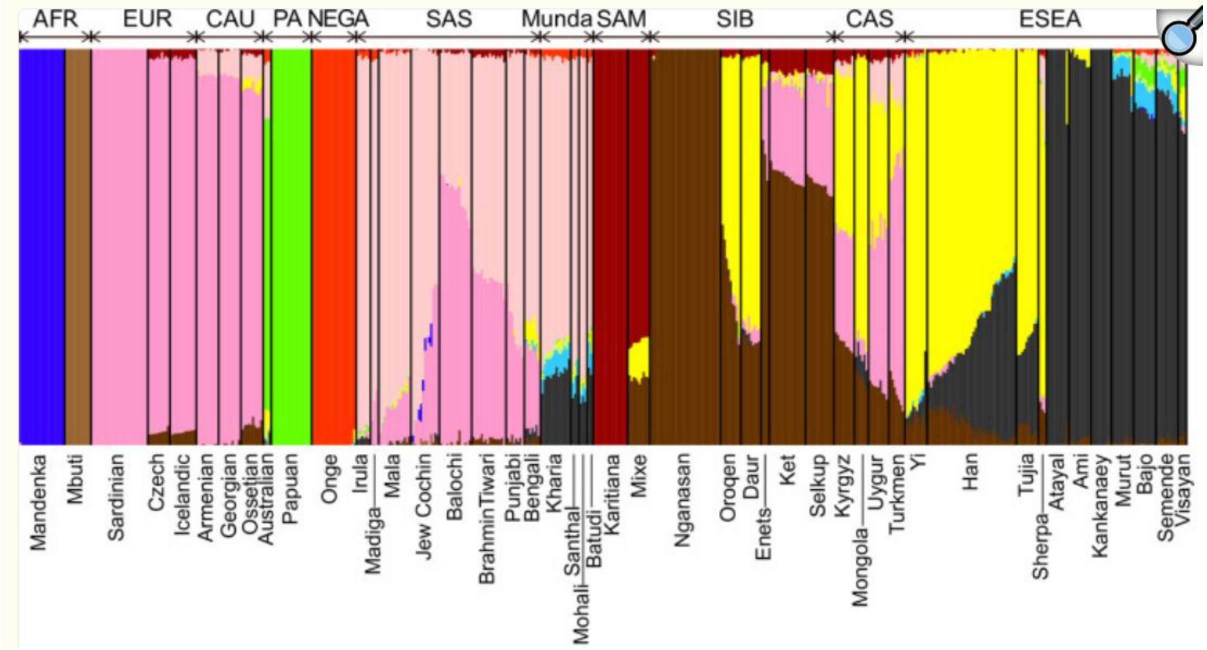
RESULTS:

Using the Affymetrix Human Origins SNP array [24], we generated genome-wide genotyping data (574,131 autosomal sites after quality control filtering) for 10 present-day human populations from Thailand (Fig 1). We merged our data with published data for ancient and present-day worldwide populations (S1 Table). To obtain an overview of population structure, we performed principal component analysis (PCA) (Fig 2). South Asian (SAS) populations lie on a previously described North-South cline [25]. Central Asian and Siberian populations lie between the European (EUR)—SAS cline and the East and Southeast Asian (ESEA) cluster. In agreement with expectations from geography, the Central Asian cline lies between the Siberian and South Asian clines. Maniq, MSEA Negritos (NEGM), are located between the ESEA cluster and Onge, the Andamanese Negritos (NEGA). Munda populations, Austroasiatic-speaking populations from India which were shown in a previous study [26] to be a genetic mixture of South Asian and Southeast Asian populations, lie between the SAS cline and ESEA cluster, as expected (Fig 2). Populations from East and Southeast Asia form a well-defined cluster, but the positions of some populations such as Sherpa, Burmese, Mon, Thai, Cambodian Khmer (Khmer C), Cham, Ede, Malay, Khmer from Thailand (Khmer T), Nyahkur, and Kuy are shifted towards the SAS cline



A principal component analysis (PCA) plot of present-day Eurasian populations.

Results of an ADMIXTURE analysis:



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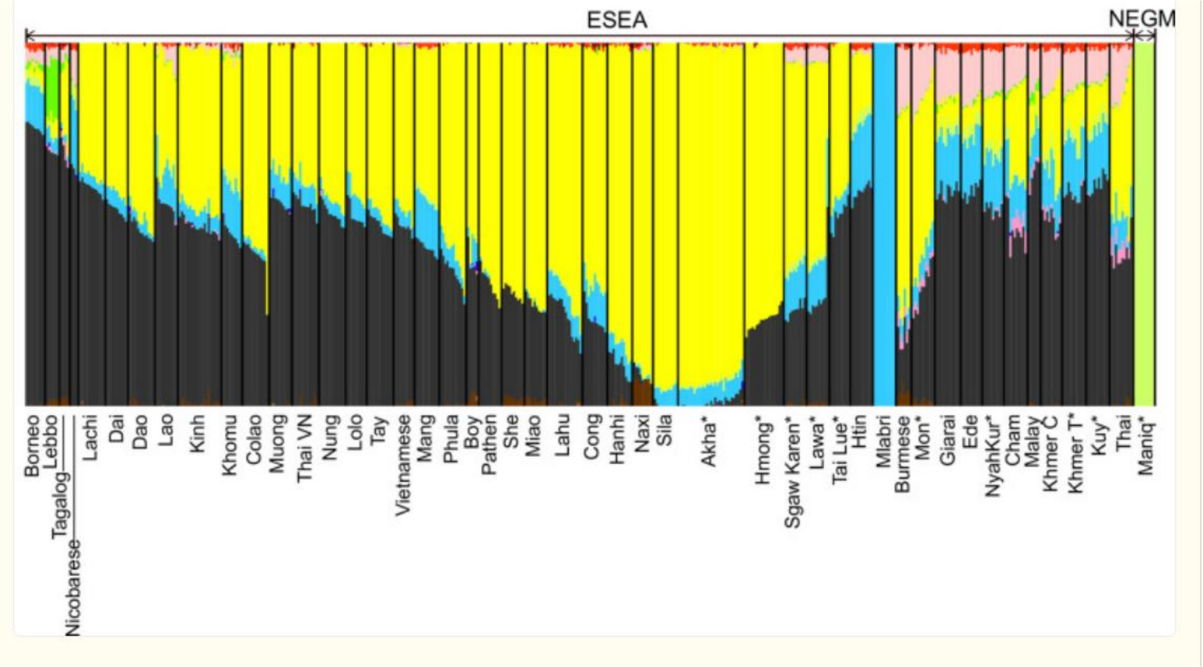

CONCLUSION:

The plot represents results for 12 hypothetical ancestral populations. Abbreviations of meta-populations are shown above the plot: AFR, Africans; EUR, Europeans; CAU, Caucasians; PA, Papuans and Australians; NEGA, Andamanese Negritos; SAS, South Asians; Munda, Austroasiatic-speaking populations (the Munda branch) from India; SAM, Native South Americans; SIB, Siberians; CAS, Central Asians; ESEA, East and Southeast Asians; and NEGM, Mainland Negritos. Asterisks after population names indicate that these populations are newly genotyped in this study. Akha, Lawa, Karen, Hmong, and Htin were officially recognized as hill tribes by the Hill Tribe Development and Welfare Programme of the Department of Public Welfare in Thailand [21]. Maniq and Mlabri are the last two hunter-gatherer groups in Thailand [45]. We failed to detect South Asian ancestry in these seven populations. The result is consistent with a recent study by Kutanan et al. [13], which investigated eight hill tribes from Thailand and detected no South Asian admixture. These populations reside in remote areas and have received minimal influence from Indian culture, thus their ancestors likely had minimal contact with South Asian populations who migrated to the region in the past.

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