Sundadonty Revisited: Dental evidence supports a mixed East Asian and Australo-Melanesian ancestry for Southeast Asians

Authors

G. Richard Scott[1], Joel D. Irish[2,3], Arielle J. Pastore[1], Hannes Rathmann[4,5,6], and Miguel E. Delgado[7,8]

Affiliations

1 - Department of Anthropology, University of Nevada Reno

2 - School of Biological and Environmental Sciences, Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University

3 - Faculty of Health Sciences, Anatomical Sciences Department, The Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, Johannesburg, South Africa

4 - Senckenberg Centre for Human Evolution and Palaeoenvironment, University of Tübingen, Rümelinstrasse 23, 72070 Tübingen, Germany

5 - Paleoanthropology Section, Institute for Archaeological Sciences, Department of Geosciences, University of Tübingen, Rümelinstrasse 23, 72070 Tübingen, Germany

6 - Institute for Clinical Epidemiology and Applied Biostatistics, University Hospital Tübingen, Silcherstrasse 5, 72076 Tübingen, Germany

7- Departamento de Antropología, Facultad de Ciencias Humanas y Sociales, Universidad del Cauca, Popayán, Colombia

8 - CONICET-División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, República Argentina

Correspondence: G. Richard Scott (grscott@unr.edu); Miguel E. Delgado (medelgado@unicauca.edu.co)

Abstract

Objectives

C.G. Turner divided the “Mongoloid” dental complex into Sinodonty and Sundadonty, but it remains unclear if the latter is a distinct complex or the product of Holocene gene flow between East Asians and the earlier inhabitants of Southeast Asia.

Materials and Methods

Dental data for 863 individuals representing 16 populations from East Asia, Southeast Asia, Australo-Melanesia, and the Pacific were investigated. Three methods were employed: rASUDAS2 analysis based on a naïve Bayesian algorithm to classify individuals into clusters, the R-matrix approach to obtain d_{ij} distances, F_{ST}, and r_{ij} rvalues among regional samples, and matrix correlation analysis to evaluate competing population history scenarios.

Results

The rASUDAS2 analysis revealed that Southeast Asians showed high variation and an indistinct dental complex, divided by East Asians (50.3%) and Australo-Melanesians (49.7%). The d_{ij} distances indicate that Southeast Asians share similarities with Australo-Melanesians and East Asians, while the Pacific groups are closer to Australo-Melanesians. The F_{ST} obtained was 0.067, while the r_{ii} values were: Southeast Asia = 0.027; Pacific = 0.057; Australo-Melanesia = 0.076, and East Asia = 0.110. The matrix correlation analysis identified the migration scenario as the best-supported model.

Discussion

Sundadonty does not represent a discrete or evolutionarily independent dental complex but rather results from admixture between Neolithic East Asian agriculturalists and Australo-Melanesians. Southeast Asians are the most biologically heterogeneous populations investigated, coinciding with archaeological, linguistic and paleogenomic evidence showing multiple migrations and population events (admixture, replacement), which occurred during the past 5000 years. This supports a complex population history and diverse ancestral components in Southeast Asia.

1. Introduction

During the Age of Discovery (Arnold 2013) and European colonial expansion, explorers encountered human populations worldwide. A common query was ‘who are these people?’ and ‘where did they come from?’ Shortly thereafter, anthropologists and historians asked this question in the following form: did a particular group occupy a geographic locality for a long period of time, or did they move into the area from another region? Using diverse sources of information, including language, biology, archaeology, and oral history, researchers would argue one of two positions: (1) once a population arrived in a region, they progressively adapted to the environmental stressors of that region and remained there until the present, i.e., local evolution hypothesis; or (2) population movement is a normal course of action in human history, so the inhabitants of an area could have been replaced or assimilated one or more times through centuries or millennia, i.e., migration hypothesis.

The origins of modern Southeast Asians have been explained by competing models that emphasize either long-term regional continuity (Hanihara, 2006; Pietrusewsky, 2005; Turner, 1990,1995) or migration and admixture (Bellwood, 2018; Matsumura and Hudson, 2005; Matsumura and Oxenham, 2014; Matsumura et al., 2015, 2019; McColl et al., 2018). Southeast Asia played a critical role in the dispersal of anatomically modern humans into Sahul by at least 50–60 thousand years ago (kya), and populations associated with these early dispersals likely contributed ancestry to later Australo-Melanesian groups (Clarkson et al., 2017; Pagani et al., 2016). A central question is whether these early inhabitants also formed the primary ancestry of modern Southeast Asians, or whether later Holocene migrations from East Asia substantially reshaped the region's biological landscape.

Researchers agree that Australia was initially settled at least 50-60 kya – derived from a population that had expanded out of Africa ~10 to 20 kya prior (Clarkson et al., 2017; Hiscock, 2013; O’Connell and Allen, 2004; Pagani et al., 2016). Between Africa and Australia, humans had to traverse India and Southeast Asia. If Southeast Asia was the springboard for the peopling of Australia, populations in this area likewise go back over 50 kya (Demeter et al., 2012, 2015; Demeter and Bae, 2020; Gosling and Matisoo Smith, 2018). Were these early settlers of Sundaland the ancestors of modern Southeast Asians or were they more closely related to extant Australians and related Melanesian populations, including those of New Guinea?

Classical authors, such as von Koenigswald (1952), proposed decades ago that Southeast Asians evolved from the mixing of East Asians and Australo-Melanesians during the Neolithic. Other researchers used components of this model to propose more sophisticated hypothesis such as the two-layer model of Bellwood (2018) to explain the origins of modern Southeast Asians, involving the following elements: (1) Sundaland was settled initially by Australo-Melanesian populations who were the primary ancestors of populations residing in both mainland and insular Southeast Asia until recent times; and (2) agriculturalists from the north, notably China, shifted south with the development of grain-based agriculture (especially millet and rice) during the late Holocene and displaced or blended with the indigenous hunter-gatherer populations of the region; this produced a mixed group with asymmetrical contributions from both East Asia and Australo-Melanesia. Craniometric analysis by Matsumura et al. (2015, 2019) found that individuals of the

Hoabinhian complex shared affinity with Australo-Melanesians; later agriculturalists in Southeast Asia showed a 'significant morphological discontinuity' from earlier groups in the region, revealing in turn an East Asian source given their close affinity with Northeast Asians.

In contrast to the Holocene migration model, C.G. Turner (1990) favored local evolution based on dental morphological research in Asian and Pacific populations. He divided the Mongoloid dental complex (sensu Hanihara, 1967) into two subdivisions – Sinodonty (Northeast Asia, Americas) and Sundadonty (Southeast Asia, Pacific). He noted that Australians shared traits with Sundadonts, dubbing them proto-Sundadonts (Turner, 1990). His argument ran counter to the position that Southeast Asians were an amalgam of Australo-Melanesians and East Asian agriculturalists. Hanihara (1992, 2006) and Pietrusewsky (2005) concurred with Turner and noted that Hoabinhian hunter-gatherers adopted agriculture during the Holocene but did not exchange genes with northern populations.

In 2005, Matsumura and Hudson analyzed metric and nonmetric dental traits in Asian and Pacific populations and concluded that the migration model was consistent with their data, challenging Sundadonty as a unique dental complex. In rebuttal, Turner (2006:455) notes that he coined the term 'Sundadonty' on the basis of a widespread dental pattern that he found throughout modern and early archaeological mainland and island Southeast Asia, and later archaeological Polynesia, Micronesia, Jomon Japan, and modern Hokkaido Ainu. In Scott and Turner (1997), box-and-whisker plots for 25 crown and root traits showed that Southeast Asian populations consistently fell between East Asians and Australo-Melanesians. To Turner, this intermediacy suggested that the generalized dentition of Southeast Asians made populations in this region the likely ancestors of all modern humans; he called this model "shifting continuity" (Turner, 1995). However, one evolutionary mechanism that could also account for intermediacy is gene flow. That is the problem at hand – does Sundadonty represent a foundational dental pattern from whence all other patterns were derived, or does it reflect gene flow between populations with two basic but highly distinct dental patterns? Recent bioarchaeological research indicates that craniometric (Matsumura et al., 2015, 2019, 2021) and dental nonmetric evidence (Matsumura & Oxenham, 2014) strongly supports demic diffusion accompanying population expansion driven by agriculture during the Neolithic period in Southeast Asia

Over the past decade, genomic and paleogenomic research has offered a new perspective on the population history of Southeast Asia and other key regions, such as the Pacific and Australo-Melanesia, improving the resolution of regional evolutionary history reconstruction and thus complicating the scenario. These findings supported an early modern human peopling of these regions around 50-60 kya, suggesting a rapid dispersal out of Africa into South Asia, Southeast Asia, and Oceania. They also highlight the role of other hominins like Denisovans in local modern human ancestry (Almeida et al., 2025; Bennett et al., 2024; Carlhoff, 2023; Liu et al., 2022; McColl et al., 2018; Oliveira et al., 2022; Soares et al., 2022; Wang et al., 2021, 2026). Archaeogenetic research indicates that most late Pleistocene to mid-Holocene Hoabinhian hunter-gatherers present Australian, Papuan, and Andamanese ancestry (i.e., Austropapuan ancestry) (Carlhoff, 2023; McColl et al., 2018; Wang et al., 2021; Wang et al., 2026), while middle to late Holocene populations present East/Northeast Asian ancestries (i.e., rice farming-related ancestries) (Bennett et al., 2024; Lipson et al.,

2018; Wang et al., 2021). This was the result of a northeast Asian southward population agricultural expansion that started 9 kya. They interacted with local populations throughout the early to mid-Holocene and became predominant by the late Holocene (i.e., Neolithic), producing differentially mixed populations across the region (Carlhoff, 2023; Wang et al., 2021). McColl et al. (2018) note there may have been two waves of agriculturalists from the north, one during the Neolithic and one during the Bronze Age. This also coincides with hypotheses proposed in the 80´s (Bellwod, 1984-985; Blust, 1985) related to changes in language, especifically the expansion of Austroasiatic languages, and the spread of agriculture from southern China into Southeast Asia (i.e, Out of Taiwan) (Blust, 2019; Mante Carlhoff, 2023; Diamond and Bellwood, 2003). Accordingly, high-resolution genome-wide data in living and ancient populations and linguistic studies confirm that recent and contemporary mainland and island Southeast Asians possess Austronesian and East/Northeast Asian ancestries with highly variable degrees of gene flow.

In the present study, we investigate dental morphological affinities among populations from Southeast Asia, East Asia, the Pacific, and Australo-Melanesia to revisit the concept of Sundadonty. Rather than treating Sundadonty as a predefined dental complex, we evaluate whether dental variation in Southeast Asia is better explained by long-term regional continuity or by admixture between East Asian and Australo-Melanesian populations. To address this question, we combine exploratory and quantitative genetic approaches, applying a Bayesian classification algorithm (rASUDAS; Scott et al., 2018a, 2025a) together with R-matrix analysis (Relethford & Blangero, 1990; Konigsberg, 2006) to assess patterns of dental morphological variation within and among populations. Finally, we test competing models of ancestry and descent within a geographically explicit framework using matrix correlation analyses. By integrating dental morphological evidence with expectations derived from recent genomic and paleogenomic research, we evaluate whether Sundadonty represents an ancestral pattern or an emergent phenotype resulting from population interaction.

Investigating human skeletal remains, particularly dental morphology, is crucial for understanding the population history of Southeast Asia and surrounding regions, given that the recovery of ancient DNA is difficult due to the scarcity of human skeletal remains earlier than 3 kya and that hot, humid environmental conditions hinder DNA preservation. Dental nonmetric traits provide an especially valuable source of information, as several studies have shown strong correlations between biological distances computed from neutral genetic markers and dental traits (e.g., Rathmann et al., 2017; Rathmann & Reyes-Centeno, 2020; Irish et al., 2020; Rathmann et al., 2023). Additionally, similar patterns of affinities have been observed using dental morphology, mtDNA haplogroups, and genome-wide data in paired samples (e.g., Delgado et al., 2019; Hubbard et al., 2015). Accordingly, dental morphology provides one of the most robust lines of evidence for reconstructing regional population history.

2. Materials and Methods

2.1 Dental dataset

Dental morphology reliably preserves human population history, in part because genetic influences are strong on dental traits. Thus, tooth crown and root traits have been intensively

used in human evolutionary studies (Delgado et al., 2019; Irish et al., 2020; Rathmann et al., 2017; Scott et al., 2018b). In the present study all data were recorded following the standards of the Arizona State University Dental Anthropology System (ASUDAS), a widely used reference that defines a range of crown and root traits and their different ordinal-scale degrees of expression in the permanent dentition, ensuring a standardized scoring procedure with negligible observer error (Scott & Irish, 2017). We employed the individual count method for trait recording (*sensu* Scott, 1980), in which bilaterally expressed traits are scored only once per dentition, using the antimere that shows the highest degree of expression (Scott & Irish, 2017). As most ASUDAS traits exhibit little to no sexual dimorphism, it is standard practice to analyze male and female individuals together (Scott et al., 2018b).

The present research uses legacy dental morphological observations recorded by Christy G. Turner II in the 1970s and 1980s before the implementation of NAGPRA and related repatriation policies. No additional examination of human remains was undertaken; this study is based solely on previously documented observations compiled for comparative research. The authors recognize the importance of responsible stewardship of legacy anthropological data and the respectful treatment of descendant communities while maximizing the scientific value of irreplaceable historical observations.

The rASUDAS2 analysis uses a naive Bayes algorithm to assign posterior probabilities for individual group assignments. In the present study, the objective was to assign individuals to one of seven major biogeographic groups based on their dental trait suite (Scott et al., 2018a, 2025a). Individuals had to be scored for at least 12 crown and/or root traits (see Scott et al., 2025a for a complete list of 25 traits and seven backups). In total, 863 individuals (Table 1) from four major geographic groups were analyzed, including three population samples from East Asia (China, Mongolia, Japan), four from Southeast Asia (Ban Chiang, Burma, Leang Tjadang, Thailand), six from Australo-Melanesia (Australia, Loyalty Islands, New Britain, New Guinea, New Hebrides, Solomon Islands), and three from the Pacific (Guam, Marquesas, Mokapu). The dataset includes both archaeological and recent populations, although sample sizes and chronological distributions were not sufficient to support a robust temporally stratified analysis across all regions.

For the R matrix analysis (detailed below), the focus is on individual dental non-metric trait scores for 861 individuals sampled from 16 populations across four major geographic regions (Table 1). For this analysis, including four pooled metapopulations (see below), two individuals were excluded because of their high percentage of missing data (<40%), so the final sample size is 861.

Dental traits are typically expressed independently of other traits (e.g., Cusp 6 expression on LM1 is independent of Cusp 7 expression on UM1). However, the same trait expressed across different members of the same morphogenetic field can show significant correlations (e.g., shoveling expression on UI1 and UI2 is significantly correlated) (Scott, 1977). To avoid issues of trait correlation, we followed the standard data preprocessing strategy and collapsed the dataset to include only traits recorded on a single tooth per field (e.g., UI1), referred to as the key tooth, which is considered the most developmentally and evolutionarily stable member of its respective field (Butler, 1939; Scott et al., 2018b). This procedure reduced the dataset to 25 traits recorded on key teeth only (Table 2). However,

because this approach reduces data coverage for individuals in which key teeth were not preserved or were less frequently observed, we adopted a more flexible data preprocessing strategy by also including what are known as "backup traits“ (Scott et al., 2025a). A backup trait is a trait scored on a non-key tooth that can substitute for the same trait on a key tooth from the same field when the latter is absent (e.g., if shoveling on UI1 could not be observed, shoveling on UI2 was used instead). This data substitution strategy is not new and has been used in several previous dental biodistance studies, albeit under different names, such as “modified key tooth analysis” (Bailey et al., 2009; Rathmann et al., 2024). Following Scott et al. (2025a), we considered the following seven backup traits: shoveling on UI2 as a backup for UI1; *tuberculum dentale* on UI1 as a backup for UC; cusp 5 on UM2 as a backup for UM1; multiple lingual cusps on LP1 as a backup for LP2; enamel extensions on LM1 as a backup for UM1; cusp 6 on LM2 as a backup for LM1; and four-cusped LM1 as a backup for LM2. Backup traits were selected only when strong developmental and statistical correspondence had previously been demonstrated between key and substitute teeth within the same morphogenetic field (Scott et al., 2025a). Although their use varied by sample, backup traits constituted less than 10% of the total traits used in the rASUDAS analysis.

Following standard procedures, we simplified the ordinal-scale dental trait scores into lower-level ranks for the rASUDAS2 and R-matrix analyses. The rASUDAS2 analysis requires templates in which ordinal scores are translated into levels of 1, 2, and sometimes 3. The R-matrix analysis, in contrast, requires binary levels of 0 or 1. For example, shoveling on UI1 is typically graded on a scale from 0 to 7, but for the rASUDAS2 template, these grades are condensed into score 1 for grades 0 and 1 (absence or minimal expression), score 2 for grades 2 and 3 (moderate expression), and score 3 for grades 4 and above (strong expression). For the R-matrix analysis, the same trait is simplified into score 0 for grades 0 and 1 (absence or minimal expression) and score 1 for grades 2 and above (moderate to strong expression). The full list of breakpoints for all traits is given in Table 2.

For the rASUDAS2 analysis, we utilized the full 25-trait battery. For the R-matrix analyses, we used a different number of traits depending on the level of analysis. First, we used the complete set of traits in an analysis that included four pooled metapopulations: Australo-Melanesia, East Asia, Southeast Asia, and the Pacific. Second, we excluded three traits—winging UI1, PRM UM3, and Tomes root LP1—because they presented a high proportion of missing data across the 16 individual population samples. This formed the basis of a second level of analysis, still representing the four major regions mentioned above.

2.2 rASUDAS2 analysis

The first step in this analysis is to screen data sheets and use only individuals who could be scored for a minimum of 12 crown and/or root traits. To analyze individuals using rASUDAS2 (https://osteomics.com), the Excel template is downloaded, which lists 25 crown and root traits along with seven backup traits (the backup is used only when the key tooth is absent). Scores are transferred from the data sheets onto the template, where ranked scores are converted into template scores of 1, 2, or 3 based on the ASUDAS. For example, the standard plaque for UI1 shoveling has absence (0) and seven grades of trait presence (1-7); that is, grades 0-1 = template score 1, grades 2-4 = template score 2, and grades 4-7 =

template score 3. For other traits, like LM1 cusp 6, grade 0 = template score 1, and grades 1-5 = template score 2.

After filling out the scores on the template for a specific sample, the completed template is processed as a batch file. The results show the most likely biogeographic group in the left-hand column (determined by the group with the highest posterior probability for a specific combination of dental traits). We focus on the percent of individuals in each sample that have the highest probability of assignment to a particular group. An alternative method is to compute the average probabilities across all groups, but Scott et al. (2025b) show that the results of the two methods are nearly identical. With rASUDAS2, under 'predict biogeographic group,' one can specify which groups to include among the following seven: Western Eurasia, Sub-Saharan Africa, East Asia, Southeast Asia & Pacific, Australo-Melanesia, American Arctic & Northern Asia, North & South America. Any number between two and seven is chosen. For this analysis, we ran batch files for all seven groups and then for just East Asia and Australo-Melanesia.

2.3 R-matrix analysis

The dental non-metric trait dataset was additionally analyzed using the relationship- or R-matrix approach. Originally developed to work with allele frequency data (Harpending & Jenkins, 1973; Harpending & Ward, 1982), the R-matrix method was later adapted for use with morphometric data (Relethford & Blangero, 1990; Relethford et al., 1997) and nonmetric trait data (Konigsberg, 2006; Irish, 2010). The present study follows the latter method and uses two levels of analysis: one includes four metapopulations, and the other uses 16 local populations representing four major regions. This procedure allows us to evaluate the consistency of our results by using different approaches. All calculations were performed in R, version 4.2.2 (R Core Team, 2025) using functions written by L. Konigsberg (http://faculty.las.illinois.edu/lylek) and custom functions published in Rathmann et al (2023). Using the R-matrix method, we estimated three key parameters of population structure useful for assessing the degree and pattern of variation:

First, we estimated F_{ST}, an index summarizing genetic differentiation among groups relative to the total amount of variation expected under panmixia (Relethford, 2006). The index ranges from 0 (indicating low genetic structure due to high gene flow) to 1 (indicating complete subdivision due to low gene flow). For example, an F_{ST} value of 0.1 means that 10% of the total variation lies between groups, while the remaining 90% lies within groups.

Second, we estimated r_{ii} values for each population, which are defined as standardized distances to the regional centroid. These distances indicate the degree of population divergence from the hypothetical pooled average group that would exist if the populations were not subdivided (Konigsberg, 2006). Within this framework, populations near the centroid are expected to exhibit greater internal variation, while those farther from the centroid tend to have less internal variation as a result of genetic drift and lower migration rates.

Third, we estimated a matrix of d_{ij} distance values between all population pairs, representing the pattern of relatedness among groups. The greater the distance between two populations, the less genetically similar they are (Relethford, 2006). To visualize the biodistance matrix, we applied Kruskal's non-metric multidimensional scaling (NMDS) to

decompose it into a two-dimensional coordinate space. In this space, spatial proximity among populations indicates closer relationships, and greater separation indicates more distant relationships. NMDS was performed using the isoMDS function from the MASS package (Venables & Ripley, 2002), and plots were generated with the ggplot2 package (Wickham, 2016).

The R-matrix can be scaled by weighting the groups under investigation by their relative population sizes to account for the confounding effects of genetic drift in small populations. Following previous work (e.g., Rathmann et al. 2017; Reyes-Centeno et al., 2017; Rathmann et al., 2023), we included published point estimates of effective population size (N_e) derived from levels of genetic linkage disequilibrium (Tassi et al., 2015), considering allele frequencies for up to ~370,000 single-nucleotide polymorphisms (SNPs). We matched the populations sampled by Tassi et al. (2015) with our dental populations using the same or geographically proximate populations with ethno-linguistic affinities (N_e values are reported in Table 1).

The R-matrix can be further scaled using an estimate of average heritability (h^2) for the traits analyzed to account for the influence of both genetic and environmental components on phenotypic variation. Although published heritability estimates for dental traits vary widely by trait and population (Scott et al., 2018b; Stojanowski et al., 2019), researchers often approximate this parameter by setting h^2=0.5 (e.g., Hanihara, 2010; Rathmann et al., 2017; Reyes-Centeno et al., 2017). In this study, however, we followed a more conservative approach and assumed complete heritability, i.e., h^2 = 1.0 (e.g., Irish, 2010; Rathmann et al., 2023). This generates what is known as 'minimum F_{ST}' and 'minimum d_{ij}' values (Relethford, 2006). Because our objective was to compare relative patterns of differentiation rather than estimate absolute genetic distances, assuming h^2 = 1.0 provides conservative minimum estimates that do not alter the spatial structure of relationships.

To construct the R-matrix, we first calculated a matrix of pairwise between-group distances using a modified version of Mahalanobis' D^2 (Mahalanobis, 1936) adapted for non-metric traits (Konigsberg, 1990). D^2 is a robust measure of between-group differentiation that accounts for correlations among traits to prevent overrepresentation of co-occurring features. Instead of the original formula proposed by Konigsberg (1990), we used the method outlined in Nikita (2015), which approximates the pooled within-group tetrachoric correlation matrix between traits using Pearson correlations – a modification shown to improve performance. From the resulting D^2 matrix, we calculated a codivergence matrix (C-matrix), which measures variance around the centroid (Konigsberg, 2006). This C-matrix was then used to compute F_{ST}, the R-matrix, and, subsequently, the r_{ii} values and d_{ij} distances.

Finally, we tested whether N_e correlates with r_{ii} values using Spearman's rank correlation rho and linear regression, to address how varying effective population sizes might influence gene flow in the studied regions. According to quantitative genetic theory, a negative correlation is expected because drift decreases as population size increases (Melton, 2018). If the correlation deviates from these theoretical expectations, it suggests the influence of other evolutionary forces, such as recent bottlenecks, asymmetrical gene flow (migration) or natural selection acting on specific populations.

2.4 Matrix correlation analyses and hypotheses testing

Two distinct hypotheses or models on the population history of Southeast Asia were evaluated using design matrices and matrix correlation analysis. These models were selected because they represent the two principal competing interpretations of Southeast Asian dental variation proposed in the literature. The comparisons include 16 populations integrating the four regions investigated (Table 1). Accordingly, the correlation between the expected pattern of diversity under a specific hypothesis or model and both the observed biological differentiation among samples, here expressed as d_{ij} distances (see below), and geographical distance between them was statistically evaluated through a two-way and three-way Mantel test (Mantel, 1967; Sokal, Oden, & Walker, 1997) using the R package vegan (v. 2.7-2) (Oksanen et al., 2025). The critical α level was set at 0.05 and p values for Mantel and partial Mantel tests were obtained after 9,999 permutations. Model comparisons were performed using matrices of biological and geographical distances against each tested hypothesis.

Given the importance of geographical distance in evolutionary processes, some comparisons were performed while holding it constant. In the present study, two design matrices were constructed on the basis of two distinct models: 1) Southeast Asians as a result of the admixture between East Asians and Australo-Melanesians and 2) Sundadonty *in situ* microevolution. Finally, to determine whether dental variation (d_{ij}) was more strongly associated with the biological/design models than with a control model (geographic distances in kilometers GEO, see below), a Dow–Cheverud test (Dow and Cheverud, 1985) was implemented. This procedure evaluates the difference between two correlation coefficients. Thus, the observed difference between them was compared against a null distribution generated by permuting the dental distance matrix while holding the explanatory matrices constant (9,999 permutations), with GEO as the control. Additionally, we tested whether Asymmetric Australo-Melanesian–East Asia Gene Flow (AGF) or Sundadonty in situ microevolution (SUNDA) better explains the structure of the d_{ij} matrix using a similar design. In this test, d_{ij} is the control. For each permutation, the difference in correlations was recalculated, and statistical significance was determined as the proportion of permuted differences equal to or greater than the observed value. This permutation framework explicitly accounts for the non-independence of pairwise distance data and allows direct comparison of competing explanatory models. All computations were performed in R (version 4.4.2) using custom functions.

2.5 Geographical Distance Calculation

Pairwise geographical distances between sampling locations were computed using the Haversine formula, which calculates the great-circle distance between two points on the Earth’s surface based on their latitude and longitude coordinates. In practical terms, these distances do not account for major topographic barriers, such as oceans, but they are useful for modeling geographical distances between populations. Pairwise distances were calculated using the Haversine formula to estimate distances between all pairs of populations. The equation accounts for Earth's curvature and provides accurate inter-site distances within a spherical model. The Haversine distance was implemented via a custom R (version 4.4.2) function applied pairwise across all sites. The resulting distance matrix

(GEO) containing the distances (in kilometers) between all pairs of populations was used in the subsequent analysis as a control model (the GEO matrix used is presented in Table S1).

2.6 Design matrices

2.6.1 Model 1. Asymmetric Australo-Melanesian–East Asia Gene Flow (AGF)

In this model, Southeast Asian populations result from asymmetric gene flow between Australo-Melanesians and East Asians. Since Australo-Melanesians are the main ancestral group, we set a distance value of 0.5 between Australo-Melanesians and Southeast Asians, implying that 50% of the ancestry of the former was shared with the latter, and a value of 0.75 between Southeast Asians and East Asians, since the latter were the migrants and thus expected to exhibit a slightly greater distance, implying that 25% of the ancestry of the latter was shared with the former. For the other comparisons, we set a value of 1, indicating higher differentiation, except for the comparison between Australo-Melanesians and Pacific Islanders, because the former were one of the ancestral populations of the latter, so we set a value of 0.5 between the two populations belonging to those regions. Since Southeast Asians and Pacific Islanders share a common Australo-Melanesian ancestor, we set their value to 0.25. This model represents a form of the two-layer hypothesis (The AGF matrix used is presented in Table S2).

2.6.2 Model 2. Sundadonty in situ microevolution (SUNDA)

In this model, Southeast Asian populations are the result of *in situ* evolution and thus show close relationships with other Sundadonts and proto-Sundadonts (i.e., Pacific groups and Australo-Melanesians) while exhibiting high differentiation from East/Northeast Asians. Accordingly, we set a value of 0.25 among Southeast Asians, Pacific Islanders, and Australo-Melanesians, modeling slight distinction among them due to an allegued spatial and temporal differentiation between Sundadonts and proto-Sundadonts. Finally, we set a value of 1 between such populations and East Asians, modeling their low contribution to the Sundadont/proto-Sundadont gene pool. This scenario models the Sundadonty dental microevolution and differentiation established by Turner (1990) (The SUNDA matrix used is presented in Table S3).

3. Results

3.1 rASUDAS2 analysis

For East Asia, the average percentage of assignments to East Asia was 45%, with an additional 20% assigned to the American Arctic and 15% to non-Arctic Native Americans. In other words, 80% of total assignments were to one of the three Sinodont groups. Except for Southeast Asia, at 12.5%, less than 5% were assigned to Australo-Melanesia, Western Eurasia, and Sub-Saharan Africa. For Australo-Melanesians, the pattern of assignment is reversed. For this group, the average assignment to Australo-Melanesia was 46%, with Western Eurasia at 22% and sub-Saharan Africa at 16%. Less than 5% were assigned to Southeast Asia and the three Sinodont groups. Southeast Asia contrasts with both East Asia and Australo-Melanesia. For these samples, the average assignment was 32% to Southeast Asia, with similar assignments to East Asia (16%) and Australo-Melanesia (22%). The remaining four groups fell between 5% and 10%. The Pacific shows close parallels with 31%

assigned to Southeast Asia, but the average percentage is much higher for Australo-Melanesia (28%) than East Asia (9%). The other four groups have average assignments from 4-12%. For both Southeast Asia and the Pacific, the assignments were more diverse than those for East Asians and Australo-Melanesians (Figure 1). These classifications do not represent direct estimates of genomic ancestry proportions but rather indicate phenetic affinities based on dental trait combinations at the individual level.

When the choice of assignments is limited to two groups (Figure 2), the patterns that emerge are striking and clear-cut. For the East Asian samples, the average assignment to East Asia was 90%, with 10% to Australo-Melanesia. For Australo-Melanesia, the pattern is reversed, with 88% of assignments to Australo-Melanesia and 12% to East Asia. Basically, this supports the position that East Asian Sinodonts and Australo-Melanesians have distinctly different dental patterns. By contrast, Southeast Asia lacks a distinct dental complex. Individuals from Southeast Asia were almost evenly classified into East Asian (50.3%) and Australo-Melanesian (49.7%) dental affinity groups. Pacific populations are also a phenetic composite of the two main patterns, although the Australo-Melanesian component (69%) is higher than the East Asian component (31%) (Figure 2). These percentages are individual-level classifications rather than direct estimations of population-level ancestry proportions.

3.2 R-matrix analysis

3.2.1 Analysis based on four metapopulations

The estimated minimum F_{ST} value for the four metapopulation samples was 0.067, indicating that 6.7% of the total variation exists between populations, while the remaining 93.3% resides within populations. In Table 4, the r_{ii} values in bold (along the diagonal), the pairwise d_{ij} distances across metapopulations (below the diagonal), and the scaled R-matrix values (above the diagonal) are presented. The highest r_{ii} values, indicating the lowest levels of inter-population variability, were observed in East Asia (0.110) and Australo-Melanesia (0.076), respectively, while the lowest values, suggesting high levels of inter-population variability, were found in the Pacific (0.057) and especially in Southeast Asia (0.027). Particularly important is the very low r_{ii} value for Southeast Asia, which indicates that these samples are the most internally heterogeneous in the analysis; this pattern is more consistent with admixture and population interaction than with a discrete, evolutionarily stable Sundadont dental complex.

A multidimensional scaling (MDS) plot (stress 0.001), based on the pairwise d_{ij} distances (Table 4) between metapopulations, is presented in Figure 3 and shows, along axis 1, large differences between Australo-Melanesia and East Asia, while the Pacific and Southeast Asia occupy intermediate positions. Along axis 2, the greatest difference is between East Asia/Pacific and Australo-Melanesia/Southeast Asia. The d_{ij} distances show phenotypic similarities between Australo-Melanesians and Southeast Asia than with the Pacific. Likewise, the distance between East Asia and the Pacific is larger than that between East Asia and Southeast Asia. Southeast Asia and the Pacific are well differentiated.

3.2.2 Analysis based on sixteen population samples

The estimated minimum F_{ST} value for all 16 population samples was 0.125, indicating that 12.5% of the total variation exists between populations, while the remaining 87.5% resides within populations. The r_{ii} values for each population are listed along the diagonal of Table 4. The highest r_{ii} values, indicating the lowest levels of inter-population variability, were observed in China (0.336) and Mongolia (0.217). In contrast, the lowest r_{ii} values, indicating the highest inter-population variability, were found in Mokapu (0.042), Marquesas (0.062), Thailand (0.062), Loyalty (0.063), Guam (0.065), Leang Tjadang (0.079), and Japan (0.093). The pairwise d_{ij} distances across populations are presented in the lower triangle of Table 4. The corresponding two-dimensional NMDS plot to visualize the inter-population affinities is shown in Figure 4. The NMDS stress value was 0.087, which is below the commonly accepted threshold of 0.1 (Kruskal & Wish, 1978), suggesting that two dimensions sufficiently capture the structure of among-population variation. Figure 4 reveals defined clusters corresponding to the four major geographic regions. It also illustrates a broad geographic gradient: East Asian populations cluster on the right side of the plot, followed by Southeast Asian populations in the center, and Australo-Melanesian populations on the left. Pacific populations fall between Southeast Asia and Australo-Melanesia in the ordination space.

Spearman's rank correlation revealed a significant positive correlation between N_e and r_{ii} (rho = 0.615, $p < 0.014$). The results of the simple linear regression analysis showed an adjusted R^2 of 0.346 and an F-statistic of 8.421 ($p < 0.012$). Figure 5 shows a scatterplot of the linear regression between N_e and r_{ii}, including the 95% confidence intervals.

3.3 Matrix correlation analysis

The results of the Mantel, partial Mantel and Dow-Cheverud tests for the 16 population samples are presented in Tables 5 and 6. The correlation between the biological and geographical distances was weak and non-significant. The AGF model presented the highest and most significant correlations with the biodistances in both Mantel ($r = 0.609$, $p = 0.001$) and partial Mantel tests ($r = 0.593$, $p = 0.001$), although the SUNDA model had a nearly significant p-value. Finally, the results of the Dow-Cheverud test (Table 6) between GEO or d_{ij} as controls and two competing population history models show that only AGF presents a strong and significant correlation. This suggests, on the one hand, that dental nonmetric variation is better explained by the biological/design models than by geography itself, and on the other, that AGF much better explains the structure of the dental distance matrix.

4. Discussion

Southeast Asia and neighboring regions have played a central role in human evolutionary history since the early Pleistocene, when hominins such as *Homo erectus sensu lato* first occupied the region nearly two million years ago. Later, during the late Pleistocene, other hominin groups, including *Homo floresiensis*, *Homo luzonensis*, and Denisovans arrived, with some contributing to the ancestry of modern human populations (Higham and Kim, 2022; Sawafuji et al., 2024). As a major corridor for dispersals out of Africa, Southeast Asia was pivotal in the settlement of Sahul, with Australia and New Guinea colonized at least 50,000 years ago (Hiscock, 2013). Contemporary and recent populations in the region exhibit exceptionally high biological, linguistic, and cultural diversity, reflecting complex

539 demographic processes involving multiple migrations, population interactions, and episodes
540 of admixture, particularly during the last 10 kya (Bellwood, 2018; Matsumura and Oxenham,
541 2014; Lipson et al., 2018; Liu et al., 2022; McColl et al., 2018; Wang et al., 2021; Wang et
542 al., 2026).

543 To explain this complexity, several population history models have been proposed,
544 most notably continuity models that emphasize long-term *in situ* microevolution and
545 discontinuity models that invoke migration, replacement, and admixture. One of the most
546 influential discontinuity-based frameworks is the “two-layer hypothesis,” originally proposed
547 by von Koenigswald (1952) and subsequently refined by later researchers. This model posits
548 that early Australo-Melanesian-related hunter-gatherers were the first widespread
549 inhabitants of Southeast Asia, locally known as Hoabinhian, and were later partially replaced
550 or admixed with agricultural populations expanding southward from East Asia, especially
551 from southern China, during the Holocene (Bellwood, 2018; Matsumura and Hudson, 2005;
552 Matsumura and Oxenham, 2014; Matsumura et al., 2015, 2019; McColl et al., 2018; Wang
553 et al., 2021, 2026).

554 In contrast, Turner’s (1990, 1995) model of local evolution, based on the distinction
555 between Sinodonty and Sundadonty, emphasized long-term regional continuity. Turner
556 argued that Sundadonty represented an ancestral dental pattern closely related to that of
557 Australians, reflecting deep population stability in Southeast Asia. This interpretation was
558 supported by some craniometric and dental studies (Pietrusewsky, 2005; Hanihara, 2006)
559 and contributed to the persistence of continuity-based models in the literature.

560 Unlike previous research (Turner, 1990; Matsumura & Hudson, 2005; Matsumura &
561 Oxenham, 2014), this study uses novel statistical methods (rASUDAS2), a quantitative
562 genetic approach (R-matrix analysis), and formally tests competing population history
563 models. The results obtained do not support the local evolution model. Our analyses
564 demonstrate that Southeast Asian populations are among the most biologically
565 heterogeneous in the dataset. rASUDAS2 classification results, global F_{ST} values, and r_{ij}
566 estimates (Tables 3 and 4), consistently reveal mixed affinities with East Asians, Pacific
567 Islanders, and Australo-Melanesians. Multidimensional scaling plots show that Southeast
568 Asian groups occupy an intermediate position between Australo-Melanesian and East Asian
569 clusters (Figures 3 and 4), indicating substantial shared ancestry. Moreover, Mantel, partial
570 Mantel, and Dow–Cheverud tests (Tables 5 and 6) and N_e – r_{ii} correlation (Figure 5) identify
571 migration as the most robust explanatory model for dental variation in Southeast Asia.
572 Collectively, these findings indicate that population expansions and gene flow, rather than
573 long-term isolation, have been primary drivers of dental diversity in Southeast Asia.

574 Recent genomic and paleogenomic research provides independent and high-
575 resolution support for this interpretation (Almeida et al., 2025; Bennett et al., 2024; Carlhoff,
576 2023; Liu et al., 2022; McColl et al., 2018; Oliveira et al., 2022; Wang et al., 2021, 2026).
577 Archaeogenetic evidence reveals marked temporal discontinuities in ancestry. Late
578 Pleistocene and early-to-mid Holocene Hoabinhian hunter-gatherers predominantly carried
579 Australo-Papuan–related (Austropapuan) ancestry (McColl et al., 2018; Wang et al., 2021),
580 indicating close genetic ties to populations of Sahul and the Andaman Islands. In contrast,
581 middle-to-late Holocene populations exhibit substantial East and Northeast Asian ancestry
582 associated with the spread of rice and millet agriculture (Bennett et al., 2024; Lipson et al.,

2018; Wang et al., 2026). This genetic transition reflects a major southward expansion of agricultural populations beginning around 9 kya, which interacted extensively with resident foragers and became demographically dominant by the late Holocene. McColl et al. (2018) suggested that at least two waves of agricultural migrants occurred during the Neolithic and later Bronze Age periods.

Population movements in this region are closely linked to cultural and linguistic transformations. The spread of agriculture from southern China into Southeast Asia corresponds with the expansion of Austroasiatic and Austronesian language families (Blust, 2019; Carlhoff, 2023; Diamond and Bellwood, 2003). High-resolution genomic studies of both ancient and living populations confirm that contemporary mainland and island Southeast Asians possess varying proportions of Austronesian and East/Northeast Asian ancestry, reflecting regionally specific histories of admixture and replacement.

In Island Southeast Asia and Remote Oceania, these demographic processes are closely tied to the Austronesian expansion, often referred to as the “Out-of-Taiwan” model (Bellwood, 2004; Gray and Jordan, 2000; Gray et al., 2009; Spriggs, 2011). Under this framework, populations associated with Austronesian languages dispersed southward from Taiwan between approximately 4–3 kya through the Philippines and Island Southeast Asia into Near and Remote Oceania. Archaeological models such as the Lapita expansion and “Express Train” hypothesis similarly propose substantial population movement accompanying the spread of agriculture, maritime technology, and Austronesian languages into the Pacific. Recent genomic studies broadly support this scenario while also revealing extensive regional admixture with pre-existing Australo-Melanesian-related populations.

When considered in this broader context, Turner’s (1990) characterization of Sundadonty as a product of regional continuity becomes difficult to sustain. Although Sundadont populations exhibit intermediate trait frequencies, this pattern is more parsimoniously explained by gene flow between Australo-Melanesian-related and East Asian-related populations. Turner’s early proposal of “shifting continuity” (Turner, 1987, 1995), which envisioned Southeast Asia as a source population for global dispersals, has been challenged by recent genetic evidence. Genomic research indicates an African origin for modern humans followed by complex Eurasian migrations.

The rASUDAS2 results further support this reinterpretation. While the algorithm reliably classifies most major genogeographic groups (Scott et al., 2018a, 2025a), Southeast Asians consistently show unstable and heterogeneous assignment patterns. Similar profiles characterize populations of known mixed ancestry in Central Asia, suggesting that the Southeast Asian pattern reflects extensive historical admixture. Thus, Sundadonty appears not as a discrete unique dental complex, but as a composite phenotype produced by repeated gene flow.

This conclusion is reinforced by comparative analyses of ancient and modern populations. Scott et al. (2018a) demonstrated that early Southeast Asian samples cluster closely with Australians, whereas later samples shift toward East Asians, mirroring Holocene demographic transitions. Similarly, Scott et al. (2021) showed that the Jomon of Japan represent a phenotypically composite population with mixed Australo-Melanesian and East Asian affinities, paralleling Southeast Asian patterns.

Archaeological and bioanthropological data are also consistent with this interpretation. Matsumura and Hudson (2005), Matsumura and Oxenham (2014), investigating dental nonmetric traits and Matsumura et al. (2019, 2021) from craniometric evidence documented gene flow from Northeast Asia into Southeast Asia, contradicting models of regional continuity. At sites such as Man Bac and Khok Phanom Di, abrupt shifts in biological affinity coincide with the appearance of agricultural material culture, indicating demographic intrusion rather than gradual local transformation.

Although previous craniometric and dental studies have questioned Sundadonty as a discrete evolutionary unit (e.g., Matsumura & Hudson, 2005; Matsumura & Oxenham, 2014), most prior work relied primarily on phenetic affinities and descriptive patterning. The present study differs by explicitly testing competing models of population history using Bayesian classification, R-matrix analysis, and matrix-correlation approaches designed to evaluate continuity versus admixture hypotheses quantitatively.

Although some authors have proposed that Sundadonty reflects long-term environmental adaptation (Hanihara, 1992), such processes alone cannot account for the pronounced heterogeneity and temporal shifts documented in both dental and genomic/paleogenomic studies. Populations often cited as relicts of early Southeast Asians, such as Philippine Negritos, display complex genetic and morphological profiles shaped by both ancient substrata and later admixture, further undermining simple continuity models (Delfin et al., 2011; Stock, 2013).

Earlier craniometric and dental studies likewise support a layered population history. Craniometric analyses by Pietrusewsky (2005) demonstrated that Australians and Melanesians share deep affinities with early Southeast Asians while remaining distinct from later Asian populations. These findings are consistent with the presence of an early Australo-Melanesian-related substratum subsequently overlaid by Holocene migrants from East Asia.

In summary, the combined dental, archaeological, linguistic, and paleogenomic evidence strongly rejects models of long-term local evolution or single-wave dispersals in Southeast Asia. Dental nonmetric variation is best explained by repeated episodes of migration, population replacement, and admixture extending from the late Pleistocene through the Holocene. Within this framework, Sundadonty represents an emergent amalgam of inherited, conserved, and recombined traits shaped by dynamic demographic processes rather than a coherent ancestral pattern. Consequently, our findings provide strong support for a discontinuity-based model of Southeast Asian population history, in which biological diversity reflects successive layers of population movement and interaction.

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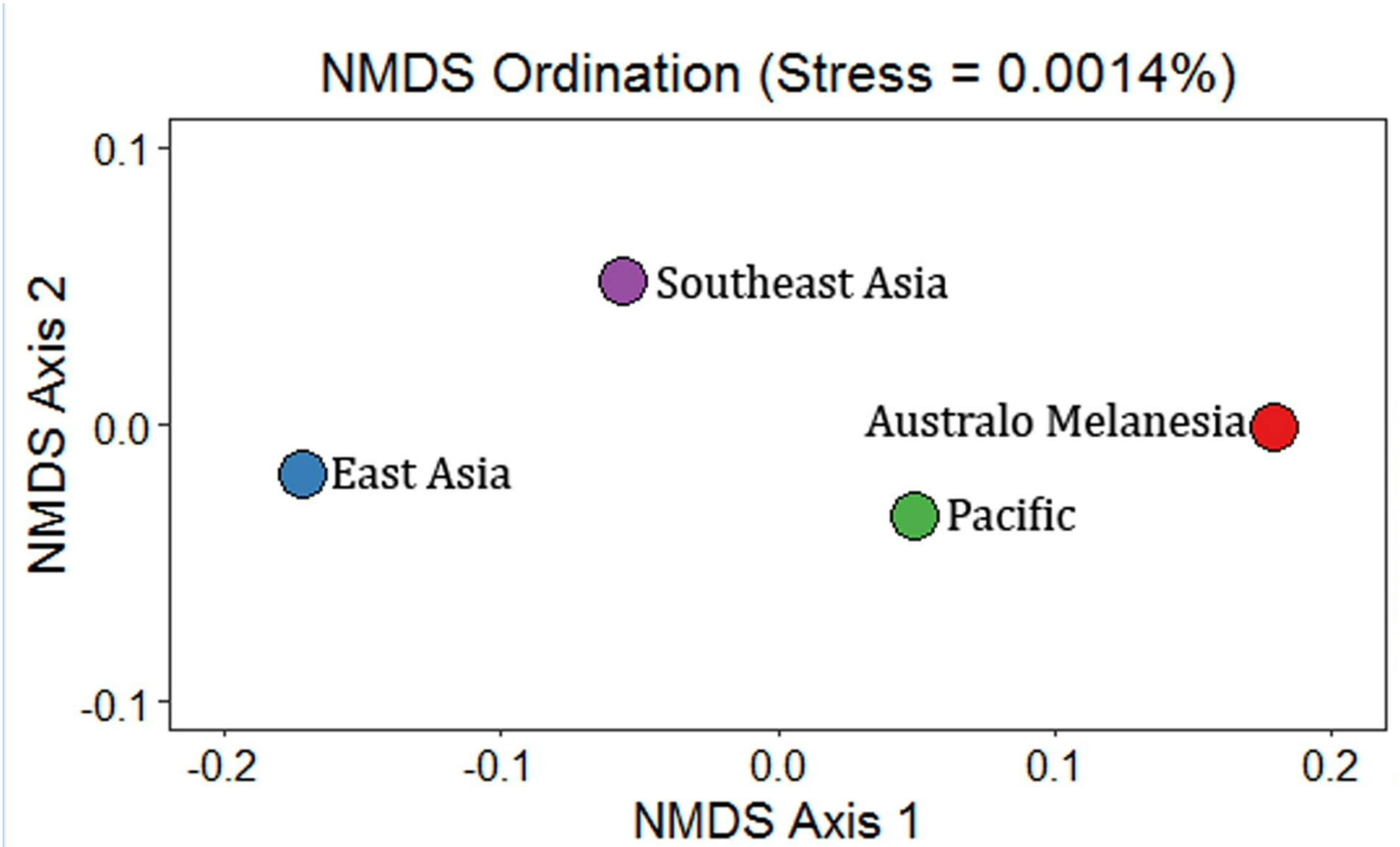
NMDS Ordination (Stress = 0.0014%)
0.1
0.0
-0.1
NMDS Axis 2
Southeast Asia
Australo Melanesia
East Asia
Pacific
-0.2
-0.1
0.0
0.1
0.2
NMDS Axis 1

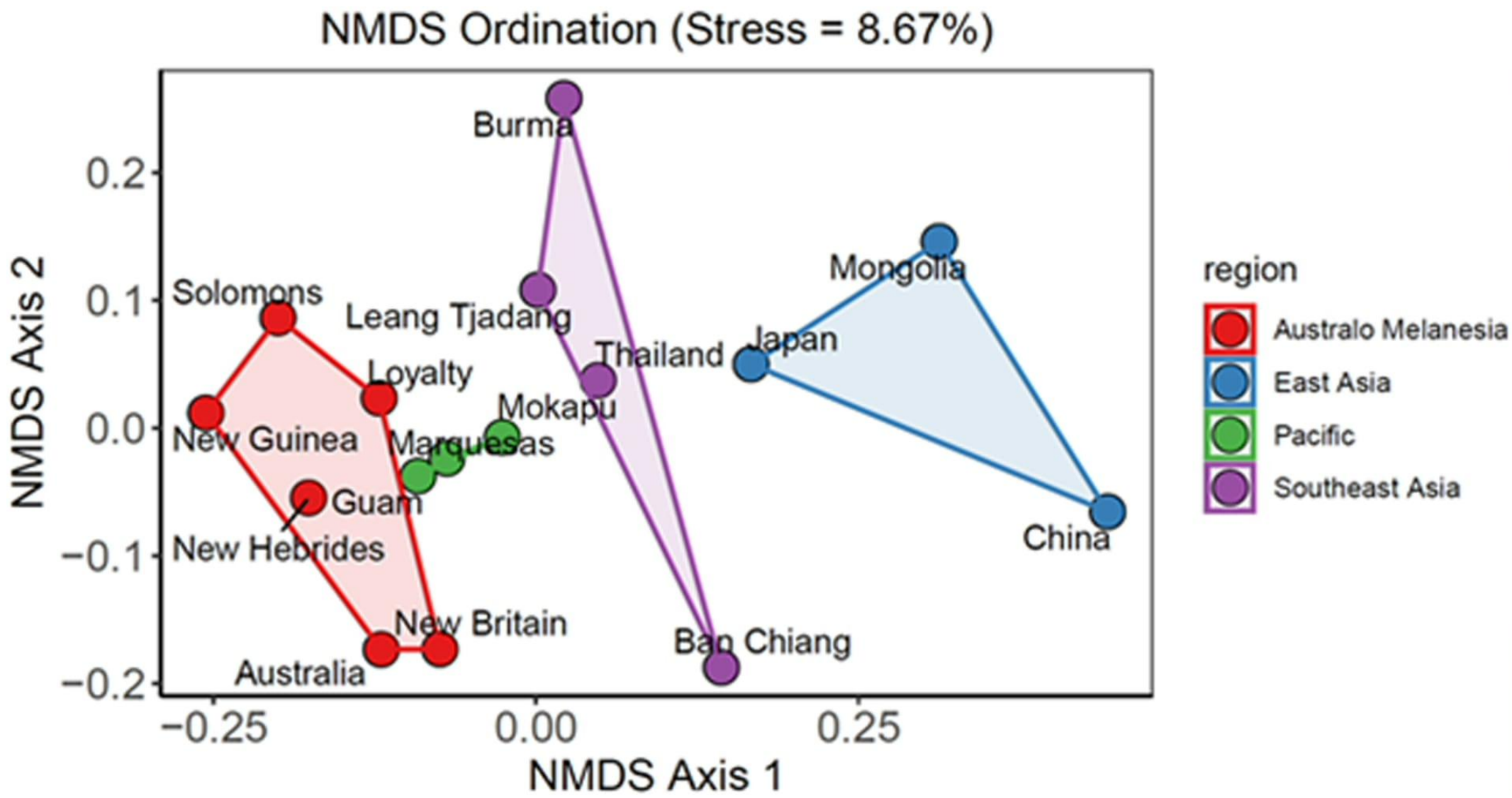
NMDS Ordination (Stress = 8.67%)
NMDS Axis 2
NMDS Axis 1
0.2
0.1
0.0
−0.1
−0.2
−0.25
0.00
0.25
Burma
Solomons
Leang Tjadang
Thailand
Loyalty
Mokapu
New Guinea
Marquesas
Guam
New Hebrides
New Britain
Australia
Ban Chiang
Mongolia
Japan
China
region
Australo Melanesia
East Asia
Pacific
Southeast Asia

Figure 1. Bar plots showing the highest percent of ancestry assignment for samples in the four regional groups when analyzed in context of seven major geographic groups.

Figure 2. Bar plots showing the highest percent of ancestry assignment for samples in the four regional groups when analyzed in the context of East Asia and Australo-Melanesia.

Figure 3. Two-dimensional NMDS plot visualizing d_{ij} distances among 4 metapopulations across four major geographic regions.

Figure 4. Two-dimensional NMDS plot visualizing d_{ij} distances among 16 population samples across four major geographic regions. Convex hulls are added to indicate affinity within geographic regions.

Figure 5. Plot showing the linear relationship between effective population size (N_e) and the standardized distances to the centroid (r_{ii}) for 16 population samples across four major geographic regions. The dotted line denotes the linear regression and the gray bands denote the 95% confidence intervals.

Table 1: Matched dental and genetic samples, sample sizes (*n*), and estimates of effective population size (N_e).

Geographic region	Population	Dental sample (n)[a]	Presumed ethnolinguistic affiliation	SNP sample (n)[b]	N_e[c]	Latitude	Longitude
Australo-Melanesia	Australia	Australia (42)	Pama-Nyungan	Australian (10)	4,400	-25	135
	Loyalty Islands	Loyalty (35)	Austronesian	Fiji (24)	3,750	-21	167
	New Britain	New Britain (73)	Austronesian/Papuan	New Guinea (27)	3,550	-6	150
	New Guinea	New Guinea (53)	Papuan/Trans New Guinea	New Guinea (27)	3,550	-5	140
	New Hebrides	New Hebrides (17)	Austronesian/Papuan	Fiji (24)	3,750	-16	167
	Solomon Islands	Solomons (23)	Austronesian/Papuan	New Guinea (27)	3,550	-8	159
East Asia	China	China (69)	Sino Tibetan	East Asia (188)	6,250	31.5	115.7
	Japan	Japan (196)	Japonic	East Asia (188)	6,250	35.7	137.8
	Mongolia	Mongol (37)	Mongolic	East Asia (188)	6,250	46.5	109.3
Southeast Asia	Ban Chiang	Ban Chiang (19)	presumed Austroasiatic	South Asia (35)	6,600	17.3	103.2
	Burma	Burma (16)	Tibeto-Burman	South Asia (35)	6,600	16.3	97
	Leang Tjadang	Leang Tjadang (71)	Austronesian	East Indonesia (10)	4,100	-4.3	120
	Thailand	Thailand (60)	Tai-Kadai	South Asia (35)	6,600	13	101
Pacific	Guam	Guam (54)	Austronesian	Polynesia (44)	2,600	13.3	144.5
	Marquesas	Marquesas (43)	Austronesian	Polynesia (44)	2,600	-9.5	-139
	Mokapu	Mokapu 1 (55)	Austronesian	Polynesia (44)	2,600	21.3	-157.5

[a] Dental non-metric trait data from Scott et al. (2025a).

[b] SNP data from Tassi et al. (2015).

[c] Values are point estimates derived from Tassi et al. (2015).

Table 2: Dental non-metric traits, key tooth, and scores for rASUDAS2 and R-matrix analyses.

Dental trait and key tooth	Ordinal scale	Coding for rASUDAS2 analysis[a]	Coding for R-matrix analysis[b]
Winging UI1	0	1	0
	1+	2	1
Shoveling UI1	0+1	1	0
(backup: UI2)	2+3	2	1
	4+	3	1
Double Shoveling UI1	0+1	1	0
	2+	2	1
Interruption Grooves UI2	0	1	0
	1+	2	1
Bushman Canine UC	0+1	1	0
	2+	2	1
Tuberculum Dentale UC	0+1	1	0
(backup: UI1)	2+	2	1
Carabellis Trait UM1	0+1	1	0
	2+3+4	2	0
	5+	3	1
Cusp 5 UM1	0+1	1	0
(backup: UM2)	2+	2	1
Enamel Extensions UM1	0+1	1	0
(backup: LM1)	2+	2	1
Hypocone UM2	0+1	1	0
	2+3	2	1
	4+	3	1
PRM UM3	0	1	0
	1	2	1
Distal Accessory Ridge LC	0+1	1	0
	2+3	2	1
Premolar Multiple Lingual Cusps LP2	0+1	1	0
(backup: LP1)	2+	2	1
Cusp 6 LM1	0	1	0
(backup: LM2)	1+	2	1
Cusp 7 LM1	0	1	0
	1+	2	1
Deflecting Wrinkle LM1	0+1+2	1	0
	3	2	1
Protostylid LM1	0	1	0
	1	2	0
	2+	3	1
Groove Pattern LM2	X and +	1	0
	Y	2	1
Four Cusped Molar LM2	5	1	0

(backup: LM1)	4	2	1
Upper Premolar Root Number UP1	1	1	0
	2+3	2	1
Upper Second Molar Root Number UM2	1+2	1	0
	3	2	1
Lower Canine Root Number LC	1	1	0
	2	2	1
Tomes Root LP1	1+2+3	1	0
	4+	2	1
Three Rooted Lower First Molar LM1	1+2	1	0
	3	2	1
One Rooted Lower Second Molar LM2	2	1	0
	1	2	1

[a] For rASUDAS2 analysis, the ordinal-scale trait scores were simplified into two-level (1 or 2) or three-level (1, 2, or 3) ranks. Thresholds follow Scott et al. (2025a).

[b] For R-matrix analysis, the ordinal-scale trait scores were simplified into two-level (0 or 1) ranks. Thresholds follow Scott and Irish (2017).

Table 3. d_{ij} distances (below the diagonal), r_{ii} values (along the diagonal) in bold, and scaled R-matrix values (above the diagonal) for four pooled metapopulations.

	Australo Melanesia	East Asia	Pacific	Southeast Asia
Australo Melanesia	**0.076**	-0.074	0.024	-0.013
East Asia	0.335	**0.11**	-0.062	0.012
Pacific	0.084	0.291	**0.057**	-0.02
Southeast Asia	0.128	0.114	0.125	**0.027**

Table 4: d_{ij} distances (lower triangle) and r_{ii} values (diagonal) for 16 populations.

	Australia	Ban Chiang	Burma	China	Guam	Japan	Leang Tjadang	Loyalty	Marquesas	Mokapu	Mongolia	New Britain	New Guinea	New Hebrides	Solomons	Thailand
Australia	**0.125**															
Ban Chiang	0.24	**0.144**														
Burma	0.399	0.338	**0.163**													
China	0.551	0.335	0.553	**0.336**												
Guam	0.144	0.243	0.261	0.558	**0.065**											
Japan	0,361	0,227	0,226	0,209	0,236	**0,093**										
Leang Tjadang	0.271	0.315	0.221	0.486	0.154	0.153	**0.079**									
Loyalty	0.134	0.288	0.224	0.612	0.093	0.235	0.123	**0.063**								
Marquesas	0.13	0.27	0.273	0.541	0.087	0.226	0.146	0.09	**0.062**							
Mokapu	0.187	0.246	0.218	0.433	0.082	0.151	0.134	0.099	0.048	**0.042**						
Mongolia	0.495	0.413	0.376	0.217	0.419	0.157	0.246	0.395	0.369	0.277	**0.217**					
New Britain	0.119	0.232	0.356	0.521	0.102	0.331	0.32	0.156	0.148	0.148	0.545	**0.125**				
New Guinea	0.208	0.394	0.37	0.89	0.127	0.43	0.233	0.087	0.162	0.189	0.59	0.188	**0.167**			
New Hebrides	0.159	0.341	0.376	0.691	0.113	0.348	0.22	0.095	0.09	0.109	0.494	0.156	0.134	**0.123**		
Solomons	0.251	0.391	0.355	0.805	0.134	0.313	0.136	0.096	0.145	0.18	0.498	0.28	0.106	0.149	**0.141**	
Thailand	0.226	0.198	0.19	0.443	0.147	0.119	0.114	0.136	0.123	0.115	0.296	0.247	0.274	0.245	0.199	**0.062**

Table 5. Mantel and partial Mantel tests between the biological (d_{ij}) and geographic (GEO) distances, and two competing population history models (AGF and SUNDA).

Matrices	Correlation	p value
d_{ij} x GEO	0.175	0.078
d_{ij} x AGF	0.609	***0.0001***
d_{ij} x SUNDA	0.354	***0.0004***
d_{ij} x AGF constant GEO	0.593	***0.0001***
d_{ij} x SUNDA constant GEO	0.326	**0.0016**

Table 6. Dow-Cheverud tests between the d_{ij} distance and the standardized difference between GEO or d_{ij} and two models tested.

Model	**r d_{ij} x model**	**r d_{ij} x GEO**	**Difference**	**p value**
AGF	0.609	0.175	0.434	***0.0001***
SUNDA	0.354	0.175	0.179	0.1368
Model	**r d_{ij} x AFG**	**r d_{ij} x SUNDA**	**Difference**	**p value**
AGF x SUNDA	0.609	0.354	0.255	***0.0016***

Distances in kilometers between all pairs of populations

	Australia	Ban Chiang	Burma	China	Guam	Japan	Leang Tjadang	Loyalty	Marquesas	Mokapu	Mongolia	New Britain	New Guinea	New Hebrides	Solomons	Thailand
Australia	0															
Ban Chiang	5829.8	0														
Burma	6167.8	669.2	0													
China	6608.9	2020.1	2536	0												
Guam	4381.6	4443.7	5106.5	3566.8	0											
Japan	6755.9	3973.3	4567.6	2094.5	2579.5	0										
Leang Tjadang	2804.7	3028.3	3412.1	4006.7	3338.5	4819.3	0									
Loyalty	3297.8	8153.2	8686.3	7996.4	4537.2	7014.6	5400.1	0								
Marquesas	9163.4	13257.3	13915.7	12003.1	8814.9	10016.9	11130	5904.8	0							
Mokapu	8921.6	10235.2	10883.2	8501.8	6189.5	6408.6	9407.5	6081.6	3976.3	0						
Mongolia	8360.9	3295.1	3545.4	1755.7	4938.8	2652.9	5746.2	9475.3	12427.3	8544	0					
New Britain	2648.8	5755.7	6334.4	5533.9	2230.3	4808.9	3327.3	2477.1	7820.3	6477.9	7082.3	0				
New Guinea	2287	4740.8	5288.3	4807	2094.6	4531.4	2217.8	3413.1	8931.5	7407.2	6475.6	1112.3	0			
New Hebrides	3469.9	7910.5	8475.2	7603.6	4090.6	6519.2	5292	555.9	5885.7	5673.6	9024.8	2160.7	3189.8	0		
Solomons	3170.4	6744.6	7335.9	6359.8	2858.9	5342.3	4329.4	1681.4	6806.9	5757.5	7797.7	1017.8	2125	1243.7	0	
Thailand	5607.4	533.2	565.4	2547.2	4704	4459.4	2846.6	8137.1	13473.8	10641	5746.2	5809.8	4749.6	7939.3	6817.8	0

Model 1. Asymmetric Australo-Melanesian–East Asia Gene Flow (AGF)

	Australia	Ban Chiang	Burma	China	Guam	Japan	Leang Tjadang	Loyalty	Marquesas	Mokapu	Mongolia	New Britain	New Guinea	New Hebrides	Solomons	Thailand
Australia	0															
Ban Chiang	0.25	0														
Burma	0.25	0	0													
China	1	0.75	0.75	0												
Guam	0.5	0.25	0.25	1	0											
Japan	1	0.75	0.75	0	1	0										
Leang Tjadang	0.25	0	0	0.75	0.25	0.75	0									
Loyalty	0	0.5	0.25	1	0.5	1	0.25	0								
Marquesas	0.5	0.25	0.25	1	0	1	0.25	0.5	0							
Mokapu	0.5	0.25	0.25	1	0	1	0.25	0.5	0	0						
Mongolia	1	0.75	0.75	0	1	0	0.75	1	1	1	0					
New Britain	0	0.25	0.25	1	0.5	1	0.25	0	0.5	0.5	0	0				
New Guinea	0	0.25	0.25	1	0.5	1	0.25	0	0.5	0.5	1	0	0			
New Hebrides	0	0.25	0.25	1	0.5	1	0.25	0	0.5	0.5	1	0	0	0		
Solomons	0	0.25	0.25	1	0.5	1	0.25	0	0.5	0.5	1	0	0	0	0	
Thailand	0.25	0	0	0.75	0.25	0.75	0	0.25	0.25	0.25	0.75	0.25	0.25	0.25	0.25	0

Model 2. Sundadonty in situ microevolution (SUNDA)

	Australia	Ban Chiang	Burma	China	Guam	Japan	Leang Tjadang	Loyalty	Marquesas	Mokapu	Mongolia	New Britain	New Guinea	New Hebrides	Solomons	Thailand
Australia	0															
Ban Chiang	0.25	0														
Burma	0.25	0.25	0													
China	1	1	1	0												
Guam	0.25	0.25	0.25	1	0											
Japan	1	1	1	0	1	0										
Leang Tjadang	0.25	0.25	0.25	1	0.25	1	0									
Loyalty	0	0.25	0.25	1	0.25	1	0.25	0								
Marquesas	0.25	0.25	0.25	1	0	1	0.25	0.25	0							
Mokapu	0.25	0.25	0.25	1	0	1	0.25	0.25	0	0						
Mongolia	1	1	1	0	1	0	1	1	1	1	0					
New Britain	0	0.25	0.25	1	0.25	1	0.25	0.25	0.25	0.25	0	0				
New Guinea	0	0.25	0.25	1	0.25	1	0.25	0.25	0.25	0.25	1	0	0			
New Hebrides	0	0.25	0.25	1	0.25	1	0.25	0.25	0.25	0.25	1	0	0	0		
Solomons	0	0.25	0.25	1	0.25	1	0.25	0.25	0.25	0.25	1	0	0	0	0	
Thailand	0.25	0	0	1	0.25	0	0	0.25	0.25	0.25	1	0.25	0.25	0.25	0.25	0

Comparative Analysis of Regional Sample Affinities