

# The Austronesian Diaspora: A Synthetic Total Evidence Model

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**Abstract:** This is an evidence-based account of a remarkable, but perhaps somewhat underestimated, series of human population movements lasting continuously for around 5000 years. Information has been collected from a wide variety of studies across a range of disciplines and subjected to critical examination. The emergent picture is presented as a *Synthetic Total Evidence Model* which traces the Austronesian Diaspora from Taiwan via a genes, language and culture trail to Island Southeast Asia. From there two distinct branches are shown to lead one across the Pacific and another through Malaysia and Indonesia then on to Madagascar. Along the way there are many confounding episodes of admixture, language shifts and cultural assimilation. The Pacific branch is shown to contain two distinct groups known as Polynesians and Melanesians with similar, but still individually characteristic, gene pools. Despite all these complexities, the evidence does build to a single unified multi-dimensional picture.

**Keywords:** Austronesia, Polynesia, Melanesia, New Zealand, Malaysia.

## INTRODUCTION

The Austronesian Diaspora is one of the most remarkable episodes in recent human history. Starting from a relatively small population based in Mainland Asia, the Austronesian-speaking peoples have expanded to fill 33 independent nations with 380 million descendants. Their genes, language(s) and culture have spread two thirds of the way round the globe. There is a story of migration, admixture and exchange, where their key attributes have not always remained united in a single package. Rather, they have become uncoupled via language shifts, cultural diffusion and evolution plus geneflow. All of these factors must be properly recognised in any comprehensive account of their movements. It is also clear that this exercise in reconstruction must be based on multidisciplinary evidence [1]. Here, we will argue that many previous accounts focussed on just one geographic region or were based on information returned from a limited set of data from a particular discipline. Narrow focus seems to have created a sort of '*pseudo-competition*' between rival theories that only embraced limited pattern and process sub-elements of a much bigger picture [2]. Today, when alternate ideas can be considered altogether in a much wider context, they blend almost seamlessly into a unified coherent account with relatively few contentious areas [3]. In presenting this synthetic view, we will explain the

origins of these ideas and critically review the evidence, old and new, upon which they are based.

## ORIGINS AND DEVELOPMENT OF SIGNIFICANT MODELS

The era of modern scholarship can be traced as starting from a single foundation reference from Hill and Sarjeantson [4] plus Bellwood [5]. The central concept is of a '*Taiwan Homeland*' with rapid dispersal of oceanic voyagers having only limited (but not zero) contact with others encountered along the way. It is now widely recognised that this version is too extreme. Kayser *et al.*'s '*Slow Boat*' model [6] allows for a much greater degree of interaction between Austronesian-speaking migrants and established indigenous residents; namely Negritos and Papuans. Key support for this general class of explanation came first from archaeological chronology, linguistics and some commensal organisms; see [1]. Much genetic evidence is in accord with this account.

The main class of alternative explanation stems from Oppenheimer's writing about an '*Eden in the East*' [7]. This book discusses his idea that Austronesians come from Asia and dispersed overland across Sundaland to become stranded on the islands of Southeast Asia by rising sea levels. Their subsequent trans-oceanic migrations were then described by various alternate forms of '*Slow Boat*' or '*Slow Train*' model (ex-Melanesia vs. ex-Island Southeast Asia etc.). These ideas are strongly driven by the disjunction between male and female genetic lineages. The persuasive power that seems to be enjoyed by this class of model is that it is lodged in hypothetical

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geological and climatic causality. The strongest argument against these ideas is that they push Taiwan out to become a migration terminus and a cultural 'backwater'. This is in serious conflict with those who see the Aboriginal Hill peoples of Taiwan as the custodians of the greatest Austronesian linguistic diversity and with the dating of archaeological sites in Taiwan, the Philippines and the Batanes Islands that lie between them [1].

The Taiwan Homeland concept has problems too, because visible traces of their supposed ancestors have been all but obliterated by more recent mainland expansion of the Han Chinese. The situation is rendered even more confusing by a number of red herrings. These include the Cham people who once dominated the vast Champa Kingdom in Vietnam and Cambodia and who even today speak Austronesian languages. However, strong genetic evidence now shows that they have experienced linguistic replacement [8]. Unidentified component(s) of the Daic people are the leading candidates for the mainland ancestors of Austronesians [9]. The general question has recently been considered critically and in-depth by Bellwood *et al.* [1]. Many other authors have also recently reviewed various aspects of the Austronesian Diaspora [10-16]. It is clear that re-construction of human movements must be based on the record of historical artefacts and supported by evidence from the genes, languages and cultures of living (and sometimes also of dead) peoples. This requires information from many academic disciplines. In our view, this mutually beneficial synergy has increasingly lead to methodological cross-fertilization and promotion of new multi-disciplinary approaches.

So, received wisdom now describes a complex and still controversial expansion pathway. The present authors suggest that this situation arises from four principal sources. First, many studies have a very narrow focus; single discipline or single target. For example, it is pretty much agreed by all investigators that Austronesian maternal genetic lineages (mitochondrial DNA; mtDNA) track back to Taiwan and/or Island Southeast Asia (ISEA) whereas their paternal lineages (Y chromosome markers aka NRY) track back more or less exclusively to Melanesia/ISEA, a seemingly impossible dichotomy! Second, many models are incomplete, at least in the sense that they are only partial accounts. Some, like the previous example of sex-limited genetic markers deal exclusively with patterns, whereas others deal with explanatory causal mechanisms and processes.

Hence, the remarkable conflict between the mtDNA and NRY data for Polynesians can be explained by gender-biased geneflow between Austronesian-speaking Mongoloids (ASM) and Papuan-speaking Australoids as explained in [1] and endorsed by Chambers and Edinur [17]. Third, in some cases there seems to be insufficient recognition of genetic admixture between populations and uncoupling of genes from various cultural elements. The former can compromise the reconstruction and dating of evolutionary trees and the latter may lead to misplaced confidence in wholly incorrect inference. Thus, data from many commensal organisms, e.g. chickens, pigs and dogs with perhaps even greater certainty, suggests that they were acquired from ISEA by Austronesians. This does not mean that the people themselves came exclusively from ISEA, only that they, have been present there at some point in the past. They may equally well have picked up these very useful items along a migration pathway starting elsewhere. Finally, there is the long-standing problem of a multiplicity of misleading descriptors used to name theoretical models, geographic areas and the peoples themselves. This difficulty is slowly becoming better resolved; see Box A.

#### **BOX A: PREFERRED TERMS FOR GEOGRAPHICAL AREAS AND THEIR PEOPLES**

##### **Nomenclature for Asian and Pacific Regions**

The terms Near Oceania and Remote Oceania are preferable to Melanesian and Polynesian and the last two properly refer to people rather than islands or open ocean spaces. Confusion arises because the so-called Melanesian region is home to both Melanesian and Polynesian people plus direct unadmixed descendants of the original Papuan settlers (*i.e.* P-SA as indicated below).

The term Island Southeast Asia should be used with extreme caution because it is always going to be unclear (due to changes in sea level) just what region is being referred to unless a timeframe is given; *i.e.* recent ISEA = WISEA + EISEA versus around 10,000 ya when ISEA = EISEA only. Hence, it is probably better to use the terms Sunda (or Sundaland) = WISEA and Wallacea = EISEA; give or take inclusion of the Philippines, which should be specified. Sahul refers to Australia plus New Guinea.

##### **Nomenclature for Asian and Pacific Peoples**

The system below was adopted to clearly distinguish modern and ancestral populations. This is

necessary to give a clear description of admixed descendants such as Melanesians whose genetic make-up may not correspond to observed cultural traits.

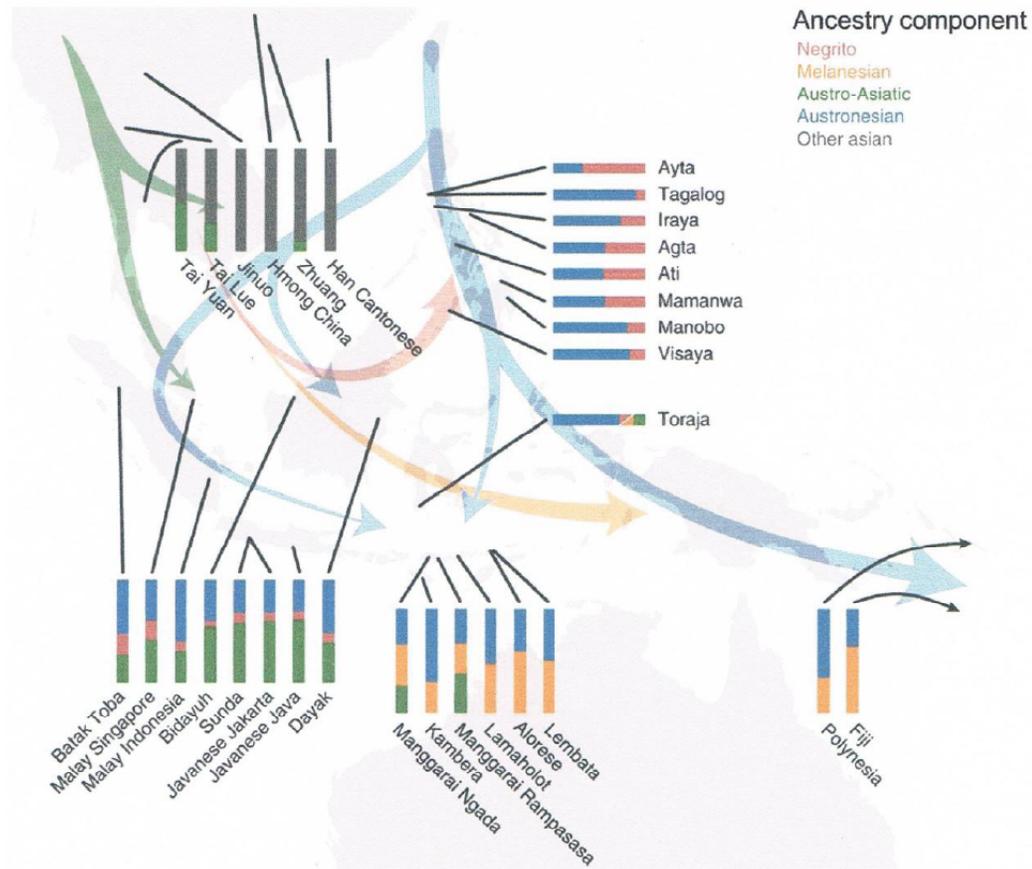
Population	Description
Taiwan aboriginal and other Asian including Filipino, Malay and Indonesian	Austronesian-speaking Mongoloid (A-SM) with increasing Negrito admixture
Australian Aborigine and Papuan interior	Papuan-speaking Australoid (P-SA)
Coastal PNG plus islands and other Melanesians	~50:50 (A-SM: P-SA) <sup>bc</sup>
Polynesian including Maori	70:30 to 87:13 (A-SM: P-SA) <sup>ad</sup>

<sup>a</sup>Lipson *et al.* [18] <sup>b</sup>Wollstein *et al.* [19], <sup>c</sup>Friedlaender *et al.* [20], <sup>d</sup>Kimura *et al.* [21] and modelled after Chambers and Edinur [17]. In the text we have sometimes used the more relaxed terms Austronesian and Papuan to refer to A-SM and P-SA groups as defined here.

For instance, the terms Melanesia and Melanesian are being replaced by the geographic term Near Oceania and describing the people who live there as

Papuan with a 100% aboriginal genepool (mainly interior Papua New Guinea, PNG) plus modern descendants of the original Austronesian settlers. Some of this latter group still have > 70% Austronesian genes and reside mainly northern coastal PNG and its offshore islands in the Bismarck Archipelago. The other admixed descendants are Melanesians having close to equal Papuan/Austronesian genetic genomic contributions and who live in coastal interior regions of the mainland and villages in the more central parts of the islands [22]. Their complex patterns of population movement in ISEA and associated genetic consequences in terms of blended genepools are shown in Figure 1.

These problems have not been fatal impediments to the development of a coherent account and there is considerable agreement between the ideas above. In fact, the only really significant difference between them is the single key question; Did Austronesian people migrate north into Taiwan as some claim [7] or south out of it [23]. Even these two apparent alternatives can



**Figure 1:** Early stages of the Austronesian diaspora; showing best-fit genomic proportions of Austronesian-speaking peoples in ISEA and their inferred population movements from [18] with permission.

be reconciled, if one allows for a degree of admixture between Austronesian voyagers ex-Taiwan and residents of ISEA [24] and as other authors have suggested [1, 2, 11, 17]. Both views of indigenous history do agree that Austronesians were not the first people to inhabit many of their present areas not excluding Taiwan itself. Their predecessors include various aboriginal and Negrito groups spread right across ISEA. We now claim that the wider picture is better captured in what has become known as the 'Synthetic Total Evidence Model' and extends to embrace further process elements such as natural selection, founder effects and genetic bottlenecks.

### THE NATURE OF THE EVIDENCE AND ITS ANALYSIS

A wide range of often contradictory information is available to scholars who might hope to untangle the deepest mysteries of the Austronesian Diaspora. It is, therefore, important to understand the nature of this information, if one wishes to make secure inferences and so arrive at a balanced evaluation of their significance.

One of the most important sources of evidence in Austronesian studies comes from archaeological remains. These often take the form of durable artefacts such as pottery shards or fishhooks, but may also be perishable plant seeds, animal bones and even human remains. Charcoal from cooking fires is also a valuable resource for carbon dating. Indeed, one of the most important properties of archaeological materials is that they can be dated, often with considerable precision. These dates need to be interpreted carefully, because they are necessarily biased towards recent dates, *i.e.* they show when sites were already occupied, rather than when they were first occupied. Carbon dating of wood is an exception to this rule, as this process returns the date when the tree started growing, not when it was used to make houses, furniture or fires. Nonetheless, within these caveats archaeological dates are valid empirical estimates of real dates and thus are fundamentally different from those obtained by genetics or linguistics as theoretical constructs beset with in-built assumptions. There is now an important interface between archaeology and genetics through the analysis of trace and ancient DNA molecules [25].

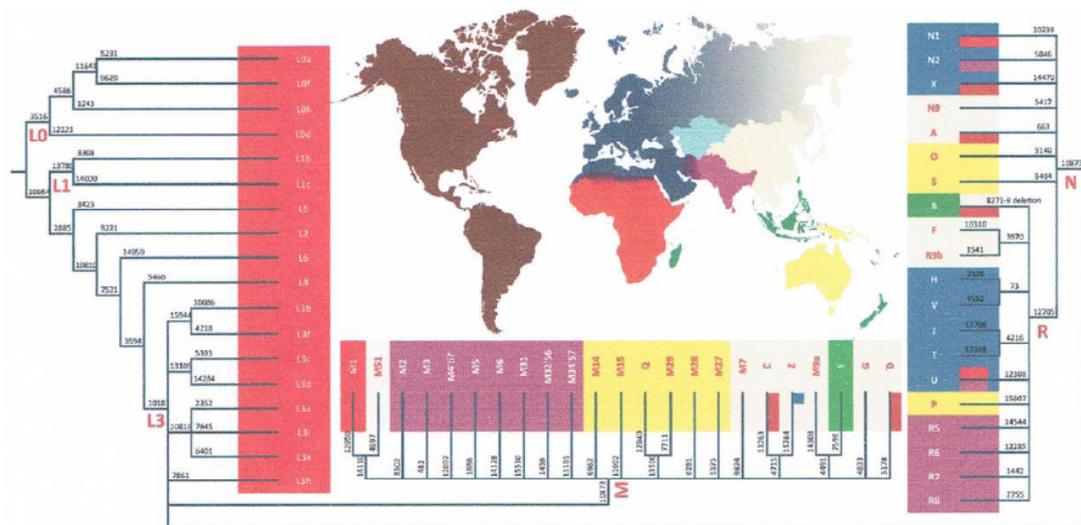
Genetic analysis has made a major contribution to reconstruction of Austronesian history. Measures of similarity and differences between particular DNA target sequences can be used to construct evolutionary trees and for tracing genealogical history. Because

mutational changes are known to accumulate in a regular fashion (the famous molecular evolutionary clock), branching events in these trees can be dated. It is important to remember that different mathematical methods may return slightly different trees from the same data, and none may be completely correct. Equally, the so called 'gene tree' returned by analysis of a single target may not be the true population tree and may conflict with other gene trees. This is not to say that molecular trees are not reliable, far from it. They should best be regarded as useful and informative hypotheses, and never treated as fact. Tree construction methods are vulnerable to all sorts of errors and can only ever be expected to return correct answers, if the underlying evolutionary process itself is actually tree-like. Hence, reticulation and admixture can lead to false inference. It is for this reason that some investigators prefer to use numerical or statistical methods [26, 27].

There are three ways to put dates on trees. First, branching events such as the settlement of a new island may be dated by historical artefacts. Other branchpoints, for which there are no archaeological records, can then be dated by comparing branch lengths. Second, branching can be related to geological changes. For instance, if a land mass or island was below the sea at some time in the past, then it is safe to say that humans arrived there later after it emerged. Finally, and in the absence of all other hard evidence, then dates can be estimated by using established rates of DNA sequence divergence for targets. Overall, most practitioners are quite sceptical about dates derived by any of these molecular methods and some may even be 'reluctant' to use them at all, *e.g.* Tumonggor *et al.* [15]. In short, it can be misleading to regard dates obtained in this manner as sufficient to constrain thinking about events in recent human history.

Despite all of the above considerations and limitations, genetics has been a particularly valuable tool in tracing the Austronesian Diaspora. In particular, mtDNA and NRY analyses have featured prominently. The great value of mtDNA and NRY for tracing ancestry is they cannot reassort and effectively do not recombine. Due to these properties they are inherited much like family names in many western societies. Figure 2 shows the global distributions the mtDNA haplogroups as an example.

Particular attention should be given to the geographical distribution of Haplogroup B. Within this



**Figure 2:** Global Distributions of Mitochondrial DNA haplogroups. This figure is reproduced from [33] with permission.

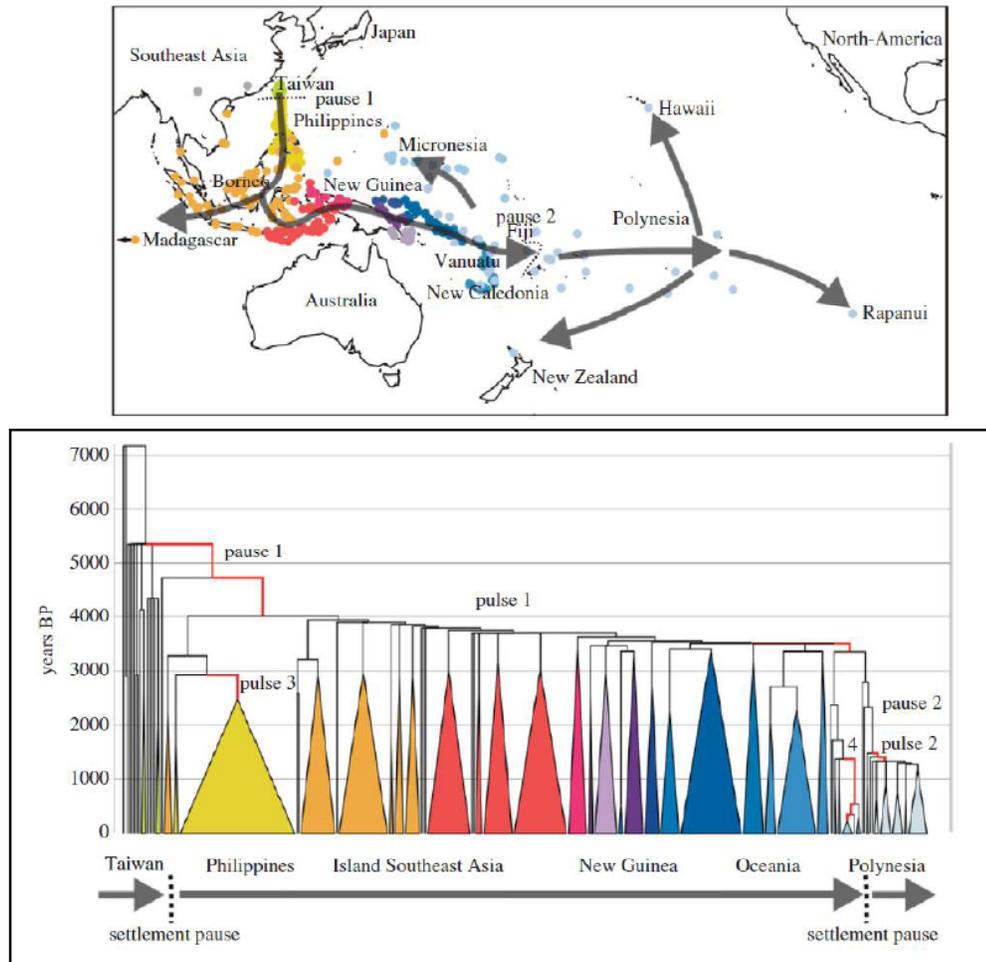
haplogroup three or four SNP markers in mtDNA give rise to the Asian-specific lineage Haplogroup B4a which is ancestral to one known as the '*Polynesian Motif*' that together with the accompanying '*COII/tRNA<sup>Lys</sup> intergenic 9-bp deletion*' that define Haplogroup B4a1a1a; see [1-3]. These last two markers are increasingly common across the Pacific and have played an especially prominent role in the field. Both are now known to be labile and subject to frequent back mutations [28], which can lead to homoplasy in trees due to convergent molecular evolution. So although data from both of these mtDNA markers should now be treated with particular care, they do remain useful diagnostic tools. In particular, complete mtDNA sequencing studies [29, 30] have been valuable extensions to these earlier surveys and have been interpreted as pointing back to native population source(s) among Taiwanese Hill Tribes (see later). A corresponding picture for the Y chromosome, including revised dating, has been constructed by two high-resolution analyses [31, 32].

Most recently large scale SNP surveys have been carried out on descendant populations of the Austronesian Diaspora [19, 21, 34]. The subsequent met analysis by Lipson *et al.* [18] now appears to be definitive; see [30] for commentary. It uses 18,412 SNPs from 1094 people representing 56 local populations and employs a new software routine called *Mix Mapper* to partition ancestry fractions and hence track ancient human population movements (see next section). The account which they develop is strongly congruent with the one developed here and introduces greater Austronesian/Negrito admixture in The

Philippines and Borneo than in our previous reconstructions, e.g. [1]. It also includes admixture between Austronesian/Negrito voyagers with Austroasiatics, who probably first entered Malaysia and Indonesia from around 10,000 ya [24]. These developments have been picked up for Southeast Asia plus Oceania [30], for Malaysia [11] and finally set in a global context [13].

Similar molecular genetic approaches have been taken using commensal organisms and disease causing bacteria and viruses [35]. The rationale for employing them as models runs that they accompanied Austronesians on migration voyages because they were useful food items (chickens, dogs, pigs and rats), valuable crop plants (see Seelenfreund *et al.* [37] for a detailed list), stowaways [55] or simply unavoidable (tapeworms [38], hepatitis B virus [39] etc.). Consequently, they should be capable of providing an independent check on trees constructed using exclusively human data. Further, they have the great advantage of being present as ancient remains found at archaeological sites or as preserved artefacts.

Linguistics has more in common with genetics than might be apparent on first encounter. Pronunciation, vocabulary and grammar all begin to diverge once populations become more or less permanently separated, albeit they do not all change at the same rate. Hence, it has been possible for scholars to construct databases of cognate words and examine the changes between them from one Austronesian language to another. These data can then be coded as characters and used to build, and even date language



**Figure 3:** Distributions and phylogenetic trees of Austronesian Languages.

This figure is taken from Gray *et al.* [40] with permission. The tree is rooted on the left hand side with two out group languages; Buyang and Old Chinese. Readers are advised to consult the original source for details regarding time estimates for the various pulse and pause phases.

trees. The tree for Austronesian languages is shown in Figure 3 and shows Taiwanese groups as being basal (*i.e.* ancestral because they fall closest to the root of the tree).

Information from studies in Comparative (*i.e.* cross-cultural) Anthropology can be used in the same way. Observational characters can be coded and used in phylogenetic analyses. However, it is more common to see investigators taking the reverse approach, *i.e.* starting from a given genetic or linguistic tree and mapping cultural features onto the branches of the tree. This allows them to observe directionality of change, the time taken *e.g.* to shift from one political system to another, and to discover if these changes have taken place once, or more frequently. A surprisingly wide range of cultural features have been examined in this way including social and political complexity [41, 42], near-shore fishing activities [43] and warp ikat weaving

[44]. However, a minor warning must be issued here, as previously. Conclusions in cross-cultural research may equally well be compromised by reticulation and homoplasy or by novel events that make geographical proximity a misleading indicator of relatedness. Cultural practice is mobile and can leapfrog great distances; *e.g.* see Sheppard [45] on Lapita pottery traditions.

### CRITICAL EVALUATION OF EVIDENCE ACROSS FIELDS

The archaeological evidence has been reviewed recently [1, 46]. All authors agree that ISEA was settled by anatomically modern humans long before Austronesian cultures developed. The descendants of these early settlers include, for example, the Orang Asli of Malaysia, the indigenous tribes of Papua New Guinea and the various Negrito peoples. Their arrival dates back to more than 50,000ybp and they had

reached places such as Niah Cave in Sarawak, Borneo and the Bismarck Archipelago north of the PNG mainland by around 28,000ybp. Subsequently, many of them have become proxy parts of the Austronesian family via language shifts. The authors above make a compelling case for the Out of Taiwan account by showing a sequential record of settlement moving south from Taiwan from around 5,000ybp via the Batanes Islands, through the Philippines and on to the northern coastal regions of PNG and its offshore islands. It is from this region that the highly distinctive Lapita pottery, as such, is first recorded. However, there is a clear trail of antecedent forms tracing back along the inferred direction of travel. This technology was carried out across Near Oceania, albeit not strictly in a set of geographically incremental steps [45] and on into Remote Oceania reaching as far as Tonga and Samoa. It seems likely that Austronesian-speaking Melanesians (as defined in this article and the preceding reference) followed the Lapitaculture people out into the Pacific and largely replaced them over much of Near Oceania and some way beyond. Their arrival then corresponds to the demise of the Lapita tradition, followed by the adoption of simpler forms.

The distribution of Austronesian languages also presents a paradox. The aboriginal people of Taiwan between them speak nine out of ten of the major Austronesian language groups (Formosan), but it is the tenth group (Malayo-Polynesian) that contains all of the Austronesian languages spoken outside Taiwan. This makes Taiwan the centre of diversity for this language group and, thus by strong inference, the origin of all Austronesian languages. The fourteen recognised indigenous tribes who inhabit Taiwan today do not represent the totality of Austronesian people who have ever lived there. At least eight major tribal groups vanished from the western plains region in the fairly recent past as they were absorbed into the majority Han culture around 300 ybp [47]. So, it is possible that one or more of them spoke an Austronesian language from the tenth group and were the ancestral population(s) for all contemporary descendent branches. Set against this proposition is the fact that some genetic studies claim to have identified the most likely candidates among the extant tribes; e.g. Paiwan, Puyuma and Saisiyat [48] vs. Amis [29]. In this case the putative missing ancestors must have been closely related to one of the competing genetic candidates (see later). Notwithstanding this debate, all of the phylogenetic reconstructions of Austronesian language trees lead back to Taiwan [40]. The review by Bellwood

*et al.* [1] strongly endorses this proposition, which has subsequently been adopted and employed to good effect by others [62, 59, 68].

Abundant, high quality genetic data are readily available for many Austronesian populations starting from the pioneering work described in [4]. It is surprising, then, that these studies have led to so much debate and controversy and so many competing theories. At the risk of making an over-simple generalisation, it seems that those researchers who work in Indonesia and Malaysia have tended to favour an 'Out of ISEA' version of the Slow Boat class of models vs. those who work in Taiwan and the Pacific who lean more towards the Out of Taiwan version. Compare for example, the '*ancient genetic highway*' which one set of workers claims [15] links the Indonesian Archipelago to the Pacific vs. the '*populated viaduct*' formed between Taiwan and Indonesia erected by [23]. Genetic influences from both directions are apparent in PNG and nowhere more apparent than in the contrasting ancestry patterns revealed by mtDNA and NRY studies [12]. The paradox can be resolved by building a new process element, gender-based gene flow, into the model. This is capable of uniting the contrasting maternal and paternal patterns. Hence, matrilineal marriage practice required Austronesian females to remain with their families where they were joined by their Papuan male partners. This explains why NRY markers in Pacific peoples map back predominantly to PNG and Asia. It does not resolve the ISEA vs. Taiwan debate.

In contrast, it is undisputed that fairly extensive admixture between Austronesians and Papuans took place in, and around, northern coastal PNG (c. 4,500ybp). This effect was firmly demonstrated by using an extensive set of autosomal SNP and STR markers [20]. Even more precise estimates were later obtained by others [19, 21] showing 20 – 30% of the Austronesian genepool in the Pacific has been replaced due to admixture. For Melanesians the corresponding figure is closer to 50%. The analysis noted earlier [18] also shows an A-SM admixture with indigenous Negritos carried into the Malay population [11].

The newly formed Austronesian populations with limited Papuan admixture are best seen as the true ancestors of Polynesians, some of whom departed to settle the uninhabited islands of Near Oceania and then moved on to Remote Oceania. They left behind a complex collection of peoples with little coherent

relationship between their physical appearance and their genes, languages and cultures [22]. The Polynesians went on to settle the widely dispersed islands of the Pacific taking Lapita culture with them, at least part of the way. The process of island hopping comes at a cost because genetic variation is shed along the route. No set of voyaging canoes can hope to capture all the genetic variation on their home island, unless absolutely all of the people set sail together. This loss of genetic variation West to East across the Pacific by these repeated founder effect events is sometimes known (rather inaccurately) as the '*genetic bottleneck in Polynesia*' [49]. Overall, it has only resulted in around a 5 to 10% reduction of variability in New Zealand Maori [2, 50]. Interestingly, it is the extensive preservation of genetic variation in terminal migrant populations that convinces investigators that the risky settlement voyages were deliberate and well planned, large scale expeditions [51], all exaggerated claims and contrary opinions notwithstanding [35]. Many of the fully dispersed and differentiated migrant Austronesian populations, such as Maori and Hawaiians, are now experiencing a new episode of admixture, this time with Europeans [26, 52], often coupled with a language shift towards the local version of English.

Those Austronesians who dispersed westwards from ISEA settled the landmasses derived from the drowning of Sundaland (from c.4,000 ybp) and encountered yet further admixture. Across Indonesia, the population has four principal sources. First, came the ancient Negrito people, followed by Austroasiatics, at some time during the last 10,000 years. This latter group is said to have arrived on an '*Early Train*' [24] and have left their mark on the contemporary population accounting for the present East-West stratification of the genepool, particularly in regard to NRY markers. This is a perhaps a signal of another episode of gender-biased geneflow between them and the third group, Austronesians, who arrived next, reflecting developments in local cultural practices [15]. Later episodes of admixture for the now settled people took place with, Arab, Chinese and Indian traders to provide the fourth source of genetic input. In Peninsular Malaysia one must add a further, fifth component to their national layer cake in the form of Malay sub-ethnic groups who arrived in fairly recent historical times from neighbouring regions, mainly Borneo and Sumatra. In genetic terms, these later immigrant populations are almost all mainstream Austronesian stock, except for some who show greater genetic affinities to

Austroasiatic lineages [53]. The full development of this work is elaborated in [11] and includes data for medically important markers such as human leukocyte antigen (HLA), killer cell immunoglobulin-like receptor (KIR), blood groups, human platelet antigen (HPA), human neutrophil antigen (HNA) and cytokines [54-58].

It is now well established by both genetic and linguistic evidence that the Austronesian Diaspora extended well beyond the confines of Asia, crossed the Indian Ocean and arrived at the Comoros [59, 60] and Madagascar [61]. These settlements involve further episodes of gender-biased admixture and have resulted in particularly complex genomic mixtures, e.g. on the Comoros Islands where the people represent a melange of African, Middle Eastern and Southeast Asian with proportions around 70:20:10 across all genes, but having a relative high proportion of Arab NRY markers coupled with relatively high proportions of Asian mtDNA lineages. On Madagascar there is continuing reciprocal genetic exchange with the African mainland.

Extensive studies on commensal organisms paint much the same picture as that from human genetics, with one or two particularly fascinating extensions. Most of the work on the plants and animals (see compilation by Storey *et al.* [35]) that accompanied the voyaging peoples can be traced to ISEA. These findings are thus compatible with both proposed distal origins for the Austronesian Diaspora, ISEA itself or Taiwan. This is a rapidly developing field as ever more samples are located and techniques to access their genetic information continue to improve rapidly. For instance, a large scale review of the available data on dogs (*Canis familiaris*) has more or less convincingly excluded the possibility of a Taiwanese origin for the Polynesian dog [62]. Once again, as these investigators suggest, this should properly be seen as pointing to the complex origins of the Polynesian culture. Disease causing organisms are not commensals in the conventional sense of the term, but they are, nonetheless, obligate human companions. Several candidates have been examined recently including *Helicobacter pylori* (responsible for stomach ulcers), hepatitis B virus and tape worms (*Taenia* spp); see [63, 39, 38] respectively. The first of these studies is particularly interesting as it clearly tracks all Pacific isolates of *H. pylori* back to Taiwan.

Commensal organisms do provide one special extension to the account so far developed in this

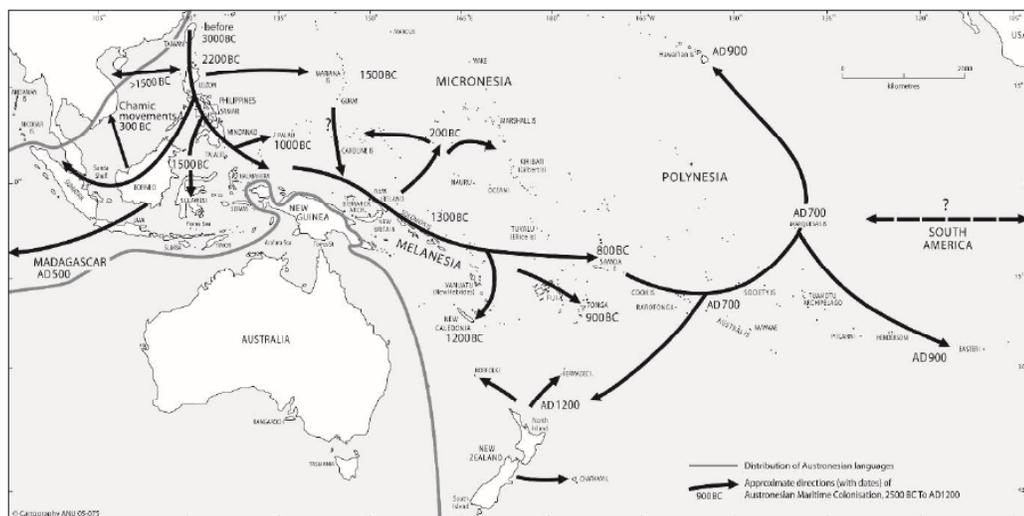
review. Across The Pacific there are some widely distributed plants that are, e.g. paper mulberry, *Broussonetia papyrifera* [64], and some that are not sourced from Asia. These latter botanic resources include the sweet potato or kumara (*Ipomoera batatus*) and the bottle gourd (*Lagenaria siceraria*) which come from South America; e.g. see review by Matisoo-Smith [65]. Now the question becomes; were they imported by Polynesians or exported by Indigenous South Americans? Venture and return by Polynesians seems the most likely scenario. There are even claims to have found Polynesian chicken bones in South America, but these are equivocal [66]. This contact episode does not seem to have left a lasting record in human genomes. There is no evidence for Polynesian genes in South America, even at well examined burial sites on offshore islands. South American genes are present, but not widespread, in the Pacific and were clearly brought there by traders and slavers after the Spanish Conquest.

**THE EMERGENT PICTURE**

Our viewpoint is presented via development of ‘The Synthetic Total Evidence Model’ or STEM for short [1, 2, 17]. This is a data-driven perspective as we found our formative experiences with alcohol metabolism genes [67] and DNA fingerprinting [50] informed pattern and process elements of the account respectively. Equally, more recent work by our team on immune system markers in New Zealand [26] and Malaysia [54-58] shows evidence of Austronesian-Papuan admixture and the role of natural selection in shaping the gene pools of these native peoples. The STEM account

includes both pattern and detailed process elements and thus goes beyond even the Out of Taiwan version of the Slow Boat model [12], which is predominantly pattern-based and does include admixture, but not repeated founder effects. The STEM has grown organically as new facts came to light. It has recently embraced insights regarding Austronesian admixture with Negrito in the Philippines and with Austroasiatics in Indonesia etc. It blends together all presently existing data with all previously described ideas in Figure 4.

The STEM account begins in Taiwan with a presently unidentified indigenous tribe (or tribes – see earlier for previously suggested candidates) moving south to the Philippines via the Batanes Islands leaving a clear ancestor–descendent genetic trail (see [1] for details). The distal source of the Taiwanese seafarers lies among the ancient Daic people of Mainland Asia, who also remain unknown for the present. From the Philippines the Austronesians moved into the Wallacea fraction of ISEA (see Box A for terminology). Here, they gradually picked up many of their commensal plants and animals and would have enjoyed a greater or lesser number of encounters with the hypothetical Fast Train Austroasiatic dispersers particularly in Indonesia and Malaysia – see Figure 1. Regardless of what took place, it is clear that Austronesian culture and languages took a strong hold in these locations, even in populations such as Negritos who still remain to some extent genetically distinct from Austronesians. These exchanges may well have continued through reticulated trading networks; see discussions in [10]. Such possibilities have been recognised in previous iterations of STEM, but now probably need to be given



**Figure 4:** The Austronesian Diaspora according to the Synthetic Total Evidence Model: from [1] with permission

greater prominence. These processes would have allowed continuous introgressive geneflow through the area and have the potential to explain some of the more enigmatic genetic data, which are the key source of on-going debates between scholars.

From ISEA one branch of the Austronesian Diaspora leads Eastwards out to Northern PNG and the Pacific (and probably even reached to South America) and a second branch leads Westwards via the Sundaland fraction of today's ISEA and out across the Indian Ocean to Africa. The Eastern Branch is associated with the development of Lapita culture and the rise of ancestral Polynesians via limited gender-biased geneflow with Papuans. There was a pause between Lapita expansion (2900 ybp) and further settlements phases – see Figure 3. Their genepool was refined by repeated founder effects as people dispersed to the far-flung corners of the Polynesian Triangle (Easter Island, Hawaii and New Zealand) arriving just 1200 to 750 ybp. It seems that even then they were willing to explore further out and voyaged to South America and brought back vegetable resources. The fact, that these crop plants became widely distributed across the Pacific, is testimony to an unseen network of trading contacts. From New Zealand, elements of the original Polynesian settlers (Māori) went on more settlement expeditions to the Auckland Islands, Chathams, Kermadecs and Norfolk Island. These islands are all quite distant from mainland New Zealand and none of them is very hospitable in terms of either resources and/or climate. Only the Chatham Island settlement by Moriori persisted and the others were quickly abandoned. Over the past 150 years mainland New Zealand Māori culture and language has experienced considerable challenges following European settlement and, as explained earlier, gradual blending of the two genepools is now taking place [52, 68]. Similar things have happened, and continue to happen, in Hawaii. The history of the Easter Islanders contains a number of well-known and utterly disastrous episodes leading to the dilution of the original genepool.

A subsequent wave of transoceanic voyagers left Island PNG following the Polynesians. These people most probably spoke Austronesian languages and their descendants have significant Austronesian gene content. They are known as the Melanesians and should be recognised a distinct component of the story that is unfolding here; see [1].

The Western Branch of the Austronesian Diaspora headed towards Indonesia and Malaysia leading to complex population structures, *e.g.* see Gomes *et al.* [69] and Morrison *et al.* [70] for an account of the Timorese, but with a preponderance of Austronesian speakers. Again there is contemporary admixture, which is probably greater in Malaysia given the significant fractions of Indian and Chinese minority ethnic groups [11]. Religions have changed from animist, through Hindu to Buddhist and on to Islam (and Christianity to a much lesser extent), leading to the complex and largely tolerant society that can be seen there today. Further migrations have taken this branch to the Comoros Islands and Madagascar, where admixed populations have developed.

## CONCLUSIONS

The account presented here represents a remarkable history of achievement, not only for the various Austronesian peoples themselves, but also for the scholars who have worked to unravel its often contradictory twists and turns. The contemporary view is informed by data from many sources. These range from oral traditions and navigation, via comparative linguistics and population genetics all the way to tapeworms. The emergent picture is becoming increasingly complex and *yet also* becoming increasingly clear as it does so. Being Austronesian now seems to be one thing and many things all at the same time. Received wisdom as presented here is not without its disputed areas, but these are where future progress may be made.

In closing, we note that new knowledge and improved interpretive understanding now help to unite this large group of dispersed peoples. These serve to provide a transcendent sense of identity via an enhanced evidence-based appreciation of shared ancestry. This also means that important new data, *e.g.* on medical genetics, collected in even one small isolated population that forms part of this diaspora, can now be seen to have greater or lesser relevance to the entire 350 million Austronesian descendants; see Kuo *et al.* [71] and Morrison *et al.* [70] for examples of this type of thinking. The extent to which any such findings are applicable is conditioned by fuller understanding of relationships between their component subgroups. The prospects a head look promising indeed, given the present intensity of effort and the way that many disciplines are now working together. It is hoped that STEM as presented here is but a single pointer to benefits still to come.

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