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## An ongoing Austronesian expansion in Island Southeast Asia

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## ABSTRACT

The Austronesian expansion into Island Southeast Asia and the Pacific was the last and most far-reaching prehistoric human migration. Austronesian languages replaced indigenous languages over nearly half the globe, yet the absolute number of Austronesian colonists was small. Recently, geneticists have identified large geographic disparities in the relative proportions of Asian ancestry across different genetic systems (NRY, mitochondrial DNA, autosomes and X chromosomes) in Austronesian-speaking societies of Island Southeast Asia and the Pacific. Surprisingly, a substantial genetic discontinuity occurs in the middle of a continuous chain of islands that form the southern arc of the Indonesian archipelago, near the geographic center of the Austronesian world. In the absence of geographic barriers to migration, this genetic boundary and swathe of Austronesian language replacement must have emerged from social behavior. Drawing on decades of comparative ethnological research inspired by F.A.E. van Wouden's structural model of Austronesian social organization, later codified by Claude Lévi-Strauss as "House societies" ("sociétés à maison"), we propose a two-stage ethnographic model in which the appearance of matrilocal "House societies" during the initial phase of the Austronesian expansion, and the subsequent disappearance of "House societies" in lowland rice-growing regions, accounts for the observed linguistic, genetic and cultural patterns.

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## Introduction

Prior to AD 1500, Austronesian was the world's most widely dispersed language family, extending more than halfway around the globe from Madagascar to Easter Island. Despite decades of debate there is as yet no consensus on either the geographic origins of the Austronesian expansion, or the social mechanisms that led to the adoption of Austronesian language and cultural traits by so many societies across the Pacific. Among geneticists and linguists, much research has been directed towards clarifying the geographic pathways of migration and colonization, with less attention paid to the processes that led to the replacement of other languages and changes in the composition of populations. Until recently, this research has been hampered by the scarcity of data (genetic, linguistic and archaeological) for Island Southeast Asia (ISEA), which played a key role in the initial phase of the Austronesian expansion (Bellwood, 2001).

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But recently more data has become available. This year our group completed analysis of nearly two thousand genetic samples from 13 Indonesian islands, along with associated linguistic data, and other researchers have published new investigations of genetic diversity in ISEA, Melanesia, Madagascar and Polynesia (Soares et al., 2011; Wollstein et al., 2010; Wilmshurst et al., 2011; Kayser et al., 2008; Kayser, 2010; Abdulla et al., 2009; Friedlaender et al., 2008; Kimura et al., 2008; Marck, 2008; Tabbada et al., 2010; Mona et al., 2009; Moodley et al., 2009; HUGO Pan-Asian SNP Consortium, 2009; Soares et al., 2008). Other studies have added to our knowledge of phylogenetic relationships within the Austronesian language family (Gray et al., 2009).

Here we propose a simple model for the Austronesian expansion that builds on these data as well as comparative ethnological research in ISEA. The model is based on an insight that dates from the earliest period of anthropological research in the region. In the 1930s, Dutch anthropologists began to argue that superficial variations in social structure – for example, patrilineality versus matrilineality – were probably not the result of successive migrations (vanWouden, 1968). Instead, Austronesian cultures shared a core set of ideas and institutions that found

expression in a cognitive classificatory system or “structure” linking social organization, cosmology and myth. As G.W. Lochter observed in 1968, “the great advance in understanding effected in the thirties was primarily the idea that accentuated matrilineal grouping, similarly marked patrilineal grouping, and double unilineal grouping could belong to one and the same structure (Lochter, 1968).” This structure later came to be identified with the concept of a “house society”, developed by Claude Lévi-Strauss. In a series of lectures at the Collège de France from 1976 through 1981, Lévi-Strauss defined “house societies” by contrasting them with lineage-based social systems (Lévi-Strauss, 1983). His initial inspiration for these “sociétés à maison” was the noble houses of Europe: the historical house of Plantagenet, or the fictional house of Usher. Lévi-Strauss observed that houses may appear in hierarchical societies as durable social groupings, which ‘reunite or transcend’ opposing categories such as descent/alliance, patrilineal/matrilineal descent, hypergamy/hypogamy, and close/distant marriage (Lévi-Strauss, 1983).

While the original concept of “sociétés à maison” covers a lot of ground, subsequently ethnologists identified a much more specific set of characteristics associated with Austronesian house societies (Fox, 1993). These include cosmological dualism, with a pronounced emphasis on the complementarity of male and female principles (vanWouden, 1968); founder-focused ideology relating to both genitor and genetrix lines of descent (Bellwood, 1996); apical demotion of these lines of descent, with an emphasis on elder/younger relationships (Fox et al., 1995); and the pervasive use of botanical metaphors to express the concept of growth from an origin (Fox et al., 1995; Fox, 1980). The relationship between these concepts and their realization in social structure became a central theme in ethnographic research, published in scores of studies of the cultures of ISEA. Unsurprisingly, the highest retention of these “Austronesian” traits occurred in the most remote islands, which were less affected by later historical developments. Here we will focus on the Austronesian expansion on three such islands: Timor, Sumba and Nias, which span the breadth of Indonesia from east to west. They also encompass the full range of variation in social structure noted by the ethnologists of the 1930s, including patrilineal, matrilineal and double unilineal systems. As we will see, the house model explains the observed genetic and linguistic patterns on these islands. Interestingly, it also implies that in the Wehali region of central Timor, the Austronesian expansion continues today.

We begin with a brief overview of the genetic, archaeological and linguistic data that have been used to characterize the Austronesian expansion. Next, we define the house model, and use it to analyze this data. Finally, we consider the effects of a later historical development, the spread of irrigated rice cultivation in Western Indonesia, and the ensuing dissolution of “sociétés à maison” in this region. This two-stage historical analysis of social behavior offers an explanation for the cultural, linguistic and genetic patterns observed today across ISEA.

#### *Austronesian genetics*

Until recently, the prehistory of ISEA was usually characterized as shaped by two population dispersals: the initial Paleolithic colonization of Sahul ~45 thousand years ago, and a much later Neolithic expansion of Austronesian-speaking farmers from Taiwan ~4 thousand years ago. Recently we genotyped an extensive battery of Y chromosome markers, including 85 SNPs/indels and 12 Y-STRs, in a sample of 1917 men from 32 communities on 13 Indonesian islands. These results point to a more complex migration history. Although comprising a series of discontinuous processes, in broad

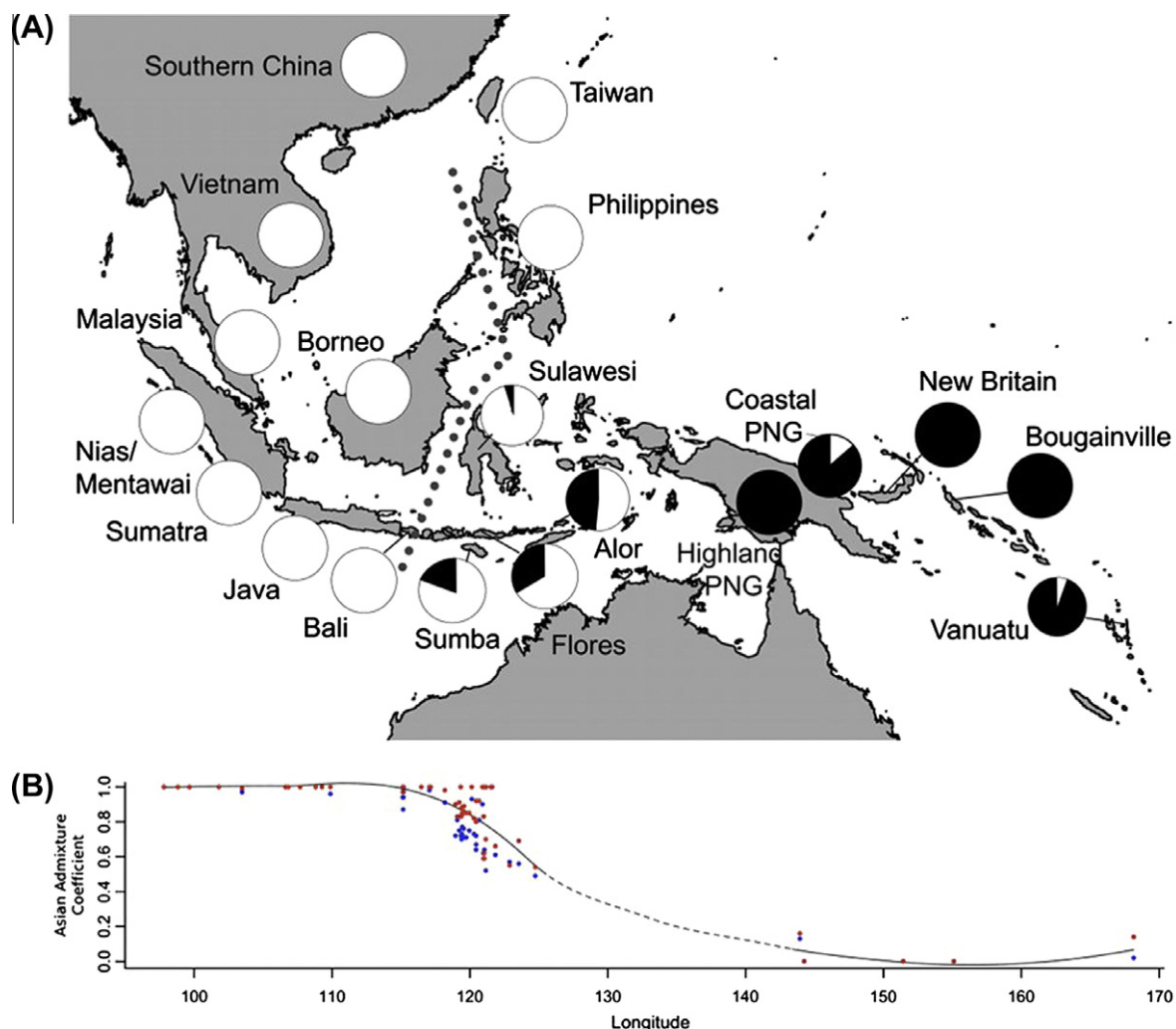
terms we can summarize this history as a four-phase colonization model.

In the first phase, the arrival of the first anatomically modern humans in the late Pleistocene introduces basal NRY C and K lineages to the entire region, including Australia and Melanesia. Later dispersals of more hunter-gatherers introduced several major subclades of haplogroup O to Indonesia (e.g. O-M119, O-M95, O-P203 and O-M122) over an extended time period (e.g., from approximately 35 to 8 kya). The third stage corresponds to the Austronesian expansion, which we associate with haplogroup O-P201 and probably O-M110 and some O-P203. Elsewhere we present a detailed argument to justify this association, based on both new samples and the discovery of novel genetic markers that clarify the dispersal of the major O subclades in ISEA (Karafet et al., 2010). The fourth phase occurred in the historic era and introduced multiple haplogroups from southern Asia, Arabia and China. A key inference from this analysis is that only a small fraction of O subclades are associated with the Austronesians; other major subclades date to earlier population movements.

We also found that the paternal gene pool is sharply subdivided between Western and Eastern Indonesia, with a boundary running between the islands of Bali and Flores (Cox et al., 2010) (Fig. 1). Analysis of molecular variance reveals one of the highest levels of between-group variance yet reported for human Y chromosome data ( $\phi_{ST} = 0.47$ ). That the Y chromosome genetic composition of these adjacent islands should be so dissimilar is surprising, because the break occurs in a narrow zone in a continuous chain of islands. Elsewhere, such a high level of population differentiation is usually associated with major geographic barriers, such as the Sahara desert or the Himalayas. The location of the division corresponds to a biogeographic frontier noted by Alfred Russell Wallace: not the famous “Wallace’s Line”, which traces the ancient sea barrier between Sahul and Sunda, but rather a second line located further to the east, between the islands of Sumbawa and Flores, which Wallace proposed based on his observation of phenotypic differences between human populations (Vetter, 2006).

Curiously, the sharp decline in Austronesian Y chromosomes to the east of Wallace’s phenotypic line is not as clearly mirrored in the maternal gene pool. Mitochondrial DNA is passed from mothers to their children; consequently, markers on this molecule can be used to trace matrilineal descent. The eastward spread of Austronesian mitochondrial DNA was not halted by the Wallace Line, nor was the spread of Austronesian languages: both reached the far Pacific. In the 1990s, several studies showed that mitochondrial DNA in Polynesia is predominantly of Asian origin, while Y chromosomes are mostly Melanesian (Melton et al., 1995; Sykes et al., 1995). Later studies confirmed this pattern: about 94% of Polynesian mtDNA is ultimately of East Asian origin, while about 66% of Polynesian Y chromosomes are Melanesian (Cox et al., 2007; Kayser et al., 2008). The immediate predecessor of the “Polynesian motif” (mtDNA haplogroup B4a1a1a) has been found in Taiwanese aboriginals, with an estimated age of 13200 YBP (95% confidence interval: 9400–17000).

As well as Polynesia, this haplogroup is also found at the extreme western end of the Austronesian-speaking world, on the island of Madagascar, where a recent study of 266 Malagasy individuals found the Polynesian motif at levels ranging from 13% to 50% in three ethnic groups. These Polynesian motif carriers shared two polymorphisms not present elsewhere, thus defining a new Malagasy motif subclade (Razafindrazaka et al., 2010). Although molecular dating was largely uninformative, the presence of a variant of the Polynesian motif in Madagascar clearly indicates an Island Southeast Asian connection. Linguistic (Dahl, 1951; Dahl, 1977) and archaeological evidence (Burney et al., 2004; Dewar, 1996; Dewar and Wright, 1993) suggests that this linkage is relatively young (less than 1.5 kya). Like the



**Fig. 1.** Local admixture rates across the Indo-Pacific region. (A) Pie charts showing mean regional admixture rates (Asian component in white; Melanesian component in black). Wallace's biogeographical line is shown as a dotted line. Regional admixture rates are shown for data reduction purposes; admixture rates for all 60 populations (with confidence intervals) are listed in the Supplementary Information for Cox et al. (2010). (B) Change in Asian admixture rates calculated from all SNPs combined (black line). Asian admixture estimated from autosomal and X chromosomal SNPs are indicated by blue and red points, respectively. Note the decline in Asian admixture beginning in Eastern Indonesia, as well as preferential retention of X chromosomal (red) versus autosomal (blue) diversity. Regions with no data indicated by a dashed line; from other evidence, the decline in the Asian component may be more pronounced than this. Reproduced unmodified from Cox et al. (2010).

Austronesian language family, prior to AD 1500 the Polynesian motif was the world's most dispersed mitochondrial lineage.<sup>1</sup>

Thus a comparison of paternal and maternal genetic markers reveals two significant patterns. First, both point to an East Asian origin for the Austronesian expansion, consistent with the linguistic evidence that the Austronesian language family arose among Taiwanese aboriginal peoples. Second, there is a very pronounced sex bias, which appears to imply that few Austronesian men ventured beyond Wallace's phenotypic line, while their female relatives continued their colonizing expeditions through the islands of Melanesia, Micronesia and Polynesia. In 2003, Hage and Marck proposed that this genetic pattern could be explained as an effect of matrilocality and matrilineal descent in Austronesian Proto-Oceanic society (Hage and Marck, 2003). According to this model, matrilocality Austronesian communities accepted husbands

from surrounding Papuan communities, and the male children of these marriages gradually displaced the Asian O clades. However, both mtDNA and NRY markers are strongly affected by genetic drift and founder effects, due to their small effective size (Cox, 2008). If the Austronesian expansion was carried out by small groups traveling in sailing canoes, as is assumed, then drift and founder effects could easily skew the demographic picture we see today. To address this issue, Cox et al developed a new sampling strategy designed to increase the statistical power of the analysis, and to clarify the sex bias revealed by the mtDNA and NRY. A small number of SNPs were identified as Ancestry Informative Markers (AIMs), which have increased power to distinguish between East Asian (southern Han Chinese) and Papuan populations (highland Papua New Guinea, which were largely isolated from Asian advances into the Pacific during the Holocene (evidence reviewed in Cox, 2008). To gain greater insight into the question of sex bias, the AIMs were chosen equally from autosomes and the X chromosome. The X chromosome spends two-thirds of its time in females and only one-third in males, whereas autosomes spend equal time in males and females, so in principle a comparison of diversity on autosomes and X chromosomes can help to reveal sex-biased migration and mixture processes (Hedrick, 2007). Thirty seven AIMs were genotyped in the largest panel of ISEA samples studied

<sup>1</sup> Soares et al. recently analyzed 157 complete mitochondrial genomes and suggest that the full Polynesian motif most likely originated in the vicinity of the Bismarck Archipelago. They hypothesize that the motif arose ~6 kya, but that Austronesian languages and culture arrived later, transmitted by small numbers of socially dominant Austronesian-speaking voyagers from ISEA in the Lapita formative period, ~3.5 kya (Soares et al., 2011). This conclusion is being debated, but we note that the model we propose here is consistent with either scenario.

to date: 1430 individuals from 60 populations, from mainland East Asia to Melanesia (Fig. 1). Consistent with the evidence for sex-biased admixture from the mtDNA and NRY studies, mean rates of Asian admixture are higher on the X chromosome than on the autosomes.

The genetic picture can be summed up as follows: all presumed “Austronesian” genetic markers (paternal, maternal and autosomal) are present among Taiwanese aborigines. This is consistent with the linguistic evidence that points unambiguously to Taiwan as the homeland of Austronesian languages. But it does not rule out the possibility that Austronesian genes might have traveled other routes into ISEA, or (as Soares et al propose) that there might have been several migrations from Taiwan along a “voyaging corridor”. Second, there is a very striking differentiation in the distribution of NRY haplogroups between Western and Eastern Indonesia. Third, all genetic systems (NRY, autosomes, X chromosome and mtDNA) exhibit a pronounced sex bias east of Wallace's phenotypic line.

#### *Austronesian archaeology*

The relationship between the Austronesian expansion and the onset of the Neolithic in ISEA has been much debated by archaeologists. Some points are not in doubt: as Donohue and Denham note, “the earliest Malayo-Polynesian speakers were agricultural; this conclusion is apparent from historical linguistic evidence and accords with archaeological evidence from Taiwan” (2010, p. 249). Rice cultivation was well established in Taiwan by at least 5000 years ago (Zhang and Hung, 2010), and many words associated with rice and associated processing and storage facilities have been reconstructed to Proto Austronesian (PAN) (Pawley, 2007). But questions remain as to whether other Neolithic cultures might have already gained a foothold in ISEA before the arrival of Austronesian-speaking voyagers from Taiwan. There are two possibilities. First, perhaps Taiwan was not the sole or even the most important route by which Asian Neolithic innovations reached the islands. Second, several food crops were originally domesticated in Melanesia (bananas (Perrier et al., 2009), sugar cane (Grivet et al., 2004), greater yam (Malapa et al., 2005) and sago (Kjaer et al., 2004)). How far into ISEA had these crops spread, at the time of the Austronesian voyages? Had a Neolithic culture begun to flourish on some of the islands before the Austronesians arrived? A relatively sparse archaeological record has left room for much speculation. Ethnobotanical and linguistic evidence suggest a significant, pre-Austronesian westward dispersal of bananas and their cultivators from New Guinea into Eastern Indonesia and possibly even further west (Denham and Donohue, 2009). Evidence from pig mtDNA points to multiple distinct migrations both eastward out of Southeast Asia, and within Wallacea itself (Lum et al., 2006; Larson et al., 2005).

In Eastern Indonesia and Melanesia, and perhaps elsewhere, incoming Asian groups encountered other food-producing societies, leading to what has sometimes been described as a “Neolithic standoff”. The rapid decline in Asian alleles in Eastern Indonesia may indicate where indigenous groups, present since the Pleistocene, were living in sufficiently large numbers to resist incursive populations spreading into the region during the mid-Holocene (Cox et al., 2010). Perhaps this demographic resistance was in part driven by indigenous agricultural traditions related to those found in New Guinea (Denham, 2005). Although only the east New Guinea highlands have yielded clear evidence for an autochthonous development of agriculture (Denham et al., 2003), indigenous agriculture may have been practiced more widely in this region than we currently have archaeological evidence for, an argument recently made from genetic evidence (Mona et al., 2007). Another possible explanation is that rice increasingly lacked power to drive the expansion of human populations as they moved into the

changing climate of the equatorial belt (Cox, 2008). Alternately, perhaps the standoff reflects some transformation in the Austronesian social structure (see Jordan et al., 2009). To date, this pattern has yet to be satisfactorily explained.

#### *Austronesian languages*

Overwhelming linguistic evidence indicates that the Austronesian language family arose in Taiwan (Donohue and Denham, 2010). Nine of the ten primary subgroups of Austronesian are attested only on Taiwan. The tenth subgroup, Malayo-Polynesian, comprises all of the Austronesian languages spoken outside Taiwan, which number approximately one thousand. This subgroup is not a catchall, but has been defined on the basis of numerous shared innovations, both regular and irregular (Ross, 2009).

The phylogeny of Malayo-Polynesian languages offers several clues about the history of this language family. The phylogenetic structure is flat and rake-like, indicative of a recent rapid multidirectional expansion (Pawley, 1999). If language diversification (cladogenesis) is linked to population expansions, then expansion pulses should leave a series of short branches in the phylogenies because there will be little time for linguistic changes to accumulate before speech communities fragment. The same is true for genetic data. In contrast, when the geographic spread of cultures is constrained by physical or social boundaries, the rate of linguistic diversification should decrease, leading to longer branches (anagenesis). The Malayo-Polynesian languages conform to the first pattern. Gray et al. (1999) used lexical data and Bayesian phylogenetic methods to construct a phylogeny of 400 Malayo-Polynesian languages. This method predicted an origin of proto-Austronesian approximately 5230 years ago, and 3800–4500 years for the Malayo-Polynesian clade. The phylogeny of Malayo-Polynesian suggests very rapid geographic expansion, with four major expansion pulses and two pauses in Pacific settlement (Gray et al., 2009).

With regard to the first pause, the emergence of Malayo-Polynesian, Gray et al note that the invention of the outrigger canoe and its sail may have enabled the Austronesians to move across the 350-km Bashi channel between Taiwan and the Philippines before spreading rapidly over the 7000 km from the Philippines to Polynesia. This result is supported by linguistic reconstructions showing that the terminology associated with the outrigger canoe complex can only be traced back to Proto-Malayo-Polynesian and not Proto-Austronesian (Pawley and Pawley, 1994).

Once this expansion was under way, with few exceptions the Austronesians would have encountered islands that were already populated. An obvious question is why the Austronesian languages replaced nearly all of the pre-existing languages in ISEA. As Peter Bellwood asks, “Why are there not far more non-Austronesian [linguistic] enclaves surviving in ISEA, as there are in western Island Melanesia. . . ?” (Bellwood, 2010).

#### **Austronesian house societies**

In 1935, F.A.E. van Wouden surveyed the ethnographies of Eastern Indonesia and concluded that over the whole region, “in spite of the extreme unilineal character of the descent systems, both patrilineal and matrilineal descent are yet taken into account” (vanWouden, 1968). Van Wouden's analysis helped guide the work of later ethnologists, and in 1996 James J. Fox revisited this topic in a study of the transformation of progenitor and progenetrix lines of origin, noting that “although Eastern Indonesia may contribute a great deal to a model of a proto-Austronesian social world, nevertheless the region represents only one area of a vast Austronesian world.” Fox's synthesis linked several analytical threads: the structuralist argument developed by van Wouden and later elaborated by Lévi-Strauss, the subsequent reconstruc-

tion of shared elements of Austronesian culture using comparative historical linguistics, and a vastly expanded ethnographic literature on Austronesian societies. Drawing on this synthesis, here we offer a structural model (sensu Lévi-Strauss) to account for the genetic, linguistic and archaeological patterns described above. For our purposes a structural model can be simply defined as the idea that “cosmos and society are organized in the same way”, by means of a core set of binary symbolic oppositions (male/female, older/younger, treetrunk/tip, cosmos/society). The key difference between this approach and the comparative method of historical linguistics is a shift in analytical focus from the reconstruction of shared cognates, to the identification of a core collection of structural principles (binary symbolic oppositions) that form a “scheme of social categories... [that] serves as the model for an all-embracing classification” (Needham et al., 1968).

In Lévi-Strauss' original concept, *sociétés à maison* are a form of social structure intermediate between the elementary and complex structures that he had previously distinguished (Lévi-Strauss, 1949). Houses were defined by their possession of a ‘domain’ consisting of both material and immaterial wealth or honors; the extensive use of fictive kinship in alliance and adoption; and the transmission of the ‘domain’ – titles, prerogatives, and wealth – via women as well as men. Lévi-Strauss' proposal that the Austronesians introduced a particular form of “house society” to ISEA was first addressed in a collection of essays in 1987; subsequently the idea was debated in numerous articles and edited volumes. In 1993, James Fox and collaborators offered an historical perspective on Austronesian house societies, based on a comparison of contemporary ethnographic studies across ISEA, coupled with historical linguistics. As Fox noted, the reconstructed lexicon of Proto-Austronesian contains the word *\*Rumaq* which Blust glosses as a descent group or house (Blust, 1980). A second relevant term is Proto-Malayo-Polynesian *\*banuaq*/*\*panua*, a more polysemous word whose glosses include inhabited territory, homeland, community and land-owing kin group (Blust, 1987). Blust also identified a large number of Proto-Austronesian terms for the physical architecture of the Malayo-Polynesian house. Along with these physical attributes, ethnographic studies refer to shared social and cosmological symbolism. Commonly, Austronesian houses define social groups and connect them to the past, using a vocabulary that emphasizes origins and founder rank. Typically, as Fox notes, the house is regarded as the ancestral embodiment of the group it represents, engaged in marital and affinal alliances with other houses.

In early twentieth century Eastern Indonesia, as van Wouden observed, the patrilineal principle dominated. But as he further noted, the underlying dualistic principle implies that female origins and descent remain significant. Houses need to form and retain alliances and to commemorate their origins. For those purposes “it is absolutely immaterial whether the principle of genealogical grouping is matrilineal or patrilineal.” Instead, “one of the most striking facts is that in almost every one of the larger regions into which the area may be divided there is a people who are sharply distinguished from their patrilineal neighbors by their matrilineal descent groups.” Van Wouden rejects the hypothesis of multiple migrations by noting two facts. First, “the various cultures in question exhibit too great a homogeneity to make it necessary to resort to migration-hypotheses.” Second, even in the most extreme examples of unilineal descent, “both patrilineal and matrilineal descent are yet taken into account.”

For example, at the extreme western edge of ISEA, communities on the island of Nias are organized as *banua* (villages) consisting of exogamous patrilineages (Schröder, 1917; Beatty, 1992). Four thousand kilometers to the east, near the eastern border of the archipelago, villages on the islands of Tanimbar consist of rows of named and unnamed houses (*uma*), linked

by matrilineal alliances and affinal relations (McKinnon, 1995). In both of these societies, and in many others, a concept of cosmological dualism is expressed in the complementarity of father (*\*ama*) and mother (*\*ina*). Houses are ranked according to their distance from an origin, and the contrast between older/younger permeates the kinship system, social precedence and cosmological myths of origin (Fox, 1996). These attributes of Austronesian societies à maison sharply contrast with the social organization of neighboring Papuan societies, which (as Bellwood observes) “seem to lack totally any concept of genealogically-based ranking, whether of persons or descent groups...” (Bellwood, 1996).

### House societies and the Austronesian expansion

Here we offer a model for the initial Austronesian expansion into ISEA, which accounts for the genetic and linguistic patterns described above. In our model, the Austronesian expansion begins with the spread of matrilineal Neolithic house societies into ISEA, which is already populated by hunter-gatherers. In Eastern Indonesia, these hunter-gatherers are Papuan. As Austronesian communities advance, their women sometimes accept husbands from neighboring Papuan communities.<sup>2</sup> As a consequence of matrilineal residence, the children of such marriages inherit their father's Papuan Y chromosome, their mother's Asian mitochondrial DNA and speak her Austronesian language. The simulation reflects the following assumptions:

- The initial population of both Austronesian colonists and indigenous hunter-gatherers is small.
- A Neolithic population expansion occurs in each Austronesian village.
- Small numbers of neighboring non-Austronesian males marry into the Austronesian matrilineal houses, at the rate alpha, for lengths of time that can vary at each settlement but are generally low.

The results of this simulation are shown in Fig. 2, in comparison with real data. Even if the migration rate ( $\alpha$ ) is quite low, there is ample time for a pronounced sex bias to develop. These results may be compared with genetic data from three ISEA populations we have studied, and with data from Polynesia. The observed genetic patterns will emerge after 50 generations if 2% of marriages are to non-Austronesians. This model accurately predicts the observed sex bias for all four genetic systems, and also accounts for the replacement of indigenous languages by Austronesian languages.

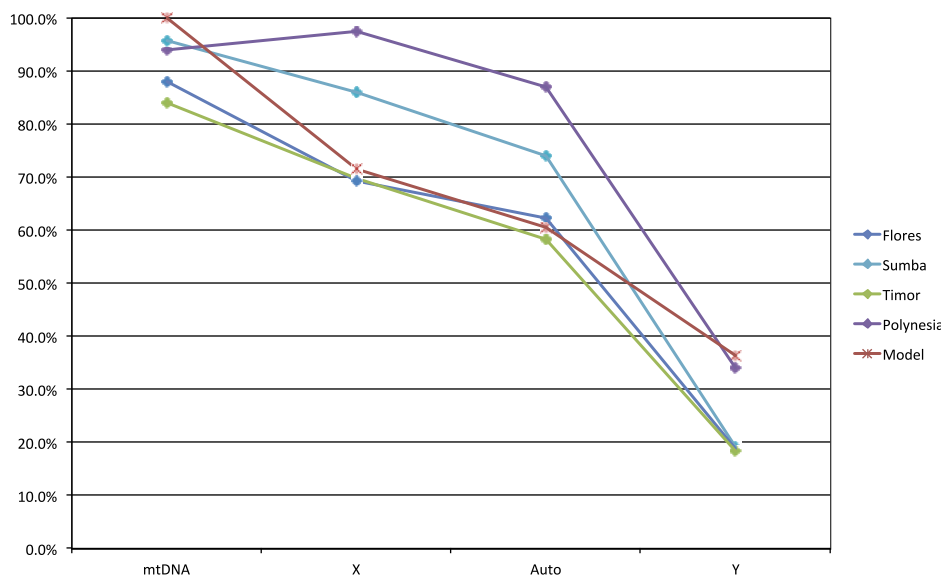
Equations for the model are as follows, where  $a$  = autosomes,  $x$  = X chromosome and  $y$  = non-recombining Y chromosome (NRY):

$$y(t) = (1 - \alpha)^t \quad (1)$$

$$a(t) = (1 - \alpha/2)^t \quad (2)$$

$$x(t) = (1 - \alpha/3)^t \quad (3)$$

<sup>2</sup> The comparison is typically presented as Austronesians versus non-Austronesians. Following common practice, for simplicity we refer to the latter as Papuan. In Eastern Indonesia, non-Austronesians were likely the ancestors of modern Papuan peoples, who have been living continuously in this region for the past 50 kya (OConnell and Allen, 2004). In western Indonesia, the character of ancestral non-Austronesians is less clear. Borneo (40,000 BP; Kennedy, 1977; Bellwood, 1997), the Philippines (22–20,000 BP; Bellwood, 1997) and Java (4000 BP; Bellwood, 1978) likely hosted Australo-Melanesian populations from the late Pleistocene to the early Holocene, thus supporting Howell's (1976) contention of an “Old Melanesia” (Howells, 1976), a swathe of Australo-Melanesian populations that once stretched across much of modern Island Southeast Asia. However, recent genetic research indicates that peoples with Asian ancestry also have a long history in western Indonesia, stretching far back into the Pleistocene (Hill et al., 2007; Karafet et al., 2010). The nature of ancestral non-Austronesian populations in western Indonesia remains an outstanding question.



**Fig. 2.** Fraction of Asian DNA in four genetic systems compared with model results for  $\alpha = 0.02$  and 50 generations. Sample sizes: Flores = 453, Sumba = 639, Timor = 529. Polynesian data from (Kayser et al., 2008; Cox et al., 2007; Kayser et al., 2008; Wollstein et al., 2010.).

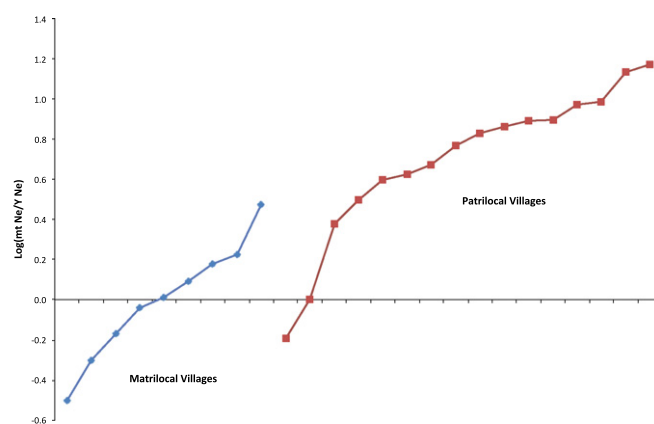
The model describes a scenario that no longer exists in most of ISEA. By now, Austronesian languages have replaced earlier indigenous languages, and most contemporary societies are patrilineal (though they retain a dualistic emphasis on the complementarity of male and female principles). But the model scenario is closely approximated in contemporary Eastern Indonesia, in the Wehali region of central Timor. Wehali is an ancient matrilineal and matrilocal society, organized as a cluster of named houses that engage in marital alliances with each other. The women of Wehali also sometimes accept husbands from neighboring Papuan villages. The Papuan villages speak Papuan (non-Austronesian) languages, and Austronesian NRY haplotypes are less common in these communities. Thus the contemporary ethnographic situation in Wehali mirrors the conditions postulated in the model for the Austronesian

expansion. To discover whether the genetic composition of Wehali houses is consistent with our model, we obtained genetic and linguistic samples from 476 men in ten villages in the Wehali region. As Fig. 2 shows, the distribution of Papuan and Austronesian haplotypes among these men agrees with the model.

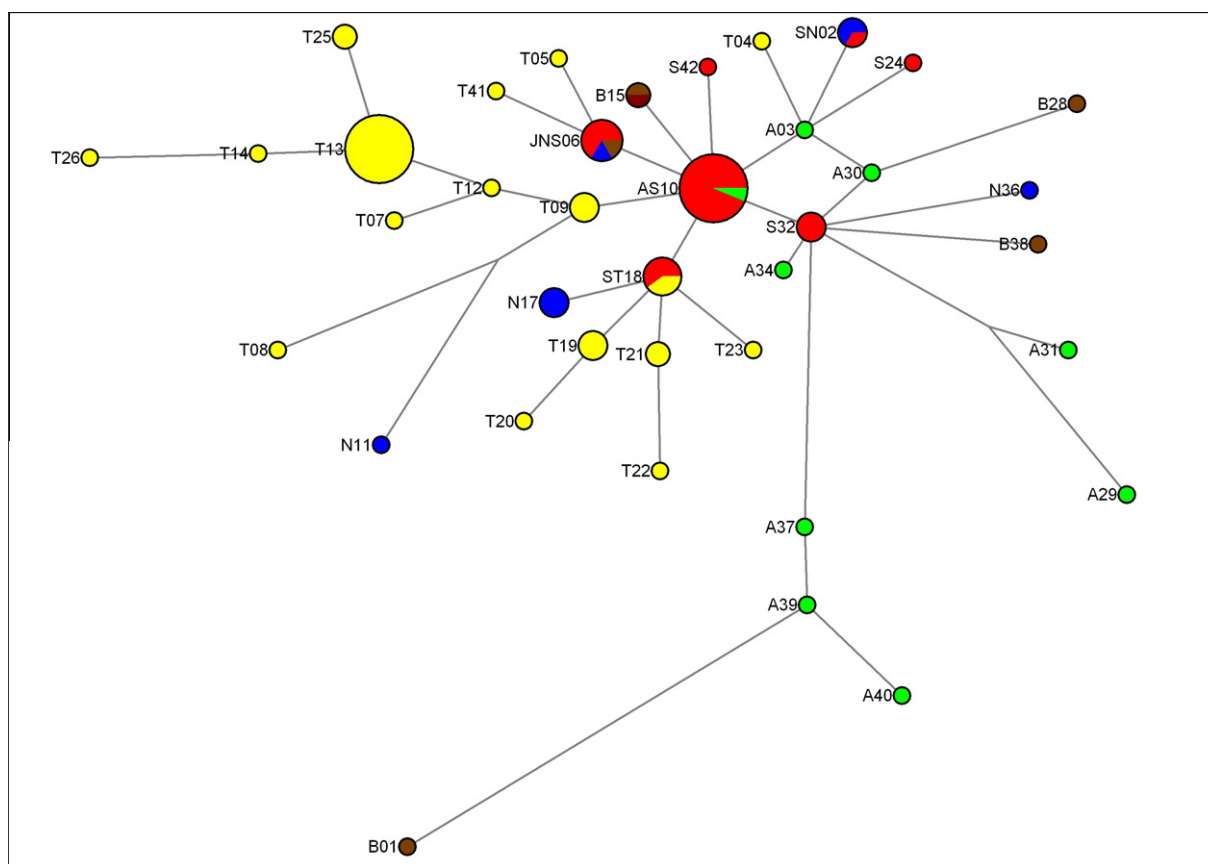
Further insights into the historical demography of these villages can be obtained by calculating the effective population size of both men and women in the villages. If the effective population size of females is less than that of males, we can conclude that there has been more in-marriage of males, consistent with a long-term matrilocal sex bias. Conversely, a patrilocal and patrilineal community should exhibit a smaller effective population size for males. Table 1 presents the results of such a comparison between the matrilocal villages of Wehali, and 13 patrilocal villages on the neighboring island of Sumba. The results support the prediction: most Wehali villages show a smaller effective population size (Ne) for females than for males; the reverse is true for all 13 patrilocal Sumbanese villages (Fig. 3). This pattern persists in the con-

**Table 1**  
Difference between effective population size calculated from haplotype data for mitochondrial DNA (mt Ne) and Y chromosome (Y Ne) for villages on Sumba and for the Wehali region of central Timor. Data and methods for estimation of effective population sizes from Lansing et al. (2008a).

| Island | Village       | mt Ne | Y Ne | mt Ne - Y Ne |
|--------|---------------|-------|------|--------------|
| Sumba  | Anakalang     | 1468  | 190  | 1279         |
|        | Bilur Pangadu | 3613  | 243  | 3370         |
|        | Bukambero     | 1998  | 214  | 1784         |
|        | Kodi          | 1384  | 175  | 1208         |
|        | Loli          | 885   | 371  | 514          |
|        | Lomboya       | 1601  | 274  | 1327         |
|        | Mahu          | 2705  | 279  | 2427         |
|        | Mamboro       | 1087  | 277  | 810          |
|        | Mbatakpidu    | 1327  | 183  | 1144         |
|        | Praibakul     | 1389  | 329  | 1060         |
|        | Rindi         | 11290 | 831  | 10459        |
|        | Waimangura    | 917   | 136  | 781          |
|        | Wanokaka      | 1566  | 334  | 1232         |
| Wunga  | 726           | 232   | 494  |              |
| Timor  | Besikama      | 1793  | 1192 | 601          |
|        | Fatuketi      | 885   | 884  | 2            |
|        | Kakaniuk      | 449   | 494  | -46          |
|        | Kamanasa      | 3687  | 2985 | 702          |
|        | Kateri        | 936   | 560  | 376          |
|        | Kletek        | 1226  | 1803 | -578         |
|        | Laran         | 1946  | 3890 | -1944        |
|        | Raimanawe     | 1998  | 677  | 1322         |
|        | Tialai        | 635   | 621  | 14           |
|        | Umaklaran     | 516   | 802  | -286         |
|        | Umanen Lawalu | 765   | 2421 | -1656        |



**Fig. 3.** Log distribution of the data shown in Table 1. This approximately continuous distribution is consistent with Lévi-Strauss' House model, which predicts that over time houses may modify their preferences for marital alliances based on genitor or genitrix. An alternative scenario of stable postmarital residence would produce distinct clumps rather than continuous variation. The largest bias for patrilocality belongs to Rindi in east Sumba, where patrilineal clans strongly favor asymmetric prescriptive alliance. The largest bias for matrilocality is found in the hamlets of Inner Wehali in Timor, site of the historic matrilocal ritual center of Wehali.



**Fig. 4.** Relationships within NRY haplogroup O-M110. Taiwanese aboriginals, green; Nias, blue; Java/Bali, brown; Sumba, red; and Timor, yellow. Note identical haplotypes shared by men from Taiwan (green), Nias (blue) and Sumba (red).

temporary population: survey data indicates that small numbers of men from neighboring Papuan communities have recently married into Wehali houses. The children of these marriages speak their mother's Austronesian language. Thus in Wehali, the Austronesian expansion described by the model is an ongoing process that has continued to the present day.

On Sumba, in recent times there have been no matrilineal/matrilocal communities. However, our model predicts that the original Austronesian colonists in Sumba belonged to a matrilineal/matrilocal house society, and that this form of social organization persisted for many generations. Consistent with this prediction, the concept of matrilineal descent is recognized by all Sumbanese societies, and named matrilineal descent groups still exist in some, as first noted by van Wouden and later confirmed by Rodney Needham's survey of Sumbanese kinship systems (Needham, 1987).

#### *The Austronesian expansion into Western Indonesia*

The model described above provides a concise explanation for the genetic, linguistic and ethnographic patterns observed in Eastern Indonesia. But what about the islands located to the west of Wallace's phenotypic line, where today only Austronesian languages are spoken? Here the genetic picture is more complex. As noted above, in this region Asian DNA is dominant, but nearly all NRY clades, including Asian lineages, appear to predate the Austronesian expansion. Thus the genetic evidence suggests that when Austronesian colonists arrived in western ISEA, they settled in a region already populated by indigenous hunter-gatherers, mostly of Asiatic origin. The model dynamics are otherwise identical to those in Eastern Indonesia, with existing Asian hunter-gatherers taking the place of Papuans (as NANS, or non-Austronesians). Evidence

for this scenario is provided by genetic, linguistic and ethnological materials from the island of Nias.

Nias is situated at the far western edge of the Indonesian archipelago. The language of Nias is an Austronesian outlier; it descends from one of the oldest branches of Malayo-Polynesian and is not closely related to other languages in the region. Nothofer has proposed that it may be a remnant from an originally larger Austronesian linguistic community, along with the language of Mentawai and some Batak languages of Sumatra (Nothofer, 1994). According to scholars of the colonial era, the island was reputed to be dangerous to mariners, and was seldom visited (Donleben, 1848; Schröder, 1917). The social organization of Nias closely resembles the patrilineal and patrilocal houses of Sumba, 3000 km to the east (Beatty, 1992; Marschall, 1977). Moreover, the architecture of Nias houses, and the custom of erecting dolmen in front of them, is strikingly similar to the houses and megaliths of Sumba (Viaro, 1981; Heine-Geldern, 1972).

We analyzed 60 samples from two villages in southern Nias and found that all of them belong to Austronesian Y chromosome haplogroups O-M110 (8 men) and O-P203 (52 men) (Karafet et al., 2010). Fig. 4 shows the distribution of haplotypes within O-M110 for Taiwanese aboriginals, as well as men from Nias, Java, Bali, Sumba and Timor. Note the clear evidence of shared haplotypes between Taiwan and Sumba (labeled in green and red) and Nias and Sumba (blue<sup>3</sup> and red). These genetic identities are observed across 14 microsatellite loci, and are therefore highly unlikely to reflect recurrent mutation. Instead, shared haplotypes between

<sup>3</sup> For interpretation of color in Figs. 1–5, the reader is referred to the web version of this article.

**Table 2**

Estimated time to most recent common ancestor (TMRCA) and standard deviations for the men who share haplogroup O-M110 (shown in Fig. 4), based on pedigree rate  $\mu = 0.0021$ .

|                 | TMRCA | 95% confidence |
|-----------------|-------|----------------|
| Taiwan          | 4700  | 976–8424       |
| Sumba and Timor | 2400  | 440–4360       |
| Nias            | 780   | 388–1172       |
| Bali            | 5129  | 2180–8060      |

Taiwan, Nias and Sumba indicate common ancestry. Furthermore, although molecular dating has considerable uncertainty, this common ancestry occurs within the time frame predicted for the Austronesian expansion into Indonesia (Table 2).

Nias, like most of the societies of Eastern Indonesia, is now a patrilineal and patrilocal society. However, consistent with van Wouden's prediction, to the east, on the neighboring island of Sumatra there exist two large and closely related house societies, of which one (the Minangkabau) is matrilineal while the other (the Batak) is patrilineal (Singarimbun, 1975). In general, with few exceptions the contemporary cultures of western ISEA are Austronesian house societies, in which named descent groups engage in marital alliances with other houses: most but not all are patrilineal. There is, however, an important exception to this generalization.

#### *The dissolution of "sociétés à maison" with irrigated rice culture*

The only major region of Indonesia where house societies are not found today is in the rice-growing areas of Java and Bali. Interestingly, on both islands there are highland regions where irrigated rice is not grown, which retain more social and cultural attributes of traditional Austronesian house societies than the lowland rice-growing villages, as several ethnographers have noted (Hefner, 1990; Reuter, 2003). Earlier studies have proposed that the productivity of rice gardening played an important role in propelling the Austronesians into ISEA. The current eastward limit of rice is to the east of Wallace's line, which also marks the sharp subdivision in the human gene pool between Western and Eastern Indonesia (Fig. 1). It has been suggested that natural climatic variation could underpin the change from rice agriculture to tuber and palm-based economies, and the decreasing ability of rice horticulture to propel the Austronesian expansion into the territory of Papuan peoples (Cox et al., 2010).

But rice is successfully grown today in garden plots in Eastern Indonesia, and appears to be a traditional crop. We suggest that the key development occurred on the other side of Wallace's line, with the development of irrigated agriculture in Java and Bali around the sixth century C.E. (Christie, 2007). The advent of wet-rice cultivation led to the dissolution of house societies on these islands as a consequence of three demographic processes: a shift to endogamous marriage, population growth, and reduced mobility. These changes were concentrated in the regions where irrigated rice could be grown. House societies vanished from the lowlands, where endogamous farming communities grew up along the rivers and irrigation canals. In Bali, these communities adapted to population growth by creating new settlements downstream (Lansing et al., 2008b; Lansing et al., 2009). The effect of these changes was to bring large-scale (inter-island) population movement to a standstill, and to magnify existing genetic differences on either side of Wallace's phenotypic line.

#### *A shift in marriage patterns*

Evidence for a shift in marriage patterns is apparent from a comparison of demographic skew in effective population sizes of Balinese villages, as compared to skew in Eastern Indonesian house

societies described above (Fig. 5). Overall the mean skew in Balinese rice-growing villages is weakly patrilocal. This may seem puzzling, since patrilocal residence is the norm in these communities. We suggest that the explanation lies in the combination of preferential endogamy and restricted mobility: both men and women tend to marry within the village where they were born. Supporting evidence for this explanation comes from two sources: surveys of contemporary marriage practices, and analysis of haplotype variation within villages.

With regard to the first point, in a survey of 252 men in 13 rice-growing villages, 84% married within their natal village. This preference fell to 34% in two highland villages, where rice is not grown.<sup>4</sup> With regard to the second point, genetic analysis of 587 Balinese men indicated patrilocal residence with very little movement on the landscape except for occasional micro-movements to nearby daughter settlements (see Lansing et al. (2008b) for a detailed analysis).

The argument, in sum, is that over the past 1500 years, the spread of wet-rice cultivation produced major changes to the demography of Bali, where the steep genetic cline shown in Fig. 1 begins. These changes were concentrated in the regions where irrigated rice could be grown (the highlands retained more of the ancient cultural features of 'house societies'). House societies vanished from the lowlands, where small, highly endogamous farming communities grew up along the rivers and irrigation canals. These communities adapted to population growth by creating new settlements downstream. These developments brought population movements across the Wallace line to a standstill, and accelerated genetic drift in the small, stationary rice-growing villages of Bali.

## Summary and conclusions

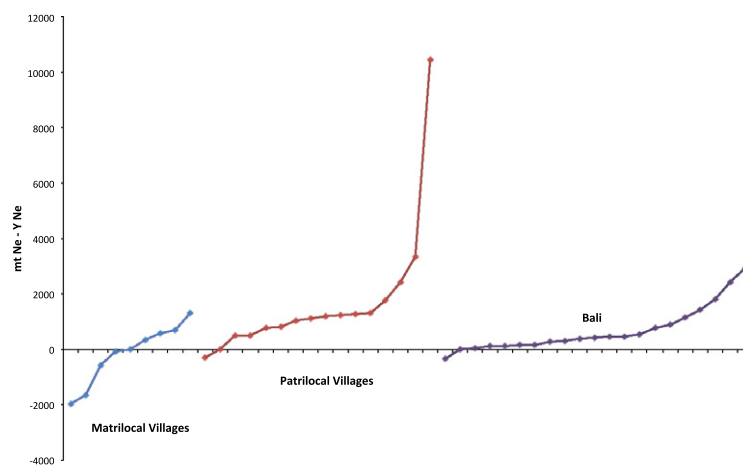
Recent studies of the genetic and linguistic traces left behind by the colonizing voyages of the Austronesians have revealed several remarkable features. Here we explain these features by modeling the demographic and linguistic consequences of a sociocultural innovation: the appearance and disappearance of house societies among Austronesian populations.

#### *The spread of Austronesian languages*

It is clear from the genetic and archaeological evidence that ISEA was already populated when the Austronesians began their colonizing voyages. The absence of other languages in ISEA prompted Peter Bellwood's question: "Why are there not far more non-Austronesian [linguistic] enclaves surviving in ISEA, as there are in western Island Melanesia...?" (Bellwood, 2010) Our model provides an explanation based on three assumptions: the initial population of both indigenous peoples and Austronesian colonists was small; the Austronesian settlements underwent a Neolithic population expansion; and Austronesian women occasionally married men from surrounding non-Austronesian villages. The children of these marriages would have spoken their mother's Austronesian language, while the total population of Austronesian speakers grew.

<sup>4</sup> The very high rate of endogamous marriage was also noticed by Leopold Howe in his study of the Balinese village of Pujung in the 1970s. He writes: "Village endogamy is very high indeed. Out of a total of 399 marriages for which I have reliable information, 82% were village endogamous. Of the 72 marriages contracted outside the village 34 were into the nearby villages of Ked and Bonjaka, and both of these were thought to be offshoots of Pujung (Bonjaka indeed is, since it was settled within living memory by people from Pujung). There is therefore good reason to include these as endogamous marriages, in which case the total goes up to 90.5%". Leopold E.A. Howe, Pujung: An Investigation into the Foundations of Balinese Culture. Doctoral thesis, University of Edinburgh, 1980.





**Fig. 5.** Difference between effective population size calculated from haplotype data for mitochondrial DNA (mt Ne) and Y chromosome (Y Ne) for villages on Bali and Eastern Indonesia.

Given sufficient time, this process will eventually lead to the replacement of non-Austronesian languages. The smaller the indigenous population at the time of Austronesian colonization, the faster this will occur. Consistent with this prediction, in an earlier study we found that on the island of Sumba, the rates of retention of Papuan words and genes vary systematically, with higher retention in areas with more dense Papuan populations at the time of the Austronesian colonization (Lansing, 2007). This analysis can be extended to explain the presence of Papuan-speaking enclaves on the island of Timor, to the east of Sumba. Timor is the largest island in Eastern Indonesia, so the ratio of Austronesian colonists to the Papuan-speaking population would have been quite small during the initial Austronesian expansion. Thus in central Timor, the Austronesian expansion continues today, as Papuan-speaking men occasionally marry into the matrilocal Austronesian villages of Wehali. Over time, this continuing process will tilt the balance in favor of Austronesian languages in the region, albeit at a much slower rate than in the initial phase of the Austronesian expansion.

#### *Sex-biased genetic skew*

Pronounced sex-biased variation in all chromosomes was initially observed for Oceania, and subsequently found in ISEA. In 2003, Hage and Marck proposed that it could be the result of matrilocal residence, and in 2009 Jordan et al used linguistic reconstruction to argue that matrilocal residence is ancestral in Austronesian societies (Jordan et al., 2009). In 2010, Gray et al argued that “the high levels of male-biased admixture detected in Polynesian genetic studies must either have occurred over this very short time span (approximately four generations), with Papuan males actively incorporated into the Austronesian expansion, or there was extended post-settlement contact between Near Oceania and Polynesia.”

Our model provides an alternative explanation, which does not require additional assumptions about either unusually high rates of admixture, or post-settlement contact between Near Oceania and Polynesia. Instead, the model predicts that the same processes of admixture occurred along the whole colonization route. Because the demographic effects are cumulative, they appear most strongly in Polynesians who live at the end of the chain of colonization.

#### *The sharp genetic cline along Wallace's phenotypic line*

It is clear that the sharp genetic cline along Wallace's phenotypic line is the result of social processes rather than geography,

because it occurs along a continuous chain of islands that have been populated for tens of thousands of years. Our model explains this break by the disappearance of house societies in lowland regions in the western islands, where irrigated rice cultivation triggered a population explosion and also brought population movement to a standstill.

#### *Conclusion: butterfly effects*

Claude Lévi-Strauss did not undertake ethnographic research in ISEA, but his reflections on house societies had a profound influence on comparative anthropological studies in the region. Subsequent ethnographic studies showed that widely dispersed Austronesian societies share not only closely related languages, but a gendered cosmology and an emphasis on origins that is not found in neighboring Melanesian societies. Today house societies are found in many parts of ISEA, and phylogenetic analysis suggests that they are not a recent innovation, but have existed since the onset of the Austronesian expansion.

The model we have proposed here traces the genetic, linguistic, demographic and cultural consequences of the prevalence of this form of social organization. In Lévi-Strauss' original conception, house societies sometimes emerge as a transitional phase in the evolution of complex societies, when competition for social rank weakens social ties based on shared unilineal descent. The house provides a way to “solidify” the “unstable relation of alliance” (Lévi-Strauss, 1987), by sanctioning ties based on either genitor or genetrix (or as the Austronesians say, *\*ama* and *\*ina*). At any given moment, a house may emphasize one relationship (for example, social ties based on shared relationship to a genitor), but there is always the possibility to strengthen alliances based on the complementary principle. Dualistic cosmologies recognize and acknowledge this potential. Thus for Lévi-Strauss, house societies are an emergent and dynamical form of social organization, which actively reshape their social environment, while varying in their immediate emphasis on patrilineal or matrilineal social relations.

But both Lévi-Strauss and van Wouden assumed that there was no inherent trajectory to the evolution of “sociétés à maison.” The genetic data reviewed here suggests otherwise for the Austronesian case. As the model shows, over a time scale of tens of generations a seemingly trivial shift in marriage preferences can produce a seismic change in language, culture and demography. The data we have reviewed here provide strong evidence that at a first approximation, this transformative potential was realized in the wake of the Austronesian colonization of ISEA.

The idea that such a subtle process could have such profound consequences seems counter-intuitive, and leads us to offer a final remark. Edward Lorenz' "butterfly effect" quickly became the canonical example of chaotic behavior in dynamical systems due to sensitive dependence on initial conditions (Hilborn, 2003). The mathematical basis of the butterfly effect is the Lorenz equations, three first order differential equations in which the iteration of initially tiny variation in initial parameterization quickly produces chaotic dynamics. Whereas in our model, the iteration of small  $\alpha$  over many generations creates new regimes of order.

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