

# Untangling Oceanic settlement: the edge of the knowable

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**Human expansion into the far reaches of the Pacific has occurred within the past 3000–4000 years. This is so recent that it is arguably the best opportunity to test models of the origin and dispersal of human groups and their domesticated plants and animals, cultural and linguistic evolution, human impacts on a pristine environment, and the lower limits for a long-term sustainable population. Multidisciplinary research is essential because these models must account for archaeological, ecological, cultural, historical, social, linguistic and (both mitochondrial and nuclear) genetic data. This synthesis has not yet been achieved for any settlement in the world, but there has been considerable progress recently on integrating these disciplines with respect to the settlement of Polynesia.**

The puzzle of Oceanic settlement, given the vast distances from Southeast Asia to eastern Polynesia (Figure 1), has long fascinated scholars. Synthesizing the main records of the past – genetics (humans and their domesticated plants and animals), linguistics, history, archaeology and paleoecology – is a multidisciplinary enterprise that must consider the complementary strengths and weaknesses of these data types. Archaeology provides the most precise dates, whereas linguistics and genetics both infer ancestral patterns from modern diversity (although ancient DNA fills some gaps). Recent advances in interpreting records of the past, especially in Polynesia, make a review of the current state of knowledge timely because, now more than ever, communication between disciplines is vital to ensure continued improvement in our understanding of human settlement into the Pacific.

## A brief background to the region

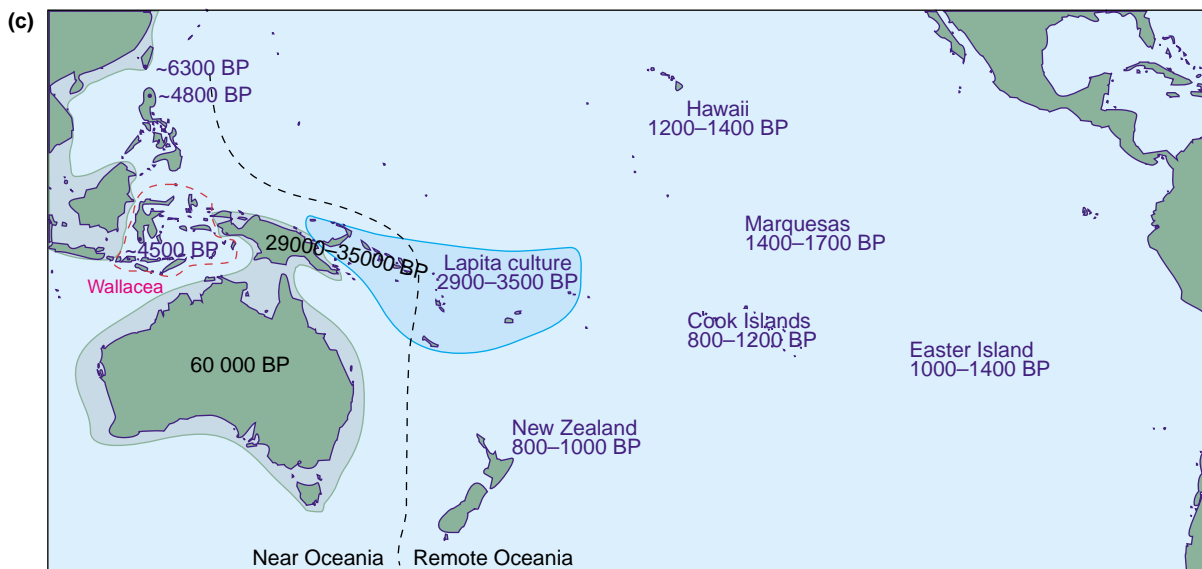
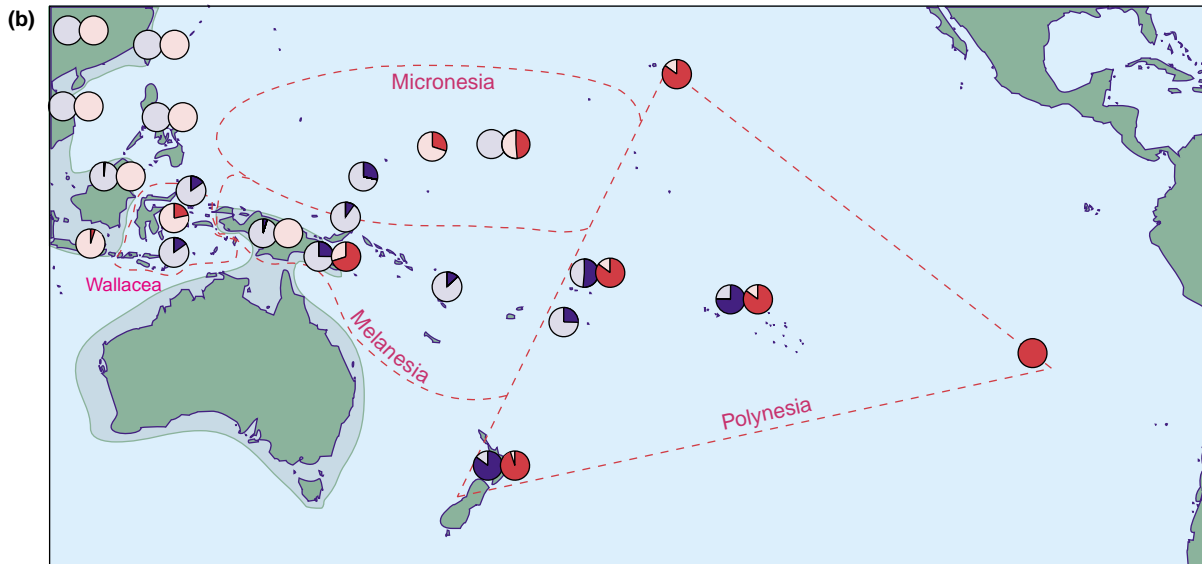
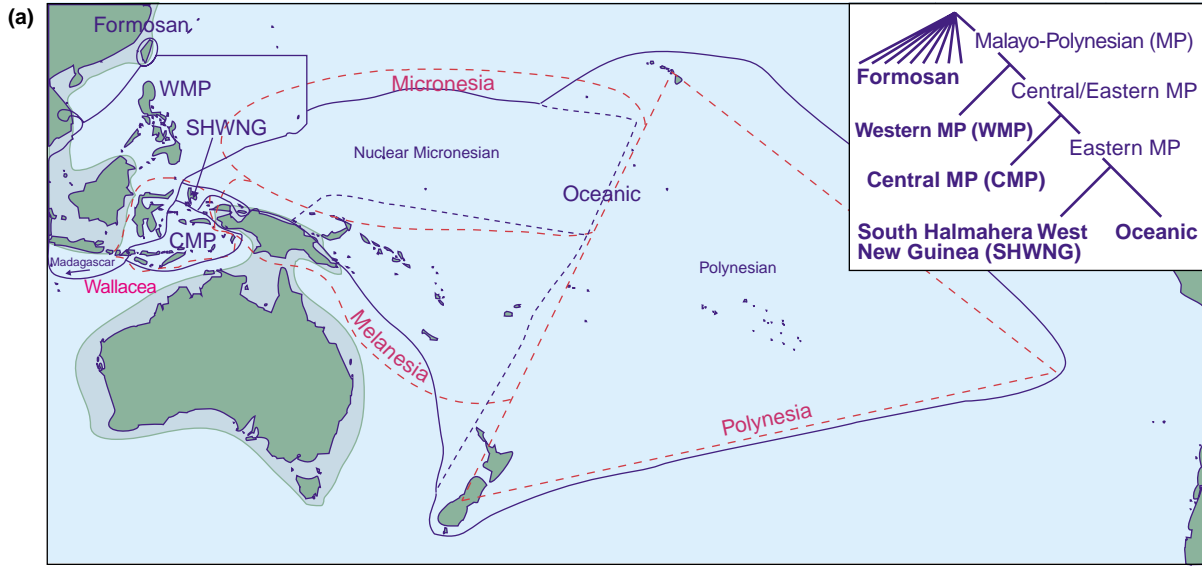
The archaeological record gives an excellent background to the arrival of modern humans into Australia and New Guinea [1,2] by 55 000–60 000 before present (BP). Although Australia and New Guinea were connected during periods of lowered sea levels, the first settlers must still have crossed open ocean from southeast Asia. By 29 000 BP, people had colonized the Bismarck and Solomon

Islands, which together with New Guinea, form ‘Near Oceania’. Reaching some of these islands required sizeable sea voyages, much longer than those being undertaken in the Mediterranean during the same period. There were local exchange networks by 18 000–20 000 BP [2], and by 9000 BP tree crops and other plants were being cultivated, making the region an important early center for plant domestication. However, population density was not high and pottery is absent [2].

Sometime around 3300–3500 BP, a new culture – Lapita – appears in the archaeological record, and in a previously unoccupied coastal niche (their stilt houses were often built over beach reefs or shallow lagoons). The ultimate geographical extent of this culture is shown in Figure 1c. Lapita is defined characteristically by a decorated pottery style and is named after an excavation site in New Caledonia in Island Melanesia. Lapita culture introduced new features, including permanent villages, a range of horticultural crops, domesticated animals (pigs, dogs, chickens and rats), fishhooks for inshore and open ocean fishing, fishing nets, sea-going canoes, stone adzes, anvils and shell bracelets. Under Green’s triple-I model [3], the genesis of this culture requires the ‘intrusion’ of a new culture, followed by ‘integration’ between the cultures, and local ‘innovation’ in technology. For example, the cultures combined aspects of an agricultural package found in slightly earlier archaeological sites from island southeast Asia with tree crops grown previously in Near Oceania, as well as making significant local technological developments [2]. Within island southeast Asia, the archaeological sites associated with agriculture form a temporal gradient. The simplest model of agricultural dispersal is a southeastward movement from continental Asia, possibly as a result of population expansion following the development of agriculture [4]. The expansion continued through Taiwan (Ta-p’en-k’eng culture 4500–5000 BP) and the Philippines (e.g. Luzon 4000–4500 BP) to Wallacea (the biogeographical zone lying between Borneo and New Guinea; Figure 1) and Near Oceania ([2]).

Although the earliest Lapita sites are found within Near Oceania, they are found within another 200 years in some parts of previously uninhabited ‘Remote Oceania’

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(Eastern Melanesia, Micronesia, and Polynesia – including sites in Vanuatu, New Caledonia, Fiji, Tonga and Samoa). New Lapita sites are still being discovered [5]. From the archaeological evidence, there appears to be a pause of 500 to 1000 years before permanent settlement of the eastern-most islands of Polynesia. The archaeological dates given in [Figure 1c](#) represent conservative estimates for permanent settlement [6]. Models of migration [7] predict that earlier exploration and temporary settlement were likely. The central islands of Eastern Polynesia (Cooks, Society Islands and Marquesas Group) were colonized initially, then the more peripheral islands (Hawaii, Rapanui/Easter Island and Aotearoa/New Zealand). However, by this time, the characteristic Lapita pottery was no longer being made, even though at least some islands had suitable materials [2]. In contrast to Near Oceania, population densities are thought to have been high in much of Polynesia (estimates of 60–100 people km<sup>-2</sup> are common). This might reflect the lower density of pathogens in Remote Oceania [2], but whatever the reason, the high population density led to the landscape being highly modified from its original condition.

Pacific languages tell a similar story, and are well integrated with archaeological studies [8]. Austronesian is a well defined family of languages that is the world's largest and the most widely distributed [9]. Its ~1200 languages are classified into ten subfamilies, nine of which are spoken only by indigenous Taiwanese (Formosans). By contrast, languages of the tenth subfamily, Malayo-Polynesian, are spoken from Madagascar (47° east) to Easter Island (109° west), and their comparative similarity suggest that they share a recent common origin. Moreover, non-Austronesian languages in Oceania are extremely diverse and are expected consequently to be much older. Although non-Austronesian languages are often lumped together in a heterogeneous catchall 'Papuan' group, they might be classified eventually into at least 12 major family groupings [2]. These linguistic relationships can be interpreted as predicting two major genetic groups in the Pacific: the older Papuan lineages and a more recent Austronesian group. However, language replacement (where one language replaces another) is well known in linguistics, and has occurred in Oceania [10]. Thus, we do not always expect a one-to-one relationship between languages and gene frequencies. In addition, borrowing between languages could be substantial [11], especially in Remote Oceania where contacts continued across hundreds of kilometers of ocean [12].

The traditional classification of Pacific islands into Polynesia, Melanesia and Micronesia ([Figure 1](#)) does not represent the complexity of the settlement of these islands. Lumped together under the term 'Melanesian' are Papuan-speakers from New Guinea, a land settled at

least 50 000 years ago, with Austronesian-speakers from Remote Oceania, who only settled within the past 3100 years. Here, we use 'indigenous Melanesians' to mean the pre-Lapita occupants of Near Oceania.

### Models for the initial settlement of Remote Oceania

The two oft-cited models for the origins of Remote Oceania peoples – the 'express train' [13] and the 'entangled bank' ([Box 1](#)) – lie at the opposite ends of a spectrum. The former predicts a strong phylogenetic (tree-like) signal reflecting initial settlement pattern, whereas the latter suggests a reticulate model with no phylogenetic signal remaining. The situation is complicated because the models are neither mutually exclusive, nor complete. One form of data (e.g. genetics) might be tree-like, whereas another (e.g. language) could be reticulate. Nor do the models account for later effects, such as continued migration. In addition, authors interpret the models differently. Each model is complex such that a dataset might disagree with one aspect of the model, but be concordant with others. It is helpful to represent the spectrum of views ([Box 1](#)) as: strong entangled bank ↔ weak entangled bank ↔ slow train ↔ express train.

A general warning from the entangled-bank model is important. Classic phylogenetic programs always output a tree for morphological, molecular, or language data, even if a tree is not appropriate. Although the programs enable estimates of the fit of the tree to the data (using consistency indices, g-statistics, etc.), they are not designed to evaluate trees versus networks. Ignoring any genetic admixture between populations can lead to inaccurate inferences of the historical processes.

The models discussed here lie along a continuum, but other versions are possible ([Box 1](#)). These models are testable because they make predictions about genes, cultures and languages. Although it sometimes appears that authors assume that models stand or fall on a single dataset, testing predictions requires that consideration be given to all classes of data: molecular genetic, linguistic and archaeological. During major migrations to previously uninhabited lands, we might expect the simultaneous transmission of genes, language and culture. By contrast, we might expect the decoupling of biology, culture and language during other periods. Thus, correspondence between the different forms of data needs to be evaluated rather than assumed.

### What does recent linguistic research tell us about Oceanic origins?

Linguistic analyses are a vital part of unraveling the patterns of human migration [4]. The express-train model of Pacific settlement predicts considerable tree-like signal in Austronesian languages. Consequently, a tree of Austronesian languages should reflect this pattern of

**Figure 1.** Map of Near and Remote Oceania, with ice-age sea levels, language families, Polynesian paternal and maternal lineages, and archaeological dates. **(a)** The distribution of Austronesian subfamilies and their phylogenetic relationships. The Malayo-Polynesian (MP) languages include Western (WMP), Central and Eastern (CEMP), Central (CMP) and Eastern (EMP) Malayo-Polynesian, as well as South Halmahera/Western New Guinea (SHWNG) and Oceanic. The Oceanic subfamily includes Nuclear Micronesian and Polynesian languages. Shading indicates the approximate coastline during the last glacial maximum. **(b)** Distribution of the predominant paternal (blue) and maternal (red) Polynesian lineages among modern populations. **(c)** Age of the earliest evidence for permanent settlement for Neolithic (black) and post-Neolithic (blue) archaeological sites throughout the region. Particularly on islands, exploration could be earlier.

### Box 1. Models of Oceanic origins: express trains and entangled banks

#### Express train

The express-train model describes the initial spread of Polynesian ancestors (Austronesians), first into Near Oceania and then into Remote Oceania. The model is as follows.

- (1) Austronesian languages arose northwestward of Near Oceania (probably in Taiwan, but ultimately from China).
- (2) The associated culture (including agriculture, horticulture, fishing, pottery, weaving and long-distance sailing) arose in the same region northwest of Near Oceania.
- (3) The Austronesian people differed genetically from the first indigenous Melanesians (who spoke non-Austronesian languages).
- (4) The Austronesian people (with their languages) moved relatively rapidly southward through the islands of southeast Asia and subsequently eastward into Remote Oceania.
- (5) There were no significant breaks between leaving Taiwan and reaching western Polynesia.
- (6) There was only limited genetic mixing between Austronesians and indigenous Melanesians during this initial expansion, and no large-scale replacement of indigenous Melanesians.

The first three points emphasize the 'Out of Asia' aspect, the last three the 'express train'. The spread of Lapita culture is the fastest in the archaeological record [68], presumably because it was largely into unoccupied niches and/or islands. However, the model says nothing about any subsequent migration and is thus incomplete, although it is usually assumed [69] that there was later admixture of indigenous Melanesians and Austronesians at least as far as Fiji and probably Samoa and Tonga. Thus the final point is:

- (7) There is ongoing genetic admixture in Near Oceania over the past 3000 years.

#### Entangled bank

In its simplest form, the entangled-bank model [70] asserts that there has been so much on-going interaction between adjacent populations that representing them (or their cultures or languages) as tree diagrams (phylogenies) is at best inappropriate and at worst seriously misleading. For example, John Terrell states, 'that these islands form an enormous geographic array of local and island populations that, in all likelihood, kept more or less in touch with one another ever since the first arrival of people at least 45 000 years ago' [70]. The strong version of the model is that, because of extensive interactions in the past, there can never be tree-like structure in these types of data, whether in Oceania or elsewhere. By contrast, the weak version does not deny that there can (sometimes) be a phylogenetic signal in the data; it is a general-purpose null model that assumes no tree-like signal. Any phylogenetic signal must be demonstrated, rather than assumed.

#### Other models of Oceanic origins

Alternatives to the express-train and entangled-bank models include several intermediate models. The 'slow-train' version of the model differs from the express version in predicting considerable genetic admixture between Austronesians and the indigenous inhabitants of the transit zones before the settlement of Remote Oceania. Both fast- and slow-train models accept that some Austronesians stopped in island Melanesia and coastal New Guinea. An 'indigenous Melanesian' model would derive Polynesian ancestry solely from the original settlers from 50 000 BP. A recent 'slow-boat' model [20] is based on genetic evidence and argues not only for a proximate Polynesian origin within Wallacea, but also for an Austronesian origin in island southeast Asia, rather than Taiwan/China. The proponents of this model consider that a genetic signal of recent dispersal (< 10 000 BP) can be traced back from Polynesia only as far as Wallacea, although the ultimate origin for such lineages in continental Asia is not in doubt.

dispersal. However, given the relatively fast travel across Island Melanesia to Tonga/Samoa, the model would not predict a robust signal (e.g. high bootstrap values) for this section of the tree. Very rapid dispersals do not allow sufficient time for languages to develop the novel linguistic innovations that define subgroups. But given the longer pause before the settlement of eastern Polynesia [2], there should be more robust support for this subgroup of languages if the founding population was from a relatively homogenous source. Testing such hypotheses requires a large database of linguistic information with a good sampling of Austronesian languages.

Fortunately, Robert Blust at the University of Hawaii has compiled such a dataset, the Austronesian Comparative Dictionary (unpublished), with over 5000 cognate sets (homologous words) for over 200 Austronesian languages. Gray and Jordan [14] converted this information into a matrix with languages as taxa and cognate words as binary characters. A variety of tests, such as skewness of tree lengths, demonstrated that there is significant tree-like signal in these data. The most parsimonious tree for the data (Figure 2) matches closely the geographical migration sequence postulated by the express-train model (Box 1). These results contradict the entangled-bank model in both its weak (null) and strong forms.

The bootstrap values, as predicted from the archaeological data, are high for the separation of the eastern Polynesian clade, but lower for the early Oceanic branches. Although there is significant phylogenetic signal in these

data, there is also evidence for borrowing between languages (e.g. the consistency index has a relatively low value of 0.26). This is not surprising, given that the Austronesians were expert navigators who dispersed as far as Madagascar and Easter Island. A well-studied example from South America of such a borrowing is described in Box 2. Recent borrowings do not erase all traces of phylogenetic signal from the initial migration-driven tree. Phylogenetic methods such as split decomposition [15] do not assume a pure tree model, and thus can be used to investigate these conflicting signals. Figure 3 shows a parsimony tree for 11 Polynesian languages and their corresponding splits graph. The splits graph shows separation between western and eastern Polynesian clades, but substantial borrowing within these groups. For example, there is signal linking Hawaii to both the Marquesian and Tahitic language groups.

Linguistic data might also be used to distinguish between the express-train and the slow-train models. According to the slow-train model, there was sufficient time for substantial borrowing from 'Papuan' languages into Oceanic ones. This means that numerous words of Papuan origin should be found throughout Oceanic languages, but should not occur in the earlier branches of the Austronesian tree (Figure 2). To the best of our knowledge, these ancient loan words are not found, but the question would repay further investigation. A third way of using language data to discriminate between hypotheses is to estimate dates of linguistic divergence. Languages do

### Box 2. Kumala – sound changes help reveal linguistic origins

Sound changes enable inferences about population histories to be made because they often change in regular ways. For example, words in the Paamese language of Vanuatu have lost typically both /<sup>\*</sup>k/ from the proto-Oceanic form and /<sup>\*</sup>a/ at the end of words [71]. In Table I, words inferred to be in a proto-language are asterisked.

Words not following these changes are likely to be more recent borrowings. The Polynesian sweet potato (kumala) illustrates this. The striking similarity of the word in many parts of the Pacific (Maori, /kuumara/: Rarotongan, /kuumara/; Samoan, /'umala/; Tahitian, /'umara/) might be taken as evidence for its antiquity among proto-Oceanic speaking peoples. However, if kumala was an old inheritance from proto-Oceanic into Paamese, then the initial /k/ and the final /a/ should have been lost, and the form should be /umal/. The fact that it is /kumala/ is consistent with it being a more recent borrowing. Botanical evidence [72] suggests an origin for the sweet potato in South America and archaeological evidence suggests that kumala cultivation has spread through Polynesia relatively recently, although before European contact [73]. Correspondingly, in the Quechua language of Peru, the term for sweet potato is strikingly similar – /kumar/. This suggests that Polynesians voyaged to South America and returned with this root crop in recent prehistory, although this possibility requires further testing.

**Table I. Observed word changes between proto-Oceanic and Paamese**

Proto-Oceanic form	Paamese	Meaning
*a kai	a:i	tree
*a ika	ai	fish
*kapika	ahi	Malay apple

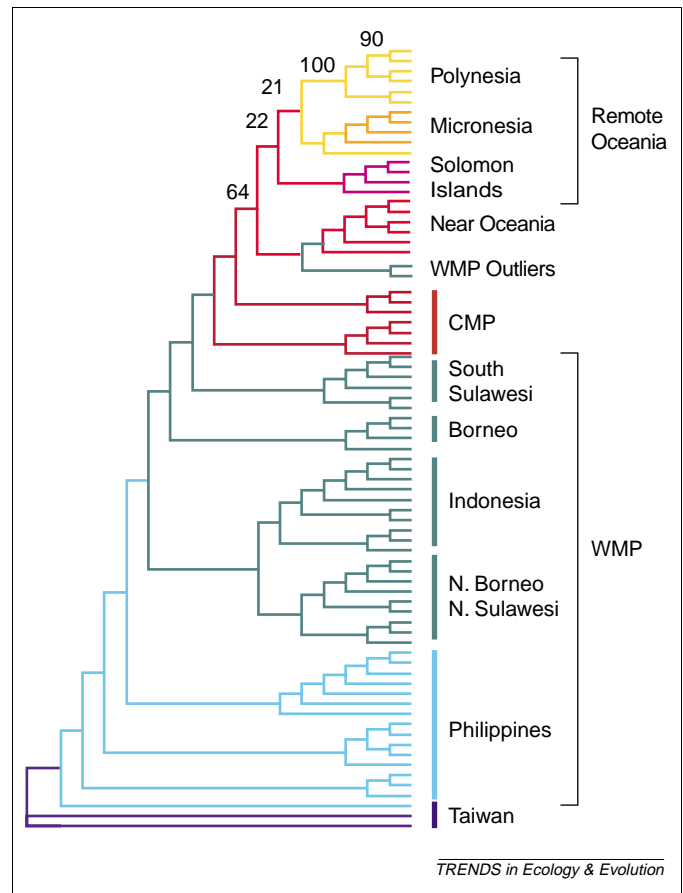
diverge with time, but Swadesh's proposal [16] that this change is sufficiently clock-like to be able to date language divergences is contentious [17]. If recent methods for dating trees with sequence data (in the presence of rate variation) can be applied to linguistic data, then this would give a significant improvement in our ability to discriminate between complex settlement scenarios. To summarize this section:

- (1) Language data generally support an express-train model with respect to both the origin of the Austronesian language family and the rate of Austronesian movement across Island Melanesia.
- (2) Split decomposition analyses of lexical data also reveal evidence of considerable post-settlement contact.

### What does recent molecular genetic work tell us about Oceanic origins?

Although Oceania is arguably the best place to reconstruct human migration, the task is full of possible pitfalls because modern genetic diversity results from a mixture of signals:

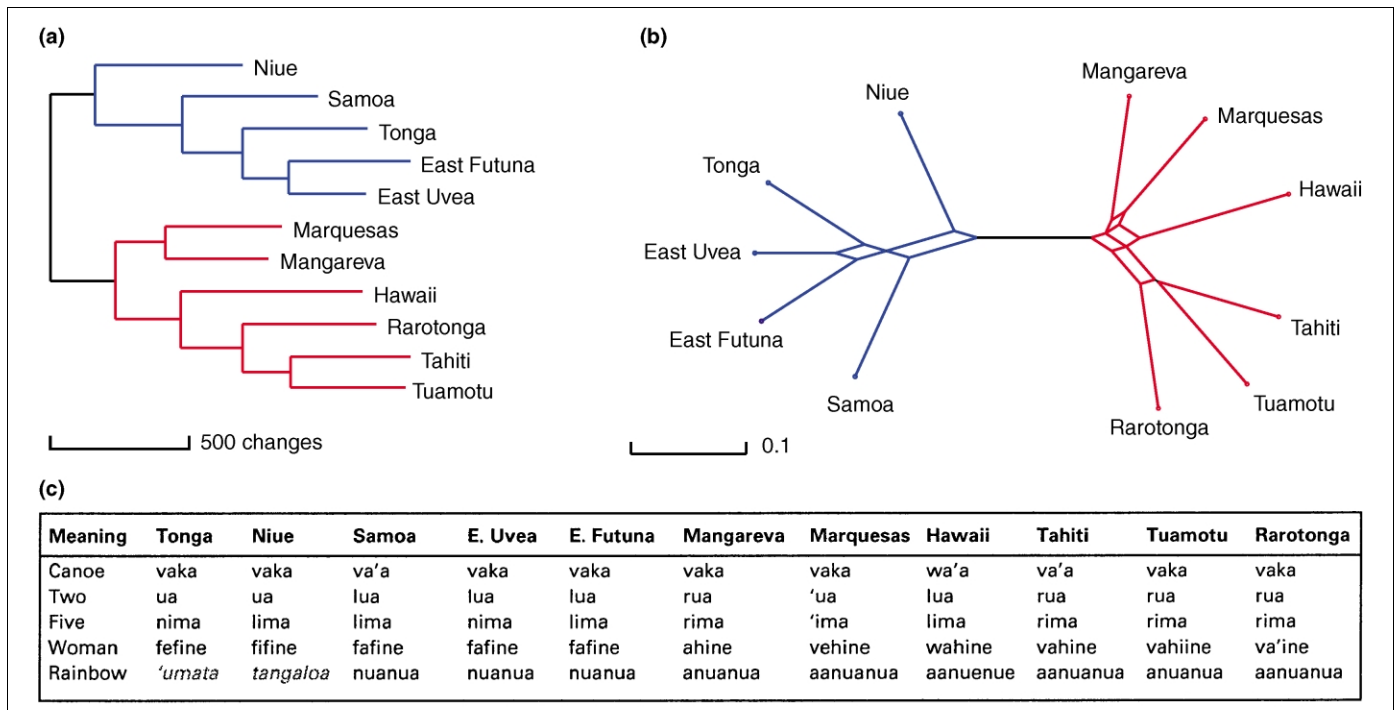
- (1) a founding population (a subset of a larger population);
- (2) genetic drift and selection (in both the founding and ancestral populations);
- (3) subsequent migration in prehistoric times (again into both the founding and the ancestral populations, and which might be different for males and females); and
- (4) 'post-contact' admixture from a variety of populations, including Europeans.



**Figure 2.** Parsimony tree for 77 Austronesian languages. The tree is rooted with two Formosan (indigenous Taiwanese) languages. Bootstrap values are shown above some of the branches in the Oceanic clade. Consistent with the suggestion of a pause in settlement, the Eastern Polynesian subgroup has strong bootstrap support (90%). Abbreviations are as in Figure 1.

A primary problem is separating the extent of admixture between dispersing (Austronesian) and indigenous populations during the initial movement across Near Oceania and Wallacea from that occurring over the subsequent 3500 years. Genetic drift and post-settlement migration render analyses difficult because current gene frequencies do not represent ancestral gene frequencies. Although the models agree in inferring that Continental Asia is the ultimate origin of genetic lineages now in Remote Oceania, they differ in the timing of the migration movements. This leads to a focus on non-recombining loci, specifically from the maternally inherited mitochondrial DNA (mtDNA) and the paternally inherited Y chromosome. Both loci provide opportunities for extracting chronological information from genetic data for comparison with archaeological dates. These two important loci also have the advantage of lower effective population sizes than the rest of the genome, resulting in higher genetic drift and greater population differentiation.

Mitochondrial DNA studies in the Pacific show a high frequency of a nine bp deletion in the COII/tRNA<sup>Lys</sup> region of the genome. The distribution of this deletion has been catalogued extensively from Madagascar to eastern Asia to Easter Island [10]. The deletion, together with three characteristic mutations in the D-loop, forms a 'Polynesian motif,' and it is useful to examine its distribution (together



**Figure 3.** Detecting potential borrowing between Polynesian languages. (a) Parsimony tree – data derived from the Pollex database [67]. (b) Splits graph for the same data as in (a), showing evidence of reticulation (borrowing) within the western (blue) and eastern (red) Polynesian clades. (c) A sample of cognate (homologous) lexical items for these languages. Noncognate terms are in an italic font.

with its predecessors with just one or two of the characteristic D-loop mutations). The full motif has its highest frequencies in Polynesia (where it predominates), and is confined largely to speakers of the central/eastern Malayo-Polynesian subgroup of Austronesian languages spoken in Wallacea and the Pacific (Figure 1). Stepping backwards phylogenetically, the ancestral lineage with two of the three D-loop mutations is found across the entire range of Austronesian language speakers from Madagascar to Easter Island. However, the earlier lineage (with only one of the three mutations) is confined to the central part of this range. Thus, this pattern of a directional series of changes provides a relative chronology of dispersal with ultimate origins (undated) in Asia. Similarly, in a dataset of 53 complete human mitochondrial genomes [18], the closest relative of the single Polynesian (Samoan) sequence is Korean, with which it shares the nine bp deletion. These two sequences then join with a Chinese sequence and these three 'Asian' mitochondrial genomes are closer (phylogenetically) to those of Europeans than to those of indigenous Melanesians. Overall, the distribution of mitochondrial lineages is consistent with an 'Out of Asia' model, whether express-train, slow-train or slow-boat, but the distribution of nine bp deletions was taken initially as support for the express train [19].

Chronological estimates of the time to the most recent common ancestor (TMRCA) of a set of sequences depend on accurate parameters and assumptions about mutation rate, generation time and prehistoric demographics, and come consequently with wide confidence intervals. The diversity of the Polynesian motif in island southeast Asia (Wallacea) has led to an estimated TMRCA of mtDNAs carrying the Polynesian motif at ~17 000 BP [20],

although this date still requires a full sensitivity analysis [21] and appears to contradict the linguistic data (Figure 2). If this date does hold up, then there might be a pre-agricultural origin of the final motif within Wallacea; only after the arrival of agriculture would there be migration into Remote Oceania. However, the paucity in Remote Oceania of common highland New Guinean lineages means there was little maternal genetic admixture between the dispersing population and indigenous Melanesians.

Y-chromosome studies enrich the picture across Polynesia and island Melanesia. There is clear evidence for male-biased European admixture among some Polynesian populations [22,23], but without a comparable gene flow of European mtDNA. In one case, careful historical work was required to trace Native American Y chromosomes back to the Polynesian slave trade [24]. In other cases, it was possible to detect post-settlement gene flow; for example, post-Lapita gene flow of Y chromosomes from island Melanesia into Tonga [25], and mtDNA into the Santa Cruz Islands [26]. Oral histories suggest subsequent migrations into Fiji [27]. Several recent studies report two Y-chromosomal lineages predominating in Polynesia [25,28,29], one of which is absent from the current population of indigenous Taiwanese. However, ancient highland New Guinean paternal lineages, which presumably represent indigenous Melanesians, are scarce in Polynesia [30]. Although both major Polynesian lineages appear to predate the earliest agricultural dates in island southeast Asia, the higher-frequency lineage appears in Wallacea and is absent further north in island southeast Asia (Figure 1), mirroring the distribution of the mtDNA Polynesian motif. Given their antiquity, the absence of

these lineages from the supposed origin of Austronesian languages and agriculture in Taiwan and southeast China does not conform to the simple express-train model.

An exciting prospect is that mitochondrial, Y-chromosomal and autosomal data [31,32] could reveal sex-specific differences in prehistoric demography, including levels of endogamy and/or migration patterns. One example of sex-biased endogamy is a matrilineal society where females tend to stay locally, but accept outside males into the group (e.g. females in early 19th century New Zealand accepted external males into the reproductive group [33]). Linguistic evidence [34] suggests proto-Oceanic societies were both matrilineal and practiced matrilocal residence, whereby husbands moved into their wife's village. Marital residence patterns can generate differences in patterns of male and female lineage diversity [35]. Historians go further [36] and report that chieftain status was inherited maternally from Madagascar to Polynesia, with high-ranking women being very influential. Population genetic modeling needs to take these factors into account.

At a more microgeographic level, the clinal decrease in genetic and linguistic diversity from west to east across the Pacific [21,37] emphasizes the role of successive founder events in shaping patterns of variation in Remote Oceania. Estimating the size of the colonizing populations becomes crucial to understanding this process. Thus far, this has been done only for New Zealand Maori, where the estimate for females of a founding population of 50–100 individuals agrees well with oral histories [21]. However, nobody as yet has presented a unifying model of Oceanic settlement consistent with all molecular, linguistic, historical and archaeological evidence.

### The ecological impact of Oceanic settlement

In Remote Oceania, evidence of initial human activity is easier to identify than it is in the rest of the world. This is a result of several factors, from the relatively short time frame of human occupation, to the decreases in general biodiversity as one moves eastward across the Pacific (new introductions are more obvious and identifiable). Similarly, the more fragile island ecosystems are disturbed more easily and obviously by human and human-associated activity such as burning and other habitat modification, hunting, and the introduction of new predators or competitors.

#### Introduction of commensal and domesticated species

One of the greatest impacts to island ecosystems is the introduction of novel flora and fauna. Pacific colonists introduced a range of plant and animal species to the relatively depauperate island environments. Human-assisted dispersal of animals dates as far back as the Pleistocene in Near Oceania, with the translocation from New Guinea to New Ireland of the possum-like cuscus (*Phalanger orientalis*) occurring possibly as early as 19 000 BP, and of a wallaby (*Thylogale brunii*) occurring perhaps around 7000 BP. Some archaeological evidence suggests that pigs (species uncertain) were introduced to New Guinea from somewhere in southeast Asia by 6000 BP; some evidence suggests it might be as early as 10 000 BP, although these early dates for pigs are debated

fiercely. Linguistic evidence suggests that proto-Oceanic speakers introduced the pig ~4000–3500 BP [38].

Despite the debates regarding early pig introductions, there is little doubt that Lapita colonists introduced several animals into Remote Oceania, including dogs (*Canis familiaris*), pigs (assumed to be *Sus scrofa*), jungle fowl (*Gallus gallus*) and the Pacific rat (*Rattus exulans*). It is unclear whether other animals such as geckos, skinks and land snails were accidental or deliberate introductions (human viruses would also be accidental introductions [39]). Not all animals made it to all locations. For example, only the rat and the dog were introduced successfully to New Zealand, and the rat and chicken to Easter Island. Sometimes, the appearance of dogs and pigs on an island occurs early, thereafter disappearing from the archaeological record, only to be re-introduced later [40]. The Pacific rat was the only commensal animal introduced to all islands that show evidence of Polynesian presence.

Mitochondrial DNA lineages shared between Pacific rat populations identify homeland regions, and disjunct variation within island rat populations suggests separate introductions from several sources [41]. This is consistent with archaeological evidence that post-settlement contact and long-distance exchange were significant in Polynesian prehistory, even in the geographical extremes of Hawaii, Easter Island and New Zealand [42]. Other domesticated animals are less straightforward in that the pigs, dogs and fowl introduced by the Lapita colonists are the same species as those introduced later by Europeans and, therefore, the respective populations are subject to more recent admixture. Thus, earlier and later lineages must be separated, a task for which DNA sequences, including ancient DNA studies, are ideal. The commensal approach has also been applied to extant populations of *Lipinia noctua*, a lizard native to New Guinea, to show that it was also transported from Near Oceania into Remote Oceania [43].

Just as with studies of humans, we need to know how well modern animal populations represent the genetic variation present in prehistory. Animal bones (rats in particular) are found in large numbers in archaeological sites throughout the Pacific, allowing ancient and modern populations to be compared. Working with animal remains is less fraught with the ethical implications of handling human remains! Thus, ancient DNA analyses of commensal animals are valuable for understanding issues in Pacific prehistory, and as a model for the evolution of island populations in general.

In one case, archaeological and modern mtDNA of the Pacific rat from the Chatham Islands (an isolated group to the east of New Zealand with a relatively simple colonization history) show that modern populations represent fairly early populations. By contrast, results from New Zealand itself are more complex. Whereas archaeological remains of rats from the South Island have the same mtDNA lineage as extant rats, two distinct lineages appear in the North Island. One is identical or related closely to extant populations, yet the second is distinct and not yet found in extant populations in New Zealand or East Polynesia [44]. Loss of diversity is not surprising. Because of competition from introduced

rodents (the brown rat *Rattus norvegicus*, the house rat *Rattus rattus*, and the house mouse *Mus musculus*), the Pacific rat is extinct on the North and South Islands except for a few pockets in Fiordland. Extant populations on offshore islands are remnants and do not represent the full original variation. Current work extends to Asian and western Pacific rat bones [45] and further analyses of Pacific pigs and dogs. In general, this sampling of remnant animal populations is exactly what researchers are facing in most human studies of population variation of origins and dispersal, and we need to consider lineage extinction in our interpretations.

Holdaway [46] reports another application of the study of commensal animals. Introduced small animals are often prey to large birds or other animal predators, and their bones are often present in natural deposits found in caves (e.g. in raptor pellets). If these remains pre-date archaeological dates for successful human settlement, then we have valuable markers of pre-settlement contact that otherwise might not show up in the archaeological record. In this way, we can tease apart potentially the different types of human contact (discovery, visitation, early settlements and later successful colonization [7]) and, therefore, better understand the total impact and history of prehistoric people in the Pacific.

#### Extinction of native species

As expected, there have been major extinctions throughout Polynesia following the arrival of humans [47,48]. As usual, there is disagreement whether this is because of physical (climate change) or biological (direct and indirect human impacts) factors. The overview is clear in the Pacific when broadened to Australia and North America, as well as Near Oceania, Fiji, Tahiti and New Zealand (Figure 4). Extinction follows human contact [49], whether in the middle of the last Ice Age in Australia [1], possibly around the glacial maximum (20 000 BP) in the rest of Near Oceania, around the end of the Ice Age (~11 000–12 000 BP in North America [50]), 3000–4000 Bp in island Melanesia [51], or in the last millennium in New Zealand [52–54]. As we become more aware of the diversity of mechanisms of human impact, the problem of accepting human impact disappears; the direct effect of ‘climate change’ on extinction is not an option for species that have already survived many Glacial/Interglacial cycles.

Hunting is just one impact, and many sites are known. A recent study of over 8400 bones from one site [55] found species that were hunted more frequently (as assessed by their presence in middens) were more likely to go extinct. For the giant flightless ratites (moa), extinction might have been fast [52]. Modeling shows that birds with slow rates of reproduction were particularly susceptible and this conclusion has now been extended to mammals [56]. Accounts by early explorers of the naïveté of the native fauna (to humans) have been collected [57] and show how easy hunting could be. Thus, comparisons between Europe and North America [50] are not relevant; humans have been in Europe for hundreds of thousand of years. It is standard evolutionary theory that animals evolve defense mechanisms (including behaviors) only for existing dangers. However, direct predation is only one mechanism. As

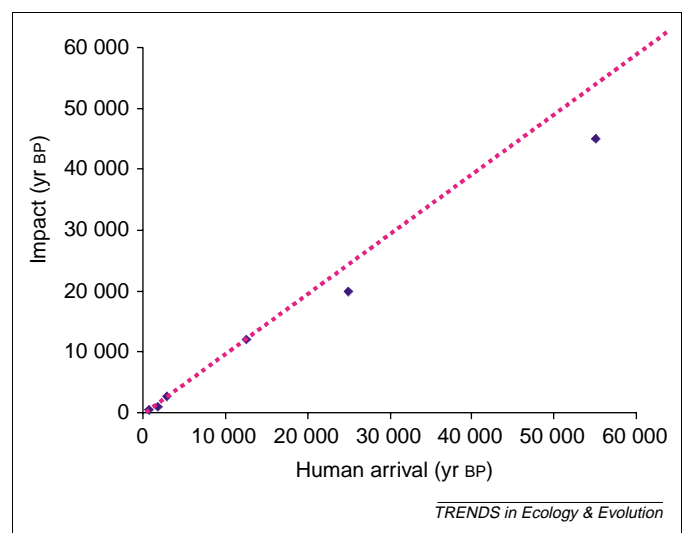
summarized earlier, human impacts also include habitat modification (including land clearance and effects of fire) and indirect effects via introduced biota. Effects will depend on many factors, including human population density [2], island size and diversity of landforms, and climate and vegetation types (e.g. Polynesian fires removed forests on the drier east coast of New Zealand, but not on the wetter west coast).

#### Ecological evidence on settlement processes

New Zealand is the last major area in Polynesia to have permanent human settlement; carefully calibrated  $^{14}\text{C}$  dates have shown no confirmed settlements before 1200 AD. However, bones of the Pacific rat several hundred (possibly up to 1000) years older than this ‘imply an early, transient, human contact’ [46]. This claim has been controversial [58] and all early dates are eliminated under the guise of ‘chronometric hygiene’. However, as mentioned earlier, studies of human migrations [7] predict a standard pattern of:

- Exploration well before outpost settlement,
- Some early settlements, then
- Migration and permanent settlement, and
- Ongoing contacts.

Was there release of commensal rats before settlement, and, if so, how long before settlement? It was common practice by European explorers to release food animals (e.g. goats, sheep, and cattle) on uninhabited islands, and, given that the Polynesians were the world’s most advanced explorers of their time, we expect them to have done the same. Oral tradition in Polynesia records exploration before settlement, although the time scale is difficult to



**Figure 4.** Testing ‘climate change’ versus ‘human impacts’ (direct and indirect) for extinction of a naïve biota. Under a global climate-change model, extinctions should be independent of human arrival times: if extinctions are human induced (direct or indirect), then they cannot occur before human arrival (i.e. not in the top left-half of the graph). Conversely, under the human-impact model, the changes will be post discovery: if extinctions are human induced, they must have occurred after human arrival (i.e. either will appear on the dashed line or in the bottom right-half of the graph). In practice, impacts on a naïve fauna are simultaneous with, or after human discovery (diamonds). Effects might be slower on larger and/or more diverse landmasses; conversely, they should be faster in smaller, more homogenous islands. Some indirect effects (such as from the release of commensal animals) could occur between initial discovery and permanent settlement.

determine. If rats were released early, then extinctions of some invertebrates and small vertebrates should precede the extinction of moa and other large taxa by habitat modification and hunting. There is indeed some evidence [54] for early extinctions before human settlement. Any release of commensal animals before permanent settlement would help separate direct and indirect 'human' impacts. The full range includes effects of commensal animals, hunting/foraging, habitat modification (including fire), and loss of prey. There is probably nowhere else in the world where we can separate so many individual factors.

Finally, early European explorers in the Pacific found 13 unpopulated islands where there was evidence of earlier human settlement [59]. All are small islands, and would not have had a large population. Some were at the lower temperature limits for growing food plants or had unsuitable coral soils. Given the intense interest in conservation biology for the sustainability of different population sizes, these case studies are potentially highly informative. In addition to ecological and psychological stresses, small populations result in high demographic stochastic variation with dire consequence for mate availability and long-term population survival.

### Conclusions and future directions

Oceanic prehistory is not simple, but it is tractable. There is a strong phylogenetic signal, together with some reticulation, for both languages and genetics. The ultimate origins of Austronesians and the more proximate origins of Polynesians and other Remote Oceanic populations will not be settled until all disciplines are better able to characterize pre-Lapita populations in Wallacea and post-Lapita population movements in Remote Oceania. Greater interaction between disciplines must occur and we consider a few examples here. First, archaeo-linguistic reconstructions of ancestral societies [60] (the historical record of male/female roles will help in this respect [33,36,61]) should help resolve differences between mtDNA and Y-chromosomal data. Second, archaeological evidence of pauses in dispersal can co-occur both with linguistic clades exhibiting high bootstrap values and with regions of heightened genetic admixture between indigenous and dispersing peoples given the additional time for interaction. Improved models of language evolution will help estimate times of divergence. If there is some selection against language change, then language in a large community might evolve more slowly than in a smaller one. By contrast, under a neutral model of language change, the rate would be independent of population size.

Genetics offers many opportunities for increased precision. Complete mtDNA genomes are much more powerful than D-loop sequences [18], although many more samples are required. New techniques [62] are increasing resolution for Y-chromosomal data. A new opportunity comes from the detection of haplotype blocks – relatively long stretches of nuclear DNA where recombination has not occurred for many generations. These blocks contain information about population history and are potential markers of selection and health [63,64]. Increased genetic study of commensal and domesticated species, such as chickens and pigs as well as for domesticated plant species

such as species of taro and breadfruit, is necessary. We need more genetic data about the sweet potato (Box 2) and bottle gourd [65], which are thought to have South American origins. Models of long-distance voyaging make getting to South America and back realistic for early Polynesians [66].

Nowhere else in the world offers the same opportunity to unravel the dramatic and complex effects of humans on the environment and on indigenous plants and animals. Everything we have learned confirms that Remote Oceania is the best location to test our understanding of human migration and impacts on a naive environment.

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