

Response to “Ancient DNA and its contribution to understanding the human history of the Pacific Islands” (Bedford *et al.* 2018)

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THE COMPLEX DEMOGRAPHIC HISTORY OF REMOTE OCEANIA

Posth *et al.* (2018) co-analysed newly generated ancient and modern genome-wide data from across Remote Oceania to shed light on the demographic history of the region, following the earliest arrival of Lapita-associated peoples around 3000 years before present (BP). Skoglund *et al.* (2016) had previously shown – in line with craniofacial analyses (Valentin *et al.* 2016) – that early Lapita settlers of Vanuatu, as well as those in Tonga, were genetically “East Asian”. However, the subsequent arrival time of the Near Oceanian (or “Papuan”; see Posth *et al.* 2018, paragraph 2) genetic component, which is necessary to explain the admixed present-day Pacific ancestry, was inferred indirectly to 1927–1239 BP using various modern Remote Oceanian proxy populations (Skoglund *et al.* 2016). In Posth *et al.* (2018), we were able to directly demonstrate the far earlier arrival of individuals with largely unadmixed Papuan genetic ancestry, related to present-day inhabitants of New Britain in the Bismarck Archipelago, in Vanuatu by c.2500 BP. Genetic data from present-day ni-Vanuatu indicated admixture with Papuan-like individuals, demonstrating almost complete replacement of the initial East Asian genetic ancestry. But our ancient DNA (aDNA) analyses showed – contrary to the later suggestion of Lipson *et al.* (2018) of a wave-like genetic turnover that was largely complete by 2300 BP – that this genetic replacement is better described as a long, incremental process with multiple gene-flow events through time. This scenario of a complex genetic replacement provides a plausible demographic mechanism to solve a long-debated conundrum: why, rather than Papuan languages, present-day ni-Vanuatu speak Austronesian languages (Blust 2008) – that is, those descended from Proto-Oceanic – assumed to

have been brought to Remote Oceania by the initial Lapita-associated peoples.

We are pleased that our work generated the discussion by Bedford and colleagues (Bedford *et al.* 2018) and are grateful for the opportunity to provide this response. Below, we aim to address the wide-range of interesting, encouraging and challenging comments on our paper – some of which elide it with that of Lipson *et al.* (2018) – which we categorise under the following broader themes: (1) integrative research on the human past; (2) limitations of inferences from current genetic data; (3) Austronesian and Papuan languages in Near and Remote Oceania; and (4) the impact of genetic research on descendant communities.

INTEGRATIVE RESEARCH ON THE HUMAN PAST

The ultimate aim of many researchers working on human population history is to provide integrated, multidisciplinary insights – drawing together all relevant data and available tools to better understand the many complex processes comprising our past. While we certainly think there is far more yet to be done in this regard, we fully agree with Kirch that our approach can “enrich our understanding of the processes involved” (Bedford *et al.* 2018). We are surprised at Sheppard’s claim that linkages between genetic and linguistic population history are merely “hypotheses . . . virtually untestable and so fairly useless” (Bedford *et al.* 2018). It is precisely the apparent “mismatch” between genetic and linguistic ancestries evident in Vanuatu – and elsewhere in Island Melanesia – that necessitates a multidisciplinary explanation. To dismiss the potential contribution of historical and/or computational linguistics to this endeavour seems overly pessimistic. Indeed, our study was in part inspired by a historical linguistic

hypothesis (Blust 2008), under which the history of the Oceanic-speaking peoples of Remote Oceania involves “two (or more) migrations by biologically, culturally and probably linguistically distinct populations” – as Blust writes (in Bedford *et al.* 2018). Our genetic analyses concluded that the demographic changes in Vanuatu were a complex, drawn-out process – a model that Blust says “could hardly provide a better match” for this hypothesis.

It is possible that the long process of genetic replacement that we infer reflects continued input from a Papuan source population that had already arrived in Vanuatu, presumably via the abrupt wave of migration for which both Burley (in Bedford *et al.* 2018) and Lipson *et al.* (2018) argue. Such a source would have to have been substantial as well as remaining largely unadmixed over a long period. Evidence of the continuing regional diversification in post-Lapita (and even during late Lapita) pottery traditions – as Bedford writes (in Bedford *et al.* 2018) – does not support such a “major wave” of migration, instead suggesting that the arrival of Papuan peoples in Remote Oceania probably happened “incrementally and unevenly” (see also Bedford & Spriggs 2018). There is, in fact, no evidence of pottery sequences found across the region that resemble a discrete ceramic tradition that might be said to represent a “second wave” analogous to Lapita; sequences in Vanuatu and elsewhere also generally show a transition from Lapita to post-Lapita traditions, rather than any abrupt change – as both Sand and Sheppard point out. While direct archaeological evidence for continued post-Lapita contact across Island Melanesia may be sparse, there are, however, a range of very distinctive cultural practices found in parts of both Vanuatu and the New Guinea/Bismarck Archipelago region in the late end of the sequence that are suggestive of later connections. While the nature of any interactions remains speculative, they include head binding, the production of fully circular pig tusks, penis sheaths and ornaments worn through the septum – the latter two noted earlier by Blust (2008).

LIMITATIONS OF INFERENCES FROM CURRENT GENETIC DATA

A number of authors in Bedford *et al.* (2018) raised the issues of how representative the aDNA evidence is for Remote Oceania, or concerns that our analyses and inferences might be biased or misleading. It should be said that even where close collaborations with appropriate community, cultural and/or governmental institutions are in place, the generation of viable aDNA data is necessarily opportunistic at present in the region. This is due to the limited amount of excavated skeletal material, as well as regionally specific aDNA preservation. While we agree that more genetic data should provide a finer-grained understanding of population history, the methods and analyses that we used are appropriate and we make statistically supported claims. However, in some cases a single data point can provide a directly observable

constraint or anchor for plausible demographic models of the past; for example, the presence of a Papuan-related individual with no detectable East Asian ancestry in Tanna, Vanuatu (TAN002) by c.2500 BP. It should also be kept in mind that unlike mitochondrial DNA (mtDNA), which presents a single genetic locus, inherited by the maternal line, a nuclear genome presents us with information on the genetic ancestry of a large number of people, the ancestors of that person. A single nuclear genome is therefore highly informative about the history of the population from which this one individual is derived.

Matisoo-Smith appears concerned that our argument “regarding rapid population replacement is based primarily on the DNA from the Teouma skulls” (Bedford *et al.* 2018). This is inaccurate on two fronts. First, the distinctive genetic inference in Posth *et al.* (2018) is that the genetic replacement in Vanuatu seems to have been incremental. Indeed, the 500-year aDNA time transect that we reported, from c.2500 to 2000 BP in Malakula, displays remarkable heterogeneity, with between 22% and 46% of these individuals’ genetic ancestry ultimately derived from East Asian sources. We showed that genetic replacement occurred over an extended period, with ALDER estimates – from both Posth *et al.* (2018) and Lipson *et al.* (2018) – revealing that admixture was still occurring after 2000 BP. Second, our argument is not based primarily on the Teouma data. Three of the earliest newly reported individuals in Posth *et al.* (2018) – dated to c.2500 BP and from Malakula, Vanuatu (MAL006) and Tonga (TON001 and TON002) – had little to no Papuan ancestry. Other authors (e.g. Sand and Pawley in Bedford *et al.* 2018) also seem to overlook some of this early direct evidence, and thus the extent and importance of the East Asian-related genetic homogeneity of Lapita-associated peoples across Remote Oceania – identified by Skoglund *et al.* (2016) and further supported by Posth *et al.* (2018) and Lipson *et al.* (2018) – may be missed.

We agree with Sand that the detail of inferences will improve when it is “possible to compare genetic data from the same chronological periods”. Indeed, Sand’s argument that “genetic conclusions for Oceania” should take account of the more recent population bottlenecks in Pacific populations caused by “the introduction of European diseases” can be read as the strongest possible case for more aDNA research across the region. Better understanding the structure of the genetic diversity that existed prior to European contact will be of huge benefit to many researchers of Pacific prehistory. With our local collaborators – and as Blust encouragingly suggests – we are currently working “to extend the kind of diachronic DNA sampling that has proven so revealing in Vanuatu” to elsewhere in Near and Remote Oceania. We also very much agree that it is misguided to make the simplistic “assumption that present-day populations in each island are the same as those that were there 4000, 3000 or 2000 years ago”; where Sand talks about population discontinuities, population geneticists would, perhaps, talk about “turnovers” or “replacements”. We have been careful to

describe historical inferences drawn on the basis of currently available modern genome-wide data in terms of “proxy sources”; that is, we identify the present-day Baining of north-east New Britain in the Bismarck Archipelago as the closest proxy source of the Papuan ancestry found in ancient Vanuatu individuals. This does not mean that the source of all Papuan ancestry is tied to this exact geographical region or to this specific present-day population and, as we show in our qpGraph analyses, present-day ni-Vanuatu genetic ancestry cannot be explained by continuing admixture with this source alone.

AUSTRONESIAN AND PAPUAN LANGUAGES IN NEAR AND REMOTE OCEANIA

Some authors in Bedford *et al.* (2018) questioned our assumption that Lapita-associated peoples were speaking a form of Proto-Oceanic (Sheppard), while others were concerned with our assumption that people arriving later from Near Oceania could still have been speaking Papuan languages (Cox and Næss), or simply miss the details of our argument (Pawley).

On the first issue, any assumed connection between Lapita and the Oceanic languages rests upon decades of linguistic and archaeological work – often carried out in concert – spanning at least 50 years (e.g. Kirch 1997; Pawley & Green 1984; Pawley & Ross 1995; Shutler & Marck 1975) and recently summarised by Kirch (2017). On the second point regarding Papuan-speaking migrants from Near Oceania, we reiterate and expand on the argument made in Posth *et al.* (2018). The present-day languages of Vanuatu are exclusively Oceanic-Austronesian, forming two major subgroupings or clades (Pawley & Ross 1995; see also Gray *et al.* 2009, fig. 1), but with a number of heterogeneously distributed “aberrant”, potentially Papuan, linguistic features. As described in Posth *et al.* (2018), these include “quinary numeral systems, rounded labial phonemes, dual exclusion of p and c phonemes, and serial verb construction” (Blust 2008; Donohue & Denham 2008; Lynch 1981; Tryon 1982) which, as we stress, are “extremely rare or absent in other Austronesian languages and shared almost exclusively with Papuan languages”. The linguistic evidence points to these Papuan-like features having arrived through the subsequent migration of Papuan speakers (Blust 2005; Blust 2008; Donohue & Denham 2008). Reconstruction of some of these rare features to the proto-languages of Vanuatu further points to early Papuan-like linguistic influence in Vanuatu – mirroring the direct aDNA evidence in Posth *et al.* (2018) and Lipson *et al.* (2018) for the early arrival of largely unadmixed Papuan genetic ancestry c.2500 BP (TAN002) and 2300 BP (TAP1), respectively. However, rather than a second, discrete migration of Papuan people, our analyses indicated a long process of interaction. In particular, our qpGraph analyses (Posth *et al.* 2018, fig. 3) showed that multiple events of genetic admixture with a group ancestral to present-day inhabitants of the Bismarck Archipelago

were necessary to explain the change in ancestry through time of the ancient inhabitants of Vanuatu.

Cox suggests – as does Næss – that it is “at least plausible that many Papuan groups in New Britain had already transitioned to Austronesian languages” in the 500 years between the arrival of Lapita 3000 BP and this earliest evidence of Papuan arrival c.2500 BP in Vanuatu. We agree that this scenario is possible but – notwithstanding the linguistic arguments outlined above – we find it a less likely explanation given the current data. This model would require that the ancestral source population for both Baining and TAN002 adopted an Austronesian language with no accompanying East Asian genetic admixture. As Cox notes, most of New Britain is today Austronesian-speaking, but the majority – if not all – of these groups that have been studied genetically have at least some East Asian ancestry (e.g. Friedlaender *et al.* 2008, fig. 7; Skoglund *et al.* 2016, fig. 2). Austronesian speakers with unadmixed Papuan genetic ancestry therefore appear to be rare. It is notable that the present-day Baining retain Papuan languages in the midst of Austronesian-speaking groups – despite having acquired a small proportion of East Asian genetic ancestry since the source population diverged (see Posth *et al.* 2018, fig. 3). We thus consider it unlikely that the ancestral population common to both Baining and late Lapita/immediately post-Lapita individuals that arrived in Vanuatu – a population with largely unadmixed Papuan genetic ancestry – spoke an Austronesian language.

Yet even if this alternative model were correct, and genetically Papuan-like people were bringing other Oceanic-Austronesian languages to Vanuatu, there is no evidence of a significant impact on or replacement of the *in situ* Austronesian languages in Vanuatu; that is, the present-day languages are monophyletic with respect to the high-order subgroupings of Oceanic languages in Near Oceania (Gray *et al.* 2009, fig. 1; Pawley & Ross 1995). Ongoing computational historical linguistics work – paired with targeted data collection – may allow estimation of the time depth of the most recent common ancestor of all present-day languages of Vanuatu, a potentially valuable contribution to this debate.

The third issue, raised by Pawley, appears to miss the temporal sequence of events that we propose – namely, an incoming population that genetically replaces the existing inhabitants, albeit incrementally, yet adopts their language. We believe that this demographic and linguistic scenario in Vanuatu is rare enough to comment upon. The further examples that Pawley proposes in his point (1) appear to be the direct opposite of what we argue for in Vanuatu. They are, instead, examples of *in situ* Papuan groups adopting incoming Austronesian languages, some with limited East Asian genetic admixture. As pointed out by Cox, this is “a commonplace process that is no oddity at all”. Language shift, whether or not underpinned by demographic changes, is a common occurrence globally, but linguistic continuity despite almost complete genetic replacement does seem uncommon in small-scale, pre-state contexts. The full

complexity of the cultural and biological interactions between Papuan and Austronesian groups in New Guinea and the Bismarck Archipelago is, understandably, beyond the scope of both the original paper and this response. Future interdisciplinary work – incorporating the direct evidence that aDNA can provide – may uncover more such complex events in the region.

THE IMPACT OF GENETIC RESEARCH ON DESCENDANT COMMUNITIES

Matisoo-Smith, Sand and Burley all raise important and pressing questions about the process of ancient and modern genetic research and/or the potential impact on descendant communities in the region of study (Bedford *et al.* 2018). Some of these structural issues, including the “‘bone rush’ and ‘industrialisation’ of ancient DNA research” described by Matisoo-Smith have huge significance for how archaeologists, anthropologists and geneticists collaborate responsibly with each other and with local communities. We agree with many of these concerns, and hope that the collaborative, multidisciplinary, community-engaged approach that we have taken can provide a positive example for future work. Regarding our work in Vanuatu, we fully agree with Sand’s comment that “ancient DNA ... cannot be used in a vacuum, separated from the anthropological context”. Our team, including indigenous researchers and co-authors who have spent decades working with communities and cultural institutions in the country, has been keenly aware of how genetic research can be received in Vanuatu. From the beginning, our team members have been committed to long-term community, public outreach and anthropological engagement with descendant communities, involving not only communication and discussion of our results, but ongoing ethnographic research projects on their potential impact.

Sand comments that we do not highlight the “extraordinary complexity” in the history of the South-West Pacific. This is to miss the main result of our paper – that the arrival of Papuan-like genetic ancestry in Vanuatu was a complex, rather than a simple, replacement of genetic ancestry, during which a lingua franca from an entirely different language family was adopted and maintained in the face of significant demographic change. This seems extraordinarily complex to us, as we repeatedly emphasise throughout our paper. Sand further states that genetic research on population history can undermine “the historical rights of the indigenous populations of Southern Melanesia, perpetuating a form of intellectual colonial power”. We reject this outright for our work in Vanuatu. Every stage of our team’s modern genetic sampling process involved explicit discussions about how this research – much like previous linguistic and archaeological research – has literally no place in disputes over land or historical rights, which in any case do not tend to take place at such a low-resolution, regional scale. We reject the notion that

having a particular genetic or linguistic ancestry should dictate how people perceive or enact their lives, and we are continuously engaged in discussion of these questions with participating communities and in ongoing research projects in Vanuatu. Specifically, on access and use of genetic data for population historical analyses, Sand comments critically on our permission to reanalyse previously published genotyping data (Parks *et al.* 2017). However, the subset of data – provided by our co-authors – that we reanalysed in Posth *et al.* (2018) has “No restrictions on use” and “No further permissions required” (Parks *et al.* 2017; Data Access Agreement, and see also <https://www.ebi.ac.uk/ega/dacs/EGAC00001000506>).

Burley describes his sense of unease, even “betrayal”, that the recent genetic work in Vanuatu has – in his view – upended archaeologists’ careful attempts to provide local empowerment through assurances of direct descent from the Lapita era. As also raised by Sand, our use of population-genetics terminology such as “turnover” or “replacement” may sound strong, but it is hard to otherwise describe such stark population genetic differences, or discontinuities, without misleading or understating their magnitude. Throughout our paper – including in the title – we stress that there is demonstrable local continuity back to the earliest Lapita settlers via the maintenance of Oceanic-Austronesian languages. Further, Burley does not indicate why contemporary Pacific Island populations cannot understand or potentially even embrace a dual or multiple-stranded heritage, which may capture more of the complexity of their history. In Vanuatu at least, intricately interwoven strands of history, from Kastom to Christianity, are already crucial in indigenous discourse on place, belonging and identity.

Many researchers working on Pacific prehistory have long embraced – as well as pioneered – interdisciplinary approaches to historical questions (see Kirch 2017). We are proud to continue within this tradition and privileged to work alongside institutions and communities in Remote Oceania that have embraced archaeological, linguistic, anthropological and, now, genetic research to understand more about their history. We are committed to continued research that is genuinely interdisciplinary, collaborative and community-orientated, and hope to further contribute to debates on the complex history of the inhabitants of the Pacific.

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