Climate Change Influenced Female Population Sizes through Time across the Indonesian Archipelago

ELSA G. GUILLOT,[1] MERYANNE K. TUMONGGOR,[2,3] J. STEPHEN LANSING,[2,4]
HERAWATI SUDOYO,[3] AND MURRAY P. COX[1]*

Abstract   Lying at the crossroads of Asia and the Pacific world, the Indonesian archipelago hosts one of the world's richest accumulations of cultural, linguistic, and genetic variation. While the role of human migration into and around the archipelago is now known in some detail, other aspects of Indonesia's complex history are less understood. Here, we focus on population size changes from the first settlement of Indonesia nearly 50 kya up to the historic era. We reconstructed the past effective population sizes of Indonesian women using mitochondrial DNA sequences from 2,104 individuals in 55 village communities on four islands spanning the Indonesian archipelago (Bali, Flores, Sumba, and Timor). We found little evidence for large fluctuations in effective population size. Most communities grew slowly during the late Pleistocene, peaked 15–20 kya, and subsequently declined slowly into the Holocene. This unexpected pattern may reflect population declines caused by the flooding of lowland hunter/gatherer habitat during sea-level rises following the last glacial maximum.

The prehistory of Island Southeast Asia is made especially complex by its position as a waypoint between mainland Asia, Australia, and the Pacific world. The region's prehistory is dominated by population movements, beginning with its first settlement by modern humans approximately 50 kya and continuing to the Islamization of Indonesia during the historic period. Reflecting the rich cultural and linguistic diversity of Indonesia's inhabitants, these eras have also left their mark on the genetic diversity of the individuals who inhabit Indonesia today (Cox et al. 2012; Jinam et al. 2012; Karafet et al. 2010; Kayser 2010; Kayser et al. 2003; Lansing et al. 2008, 2009; Mona et al. 2009; Wilder et al. 2011; Xu et al. 2012).

[1]Institute of Fundamental Sciences, Massey University, Palmerston North, New Zealand.

[2]Department of Anthropology, University of Arizona, Tucson, AZ.

[3]Eijkman Institute for Molecular Biology, Jakarta, Indonesia.

[4]Santa Fe Institute, Santa Fe, NM.

*Correspondence to: Murray P. Cox, Institute of Fundamental Sciences, Massey University, Palmerston North 4442, New Zealand. E-mail: m.p.cox@massey.ac.nz.

Although movements of people into and through Island Southeast Asia are known with some accuracy, other aspects of Island Southeast Asian prehistory remain largely obscure. Two key questions concern population sizes across the region (from its initial settlement through to modern times: Did climatic fluctuations during the late Pleistocene play important roles in contemporary population density? Did populations grow rapidly with the adoption of farming practices during the Neolithic? Estimating past population sizes from archaeological data has proven challenging (Steele and Shennan 2009; Wichmann and Holman 2009). When traditional anthropology falters, population genetics can perhaps offer a different perspective.

Inferences made from simple summaries of the data [e.g., Tajima's D (Tajima 1989) and Fu's F (Fu 1997)] suggest that Indonesian populations may have increased in size, with growth stronger in the center of the archipelago (Bali, Sulawesi, Sumba, and Flores) and weaker toward the eastern and western peripheries (Tumonggor et al. 2013). However, these summaries represent long-term average estimates, which may be misleading if population sizes have fluctuated through time rather than exhibiting a simple monotonic change. Further, many of these simple summary statistics can be conflated with other demographic factors, and their statistical power is therefore relatively low (Pilkington et al. 2008).

Here, we apply a model-free statistical inference procedure, the Bayesian skyline plot (BSP), which permits a more nuanced evaluation of past population sizes (Drummond et al. 2005). BSPs are founded on coalescent theory, which describes the evolution of genetic lineages within a population. This method can be used to infer the size of populations at different points in the past. Importantly, BSPs employ Bayesian statistics and Monte Carlo inference to explicitly model the level of uncertainty in estimates of past population sizes.

Thus far in the study of human prehistory, BSPs have mostly been applied to large regional samples, often on continental scales (Atkinson et al. 2008, 2009; Fagundes et al. 2008; Shennan 2009) or restricted to specific genetic lineages (e.g., mitochondrial DNA haplogroups; Soares et al. 2011). However, the history of haplogroups cannot be disassociated from the dynamics of the populations from which they derive (Peng and Zhang 2011). In this study, we instead focused on the evolution of small self-defined communities. BSPs have recently been inferred for a handful of indigenous populations from the Philippines (Gunnarsdóttir et al. 2011) and Malaysia (Jinam et al. 2012), where a characteristic pattern of growth and decline was detected. We extended this analysis to a large number of Indonesian populations. We focused on 55 village communities from four Indonesian islands (Bali, Flores, Sumba, and Timor) that span the Indonesian archipelago—from Bali, where genetic ancestry largely traces back to Asian sources, to Timor, with its genetic roots firmly planted in Papuan soil (Cox et al. 2010; Tumonggor et al. 2013). By leveraging data from 2,104 Indonesian volunteers, we present a new picture of population size changes across Island Southeast Asia from its first settlement to modern times.

Methods

Ethics. Biological samples were obtained by M.K.T., H.S., J.S.L., Golfiani Malik, Wuryantari Setiadi, and Loa Helena Suryadi of the Eijkman Institute for Molecular Biology, Jakarta, Indonesia, with the assistance of the Indonesian Public Health clinic staff, following protocols for the protection of human subjects established by both the Eijkman Institute and the University of Arizona institutional review boards. Permission to conduct research in Indonesia was granted by the State Ministry of Research and Technology, Republic of Indonesia.

Samples. Mitochondrial DNA diversity was screened in 2,104 consenting, closely unrelated, and apparently healthy individuals drawn from across the Indonesian archipelago (Table 1) (Tumonggor et al. 2013). Samples were collected in 55 populations from four island groups: 21 communities on Bali ($n = 486$), 9 communities on Flores ($n = 458$), 14 communities on Sumba ($n = 634$), and 11 communities on Timor ($n = 526$). Sequences are available for a minimum of 18 individuals per population (mean $n = 39$). Figure 1 shows the geographical locations of sampled populations. Participant interviews confirmed ethnic, linguistic, and geographic classifications for at least two generations into the past.

Extraction and Sequencing. DNA was extracted from peripheral blood and
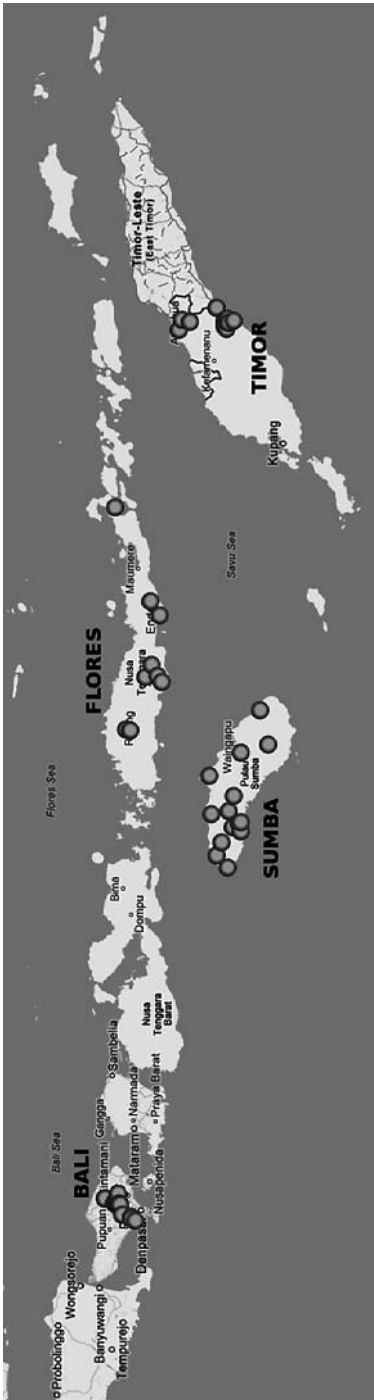
Figure 1. Geographic locations of 55 communities sampled across four Indonesian islands: Bali, Flores, Sumba, and Timor.

Table 1. Indonesian Communities with Sample Size and Inferred Modern Female Effective Population Size (N_{ef})

ISLAND/COMMUNITY	SAMPLE SIZE	MODERN N_{ef} (95% CREDIBLE INTERVAL)
Bali		
Abian Kebon	37	9,400 (1,900–44,900)
Bena	18	3,400 (600–22,800)
Calo	23	2,600 (400–16,900)
Gadon	19	16,500 (3,700–91,600)
Kebon	20	900 (100–10,000)
Kedisan Kaja	20	1,400 (200–10,500)
Kedisan Kelod	20	1,800 (200–14,200)
North Batur	19	3,300 (600–20,100)
Pujung Kaja	20	1,700 (200–13,600)
Sebatu	38	1,500 (300–8,800)
South Batur	25	7,400 (1,600–47,600)
Subak Bayad	20	2,900 (500–21,000)
Subak Bonjaka	21	1,800 (200–15,700)
Subak Jasan	23	2,500 (400–21,300)
Subak Jati	20	4,200 (700–27,100)
Subak Pakudui	19	800 (100–6,600)
Subak Tegal Suci	23	1,400 (200–9,700)
Sungi	20	2,400 (400–14,200)
Timbul	18	3,200 (600–20,500)
Tungkub	18	5,500 (1,000–36,000)
Yeh Tampuagan	45	5,400 (1,200–29,400)
Flores		
Bama	49	2,400 (400–15,400)
Bena	46	6,200 (1,200–35,600)
Boawae	26	48,800 (10,900–318,000)
Cibol	55	1,300 (200–10,400)
Rampasasa	106	3,000 (600–16,400)
Seso	66	7,900 (1,800–31,200)
Wogo	36	7,500 (1,500–37,800)
Woloara	29	12,600 (2,700–57,100)
Wolotopa	45	10,100 (2,200–44,700)

buccal swabs. DNA extractions, polymerase chain reaction amplifications, and Sanger sequencing were performed as described elsewhere (Tumonggor et al. 2013); 350 bp of the first hypervariable segment (HVS1) were sequenced and analyzed further. All individuals showed indigenous Indonesian ancestry.

Summary Statistics. Point estimates of relative population sizes were obtained with unbiased estimators of the population mutation rate. Four summaries—θ_π (Tajima 1983), θ_k (Ewens 1972), θ_S (Watterson 1975), and θ_h (Charkraborty and Weiss 1991)—were calculated with Arlequin version 3.11 (http://cmpg.unibe.ch/software/arlequin3/; Excoffier et al. 2005). Assuming constant population sizes and a single underlying mutation rate, we noted that these estimates scale linearly

ISLAND/COMMUNITY	SAMPLE SIZE	MODERN N_{ef} (95% CREDIBLE INTERVAL)
Sumba		
Anakalang	47	3,400 (600–21,700)
Bukambero	50	4,800 (800–30,100)
Bilur Pangadu	54	9,400 (2,100–49,200)
Kodi	42	3,000 (500–18,000)
Lomboya	49	4,100 (700–27,100)
Loli	34	4,200 (600–37,300)
Mahu	45	10,700 (2,400–21,800)
Mamboro	52	1,900 (300–13,800)
Mbatakapidu	41	3,200 (600–20,200)
Praibakul	57	5,100 (800–34,900)
Rindi	28	29,000 (7,200–172,000)
Waimangura	50	4,200 (500–43,200)
Wanokaka	52	5,300 (1,100–29,500)
Wunga	33	1,700 (300–12,100)
Timor		
Besikama	42	5,500 (1,000–30,100)
Fatuketi	35	2,700 (400–22,900)
Kakaniuk	49	700 (100–7,500)
Kamanasa	67	11,800 (2,200–94,800)
Kateri	50	5,000 (700–57,900)
Kletek	69	1,700 (200–15,500)
Laran	50	6,300 (1,100–48,500)
Raimanawe	50	5,200 (900–40,300)
Tialai	24	1,700 (200–13,900)
Umaklaran	41	1,800 (200–19,500)
Umanen Lawalu	49	1,600 (200–13,900)

Effective sizes are rounded to the nearest hundred.

[a]Note that 95% credible intervals reach their greatest breadth at the present. For most population size estimates in the past, these bounds can be as much as an order of magnitude smaller.

with the female effective population size, $N_{ef} = \theta/2\mu$. Rank correlations were performed to test these associations (R Development Core Team 2013).

BSPs. We explored how the effective population size of women has changed through time across the Indonesian archipelago. Historic population sizes were inferred via computationally intensive Markov chain Monte Carlo on the sample genealogy with a coalescent-based algorithm. BSPs are implemented in BEAST version 1.7.0 (http://beast.bio.ed.ac.uk/; Drummond et al. 2005, 2012) and assume a priori that sampled populations are unstructured. To explore the effects of possible metapopulation structure, we first analyzed all 55 populations separately, before subsequently combining them into their four island groups. This two-phase

framework allows us to determine the extent to which migration and population substructure may have influenced Indonesian prehistory (Cox and Hammer 2010). To check the robustness of our inferences, island groups were independently sub-sampled 10 times ($n = 50$ individuals each).

BSPs are described in detail elsewhere (Drummond et al. 2005; Ho and Shapiro 2011; Minin et al. 2008; Strimmer and Pybus 2001). In brief, this method infers historical population sizes from the shape of the genealogy (or tree) relating a sample of individuals. Coalescent theory (Kingman 1982) describes a backward-in-time process whereby a given pair of lineages shares a common ancestor, and the two lineages join (or coalesce). This process continues until only one lineage is left—the most recent common ancestor of the sampled individuals. The speed at which lineages coalesce primarily depends on the size of the population in which those individuals live. Two individuals are more likely to share a parent in a small population (thus, coalescent events occur frequently), whereas two individuals are less likely to share a parent in a large population (thus, coalescent events are more rare). This distribution of coalescent events is recorded in the genealogy of mitochondrial lineages. Working in reverse, the distribution of nodes (or coales-cence points) in the genealogy can be used to estimate population sizes from the present backward into the past. BSPs employ computationally intensive statistics to infer population size changes that best fit the observed genealogy. Importantly, the method also places credible intervals on these population size estimates.

BSPs must be interpreted with care. Recent population growth (which is not observed here) can mask earlier demographic history (Grant et al. 2012). Similarly, population structure can alter the distribution of coalescence points (Pannell 2003). We explore in detail the role played by population structure. Throughout this analysis, we focus on general trends across multiple independently sampled populations, rather than the detailed interpretation of individual graphs.

BSPs used the Hasegawa-Kishino-Yano substitution model with heterogene-ity allowed among sites according to a Γ distribution together with a lognormal molecular clock model (Drummond et al. 2006; Kitchen et al. 2008; Soares et al. 2011). Piecewise linear reconstructions with five change points were started with an unweighted pair group method with arithmetic mean tree. Inferences are scaled to chronological time with a mutation rate of 1.64×10^{-7} events/nucleotide/year for the HVS1 sequence variation (Soares et al. 2009). Graph axes can be linearly scaled for alternative mutation rates, such as the higher estimates proposed by Scally and Durbin (2012). Markov chains were run for 5×10^5 steps with a 5×10^4 step burn in. Output files were analyzed in Tracer version 1.5 (http://tree.bio.ed.ac.uk/software/tracer/). Markov chains were tested for convergence to their stationary distributions, and demographic reconstructions were only accepted if the estimated sample size of all inferred parameters exceeded 100. The influence of all starting parameters, including sample size and number of change points, was checked, but found to have little impact on final results.

We note that BSPs are computationally intensive. The following results re-quired approximately 10,000 computer hours on fast Intel Xeon X5690 processors.

Computations were run on UNIX-based high-performance computing clusters at Massey University (Palmerston North, NZ).

Effective female population sizes were calculated by scaling median BSP estimates with a generation time of 25 years (Fenner 2005). Population substructure was explored by summing the population-level effective sizes and comparing them with pooled island group size estimates. The time of peak population size is defined as the point at which each population reaches its maximal effective population size. Land surface area as a function of time was reconstructed from sea level curves in Coller (2007) and land area estimates in Sathiamurthy and Voris (2006).

Results

BSPs illustrating changes in N_{ef} through time are presented for all 55 Indonesian populations in Figure 2. The *y*-axis shows the female effective size of each population, and the *x*-axis shows time, in years, moving backward into the past. Population sizes have not fluctuated rapidly through time. A trend common for all the plots is slow population growth during the Pleistocene before population size declines again during the Holocene. Growth rates during the Pleistocene were on the order of 0.18 individuals per year, with later population declines of around 0.31 individuals per year (Figure 3). Extended BSP runs (Heled and Drummond 2008), computed for a subset of populations, infer nonzero change points, thus providing statistical evidence that population sizes have changed through time. Curiously, population sizes typically peaked 15–20 kya, well before the period of population growth that is generally assumed to have occurred during the Neolithic.

Effective female population sizes vary greatly between communities, with average through-time values ranging broadly from 1,000 to 15,000 (Figure 3). The 95% credible intervals increase markedly toward the present, such that estimates of modern effective sizes lack strong statistical support. Community sizes and trends through time are similar between islands, with no clear distinctions between islands dominated by Asian ancestry (e.g., Bali) and islands dominated by Papuan ancestry (e.g., Timor).

Two community outliers warrant particular attention—the inferred population size of Boawae (Flores) approaches 50,000, whereas that of Rindi (Sumba) reaches approximately 30,000. Both groups differ from surrounding populations by suggesting rapid demic growth right up to the present. Boawae can be distinguished from other population samples in that it once hosted a minor princedom. Boawae later became an administrative center during the Dutch colonial era and now acts as an urbanized district capital (*kecamatan*). Previous research has noted the diverse genetic profile of this sample, which inadvertently includes a large proportion of civil servants with ancestry from elsewhere in Indonesia (Lansing et al. 2008). We propose that the Boawae analysis is dominated by this large-scale (although transient) immigration, therefore reflecting a biased composite sample from across Indonesia, not the local community at Boawae.

Conversely, Rindi has remained relatively isolated but is the site of the
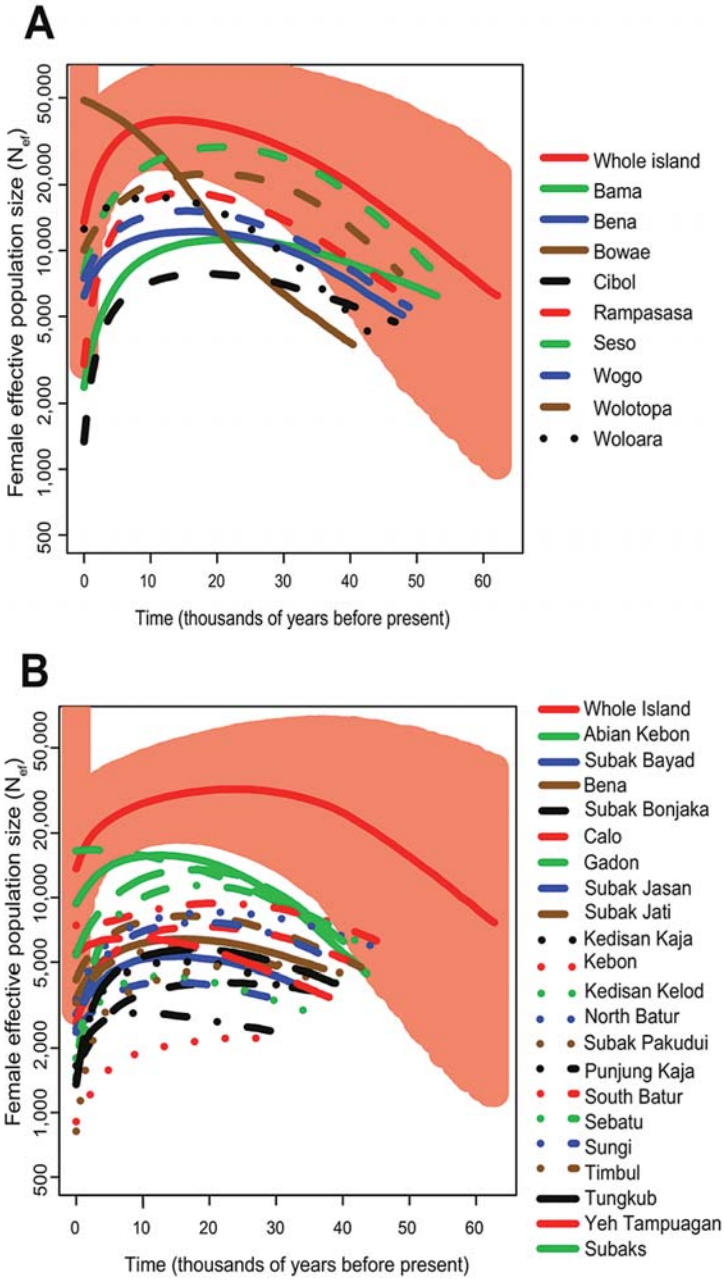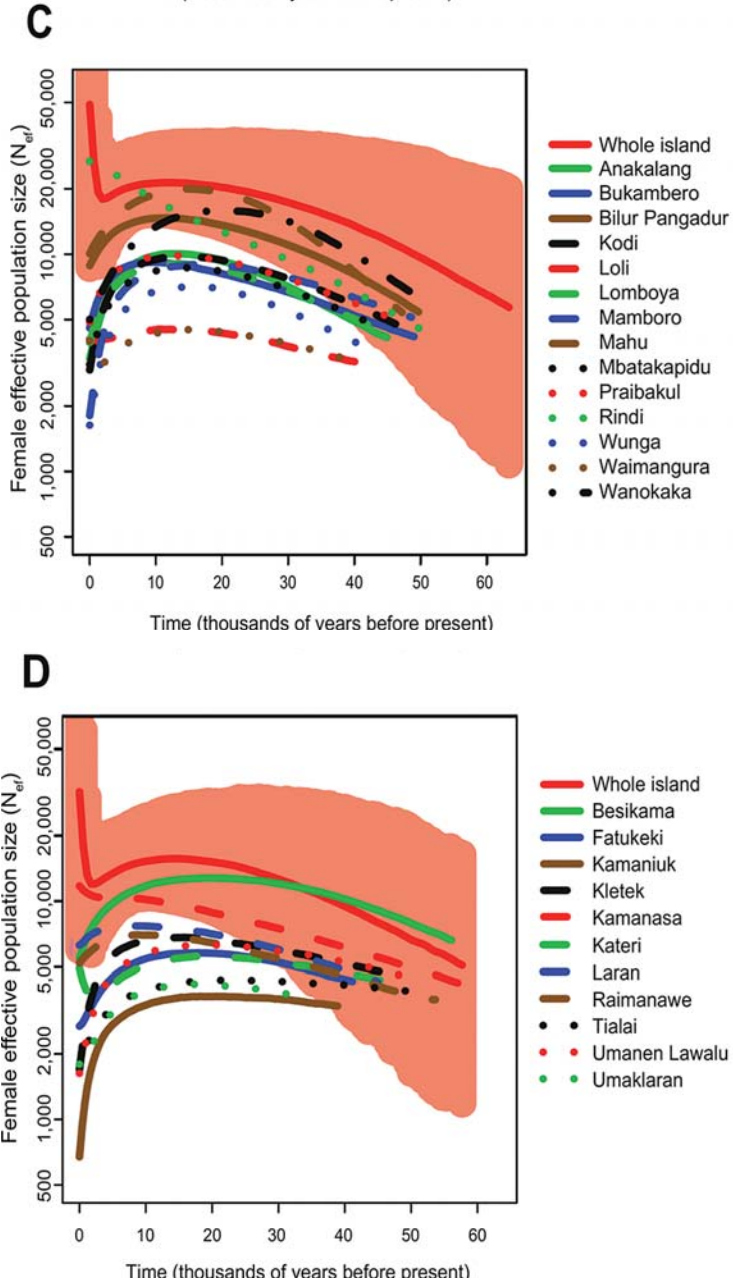
Figure 2. BSPs of female effective population sizes (N_{ef}) through time for communities on Flores (A), Bali (B), Sumba (C), and Timor (D). Effective sizes are plotted on a log scale. Shaded areas represent the 95% credible interval for each island metapopulation (i.e., all populations pooled from a given island).
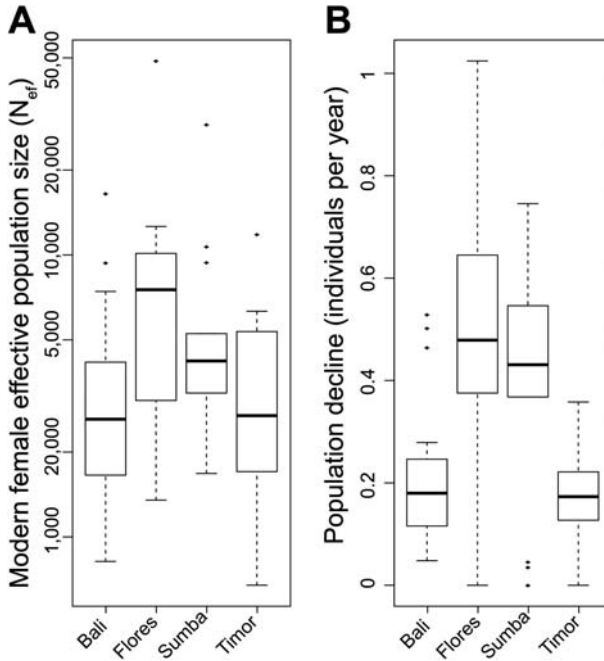
Figure 3. (A) Distribution of modern female effective population sizes (N_{ef}). (B) Distribution of rates of population decline following peak population size.

most powerful chiefdom in eastern Sumba. The social system in Rindi is strongly biased toward patrilocality (Forth 1981), which has had a substantial impact on the community's genetic diversity. Indeed, Rindi exhibits the most extreme difference in male versus female effective sizes of any of our sampled communities (Lansing et al. 2011). Patrilocal marriage practices favor high female immigration, whereby husbands remain in Rindi but wives are attracted from elsewhere in Sumba. This activity increases the genetic diversity of female lineages and likely accounts for the observed increase in N_{ef} over time.

We note that the 95% credible intervals are broad for all population size estimates, especially at the present, and we are therefore reluctant to dwell on exact values, instead emphasizing relative trends. Nevertheless, BSPs closely mirror estimates from summary statistics that contain information about effective population sizes. Modern N_{ef} values calculated from BSPs are highly correlated with θ_π ($r_S = 0.39$, $p = 0.003$), θ_k ($r_S = 0.92$, $p < 0.001$), θ_S ($r_S = 0.69$, $p < 0.001$), and θ_h ($r_S = 0.80$, $p < 0.001$).

Curiously, when modern census sizes are available, our estimates of effective population size often exceed these by an order of magnitude. The number of households in these communities, which is defined as the number of male family heads, averages around 280 (Lansing et al. 2008). We believe that this
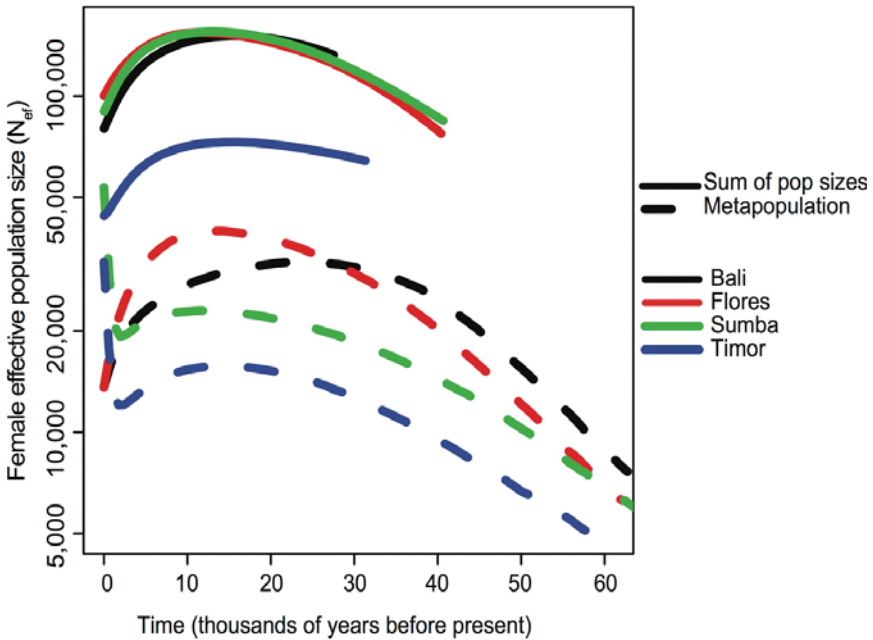
Figure 4. BSPs of female effective population sizes (N_{ef}) through time for each island metapopulation (dashed lines) and the sum of effective population sizes for individual island communities (solid lines). Effective sizes are plotted on a log scale.

discrepancy may have two causes. First, individual households may actually contain multiple generations of reproductive age women. Second, BSPs assume that sampled communities form natural populations, but Indonesian communities are typically structured with evidence of frequent interpopulation migration (Lansing et al. 2007).

A metapopulation structure can affect the coalescent reconstruction of population history (Pannell 2003). To explore the effects of structure and migration in these Indonesian communities, we pooled communities within island groups and ran single BSPs for Bali, Flores, Sumba, and Timor (Figure 4, dashed lines). Overall trends broadly mirror those of individual communities, thus suggesting that BSPs are relatively insensitive to population structure when inferring relative changes in effective population size through time. However, numeric size estimates are less concordant. Population sizes inferred for island groups as a whole are typically much smaller than the sum of population sizes inferred for individual communities on those islands. This suggests that migration between communities inflates individual population estimates because shared haplotypes may be counted multiple times in different communities.

Across all four islands, populations reached their peak sizes during the late Pleistocene (Figure 5). Excluding three populations that have grown continuously
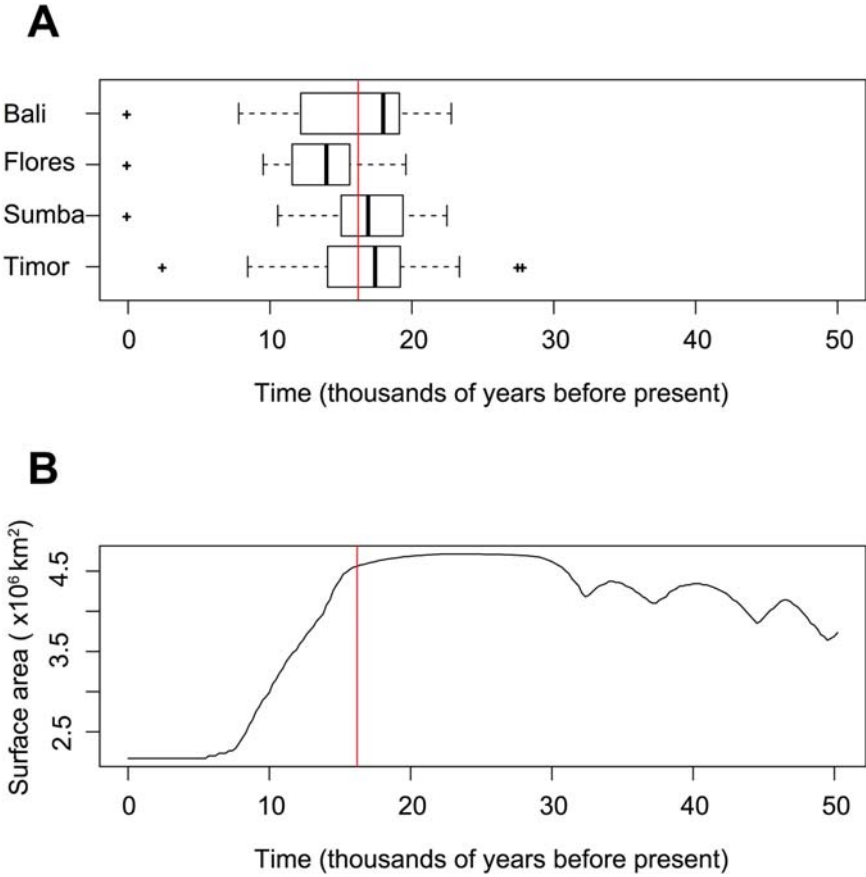
A

B

Figure 5. (A) Distribution of times of peak population size. (B) Surface area of the Sunda Shelf since its settlement by modern humans (Sathiamurthy and Voris 2006). The vertical line on both plots shows the mean time of peak population size excluding the three populations with maximal population size in the present.

to the present, population sizes peaked on average approximately 16 kya. This date closely matches the time at which sea levels began to rise at the end of the last glacial maximum, which in turn is tightly linked to a precipitous decline in the land area of the Sunda Shelf.

Discussion

We infer that Indonesian populations grew slowly through the late Pleistocene, peaked 15–20 kya, and then declined slowly through the Holocene. Curiously, the trends of past population sizes do not differ substantially between islands,

even though Balinese women largely carry mitochondrial DNA variants with Asian ancestry, whereas the mitochondrial DNA genomes of Timorese women predominantly derive from Papuan progenitors (Cox et al. 2010; Karafet et al. 2010; Xu et al. 2012).

We note that peak population sizes occur around the last glacial maximum (Figure 5). During this period, sea levels were at their lowest, and Indonesia was dominated by vast continental landmasses (Bellwood 2007). As sea levels rose, the large Sunda Shelf fragmented into isolated islands, likely scattering Southeast Asian populations and altering existing patterns of exchange between them. Because of this massive flooding, over two million square kilometers of lowland plains were lost across continental Sundaland alone, including the extensive and extremely fertile river valleys lying between Sumatra, Java, and Borneo. Indigenous populations were forced up into mountainous tropical forests, which have been called "green deserts" for their paucity of resources for hunter/gatherer communities. We propose that population declines observed during the tail end of the Pleistocene reflect this influential geological event.

Conversely, we do not see increasing population sizes during the Holocene. Geographical expansion and population growth are usually considered synonymous (Excoffier et al. 2009), but at least, in theory, can be mutually exclusive. Indonesia shows strong evidence for geographical expansions (Soares et al. 2008), not least a proposed major influx of Austronesian-speaking populations approximately 4 kya (Karafet et al. 2010; Tumonggor et al. 2013). Competing demographic scenarios predict strong population growth during the Neolithic (Bellwood 2007; Oppenheimer 1999). An association between growth and the rise of farming societies has recently been shown for Europe and eastern Asia, although much more weakly for sub-Saharan Africa (Cox et al. 2009; Gignoux et al. 2011). We also observe this pattern with BSPs for Europe (data not shown), but instead propose slow declines in population size during the Holocene for Indonesia. Even though the spread of farming groups is well documented genetically, with several mitochondrial lineages reflecting mid-Holocene population dispersals in Island Southeast Asia (Hill et al. 2007), we suggest that these dispersals did not substantially increase Indonesia's overall population size. Perhaps the spread of Neolithic populations occurred concomitantly with the assimilation or replacement of earlier hunter/gatherer groups, rather than providing an additional population load as communities expanded. If so, this scenario has implications for traditional wave-of-advance models (Ammerman and Cavalli-Sforza 1979), which often assume that the geographic expansion of farming populations is coupled with strong population growth. Rapid population growth was observed during the European colonization of North America, when settlers moved increasingly westward in search of freehold farmland (Billington 1974). However, colonial era expansions were often fueled by overpopulated urban sources in Europe, and this long-distance migration may have differed substantially from the processes driving the expansion of Neolithic farmers. How these two models agree or differ would benefit from further consideration.

We also note that recent, historic increases in population size are not reflected in these analyses. Indonesia has experienced an extreme, recent population growth, particularly during the colonial period. For instance, the population of Java increased 20-fold within 200 years—from approximately 7 million people in 1830 (Bleeker 1869) to approximately 140 million inhabitants today (Central Intelligence Agency 2013). However, mutation rates are correspondingly low (e.g., 1.64×10^{-7} events/nucleotide/year; Soares et al. 2009), and these recent size changes are not yet adequately reflected in the genetic record. Our estimates of community sizes are therefore not optimally reliable for the very recent past. Alternately, the lack of any strong growth signal may be caused by our focus on small, relatively marginal populations, especially on the sparsely populated eastern Indonesian islands of Flores, Sumba, and Timor. These communities may have experienced recurrent extinctions and recolonizations coupled with weak population growth, in marked contrast to the densely populated western islands of Sumatra and Java.

Comparative data are largely unavailable, but BSPs have been used to infer population size changes in four communities on Mindanao in the Philippines ($n = 92$), including one negrito group, the Mamanwa (Gunnarsdóttir et al. 2011). Identical patterns were observed in four communities from peninsular and island Malaysia ($n = 86$; Jinam et al. 2012). In both cases, whole mitochondrial DNA genome sequences were generated, but only for a very small number of samples. This alternative strategy involves deep, whole mitochondrial DNA genome sequencing of relatively few samples (i.e., tens of individuals) compared with our shallow HVS1 sequencing of many samples (i.e., thousands of individuals). Interestingly, however, all three sets of results are remarkably similar. All analyses show population growth during the Pleistocene, followed by population peaks 15–20 kya and a decline in effective population sizes during the Holocene. Seeing the geographical distribution of these samples (from Malaysia through Indonesia and the Philippines), we suggest that the pattern described here holds for large tracts of Island Southeast Asia, and even for populations with very different histories (e.g., western Indonesian groups and Philippine negritos). This has implications for genetic reconstructions of population history for small ethnic groups (Heyer et al. this issue), as well as studies of language evolution (Dunn et al. this issue; Reid this issue). Southeast Asian groups have extremely diverse cultures and histories, but common patterns of population size change emphasize the substantial impact of common environmental forces. These must be taken into account when studying community histories and population interactions.

Previous research has shown that the rich genetic diversity of Indonesia is driven by 50,000 years of population movements into and within Indonesia. Despite this complexity, Indonesian populations have surprising consistency in one key demographic factor: their dynamics of past population size. Communities from Bali to Timor have different origins, population histories, local environments, and selection pressures. However, they all exhibit broadly similar trends in community size through time. Although strictly recording the history of women, the histories of men and women are necessarily coupled, and our mitochondrial estimates likely

reflect changes in these communities as a whole. Developments to modify BSPs for Y-chromosome data will confirm whether this assertion is valid. Regardless, we suggest that the biggest influence on population size changes through Indonesian prehistory is not the expansion of Neolithic farming groups, but a regional decline in population size following the flooding of lowland Indonesia caused by a warming climate in the Arctic. This rapid change from a continental landmass to the modern maritime nation still resonates in the genomes of Indonesian people today.

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