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Original Article:

Reconstructing the Demographic History of Orang-utans using Approximate Bayesian Computation

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1 **Abstract**

2 Investigating how different evolutionary forces have shaped patterns of DNA variation within
3 and among species requires detailed knowledge of their demographic history. Orang-utans,
4 whose distribution is currently restricted to the Southeast Asian islands of Borneo (*Pongo*
5 *pygmaeus*) and Sumatra (*Pongo abelii*), have likely experienced a complex demographic
6 history, influenced by recurrent changes in climate and sea levels, volcanic activities and
7 anthropogenic pressures. Using the most extensive sample set of wild orang-utans to date, we
8 employed an approximate Bayesian computation (ABC) approach to test the fit of 12 different
9 demographic scenarios to the observed patterns of variation in autosomal, X-chromosomal,
10 mitochondrial and Y-chromosomal markers. In the best-fitting model, Sumatran orang-utans
11 exhibit a deep split of populations north and south of Lake Toba, probably caused by multiple
12 eruptions of the Toba volcano. In addition, we found signals for a strong decline in all
13 Sumatran populations ~24 ka, probably associated with hunting by human colonizers. In
14 contrast, Bornean orang-utans experienced a severe bottleneck ~135 ka, followed by a
15 population expansion and substructuring starting ~82 ka, which we link to an expansion from
16 a glacial refugium. Therefore, we showed that orang-utans went through drastic changes in
17 population size and connectedness, caused by the recurrent contraction and expansion of
18 rainforest habitat during Pleistocene glaciations, and probably also by the impact of hunting
19 by early humans. Our findings also emphasize the fact that important aspects of the
20 evolutionary past of species with complex demographic histories might remain obscured
21 when applying overly simplified models.

22 **Introduction**

23 Patterns of DNA variation are the result of both adaptive and non-adaptive processes, and the
24 debate about the relative importance of natural selection and random genetic drift in shaping
25 genetic diversity within and among species is still ongoing (e.g. Hahn 2008; Nei *et al.* 2010).
26 A common approach to detect signals of selection aims at identifying genomic regions that
27 show marked deviations in DNA variation from a neutral equilibrium model (reviewed in
28 Nielsen 2005). However, in certain demographic scenarios, such as population size changes or
29 population subdivision, random genetic drift can result in similar deviations as selection (e.g.
30 Excoffier *et al.* 2009; Teshima *et al.* 2006). Therefore, confounding effects of demographic
31 processes can only be unravelled from selective signals if the demographic history is
32 explicitly taken into account when formulating the expectations under the neutral model
33 against which observed patterns of DNA variation are tested (e.g. Haddrill *et al.* 2005; Stajich
34 & Hahn 2005). Consequently, methods to reconstruct the demographic history of natural
35 populations have recently generated great interest among evolutionary geneticists, as recent
36 technical advances allow conducting genome-wide studies of selection in a large variety of
37 species (reviewed in Ellegren 2014).

38 Orang-utans, currently restricted to two distinct species on Borneo (*Pongo pygmaeus*) and
39 northern Sumatra (*Pongo abelii*) (Wich *et al.* 2008), are the only Asian great apes and are
40 phylogenetically most distant to humans (Groves 2001). Their ancestral position in the lineage
41 leading to African great apes and modern humans has evoked great interest in this taxon in the
42 overall effort to reconstruct the adaptive evolutionary history of great apes in general and
43 humans in particular (Locke *et al.* 2011; Prado-Martinez *et al.* 2013). However, orang-utans
44 might have experienced a complex demographic history, as their distribution has been subject
45 to major changes during the Pleistocene. The ancestors of extant orang-utans have
46 sequentially colonized the islands of the Sunda archipelago arriving from the Southeast Asian
47 mainland (Delgado & Van Schaik 2000; Rijksen & Meijaard 1999). Since then, their
48 population history was strongly influenced by geological and climatic events: rising and
49 falling sea levels cyclically connected and isolated the islands of Sundaland, allowing for
50 potential terrestrial migration between the islands at certain points in time (Voris 2000).

51 Major volcanic eruptions, mainly on Sumatra and Java, might have led to the extinction of
52 local orang-utan populations and subsequent re-colonisations (Muir *et al.* 2000). Of special
53 interest here is the Toba volcano on northern Sumatra, which has seen at least four major

54 eruptions during the last 1.2 million years (Chesner *et al.* 1991). This sequence of eruptions
55 culminated in the Toba supereruption ~73 ka, which is considered to be the most powerful
56 volcanic eruption within the last 25 million years (Chesner *et al.* 1991) and is thought to have
57 had severe consequences for flora and fauna on Sundaland (Williams *et al.* 2009). In the Late
58 Pleistocene, all orang-utan populations on the mainland, southern Sumatra and Java went
59 extinct (Delgado & Van Schaik 2000; Rijksen & Meijaard 1999). Climatic changes during the
60 Pleistocene might have been responsible for the southward shift of the distribution and the
61 disappearance of orang-utans from the mainland (Jablonski 1998). Moreover, anthropogenic
62 factors, such as prehistoric hunting by hunter-gatherer societies, are likely to have played a
63 significant role in the decline and extinction of orang-utans populations on insular Southeast
64 Asia (Delgado & Van Schaik 2000).

65 Genetic signals of these past demographic changes have been found in studies of genetic
66 diversity in extant orang-utan populations on Borneo and Sumatra. Most genetic studies
67 analysing autosomal and mitochondrial DNA (mtDNA) agree that Sumatran orang-utans
68 show a higher level of sequence diversity and corresponding long-term effective population
69 size (N_e) (Locke *et al.* 2011; Muir *et al.* 2000; Prado-Martinez *et al.* 2013; Steiper 2006;
70 Zhang *et al.* 2001), even though Sumatran orang-utans have a much smaller current census
71 size and a more restricted distribution than Borneans (~6,600 vs. ~54,000 individuals, Wich *et al.*
72 2008). This large N_e of the Sumatran species was interpreted as a signal of immigration
73 from multiple differentiated populations into the current Sumatran gene pool (Muir *et al.*
74 2000; Steiper 2006). However, Y-chromosomal diversity in orang-utans shows the opposite
75 pattern compared to mtDNA and autosomal data, with a smaller N_e on Sumatra than Borneo
76 (Nater *et al.* 2011). Such contrasting patterns of N_e between species and among genomic
77 regions hint at complex population dynamics that have so far not been properly investigated.

78 Recently, Locke *et al.* (2011) used extensive single-nucleotide polymorphism (SNP) data
79 from whole-genome resequencing of five Bornean and five Sumatran orang-utans to model
80 the demographic history of the two species. They found that a model with a population split
81 ~400 ka with subsequent gene flow between Borneo and Sumatra fits the observed data best.
82 Furthermore, Locke and colleagues inferred that Sumatran orang-utans underwent a
83 continuous exponential population growth since the population split, while Bornean orang-
84 utans were subject to a continuous exponential decline. Given the large amount of genetic
85 data, the study by Locke and colleagues is currently regarded as the most accurate
86 reconstruction of demographic history in orang-utans to date. However, the demographic

87 modelling approach by Locke and colleagues did not take several idiosyncrasies of orang-utan
88 biology into account, thus severely limiting the conclusions that could be drawn from their
89 findings.

90 First, it has been shown that biased sampling and disregard of population structure will
91 produce misleading results regarding N_e and its temporal changes (Chikhi *et al.* 2010; Stadler
92 *et al.* 2009). The study by Locke and colleagues incorporated data from only five captive
93 individuals each from Borneo and Sumatra without further provenance information. This
94 limited genetic sampling is unlikely to represent the entire genetic diversity present on both
95 islands. Second, given this lack of detailed sample provenance, the analyses were restricted to
96 models that treated Bornean and Sumatran orang-utans as single panmictic populations each.
97 Previous work, however, unequivocally showed that both Bornean and Sumatran orang-utans
98 are deeply structured genetically (Arora *et al.* 2010; Nater *et al.* 2011; Warren *et al.* 2001).
99 Especially on Sumatra populations north and south of Lake Toba exhibit high genetic
100 differentiation (Nater *et al.* 2013; Nater *et al.* 2011). Third, Locke and colleagues did not test
101 complex demographic models including population bottlenecks or recent declines, as
102 suggested in previous genetic studies. For example, genetic signals of a bottleneck with
103 subsequent population expansion on Borneo might be linked to a glacial refugium or the
104 impact of the Toba supereruption ~ 73 ka (Arora *et al.* 2010; Steiper 2006), and patterns of a
105 recent population decline in Sabah, Borneo, are most likely attributable to recent
106 anthropogenic pressures (Goossens *et al.* 2006).

107 Reconstructing the demographic history of a species has long been hindered by the fact that
108 full-likelihood methods were restricted to relatively simple demographic models (e.g. Hey &
109 Nielsen 2004; Wilson *et al.* 2003), which might not capture all relevant processes in complex
110 demographic settings. This restriction is mainly caused by the fact that the computation of the
111 likelihood function of complex demographic models with many parameters is either
112 intractable or computationally too expensive, especially for large data sets (Marjoram *et al.*
113 2003). Approximate Bayesian computation (ABC) allows circumventing these problems by
114 approximating the likelihood functions with simulations of genetic data under a given
115 demographic model (Beaumont *et al.* 2002; Marjoram *et al.* 2003). In order to estimate the
116 model parameters, parameter values are drawn from predefined prior distributions and used to
117 simulate genetic data matching the observed data in type of markers and number of loci. Both
118 observed and simulated data are then reduced to a set of summary statistics and the Euclidian
119 distance between the observed and the simulated summary statistics is calculated. Based on

120 the subset of simulations with the smallest Euclidian distance between observed and
121 simulated data, the posterior distribution of the model parameters can be approximated and
122 the relative fit of different demographic models to the data can be assessed.

123 Here we present an ABC modelling approach of the demographic history of orang-utans
124 based on autosomal and sex-linked marker systems. We aim to improve the current
125 knowledge of demographic history by applying three major improvements over previous
126 studies. First, we capitalize on the knowledge base of behavioural ecology and population
127 genetics of orang-utans in order to test realistic demographic models. Second, due to our
128 extensive set of orang-utan samples with detailed and reliable provenance, we are able to
129 investigate models incorporating population substructure in both orang-utan species, which
130 allows us to disentangle changes in population size from confounding effects due to changes
131 in population structure. Third, by combining autosomal and sex-linked markers into a
132 combined demographic analysis, we make use of the specific information content of different
133 marker systems in this species with its heavily sex-biased dispersal. Due to strong female
134 philopatry in orang-utans (Arora *et al.* 2012; Galdikas 1995; van Noordwijk *et al.* 2012),
135 mitochondrial markers contain information about population split times without the
136 confounding influence of gene flow. In contrast, Y-chromosomal loci should have more
137 power than autosomal markers to reveal low levels of male-mediated gene flow.

138 **Materials & Methods**

139 **Sample Collection and Genetic Markers**

140 A representative sampling scheme covering the whole range of a species is crucial for
141 accurate reconstruction of demographic history (Stadler *et al.* 2009). We used an extensive set
142 of samples from wild-born orang-utans from ten sampling locations, covering the entire
143 distribution of the genus (Figure 1, see Supporting Material for detailed information about
144 sample origin). Samples were analysed for several genetic marker systems with different
145 modes of inheritance and effective population sizes (Table 1), thus ensuring representation of
146 both male and female population history, an important aspect in demographic reconstructions
147 in species with strongly sex-biased dispersal (Nater *et al.* 2011; Nietlisbach *et al.* 2012).

148 The autosomal microsatellite data contained genotypes of 25 microsatellite markers from a
149 total of 237 individuals (Arora *et al.* 2010; Greminger *et al.* 2014; Nater *et al.* 2013). We also
150 included sequences from three mtDNA genes with a total length of 1,355 bp from 118

151 individuals (Nater *et al.* 2011), and Y-chromosomal haplotypes based on 11 Y-linked
152 microsatellite loci from 129 individuals (Nater *et al.* 2011). We complemented the data set by
153 additionally sequencing 8,055 bp of the non-coding X-chromosomal region Xq13.3
154 (Kaessmann *et al.* 2001) in 36 individuals and four non-coding autosomal regions (Fischer *et*
155 *al.* 2006) of a total of 8,238 bp in 22 individuals. Basic summary statistics for all marker
156 systems are provided in Table 2. The primers and cycling conditions used for PCR
157 amplification and sequencing of the X-chromosomal and autosomal regions are described in
158 the Supporting Table S1.

159 **Approximate Bayesian Computation**

160 *Model Selection Procedure*

161 We reconstructed the demographic history of orang-utans using an ABC approach
162 implemented in the software package ABCtoolbox v1.1 (Wegmann *et al.* 2010). To achieve
163 this goal, we first performed a model selection procedure, in which we used a hierarchical
164 approach to test a total of 12 different demographic models (Figure 2) with increasing levels
165 of complexity (see Supporting Tables S3 and S4 for more details about model
166 parameterisation and prior distributions).

167 We started by testing four relatively simple models that assumed a single population for each
168 of the two orang-utan species (Figure 2A). The first model in this set (I2) assumed constant
169 population sizes and no migration between the two populations. The second model (IM2)
170 incorporated asymmetric migration after the population split, up to a point in the past where
171 migration between Borneo and Sumatra ceased. Gene flow in all models with migration was
172 strictly male-mediated, as recent genetic and behavioural findings showed extreme female
173 philopatric tendencies in orang-utans (Arora *et al.* 2012; Nater *et al.* 2011; van Noordwijk *et*
174 *al.* 2012). The third model (IM2-GR) additionally allowed the two populations to change size
175 exponentially after the population split and corresponded largely to the favoured model in the
176 genomic study by Locke *et al.* (2011). In the fourth and most complex 2-population model
177 (IM2-BN-GR), both populations retained a constant size after the population split, with the
178 possibility for a sudden population size rescale followed by exponential growth or decline.

179 In order to test more biologically relevant demographic scenarios, we designed a series of 10-
180 population models that incorporated the repeatedly reported extensive population substructure
181 in extant orang-utan populations (Arora *et al.* 2010; Goossens *et al.* 2005; Kanthaswamy *et al.*
182 2006; Nater *et al.* 2013; Nater *et al.* 2011; Warren *et al.* 2001). The use of ten extant

183 population units models is justified by previously published data (Arora *et al.* 2010;
184 Greminger *et al.* 2014; Nater *et al.* 2013; Nater *et al.* 2011), and the combination of patterns
185 of population differentiation in both mtDNA and autosomal microsatellite markers, pointing
186 to six populations on Borneo, one Sumatran population south of Lake Toba, and three
187 Sumatran populations north of Lake Toba (see validation for ten population units in
188 Supporting Figures S1 and S2). For all 10-population models, we assumed equal population
189 sizes and equal symmetric migration rates among all populations within Borneo and among
190 all populations north of Lake Toba, respectively, as well as a separate population size
191 parameter for the population south of Lake Toba. We included asymmetric migration rates
192 between Borneo and south of Lake Toba, and between north of Lake Toba and south of Lake
193 Toba.

194 To assess to what extent the additional population units improve model fit, we first tested the
195 best-fitting 2-population model against two basic 10-population models (IM10 and IM10-
196 BOSU, Figure 2B). The IM10 model incorporated the population splitting sequence derived
197 from mtDNA data, i.e. the populations north and south of Lake Toba show the oldest split,
198 while Bornean populations diverged after this split (Nater *et al.* 2011). As this is in
199 discordance with the current species designation (Groves 2001), which assigns a single
200 species each to Sumatra and Borneo, we also tested this model against a model following the
201 species split pattern (IM10-BOSU), i.e. with the oldest split between Sumatra and Borneo, to
202 see if incomplete lineage sorting could be responsible for the particular phylogenetic pattern
203 observed for mtDNA.

204 We further tested for the presence of population size changes in the demographic history of
205 orang-utans, as suggested by previous studies (Arora *et al.* 2010; Goossens *et al.* 2006; Locke
206 *et al.* 2011; Steiper 2006). First, we tested for signals of recent declines on Sumatra (IM10-
207 DECSU), Borneo (IM10-DECBO) or both islands (IM10-DECALL) (Figure 2C).

208 In a second test, we evaluated the support for a bottleneck on Borneo (IM10-BNBO-DECSU),
209 possibly linked to a refugium during the penultimate glaciation (Arora *et al.* 2010) (Figure
210 2D).

211 Last, we tested for evidence for a bottleneck on Sumatra linked to the Toba supereruption,
212 either allowing for a broad prior range of the magnitude of decline (IM10-BNBO-TOBA-
213 DECSU) or restricting to a severe bottleneck of less than 100 individuals in each of the four

214 Sumatran populations (IM10-BNBO-RECOL-DECSU), resembling a founder effect after
215 local extinction and re-colonization events on Sumatra (Figure 2E).

216 *ABC Data Simulation*

217 To simulate genetic data under different demographic models, we used the software
218 FASTSIMCOAL v1.1.2 (Excoffier & Foll 2011). Simulations for the different marker
219 systems were run with the same set of parameters, whereby the effective population sizes
220 were scaled 1 to 0.75, 0.25, and 0.25 for autosomal, X-chromosomal, mitochondrial and Y-
221 chromosomal markers, respectively. We then used ARLSUMSTAT v3.5.1.3 (Excoffier &
222 Lischer 2010) to calculate a total of 259 summary statistics for each simulated data set as well
223 as for the observed data set (Supporting Table S5). The summary statistics were chosen in
224 order to capture the information in the genetic data about population differentiation, within
225 population diversity, and population size changes. To avoid problems with unreliable phasing,
226 we only used summary statistics that do not require phased sequence data for X-chromosomal
227 and autosomal loci. Since the number of simulated populations differed between the 2-
228 population and 10-population models, summary statistic would not be directly comparable
229 between the two sets of models. Therefore, when running the 10-population models, we
230 applied a script that pooled the simulated data into a Bornean and a Sumatran group after each
231 simulation step. Summary statistics were then also calculated island-wise, in order to be able
232 to directly compare to the 2-population models.

233 We first performed an initial run of 2×10^6 simulations with the standard rejection sampler
234 (Tavare *et al.* 1997). These simulations were used for both model selection and validation. To
235 reduce the dimensionality of the summary statistics, we performed a principal component
236 analysis (PCA) with the “prcomp” function in R version 2.12.1 (R Development Core Team
237 2010). A 100,000 random simulations from each of the two compared models were pooled
238 and standardised, and these summary statistics were used to extract the loadings of the first
239 ten principal components. We then transformed both the simulated and the observed data and
240 used it to perform a multinomial logistic regression with the R package “abc” version 1.6. For
241 this, we used the 0.1% of the simulations with the smallest Euclidean distance between the
242 transformed summary statistics and the observed data.

243 In order to assess model fit, we also calculated the marginal densities and the probability of
244 the observed data under the general linear model (GLM) used for the post sampling regression
245 for each model with ABCtoolbox (Leuenberger & Wegmann 2010). For this, we again
246 transformed both the simulated summary statistics as well as the observed data with the

247 loadings for the first ten principal components. This time, PCA loadings were obtained for
248 each model separately by using 100,000 random simulations. The GLM was built from the
249 2,000 simulations closest to the observed data, and we assessed the goodness of fit of all
250 tested models to the observed data by calculating the p-value of the observed data under the
251 GLM (Supporting Table S6). The p-value is representing the proportion of the retained
252 simulations showing a lower or equal likelihood under the inferred GLM as compared to the
253 observed genetic data (Wegmann *et al.* 2009a). Thus, low p-values indicate that the observed
254 data is unlikely to have been generated under the inferred GLM, implying a bad model fit.

255 *Parameter Estimation*

256 To obtain good estimates of the posterior distributions of the parameters for the best-fitting
257 model (IM10-BNBO-DECSU), we used a MCMC without likelihood method (Wegmann *et al.*
258 *et al.* 2009b). To reduce the dimensionality of the data and extract as much information as
259 possible about the model parameters, we used the first 20,000 simulations with the standard
260 sampler to define the first 12 orthogonal components of the summary statistics that maximise
261 the covariance matrix between summary statistics and model parameters. For this, we applied
262 a partial least-squares (PLS) regression approach (Boulesteix & Strimmer 2007) as
263 implemented in the “pls” R package (Mevik & Wehrens 2007) and used the R script provided
264 in the ABCtoolbox package. We defined the optimal number of PLS components by assessing
265 the drop in the root mean squared error for each parameter with the inclusion of additional
266 PLS components. This way, a large set of summary statistics is reduced to a number of
267 independent components, whereby summary statistics that are most informative about the
268 model parameters are weighted more than summary statistics that do not show much response
269 to changing parameter values (Wegmann *et al.* 2009b). The initial simulations were also used
270 to define the tolerance distance based on a tolerance level of 0.1 and to calibrate the transition
271 kernel of the MCMC run with a rangeProp setting of 1 unit of standard deviation (Wegmann
272 *et al.* 2009b; Wegmann *et al.* 2010). We then ran a total of 10^7 iterations with the MCMC
273 sampler, followed by a ABC-GLM post sampling regression (Leuenberger & Wegmann
274 2010) on the 10,000 simulations with the smallest Euclidean distance to the PLS components
275 of the observed summary statistics. Finally, we used R to plot the posterior distributions of
276 important model parameters.

277 *ABC Validation*

278 The performance of ABC in model selection and parameter estimation in complex
279 demographic settings inevitably suffers from the loss of information when the observed and

280 simulated genetic data are reduced to a set of summary statistics (Robert *et al.* 2011). This
281 necessitates a careful validation of the employed ABC procedure in order to avoid biases in
282 the approximation of posterior probabilities of evaluated models and the estimation of model
283 parameters. Accordingly, we validated our model selection and parameter estimation
284 approach with four different procedures. The first three validation approaches made use of so
285 called pseudo-observed data sets (*pods*), whereby parameter combinations are randomly
286 drawn from the prior distributions and the corresponding summary statistics were simulated
287 under a given model. These sets of summary statistics were then treated as if it were real
288 observed data, but since the model and the corresponding parameter values that generated
289 these summary statistics were known, we could use the *pods* to validate both our model
290 selection and parameter estimation procedure.

291 In the first validation step, we investigated the model misclassification rate for each pair-wise
292 model comparison by generating 100 *pods* under each model with parameters randomly
293 drawn from the prior distributions. We then performed the same model selection procedure as
294 with the real observed data and counted the number of assignments to each model. We
295 derived the model misclassification rate by counting all assignments of *pods* to a model other
296 than the one generating it (Figure 2).

297 Second, we assessed the accuracy of the parameter estimation, both in terms of different point
298 estimators (mode, average and median) and over the whole posterior distribution under
299 different tolerance levels (proportion of retained simulations). For this, we generated 1,000
300 *pods* under the best-fitting model (IM10-BNBO-DECSU) and performed the same parameter
301 estimation procedure on each *pods* as for the real data. The accuracy of the point estimators
302 was assessed using the average of the root mean squared errors (RMSE) over all 1,000 *pods*
303 (Supporting Table S7), while the root mean integrated squared error (Leuenberger &
304 Wegmann 2010) was used to assess accuracy over the whole posterior distribution
305 (Supporting Table S8). The results indicated that accuracy of the posterior distributions is
306 little affected by varying tolerance levels and that the mode of the distribution is the most
307 accurate point estimator for parameter estimation.

308 Third, to increase confidence in the parameter estimates of the best-fitting model, we checked
309 for biased posterior distributions by producing 1,000 *pods* under the best-fitting model with
310 parameter values drawn from the prior distributions. We used ABCtoolbox to calculate the
311 posterior quantiles of the true parameter values within the estimated posterior distributions for
312 each *pods* and used a Kolmogorov-Smirnov test for uniformity in R (Wegmann *et al.* 2009b).

313 Significant deviation from uniformity after sequential Bonferroni correction (Rice 1989)
314 would indicate biased posterior distributions (Cook *et al.* 2006). The distribution of posterior
315 quantiles within which the true values of the *pods* fell did not significantly deviate from the
316 expectation of uniformity for most parameters (Supporting Figure S4). In most cases where
317 the posterior quantiles were not distributed uniformly, data points were overrepresented in the
318 centre of the histogram, indicating that the posterior distributions were estimated too
319 conservatively.

320 In a last validation approach, we tested if the best-fitting model (IM10-BNBO-DECSU) and
321 the corresponding posterior distributions of the model parameters are able to reproduce the
322 summary statistics of the observed data. For this, we randomly sampled 10,000 parameter sets
323 from the inferred posterior distributions and used these to simulate genetic data under the
324 best-fitting model. We then carried out a PCA transformation of the simulated data and
325 plotted the first 16 principal components to check if the transformed observed data fell within
326 the distribution of the simulated data (Supporting Figure S5). This was the case for all the first
327 16 principal components, suggesting that the best-fitting model and its inferred parameter
328 estimates are well able to explain the observed data.

329 **Results**

330 **Model Selection**

331 We tested 12 demographic models, evaluating the impact of multiple demographic processes
332 on the current genetic makeup of orang-utan populations (Figure 2). We first compared
333 simple models that treated Bornean and Sumatran orang-utans as single populations, but
334 differed in the opportunity for migration after the population split (IM2 vs. I2, Figure 2A). We
335 found substantial support for the model allowing migration after the split (IM2, Bayes factor,
336 i.e. ratio of model posterior probabilities (BF) 5.18). However, this simple isolation with
337 migration model achieved only a very poor fit to the observed data, as shown by the
338 probability of the observed data under the general linear model used for parameter estimation
339 (GLM p-value) of 0.003, indicating that additional processes were involved in shaping the
340 gene pool of orang-utans. Of all four 2-population models tested, we observed a very strong
341 support for a model that allowed a sudden change in population size for both populations
342 followed by exponential growth (IM2-BN-GR vs. I2, IM2, IM2-GR, BF 36.79). Still, this

343 model did not achieve a good fit to the observed data, as evidenced by a p-value of the
344 observed data under the GLM of only 0.017 (Supporting Table S6).

345 The poor model fit of all tested 2-population models can be explained by the extensive
346 population substructure within the two orang-utan species (Arora *et al.* 2010; Kanthaswamy *et*
347 *al.* 2006; Nater *et al.* 2013; Nater *et al.* 2011; Warren *et al.* 2001), which differs to a great
348 extent for female- and male-mediated marker systems (Nater *et al.* 2011; Nietlisbach *et al.*
349 2012). Accordingly, the N_e for each marker system varies to a large degree and cannot be
350 described accurately with just one population size parameter per island. In agreement with
351 this notion, we found that a basic model with ten current population units (IM10) achieved a
352 better fit to the observed genetic data (GLM p-value 0.224) than all the 2-population models
353 (Supporting Table S6), and also obtained much stronger statistical support when directly
354 compared against the best 2-population model (IM10 vs. IM2-BN-GR, BF 830.21, Figure
355 2B). However, in our case, a better fit of the 10-population model compared to the 2-
356 population models was not unexpected, since part of the observed genetic data was used
357 beforehand to derive the number of population units in the 10-population models. When we
358 computed summary statistics for the IM10 model without pooling the genetic data for the
359 Sumatran populations north and south of Lake Toba, the model fit was still poor (GLM p-
360 value 0.019). In order to improve model fit, we first tested whether a population split
361 sequence following the species designation fits the data better than the pattern suggested by
362 mtDNA data (deepest split within Sumatran orang-utans north and south of Lake Toba). This
363 was strongly rejected by the observed data (IM10 vs. IM10-BOSU, BF 45.45, Figure 2B).

364 We then further tested for recent population declines on Sumatra (IM10-DECSU vs. IM10,
365 BF 57.03), on Borneo (IM10-DECBO vs. IM10, BF 0.48) or on both islands (IM10-DECALL
366 vs. IM10-DECSU, BF 0.94, Figure 2C). Incorporating a population decline on Sumatra
367 considerably improved the model fit (GLM p-value 0.553).

368 Next, we tested a model incorporating a bottleneck on Borneo together with a recent decline
369 on Sumatra (Figure 2D), which revealed substantial support for a bottleneck on Borneo
370 (IM10-BNBO-DECSU vs. IM10-DECSU, BF 3.60).

371 Finally, we evaluated the statistical support for a bottleneck on Sumatra associated with the
372 Toba supereruption (Figure 2E). We found substantial support against a bottleneck on
373 Sumatra in general (IM10-BNBO-DECSU vs. IM10-BNBO-TOBA-DECSU, BF 3.29), and

374 overwhelming support against a severe bottleneck (less than 100 individuals per population)
375 (IM10-BNBO-DECSU vs. IM10-BNBO-RECOL-DECSU, BF 10,887.60).

376 After performing a series of hierarchical model selection steps, we were able to identify a
377 demographic model (IM10-BNBO-DECSU) capable of reproducing the observed patterns of
378 DNA variation in the two current orang-utan species. Therefore, this model is likely to
379 capture the biologically most relevant processes in the demographic history of orang-utans.

380 **Parameter Estimation**

381 We estimated the model parameters for the selected 10-population model (IM10-BNBO-
382 DECSU, Figure 3) based on a total of 10 million simulations (Table 3, Figure 4). The
383 parameter estimates point to a current N_e of ~970 diploid individuals in each of the six
384 Bornean populations. We found support for a bottleneck on Borneo starting ~135 ka and
385 ending ~82 ka, during which N_e on Borneo was reduced from an ancestral N_e of ~17,000
386 individuals to ~2,600 individuals. The bottleneck on Borneo was followed by population
387 recovery and substructuring, with a current total N_e of all Bornean populations of ~6,150
388 individuals.

389 On Sumatra, the three populations north of Lake Toba suffered a decline ~24 ka from a N_e of
390 ~10,500 to currently only ~960 individuals in each of the three populations, corresponding to
391 a total N_e in the meta-population north of Lake Toba of ~38,300 and ~3,300 individuals
392 before and after the decline, respectively. We estimated that population structure north of
393 Lake Toba was established ~860 ka, with an ancestral effective population size of ~14,400
394 individuals. The population south of Lake Toba also went through a recent decline ~24 ka
395 from a N_e of ~24,200 individuals in the ancestral population to currently only ~1,030
396 individuals. Thus, Sumatran orang-utan populations first expanded during the Middle
397 Pleistocene before experiencing an island-wide population crash in the Late Pleistocene or
398 Early Holocene.

399 We inferred the population split time between Borneo and south Toba as ~1.13 Ma, and
400 between north and south of Lake Toba as ~3.39 Ma. Gene flow between Borneo and Sumatra
401 appears to have ceased ~87 ka, but this parameter was associated with a broad posterior
402 distribution. We found no evidence for asymmetric migration rates between Borneo and south
403 of Lake Toba, and between south of Lake Toba and north of Lake Toba. The migration rates
404 between the two islands were comparable to the migration rates over the Toba caldera on

405 Sumatra, while migration rates among the populations on Borneo and among those north of
406 Toba, respectively, were estimated to be about a magnitude higher.

407 **Discussion**

408 Our modelling approach capitalized on the use of multiple genetic marker systems and an
409 extensive set of geographically well-defined samples, in contrast to previous studies, which
410 based their findings on a small number of captive individuals with poorly recorded
411 provenance (Locke *et al.* 2011; Mailund *et al.* 2011; Mailund *et al.* 2012). Thus, our study
412 was able to shed light on important aspects of orang-utan demographic history that so far
413 remained unexamined due to non-representative sampling and dismissal of within-species
414 population structure. For instance, the inferred model by Locke *et al.* (2011) of a continuously
415 expanding Sumatran orang-utan population with a substantially larger current N_e as compared
416 to Bornean orang-utans was unrealistic in the light of current species distribution and
417 abundance, and did not capture recent population dynamics. Our results indicate that such
418 misleading signals are the result of a recent decline and deep divergence of orang-utan
419 populations on Sumatra, which yields a larger long-term N_e for Sumatran orang-utans as
420 compared to Bornean orang-utans in oversimplified demographic models.

421 **Inference of Best-Fitting Model**

422 We inferred that a model with comprehensive population structure, a bottleneck on Borneo
423 and a recent decline on Sumatra (IM10-BNBO-DECSU) fits the observed data significantly
424 better than a range of simplified models that treat each orang-utan species as a single
425 panmictic population. Estimation of demographic parameters under this model revealed a
426 population split time between Borneo and Sumatran populations south of Lake Toba of just
427 over a million years ago, followed by bidirectional gene flow. This species split time estimate
428 is considerably older than estimates obtained using whole genome data, suggesting a species
429 split time of between 330 and 600 ka (Locke *et al.* 2011; Mailund *et al.* 2011; Mailund *et al.*
430 2012). Such recent species split estimates are, however, in disagreement with findings based
431 on mitochondrial DNA, which yielded divergence time estimates of island specific mtDNA
432 lineages of 1–5 Ma (Nater *et al.* 2011; Steiper 2006; Warren *et al.* 2001; Xu & Arnason 1996;
433 Zhang *et al.* 2001; Zhi *et al.* 1996).

434 The discrepancy between model-based species split estimates using exclusively autosomal
435 data and mtDNA divergence time estimates from phylogenetic methods is owed to two

436 idiosyncrasies in the biology of orang-utans. First, due to the pronounced philopatric
437 tendencies of female orang-utans (Arora *et al.* 2012; Galdikas 1995; Nietlisbach *et al.* 2012;
438 van Noordwijk *et al.* 2012), mtDNA has likely experienced only little if any gene flow
439 between the two species after the species split. Therefore, the coalescent time of island-
440 specific mitochondrial lineages is expected to predate the population split between Borneo
441 and Sumatra, depending on N_e in the ancestral population (Nichols 2001). Second, due to
442 male-mediated gene flow, model-based approaches using solely autosomal data are likely to
443 underestimate species split times, as disentangling the contributions of migration and split
444 time remains challenging (Hey & Nielsen 2004). The recent split time estimates from
445 autosomal genomic data might reflect the end of an initial period of frequent, but strictly
446 male-driven gene flow after the species split. Such complex temporal fluctuations in
447 migration rates, as expected during glacial cycles for Sundaland species, are so far not
448 properly addressed in any applied demographic model. Still, combining markers with
449 different inheritance patterns as done in this study is likely to improve the estimates of both
450 migration rates and split times in species with sex-biased dispersal such as orang-utans.

451 Our findings of recent gene flow between Bornean and Sumatran orang-utans are in
452 agreement with previous observations (Becquet & Przeworski 2007; Muir *et al.* 2000;
453 Verschoor *et al.* 2004). In their genomic study, Locke and colleagues (2011) found an
454 unexpectedly high incidence of low-frequency mutations shared between Borneo and
455 Sumatra, which also hints at recent gene flow between the two islands. Contrary to studies
456 that indicated the presence of impassable dispersal barriers on the exposed Sunda shelf, either
457 due to large river systems (Harrison *et al.* 2006) or a putative savannah corridor (Bird *et al.*
458 2005; Gathorne-Hardy *et al.* 2002), it seems that habitat conditions during glacial periods did
459 at least sporadically allow male orang-utans to cross the exposed Sunda shelf. However, given
460 the strict and long lasting separation of mtDNA lineages on both islands (Nater *et al.* 2011), it
461 appears that the exposed shelf was not covered with forest able to sustain orang-utan
462 populations over prolonged periods. In fact, large parts of the Sunda shelf between Borneo
463 and Sumatra were covered with nutrient-poor sandy soils (Bird *et al.* 2005; Slik *et al.* 2011).
464 Forests on such soil types are characterized by low growth and productivity (Paoli *et al.*
465 2010). These constraints might explain why orang-utan populations on both islands could not
466 expand onto the exposed shelf to an extent where population admixture and thus exchange of
467 mtDNA lineages was possible.

468 **Glacial Cycles and Population Size Changes**

469 Since we also tested models that incorporated sudden population size changes, we were able
470 to detect signals of a population bottleneck on Borneo. In contrast to Sumatra, the currently
471 observed pattern of strong population differentiation on Borneo (Arora *et al.* 2010; Warren *et*
472 *al.* 2001) seems to have been established only recently, as parameter estimation indicated that
473 Bornean orang-utans were organized at least temporarily as a single panmictic population
474 before ~80 ka. At ~140 ka, the ancient population on Borneo experienced a sudden drop in N_e
475 from ~17,000 to ~2,500 individuals, which then recovered again to the current total N_e of
476 ~6,000 for all Bornean orang-utans. Such a change in both N_e as well as population structure
477 could be explained by a common Bornean refugium during either the penultimate (190–130
478 ka) or last (110–18 ka) glacial period, when the drier and more seasonal climate might have
479 caused a drastic reduction of rainforest coverage on Borneo (Bird *et al.* 2005; Gathorne-Hardy
480 *et al.* 2002; Morley 2000). Population contractions with subsequent expansions likely
481 occurred multiple times on Borneo during Pleistocene glacial and interglacial cycles, but
482 incorporating such complex population dynamics into a demographic model is currently not
483 feasible with the data at hand.

484 Interestingly, a similar signal of a glacial refugium with subsequent population structuring, as
485 observed in Bornean orang-utans, has been found in western gorillas (*Gorilla gorilla*). By
486 using a demographic modelling approach comparable to our study, Thalmann *et al.* (2011)
487 found that the two subspecies of western gorillas (*G. g. gorilla* and *G. g. diehli*) diverged only
488 about ~18 ka, thus directly following the last glacial maximum (LGM) 19–26 ka (Clark *et al.*
489 2009). Furthermore, the ancient population of western gorillas exhibited a N_e of just ~2,500
490 individuals as compared to 22,000 and 17,000 individuals in the two subspecies after the
491 population split. Therefore, it seems that western gorillas, similar to Bornean orang-utans,
492 were constrained to a relatively small refugial population during glacial periods from which
493 they subsequently expanded when the climate got warmer and wetter during interglacials.

494 **Geological Processes and Population Size Changes**

495 Linking bottleneck signals to specific environmental processes is difficult due to the large
496 confidence intervals associated with most parameter estimates. For instance, the 90%-highest
497 posterior interval for the estimate of the start of the bottleneck on Borneo (21–348 ka) also
498 overlaps with the Toba supereruption on northern Sumatra ~73 ka (Chesner *et al.* 1991). It has
499 been hypothesized that this colossal explosive eruption might have had a strong global

500 impact, causing a severe bottleneck in humans (Rampino & Ambrose 2000). However,
501 evidence presented here points toward climatic changes during the glacial periods rather than
502 the Toba supereruption as being the main cause for the detected bottleneck on Borneo, as our
503 results showed that the supereruption did not even have a strong impact on the Sumatran
504 populations despite their much closer geographic proximity. Models incorporating a severe
505 bottleneck in the Sumatran populations around the time of the supereruption were clearly
506 rejected and the signal of a recent population decline on Sumatra was considerably younger
507 than the Toba supereruption. Studies indicate that the destruction caused by the Toba
508 supereruption had been geographically limited, as shown by the distribution of rainforest
509 refugia in Southeast Asia (Gathorne-Hardy *et al.* 2002), including on Mentawai Island around
510 350 kilometres from the Toba caldera (Gathorne-Hardy & Harcourt-Smith 2003), as well as
511 the similar composition of Southeast Asian fossil sites before and after the date of the
512 supereruption (Louys 2007). Given the proximity of contemporary populations of Sumatran
513 orang-utans to the Toba caldera and the strong dependency of orang-utans on intact rain forest
514 habitat, they are undoubtedly one of the most striking examples illustrating the limited impact
515 of the Toba supereruption on the local flora and fauna in Southeast Asia. However, the lack of
516 bottlenecks signals in the Sumatran populations does not imply that the activity of the Toba
517 volcano did not influence the population history of Sumatran orang-utans at all. Rather, the
518 results of this study, as well as previous findings (Nater *et al.* 2013; Nater *et al.* 2011),
519 showed strikingly that the Toba eruptions must have repeatedly caused devastating damage to
520 the local surroundings, which led to a long-lasting separation of gene pools north and south of
521 Lake Toba.

522 In contrast to Toba as cause for the bottleneck on Borneo, a contraction of rainforests
523 following the colder and drier climate during the last glacial period well explains the absence
524 of a similar bottleneck in the Sumatran population history. During the generally drier glacial
525 periods, large parts of Sumatra experienced considerably more rain fall compared to Borneo
526 (Gathorne-Hardy *et al.* 2002; Whitten *et al.* 2000), because the Barisan mountain range
527 running the length of Sumatra acted as a barrier for the wet monsoon winds, causing high
528 precipitation along its western slopes (Whitten *et al.* 2000). This mountain ridge effect in
529 combination with the close proximity to the sea during glacial periods, when sea levels were
530 low, might have allowed large areas of rainforest to persist on Sumatra during glacial periods
531 (Gathorne-Hardy *et al.* 2002). Thus, Sumatran orang-utans were almost certainly not forced
532 into glacial refugia to the same extent as Borneans.

533 **Anthropogenic Impacts on Orang-Utan Populations**

534 While Sumatran orang-utans did not seem to go through glacial bottlenecks, we found
535 evidence for recent and drastic declines in population sizes north and south of Lake Toba.
536 These signals of population decline cannot be attributed to the large-scale human-induced
537 habitat degradation that started in the last century (Rijksen & Meijaard 1999), of which
538 genetic signals were found in previous studies of Bornean orang-utans (Goossens *et al.* 2006;
539 Sharma *et al.* 2012). Rather, our results point toward an earlier decline in the Late Pleistocene
540 or Early Holocene. In the Late Pleistocene, orang-utans went extinct on the Southeast Asian
541 mainland as well as in many Sundaland regions (Delgado & Van Schaik 2000; Jablonski
542 1998; Rijksen & Meijaard 1999). Furthermore, the Pleistocene-Holocene boundary is
543 characterized by the disappearance of many large-bodied animals world-wide (Koch &
544 Barnosky 2006), including large parts of the megafauna in Southeast Asia (Louys *et al.* 2007).
545 The increased occurrence of megafaunal extinctions during this period has been attributed to
546 climatic changes following the LGM, the impact of human hunting and human-induced
547 habitat changes, or the combination of these two factors (reviewed in Koch & Barnosky
548 2006).

549 Both climatic and anthropogenic factors might have played a role in the decline and local
550 extinctions of orang-utan populations in the Late Pleistocene. During the LGM, the drier and
551 more seasonal climate caused a shifting of zones of evergreen rainforest toward the equator
552 (Flenley 1998; Jablonski 1998; Morley 2000), likely causing populations in southern China to
553 go extinct. The warmer climate following the LGM was accompanied by rising sea levels,
554 which drastically increased the extent of coastlines in Sundaland (Voris 2000). This
555 enlargement of coastal habitat might have promoted an expansion of early modern humans on
556 Sundaland, leading to increased hunting pressure on large-bodied animals, including orang-
557 utans (Hill *et al.* 2007; Soares *et al.* 2008). Such hunting by modern humans might have
558 caused the local extinctions of orang-utans on many Sundaland islands, and led to a strong
559 decline in Sumatran populations north and south of Lake Toba. Bornean orang-utans did not
560 seem to be as strongly affected by human hunting, probably because the large size and low
561 productivity of Borneo left enough inland areas with relatively low human densities (Delgado
562 & Van Schaik 2000).

563 Our modelling approach revealed that the two recognised orang-utan species experienced
564 drastically different demographic histories. Sumatran orang-utans exhibit a deep and
565 temporally stable population structure, including an old divergence of gene pools north and

566 south of Lake Toba with limited amount of gene flow over the Toba caldera. The populations
567 on Sumatra recently suffered a strong decline, which, in combination with the strong
568 population structure, explains the high genetic diversity found in recent genomic studies
569 despite their low current census size (Locke *et al.* 2011; Prado-Martinez *et al.* 2013). In
570 contrast, we find that the population structure currently observed within Bornean orang-utans
571 has been established only recently and the population went through at least one bottleneck
572 most likely associated with a glacial refugium.

573 These results strongly suggest that special consideration needs to be given to demographic
574 factors when analysing adaptive evolutionary processes in great apes. Due to their strong
575 dependence on intact forest habitat, most great ape taxa were severely affected by the climate
576 shifts during glacial periods, which were accompanied by drastic changes in forest coverage
577 in the tropics (Flenley 1998; Morley 2000). Accordingly, great ape populations experienced
578 population bottlenecks, founder events, population expansions and population structuring as
579 recent as 15,000 years ago (Clark *et al.* 2009). Given the long generation time of all great apes
580 (18–30 years, Wich *et al.* 2009), great ape populations will likely not have reached an
581 equilibrium state for most genomic regions. Thus, population expansions and substructuring
582 caused by relatively recent climatic changes might produce erroneous signals of selective
583 sweeps if demography is not taken into account. Our results therefore emphasize the need to
584 further advance the development of tools to jointly estimate demography and selection in
585 order to unravel the convoluted evolutionary history of great apes (Li *et al.* 2012).

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Data Accessibility

Sequence data not published previously is accessible under GenBank accession numbers XXXX-YYYY.

Author Contributions

AN, MPG, CPvS, and MK designed the study; BG, IS, EJV, and KSW provided samples; AN, MPG, and NA performed laboratory procedures; AN and MPG conducted genetic data analysis; AN performed demographic modelling; AN wrote the manuscript; MPG, NA, CPvS, and MK critically revised the manuscript and provided comments at all stages; BG, EJV, and KSW edited the final manuscript.

Table 1: Sample sizes for the different marker systems in the ten geographic regions

Sampling region ^a	mtDNA	Y-STRs	Autosomal STRs	Autosomal regions	Xq13.3
North Kinabatangan (NK)	6	10	32	4	3
South Kinabatangan (SK)	13	15	76	4	3
East Kalimantan (EK)	7	9	34	4	5
Sarawak (SR)	8	2	12	2	1
Central Kalimantan (CK)	9	9	68	2	2
West Kalimantan (WK)	9	8	32	4	4
Batang Toru (BT)	8	8	18	4	3
North Aceh (NA)	7	15	32	6	3
Langkat (LK)	14	15	66	10	6
West Alas (WA)	37	38	104	4	7
Total	118	129	474	44	37

^a, sampling regions corresponding to Figure 1. Sample sizes are given as number of sampled chromosomes. The light grey shading refers to Bornean populations, middle grey to Sumatran populations north of Lake Toba, and dark grey to the Sumatran population south of Lake Toba.

Table 2: Summary statistics for the marker systems used in the ABC analysis.

Sequences	L _{Bases} ^a	Group	N _{Ind} ^b	N _{Seg} ^c	π ^d	θ_w ^e	D ^f
mtDNA (16S, ND3, CYTB)	1,355	Borneo	52	19	0.0022	0.0031	-0.92
		South Toba	8	1	0.0002	0.0003	-1.05
		North Toba	58	41	0.0100	0.0066	1.79
Autosomal regions (Chr2a_R17, Chr9_R16, Chr12_R1, Chr19_R7)	8,238	Borneo	10	19.50 ±4.56	0.0033 ±0.0011	0.0027 ±0.0006	0.68 ±0.66
		South Toba	2	13.50 ±7.79	0.0037 ±0.0020	0.0036 ±0.0020	0.08 ±0.49
		North Toba	10	28.75 ±4.66	0.0046 ±0.0012	0.0040 ±0.0006	0.51 ±0.52
Xq13.3	8,055	Borneo	18	6	0.0001	0.0002	-1.11
		South Toba	3	33	0.0027	0.0027	0.00
		North Toba	15	54	0.0020	0.0020	-0.09
Microsatellites	N _{Loci} ^g	Group	N _{Ind}	N _A ^h	H _O ⁱ	H _E ^j	G-W ^k
Autosomal-STR	25	Borneo	127	7.16 ±4.13	0.53 ±0.22	0.61 ±0.25	0.90 ±0.15
		South Toba	9	3.84 ±1.18	0.60 ±0.23	0.62 ±0.16	0.72 ±0.22
		North Toba	101	6.32 ±3.11	0.61 ±0.16	0.65 ±0.16	0.82 ±0.17
Y-STR	11	Borneo	53	3.18 ±2.48	-	0.31 ±0.33	0.90 ±0.14
		South Toba	8	1.27 ±0.65	-	0.08 ±0.19	0.88 ±0.18
		North Toba	68	1.91 ±1.64	-	0.12 ±0.24	0.91 ±0.17

Statistics are provided as average and standard deviation for marker systems with multiple independent loci; ^a, sequence length in base pairs; ^b, number of sampled individuals; ^c, number of segregating sites; ^d, nucleotide diversity; ^e, Watterson's θ per base pair; ^f, Tajima's D (Tajima 1989); ^g, number of loci; ^h, number of alleles; ⁱ, observed heterozygosity; ^j, expected heterozygosity; ^k, Garza-Williamson index (Garza & Williamson 2001);

Table 3: Estimates of the model parameters for the selected 10-population model with a bottleneck on Borneo and a recent decline on Sumatra (IM10-BNBO-DECSU).

Parameter ^a	Prior ^b	Mode	Mean	90%-HPD ^c
N _{NOWBO} [ind] (6)	logunif[100;10,000]	974	1,028	348–3,011
N _{NOWNT} [ind] (3)	logunif[100;10,000]	963	933	239–3,613
N _{NOWST} [ind] (1)	logunif[100;10,000]	1,034	952	189–4,514
N _{BNBO} [ind] (1)	logunif[100;10,000]	2,598	1,486	286–9,988
N _{ANCB} [ind] (1)	logunif[1,000;100,000]	17,046	12,344	2,171–89,115
N _{STRUCNT} [ind] (3)	logunif[1,000;100,000]	10,508	11,278	1,886–78,264
N _{ANCNT} [ind] (1)	logunif[1,000;100,000]	14,407	10,519	1,565–70,259
N _{ANCAST} [ind] (1)	logunif[1,000;100,000]	24,193	13,991	2,629–99,070
T _{BNENDBO} [yrs]	unif[8,750;400,000]	81,946	149,580	8,848–283,785
T _{BNSTARTBO} [yrs]	T _{BNENDBO} + unif[250;100,000]	135,076	191,001	20,855–348,145
T _{SPLITBO} [kyrs]	unif[400;1,500]	1,128	960	497–1,436
T _{DECSU} [yrs]	unif[1.0;3.5]	23,651	36,200	4,119–67,272
T _{STRUCNT} [kyrs]	unif[75;1,500]	861	820	267–1,398
T _{SPLITNT} [kyrs]	unif[1,500;4,000]	3,392	2,995	2,101–3,999
T _{MIGSTOP} [yrs]	unif[2.5;4.2]	87,034	161,862	8,849–310,833
Log(m _{BO-ST}) [migrants/ind/gen]	unif[-5.0;-3.0]	-3.55	-3.96	-4.79–-3.09
Log(m _{ST-BO}) [migrants/ind/gen]	unif[-5.0;-3.0]	-3.42	-3.84	-4.61–-3.10
Log(m _{NT-ST}) [migrants/ind/gen]	unif[-5.0;-3.0]	-3.89	-3.98	-4.81–-3.14
Log(m _{ST-NT}) [migrants/ind/gen]	unif[-5.0;-3.0]	-3.65	-3.92	-4.71–-3.06
Log(m _{BO}) [migrants/ind/gen]	unif[-4.0;-2.0]	-2.52	-2.90	-3.66–-2.02
Log(m _{NT}) [migrants/ind/gen]	unif[-4.0;-2.0]	-2.51	-2.89	-3.65–-2.03

^a, BO = Borneo, NT = Sumatra north of Lake Toba, ST = Sumatra south of Lake Toba, N_{NOW} = current effective population size, N_{BN} = effective population size during population bottleneck, N_{ANC} = ancestral effective population size, N_{STRUC} = effective population size before recent decline, T_{BNEND} = time since population bottleneck ended, T_{BNSTART} = time when population bottleneck started, T_{SPLIT} = population split time, T_{DEC} = time since population decline, T_{STRUC} = time since establishment of population structure, T_{MIGSTOP} = time since migration between Borneo and Sumatra stopped, m = migration rate per individual per generation (an illustration of the meaning of the different model parameters can be found in Figure 3), the number in brackets next to the population size parameters refer to the number of simulated populations of this size each; ^b, The prior distributions for the parameter values were either uniform or loguniform within the boundaries provided in squared brackets; ^c, 90%-highest posterior density interval.

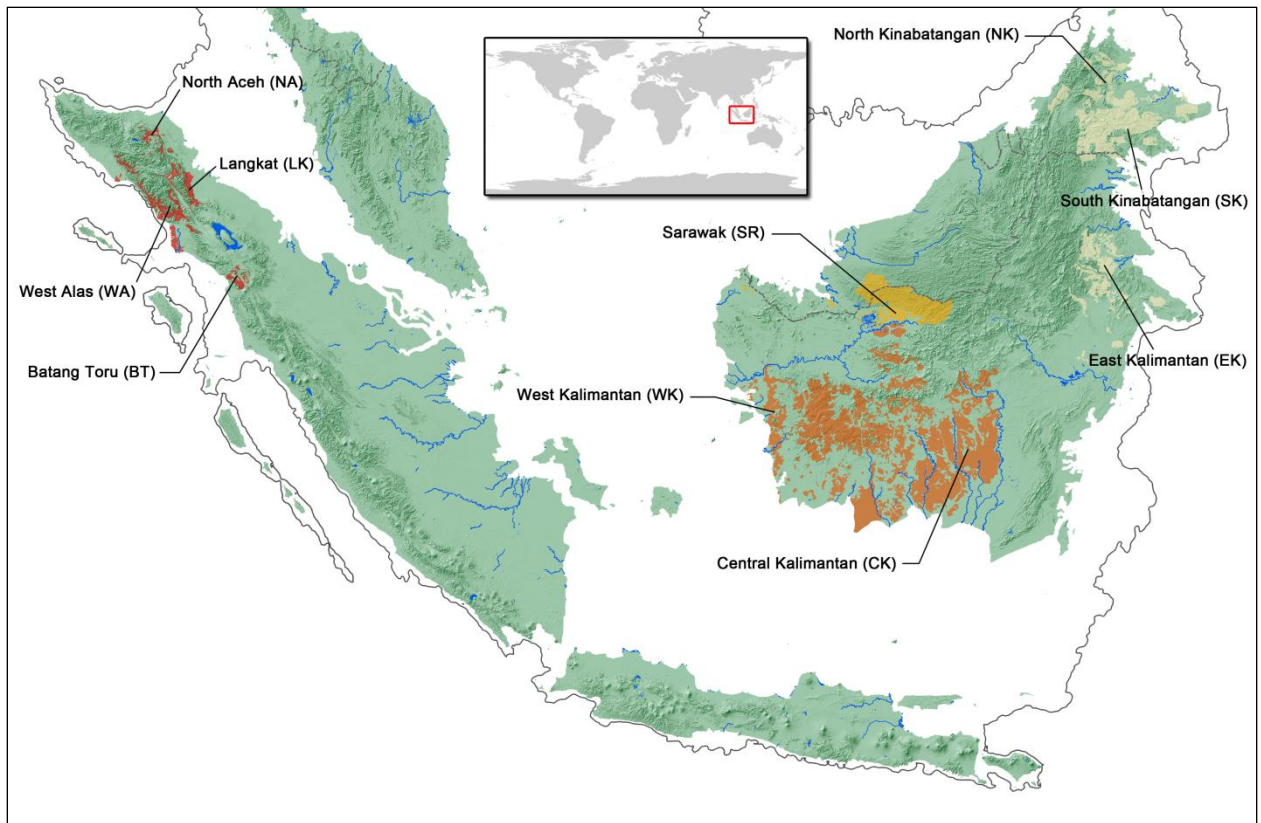
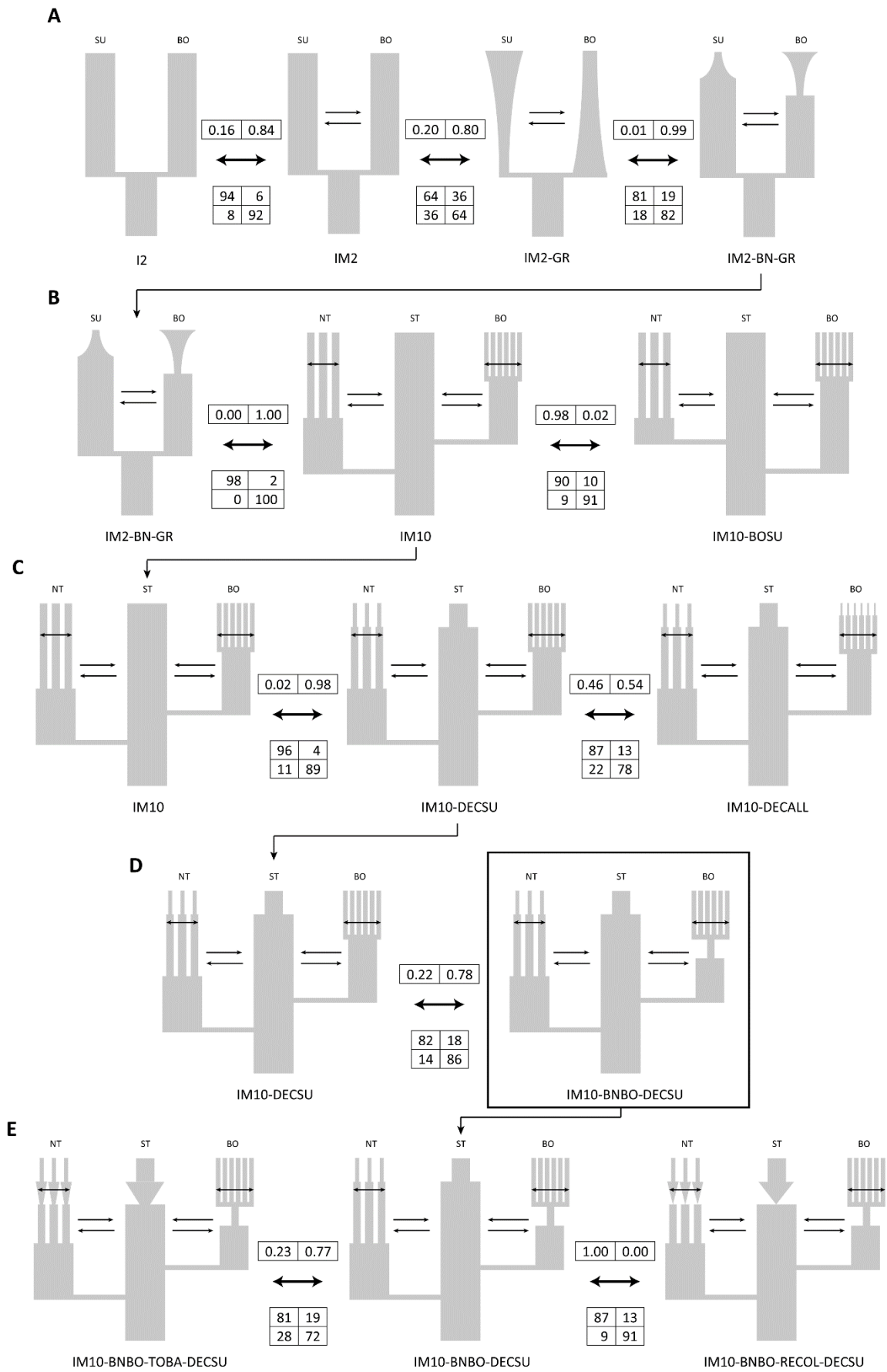


Figure 1: Map of sampling regions in Sundaland used for the demographic modelling. Shaded areas represent the current distribution of the Sumatran orang-utans and the three subspecies of Bornean orang-utans. The grey line indicates the extent of the exposed Sunda shelf during the LGM (19–26 ka, -120 meters below current sea level).



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Figure 2: Schematic representation of the hierarchical model testing procedure. The 12 tested demographic models can be divided into four 2-population models and eight 10-populations models (IM10-DECBO not shown). The box above the left-right arrow shows the model posterior probabilities for each model comparison pair. The overall best-fitting model (IM10-BNBO-DECSU) is shown in a black frame. The box below the left-right arrow shows the power to distinguish between the two compared models as evaluated in a cross-validation procedure with 100 validations for each model, with the upper left and lower right boxes showing the correct model assignments for model 1 and model 2, respectively (SU = Sumatra, BO = Borneo, NT = Sumatra north of Lake Toba, ST = Sumatran south of Lake Toba). A) Comparison of four 2-population models, testing gene flow after the population split, exponential population growth or decline after the population split, and sudden population size change followed by exponential growth or decline. B) Comparison between the best fitting 2-population model and two 10-population models incorporating population structure. C) Tests of recent population declines on Sumatra, and Sumatra as well as Borneo. D) Test of population bottleneck on Borneo. E) Testing of a population bottleneck on Sumatra associated with the Toba supereruption 65–75 ka. The leftmost model implements a bottleneck in all four populations on Sumatra, followed by exponential population recovery. The rightmost model is similar, but restricts the bottleneck to a size of less than 100 surviving individuals per population, thus representing a scenario where regions devastated by the Toba eruption were recolonized from other areas after restoration of the rain forest habitat.

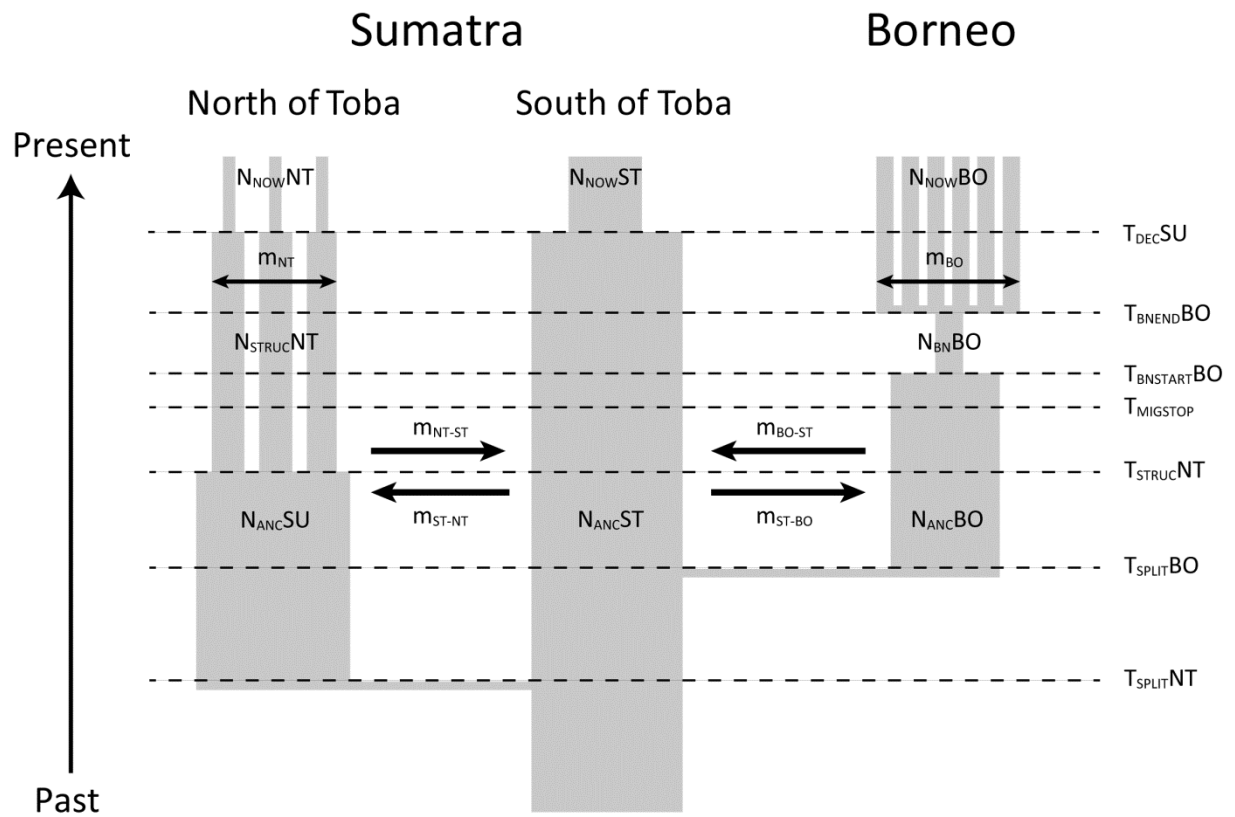


Figure 3: Schematic representation of the selected 10-population model with a bottleneck on Borneo and recent population declines in all Sumatran populations (IM10-BNBO-DECSU).

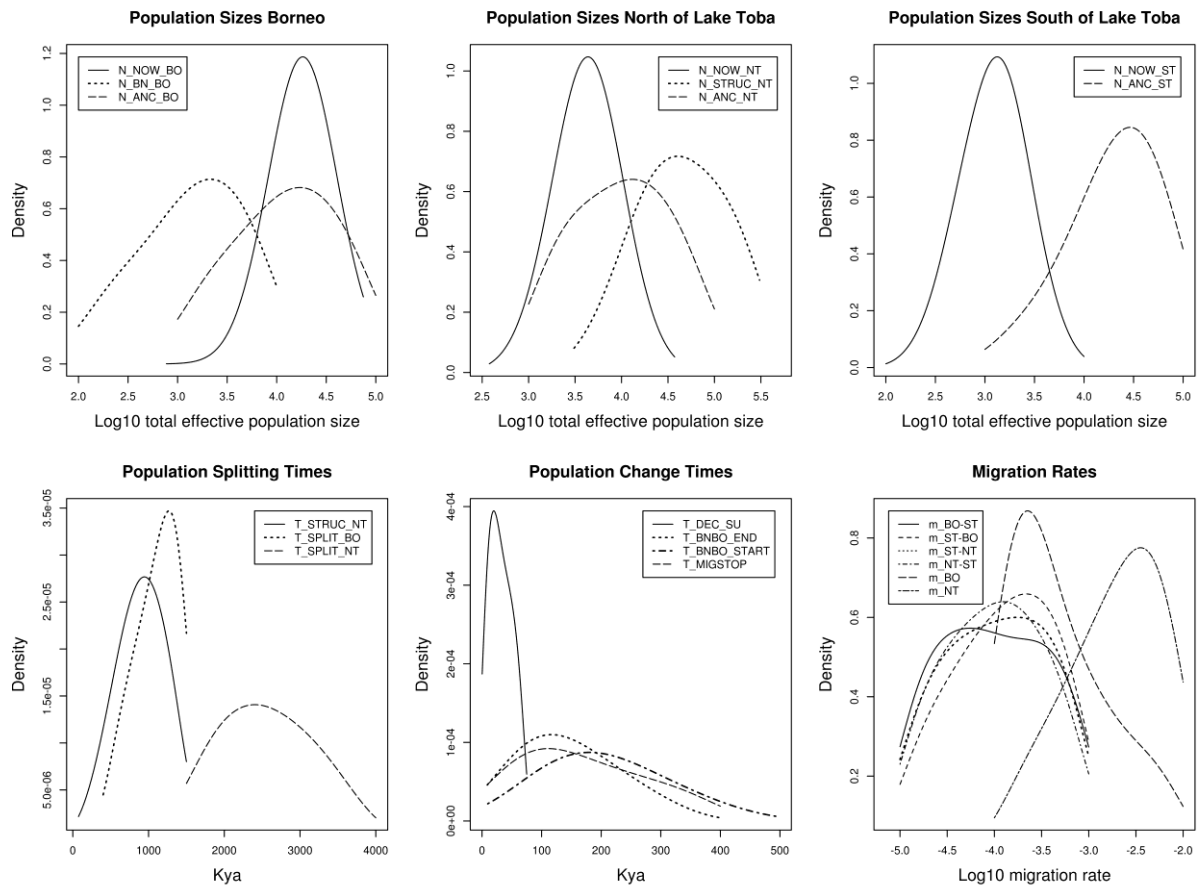


Figure 4: Posterior distributions of important model parameter under the selected 10-population model (IM10-BNBO-DECSU). The abbreviations of the model parameters correspond to the labels in Figure 3. For better comparability, the effective populations sizes of the structured meta-populations on Borneo and north of Lake Toba are given as the total effective sizes according to the formula $N_e = D \times N \times (1 + (1 / (4 \times N \times m)))$, with D corresponding to the number of subpopulations, N to the mean subpopulation size and m to the total migration rate per individual per generation within the meta-population (Nichols *et al.* 2001).