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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 *et al.* 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  $\sim 73$  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  $2 \times 10^6$  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 <sup>a</sup>	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

<sup>a</sup>, 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.

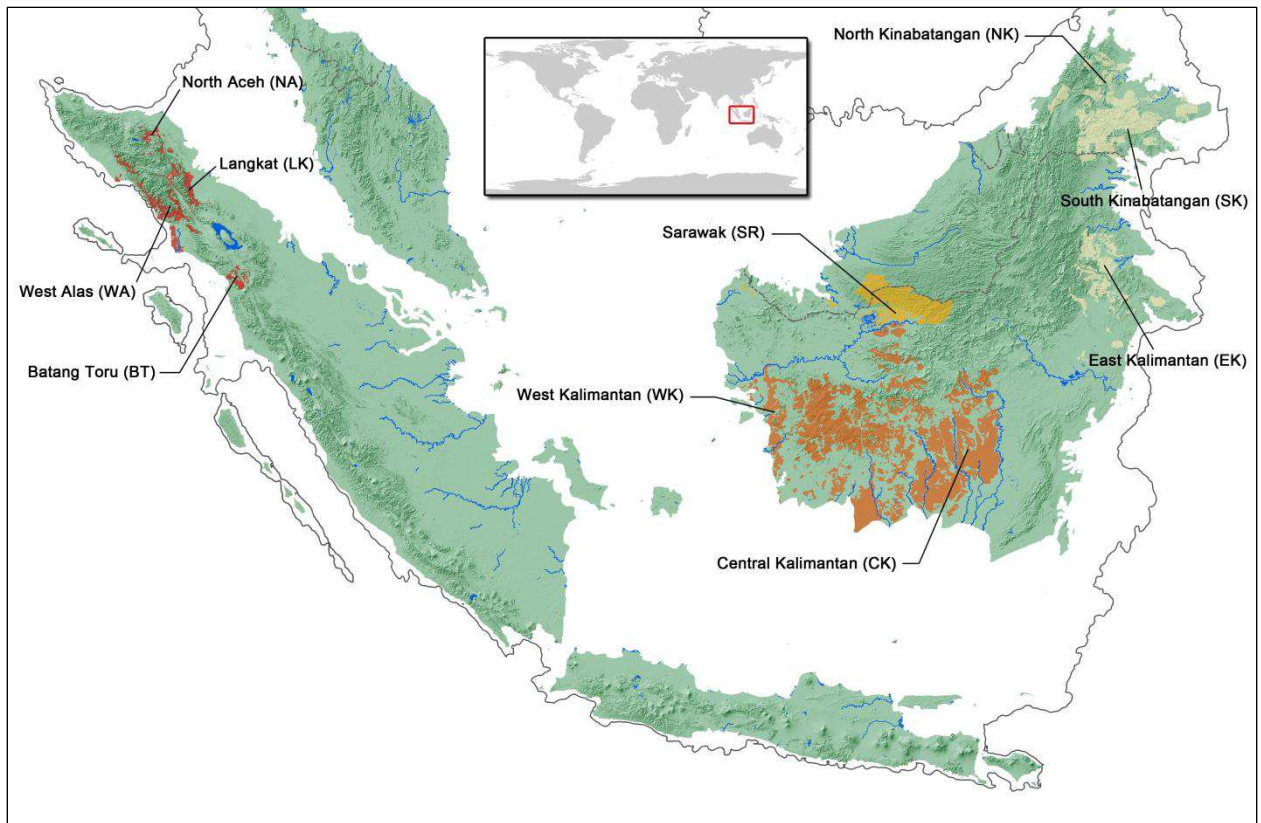
Sequences	L <sub>Bases</sub> <sup>a</sup>	Group	N <sub>Ind</sub> <sup>b</sup>	N <sub>Seg</sub> <sup>c</sup>	$\pi$ <sup>d</sup>	$\theta_w$ <sup>e</sup>	D <sup>f</sup>
mtDNA (16S, ND3, CYTB)	1,355	Borneo	52	19	0.0022	0.0031	-0.92
		South Toba	8	1	0.0002	0.0003	-1.05
		North Toba	58	41	0.0100	0.0066	1.79
Autosomal regions (Chr2a_R17, Chr9_R16, Chr12_R1, Chr19_R7)	8,238	Borneo	10	19.50 $\pm 4.56$	0.0033 $\pm 0.0011$	0.0027 $\pm 0.0006$	0.68 $\pm 0.66$
		South Toba	2	13.50 $\pm 7.79$	0.0037 $\pm 0.0020$	0.0036 $\pm 0.0020$	0.08 $\pm 0.49$
		North Toba	10	28.75 $\pm 4.66$	0.0046 $\pm 0.0012$	0.0040 $\pm 0.0006$	0.51 $\pm 0.52$
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 <sub>Loci</sub> <sup>g</sup>	Group	N <sub>Ind</sub>	N <sub>A</sub> <sup>h</sup>	H <sub>O</sub> <sup>i</sup>	H <sub>E</sub> <sup>j</sup>	G-W <sup>k</sup>
Autosomal-STR	25	Borneo	127	7.16 $\pm 4.13$	0.53 $\pm 0.22$	0.61 $\pm 0.25$	0.90 $\pm 0.15$
		South Toba	9	3.84 $\pm 1.18$	0.60 $\pm 0.23$	0.62 $\pm 0.16$	0.72 $\pm 0.22$
		North Toba	101	6.32 $\pm 3.11$	0.61 $\pm 0.16$	0.65 $\pm 0.16$	0.82 $\pm 0.17$
Y-STR	11	Borneo	53	3.18 $\pm 2.48$	-	0.31 $\pm 0.33$	0.90 $\pm 0.14$
		South Toba	8	1.27 $\pm 0.65$	-	0.08 $\pm 0.19$	0.88 $\pm 0.18$
		North Toba	68	1.91 $\pm 1.64$	-	0.12 $\pm 0.24$	0.91 $\pm 0.17$

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

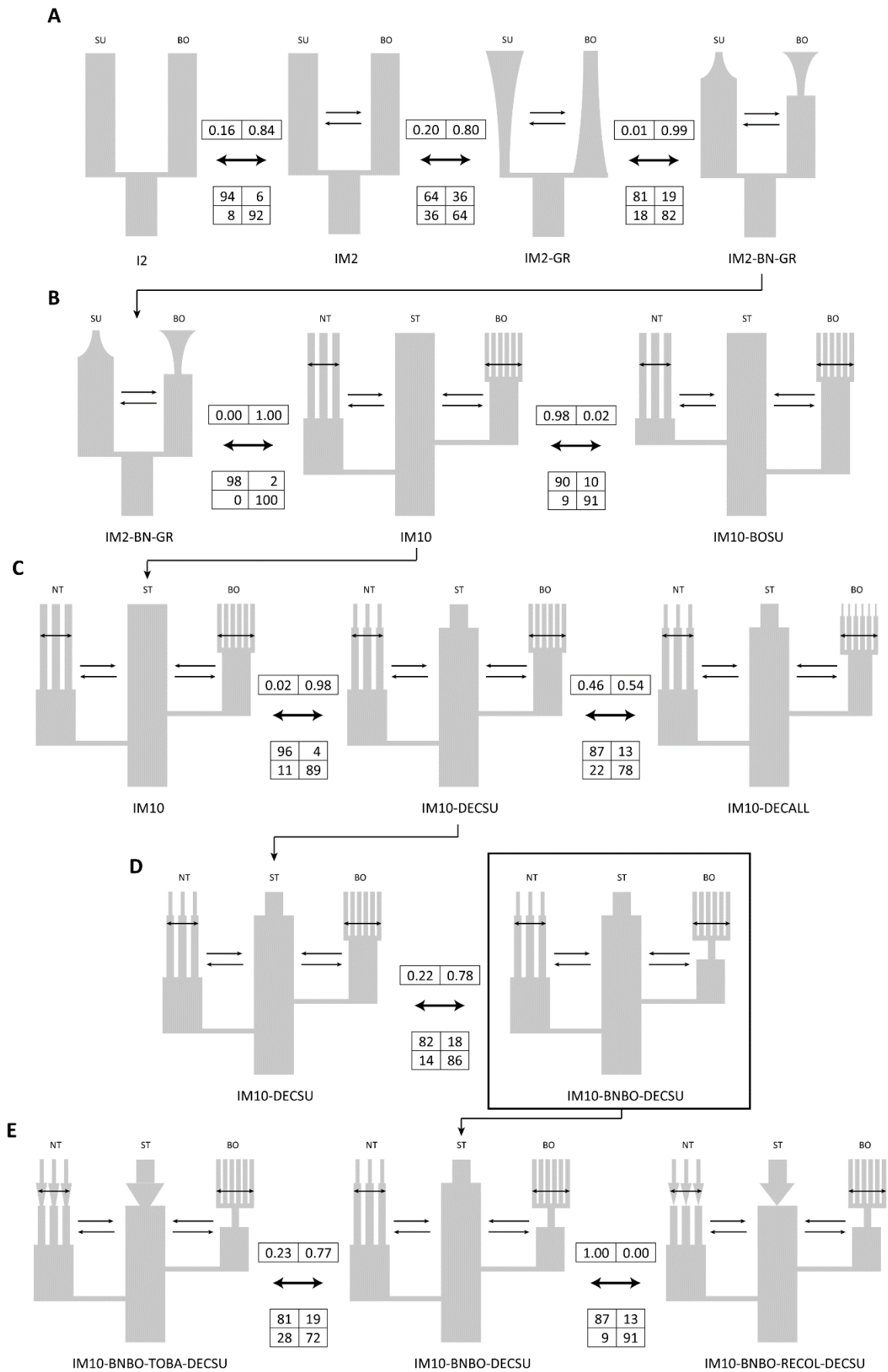
**Table 3:** Estimates of the model parameters for the selected 10-population model with a bottleneck on Borneo and a recent decline on Sumatra (IM10-BNBO-DECSU).

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

<sup>a</sup>, BO = Borneo, NT = Sumatra north of Lake Toba, ST = Sumatra south of Lake Toba, N<sub>NOW</sub> = current effective population size, N<sub>BN</sub> = effective population size during population bottleneck, N<sub>ANC</sub> = ancestral effective population size, N<sub>STRUC</sub> = effective population size before recent decline, T<sub>BNEND</sub> = time since population bottleneck ended, T<sub>BNSTART</sub> = time when population bottleneck started, T<sub>SPLIT</sub> = population split time, T<sub>DEC</sub> = time since population decline, T<sub>STRUC</sub> = time since establishment of population structure, T<sub>MIGSTOP</sub> = 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; <sup>b</sup>, The prior distributions for the parameter values were either uniform or loguniform within the boundaries provided in squared brackets; <sup>c</sup>, 90%-highest posterior density interval.



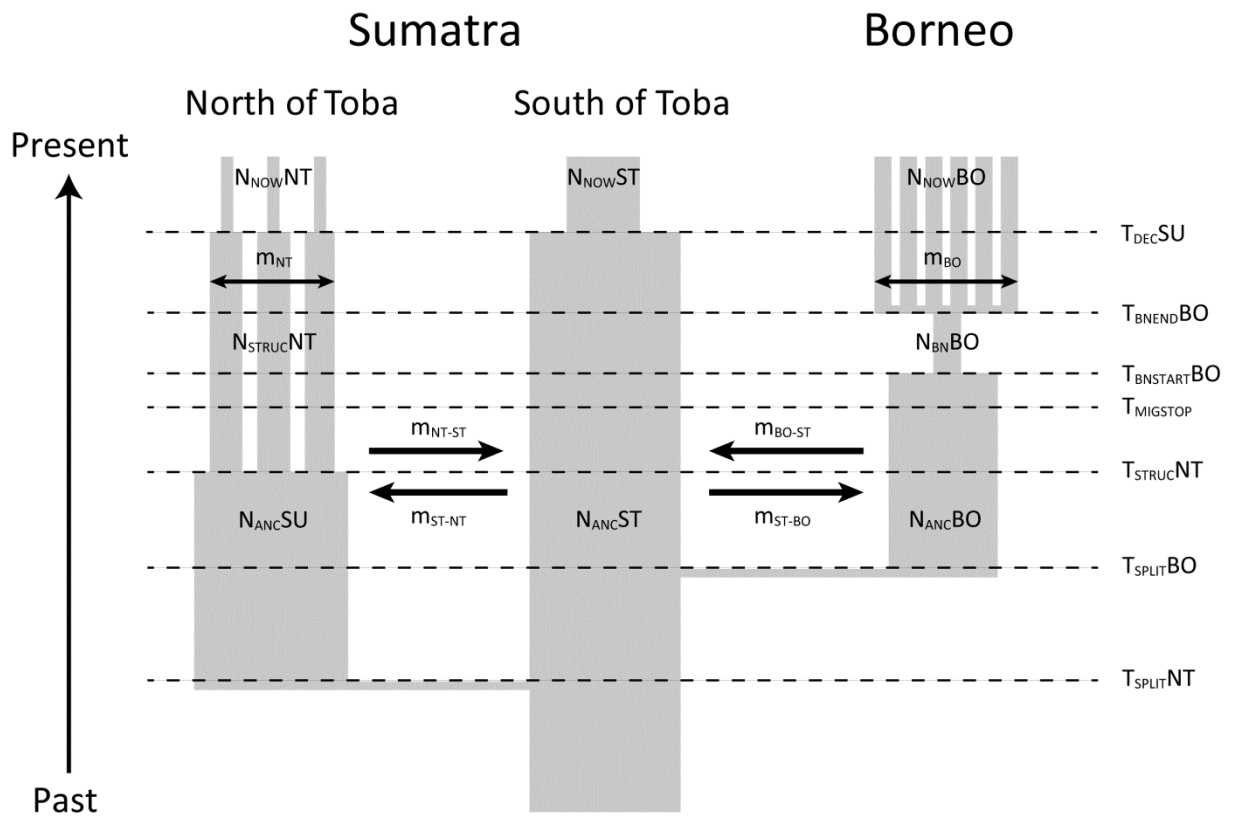
**Figure 1:** Map of sampling regions in Sundaland used for the demographic modelling. Shaded areas represent the current distribution of the Sumatran orang-utans and the three subspecies of Bornean orang-utans. The grey line indicates the extent of the exposed Sunda shelf during the LGM (19–26 ka, -120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



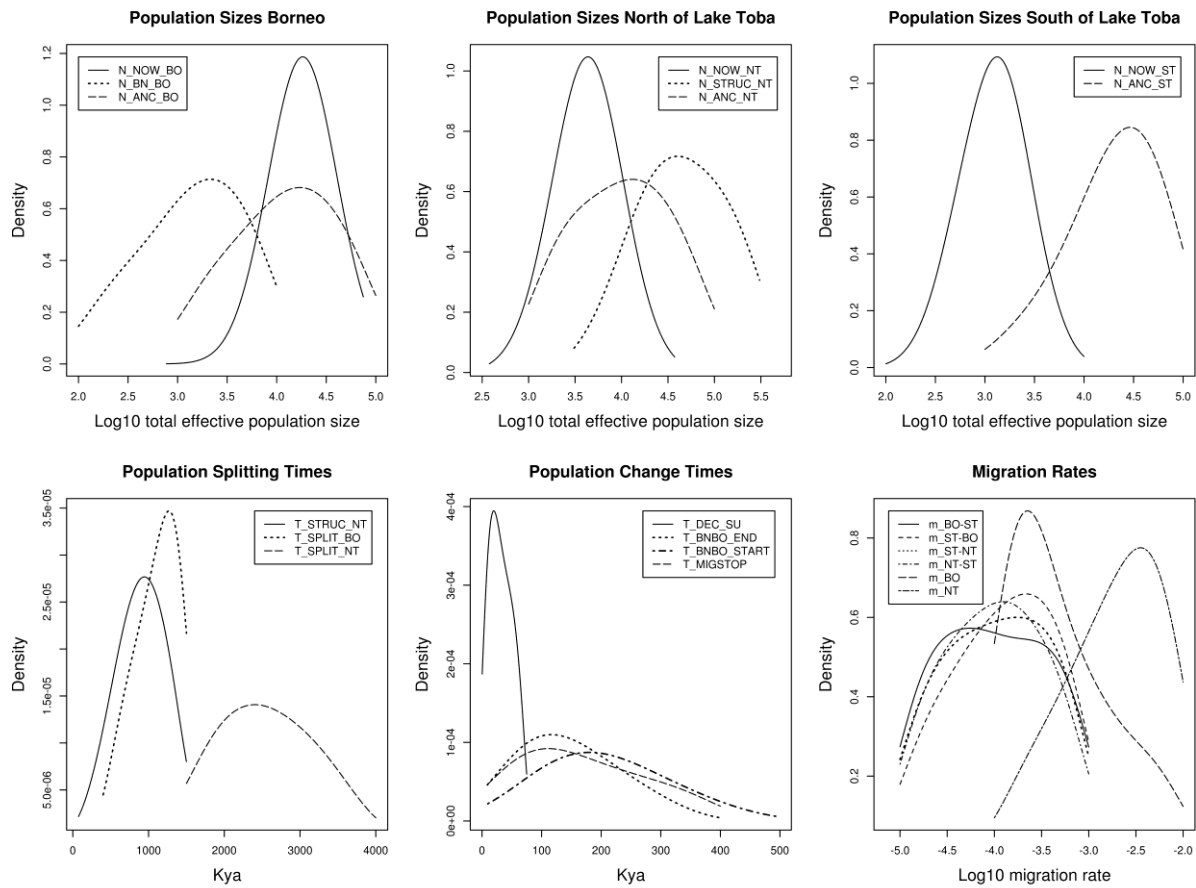
Demographic History of Orang-utans (*Pongo* spp.)



**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).