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1 On the demographic history of chimpanzees and some
2 consequences of integrating population structure in chimpanzees
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16 **Abstract**

17 Reconstructing the evolutionary history of great apes is of particular importance for our understand-
18 ing of the demographic history of humans. The reason for this is that modern humans and their hominin
19 ancestors evolved in Africa and thus shared the continent with the ancestors of chimpanzees and gorillas.
20 Common chimpanzees (*Pan troglodytes*) are our closest relatives with bonobos (*Pan paniscus*) and most
21 of what we know about their evolutionary history comes from genetic and genomic studies. Most evolu-
22 tionary studies of common chimpanzees have assumed that the four currently recognised subspecies can
23 be modelled using simple tree models where each subspecies is panmictic and represented by one branch
24 of the evolutionary tree. However, several studies have identified the existence of significant population
25 structure, both within and between subspecies, with evidence of isolation-by-distance (IBD) patterns.
26 This suggests that demographic models integrating population structure may be necessary to improve

27 our understanding of their evolutionary history. Here we propose to use n -island models within each
28 subspecies to infer a demographic history integrating population structure and changes in connectivity
29 (*i.e.* gene flow). For each subspecies, we use SNIF (structured non-stationary inference framework),
30 a method developed to infer a piecewise stationary n -island model using PSMC (pairwise sequentially
31 Markovian coalescent) curves as summary statistics. We then propose a general model integrating the
32 four subspecies metapopulations within a phylogenetic tree. We find that this model correctly predicts
33 estimates of within subspecies genetic diversity and differentiation, but overestimates genetic differenti-
34 ation between subspecies as a consequence of the tree structure. We argue that spatial models integrating
35 gene flow between subspecies should improve the prediction of between subspecies differentiation and
36 IBD patterns. We also use a simple spatially structured model for bonobos and chimpanzees (without
37 admixture) and find that it explains signals of admixture between the two species that have been reported
38 and could thus be spurious. This may have implications for our understanding of the evolutionary history
39 of the *Homo* genus.

40 **Key words** demographic history, population structure, chimpanzees, connectivity, fragmentation, hu-
41 man evolution

42 1 Introduction

43 Common chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are great apes found in western and
44 central Africa, and they are the closest relatives to humans from which they diverged between 5 Mya [1,
45 2] and 7-8 Mya [3]. The current taxonomy of the genus *Pan* recognises bonobos as one unique species,
46 geographically separated from common chimpanzees by the Congo river and from which it would have
47 diverged between 0.9 and 2 Mya [2, 4, 5, 6]. Unlike bonobos, it is currently considered that common
48 chimpanzees are further divided into four subspecies [2, 7]. Western chimpanzees, *P. t. verus*, occur in the
49 most western part of the species geographic range, from Senegal on the west to Ghana on the east (see Fig.
50 1). The other three subspecies are separated from Western chimpanzees by the Dahomey gap, and their
51 distribution ranges from Nigeria on the west to Tanzania on the east. From west to east, Nigeria-Cameroon
52 chimpanzees (*P. t. ellioti*) are separated from Central chimpanzees (*P. t. troglodytes*) by the Sanaga river,
53 and Eastern chimpanzees (*P. t. schweinfurthii*) are separated from Central chimpanzees by the Ubangi river
54 (Fig. 1).

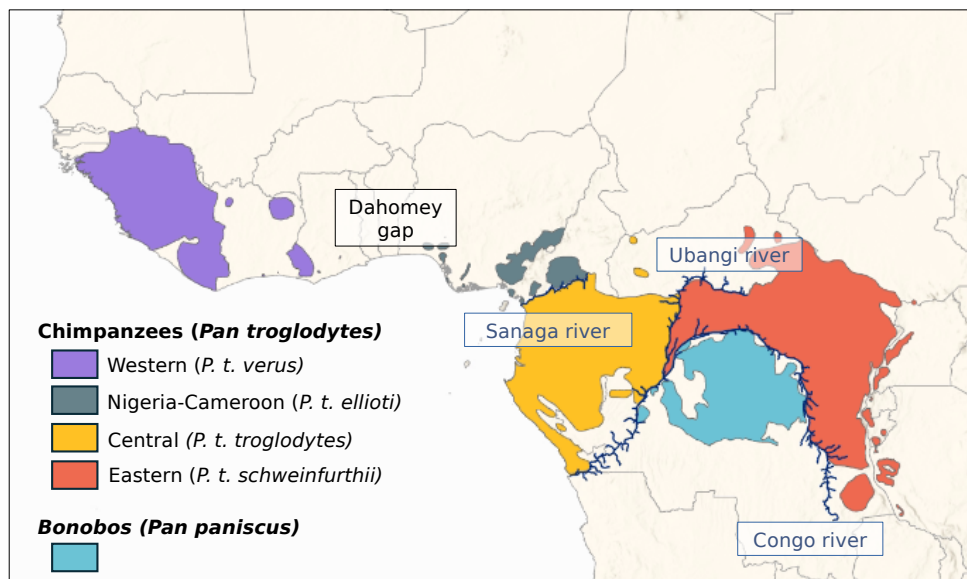


Figure 1: Distribution of the *Pan* genus. Data were extracted from the IUCN Red List of Threatened Species [8, 9].

55 Genetic and genomic analyses suggest that the four subspecies of common chimpanzees form two dis-
56 tinct monophyletic groups that split around 400-600 kya, with Western and Nigeria-Cameroon chimpanzees
57 forming one clade and Central and Eastern chimpanzees forming the other clade [2, 10, 11, 12, 13, 4]. Sev-

58 eral studies estimate that Western and Nigeria-Cameroon chimpanzees probably split between 250-500 kya
59 [2, 6], while Eastern and Central chimpanzees separated more recently, around 90-250 kya [2, 11, 12, 6].
60 The existence and the magnitude of gene flow between subspecies, today or in the past, remains however
61 unclear [13, 12, 11, 2, 14]. Indeed, if the delimitation of the subspecies reflects mostly current geographic
62 barriers (the Dahomey gap, the Sanaga and the Ubangi rivers), it is very likely that these barriers were more
63 or less permeable in the past [15], and it has also been suggested that the ancestral population of common
64 chimpanzees used to cover a wider and more continuous geographic range [16]. Furthermore, studies using
65 models of isolation with migration (IM) have found signals of gene flow between subspecies, even though
66 there is little consensus regarding the pairs of subspecies involved (see Figure 1 in Brand *et al.* [14] for a
67 summary). For instance, Brand *et al.* [14] have identified introgressed segments from Western chimpanzees
68 in Eastern chimpanzees, previously suggested by Hey [11], whereas Wegmann and Excoffier [13] found
69 gene flow from Western to Central chimpanzees. Other studies have identified isolation-by-distance (IBD)
70 patterns, where genetic distance increases with geographic distance [17, 18]. Taking the four subspecies as
71 a single unit, Lester *et al.* [18] computed pairwise F_{ST} values between samples both within and between
72 subspecies. They suggested that patterns of genetic diversity and differentiation could indeed correspond
73 to a model with continuous gene flow across the whole *P. troglodytes* species geographic range, with the
74 exceptions of a few highly isolated populations [18]. Patterns of IBD were also identified across Central and
75 Eastern chimpanzees in an earlier study by Fünfstück *et al.* [17], questioning the classification of these two
76 populations as distinct subspecies [17].

77 Additionally, several studies have pointed out the existence of structure within subspecies [17, 18, 19,
78 20, 21, 2, 6]. Central and Eastern chimpanzees could thus correspond to a set of populations that were
79 connected by gene flow in the recent past, thus explaining the IBD pattern still detectable today [22, 17, 19].
80 In Nigeria-Cameroon chimpanzees, Mitchell *et al.* [20] identified two genetically distinct populations, one
81 located in the forests of western Cameroon and another one in central Cameroon. Prado-Martinez *et al.*
82 [2] also suggested the existence of substructure as they identified three Nigeria-Cameroon individuals who
83 could belong to a distinct population than the rest of their sample. Finally, population structure has been
84 identified as well in Western chimpanzees [21].

85 In parallel, much work has been done to reconstruct the demographic history of common chimpanzees
86 using genetic and genomic data [2, 13, 7, 1, 11, 10, 21, 12, 23, 22, 19, 5]. Prado-Martinez *et al.* [2] used
87 the Pairwise sequential Markovian coalescent (PSMC) method of Li and Durbin [24] on common chim-

88 panzee individual genomes to reconstruct what Prado-Martinez *et al.* [2] interpreted as a history of effective
89 population size (N_e) changes through time. This method is particularly suited for endangered species, for
90 which genomic data can be limited [25, 26, 27] because it only requires one single diploid genome. The
91 interpretation of the PSMC curve is however not trivial [28, 29, 30, 31]. Indeed, whereas the interpretation
92 of Prado-Martinez *et al.* [2] in terms of changes in N_e is potentially valid, several studies have shown that
93 ignoring population structure can lead to the inference of spurious population size changes [32, 33]. In the
94 case of the PSMC method, Mazet *et al.* [28] have shown that under structured population models, the PSMC
95 curve will not only be influenced by changes in N_e , but also by population structure, and subsequently by
96 changes in migration rates between populations [28, 29, 30, 31]. Given that population structure has been
97 identified in common chimpanzees, both across the four subspecies and within subspecies, this means that
98 there is currently no general model that would allow us to interpret the PSMC curves, while accounting for
99 the observed patterns of IBD. Indeed, the current models of divergence represent the evolutionary history
100 of the species and subspecies as successive splits of constant-size panmictic populations, which are incom-
101 patible with the PSMC curves. Altogether chimpanzees may represent interesting models to study ancient
102 population structure and how it influences patterns of genomic diversity in present day populations. The
103 current study benefits from work already done in humans but could also provide some interesting avenues
104 of research for geneticists interested in ancient population structure in humans, by providing comparative
105 data, and prompting similar work in other great apes.

106 Mazet *et al.* [28] introduced the IICR (inverse instantaneous coalescent rate), and showed that the PSMC
107 is actually an estimate of the IICR and corresponds to changes in N_e under total panmixia but not necessarily
108 under other demographic models. Mazet and colleagues also showed in several studies that the IICR can be
109 characterized for any model of population structure under the coalescent, which opened the way to doing
110 demographic inference using the PSMC as a summary statistic [29, 30, 34, 31]. To that purpose, Arredondo
111 *et al.* [31] developed a method that allows to infer the parameters of a stepwise stationary n -island model
112 [35] from a PSMC curve. For example, it allows to infer the number of islands or demes, n , their size N
113 (in diploids), and the times, t_i , at which gene flow, $M_i = 4Nm_i$, may have changed by simply specifying a
114 range of possible values for each one of these parameters. This method is implemented in SNIF (structured
115 non-stationary inference framework).

116 In the present study, we ask whether it is possible to integrate population structure within each subspecies
117 of common chimpanzees and infer a reasonable demographic history that explains the PSMC curves within

118 one single model for each subspecies and then for the species as a whole. First, we use SNIF [31] to infer
119 non-stationary n -island models for each subspecies of common chimpanzees, assuming constant deme size,
120 using the PSMC curves generated by Prado-Martinez *et al.* [2]. At each step we validate the inference steps
121 by generating IICR curves from the inferred demographic models and by applying SNIF to the inferred IICR
122 curves. From the resulting inferences, we then propose a model of demographic history for the four sub-
123 species, integrating the n -island models and a tree model consistent with previous research. For all inferred
124 models (for each subspecies and for the general model), we predict genetic diversity (nucleotide diversity)
125 and differentiation (F_{ST}) both within and between subspecies and compare the predicted values to empirical
126 estimates. We found that a model of structured populations with successive population splits and variable
127 migration rates is sufficient to explain both the PSMC curves and several statistics of genomic diversity. We
128 also find some discrepancies between the observed and predicted F_{ST} values between subspecies and use
129 these to identify future directions for research. In particular we suggest that models incorporating spatial
130 structure should be explored. As a proof of concept we use a simple example of stepping-stone model and
131 show how signals interpreted as signatures of admixture events between chimpanzees and bonobos could
132 actually be explained by population structure alone. These results are thus of great importance for the anal-
133 ysis of primate genomes in general and of humans in particular, where admixture events have been inferred,
134 and for which population structure has also been invoked as a possible explanation [36, 37, 38].

135 **2 Materials and Methods**

136 **2.1 Data: PSMC curves**

137 The PSMC curves of the chimpanzees used here were retrieved from the study of Prado-Martinez *et al.* [2]
138 who kindly shared the *.psmc* files. We only kept the PSMC curves that were computed on genomes with
139 a coverage higher than 12X. In total, this corresponded to a total of 17 individuals, namely three Eastern
140 chimpanzees (*P. t. schweinfurthii*), four Central chimpanzees (*P. t. troglodytes*), five Nigeria-Cameroon
141 chimpanzees (*P. t. ellioti*) and five Western chimpanzees (*P. t. verus*). The PSMC files were used to
142 reproduce the PSMC curves (Fig. S3).

2.2 Inference of demographic histories for each subspecies under non-stationary n -island models

We used SNIF (Structured Non-stationary Inferential Framework), a freely available program (<https://github.com/arredondos/snif>) based on a method developed by Arredondo *et al.* [31] to infer parameters of piecewise stationary n -island models. SNIF assumes that the number of demes (n) and their size (N diploids) are unknown and constant through time, whereas scaled migration rates ($M = 4Nm$, where m is the proportion of migrating genes at each generation) are allowed to vary over time in a piecewise manner. Note that throughout the whole paper, deme sizes are given in number of diploid individuals.

More specifically, SNIF assumes that the PSMC can be decomposed by dividing time into periods, called "components" (c), during which migration rate, M_i for component c_i , is constant. SNIF will infer the best timing (t_i) and duration ($t_{i+1} - t_i$) for these components to fit the observed PSMC/IICR curve for a given and fixed value of c provided by the user. To estimate the parameters of the model, SNIF minimizes a distance computed between the observed PSMC/IICR and the IICR simulated under the piecewise stationary n -island model (see Arredondo *et al.* [31] for details). The user must specify ω , a parameter that weights the computation of the distance between observed and simulated IICR curves by giving more weight to either recent or ancient times. The size of the parameter space explored by SNIF is defined by the user, who specifies a range of values for the parameters of the model, namely the number of islands n , their size N (in number of diploids), the scaled migration rates $M_i = 4Nm_i$ for each component c_i with $i \in \{0, \dots, c - 1\}$, and the times t_i (in generations) separating the components c_i and c_{i+1} (for instance t_1 separates the first component c_1 that starts at $t_0 = 0$ and the second component c_2 that ends at t_2). To scale and compare IICR curves to PSMC curves, a mutation rate (μ) and a generation time (g) are also required. The following values were used for the chimpanzee data: $\mu = 1.5 \times 10^{-8}$ per bp per generation [14] and $g = 25$ years [2].

To reduce computation time and improve consistency across runs, we first ran inferences using a wide parameter space to identify the range of parameter values that were more likely to produce IICR curves reasonably close to the observed PSMC. This allowed us to then re-run the analyses on a smaller parameter space, making the optimization algorithm more efficient for the same number of iterations. For this exploratory step, the following ranges were used: $n \in [2; 100]$, $N \in [10; 2 \times 10^4]$, $M_i \in [0.01; 100]$, and $t_i \in [4 \times 10^2; 4 \times 10^5]$. We also identified values for c and ω that would best describe the observed PSMC curves. We tested $c \in \{4, 5, 6, 7, 8\}$ and $w \in \{0.5, 1\}$ (1 being the default value). SNIF was run ten times for

172 each combination of c and ω value, and each run used 50 iteration steps of the optimization algorithm. The
 173 inference is expected to improve as c increases, since it allows the algorithm to add more changes in M and
 174 thus better fit the observed PSMC/IICR curve. We allowed c to vary between four and eight because the
 175 minimum number of components required to explain two humps in a PSMC is $c = 4$ [28] and because we
 176 considered that using more than eight components might lead to over-parametrization (see next section on
 177 the validation process).

178 This exploratory step allowed us to significantly reduce the parameter space as can be seen in Table 1,
 179 where the ranges for N and n were halved or nearly halved. We also found that $\omega=0.5$ generated the best fit
 180 to the observed data and we identified the most likely time windows (t_i) for the changes of migration rates
 181 (see Table S1). The latter significantly reduced the time required by the optimization algorithm as the t_i
 182 and M_i values can vary over several orders of magnitude. In particular, the distance between the target and
 183 inferred IICR was on average smaller for the same number of iterations when we constrained the t_i values
 184 (based on preliminary runs) than when we did not (results not shown). We finally found that using seven
 185 components for Western, Nigeria-Cameroon and Eastern chimpanzees, and eight components for Central
 186 chimpanzees provided a good balance between model complexity and increase in fit to the observed PSMC
 187 (and validation, see next section). For Western chimpanzees, we further specified not to fit the very recent
 188 past (< 20 kya), because we noticed that SNIF would try to fit the most recent increase (forward in time)
 189 in the IICR that we wanted to ignore as it differs in magnitude between the individuals of this subspecies.
 190 Table 1 summarizes the parameter space used for the analysis of all individuals of the different subspecies
 191 and for the results shown further down. Using this final parameter space, SNIF was run ten times on each
 192 PSMC curve, each run used 50 iteration steps of the optimization algorithm.

Table 1: Parameter space used to run SNIF

Subspecies	Sample size	c	ω	n_{min}, n_{max}	N_{min}, N_{max}	$M_{i,min}, M_{i,max}$	t_i
Western	5	7	0.5	2,60	10,10000	0.01,50	Constrained*
Nigeria-Cameroon	5	7	0.5	2,30	10,10000	0.01,50	Constrained*
Central	4	8	0.5	2,60	10,10000	0.01,50	Constrained*
Eastern	3	7	0.5	2,50	10,10000	0.01,50	Constrained*

* see Supp. Table S1 for the explicit specified time windows

193 2.3 Validation of the inferred scenarios

194 Once we had inferred demographic scenarios, we performed a validation step as recommended by Arredondo
195 *et al.* [31]. They suggested to simulate pseudo-observed data (POD) under an inferred scenario S^* , here in
196 the form of IICR or PSMC curves, and to analyse these POD using SNIF with the same parameter ranges
197 and c and ω values as those used to analyse the original observed PSMC curves. This procedure is some-
198 what similar to the validation process used in Approximate Bayesian Computation (ABC, [39]). In practice,
199 SNIF allows the user to generate a *ms* command [40] to simulate coalescent times (T_2) under an inferred sce-
200 nario S^* . This command is used by SNIF as an input to, first, produce a pseudo-observed IICR curve using
201 simulated T_2 values, and second, infer the best stepwise stationary n -island model. This allows to quantify
202 the discrepancy between the inferred model and the pseudo-observed underlying one. It is also possible to
203 produce a *ms* command to simulate genomic data (by adapting the *ms* command using appropriate mutation
204 and recombination rates and generation time) and run the PSMC method to produce a PSMC curve that can
205 then be used as POD. Note that using genomic data instead of T_2 values is more time consuming (several
206 hours to produce a pseudo-observed PSMC curve) and can only be applied to a limited number of simu-
207 lated scenarios. Here, we performed the validation step using both simulated IICR and simulated PSMC, as
208 explained below and in the Supplementary material.

209 Different individuals of the same subspecies exhibit PSMC curves that can differ more or less signif-
210 icantly in the recent past (see Figure S3 and Results). In addition, running SNIF on a particular PSMC
211 curve can generate slightly different scenarios (see Results) generally characterized by similar connectivity
212 graphs. Instead of trying to validate many similar scenarios, we arbitrarily chose an average scenario for
213 each subspecies based on parameter values close to the median of the distribution of the inferred values.
214 For instance, we found that the inferred values for n varied between 12 and 48 for Western chimpanzees,
215 with 50% of inferred values between 17 and 31, and we thus selected a scenario with $n = 25$ and extracted
216 the corresponding *ms* command. This *ms* command then served to produce as many independent IICR or
217 PSMC curves as there were individuals in that subspecies. This allowed us to quantify the variation of
218 inferred parameter values and compare it to the variation observed when analysing the empirical data. For
219 each run, we simulated 10^6 T_2 values to produce an IICR curve, and simulated 10 genomic sequences of 100
220 Mb to produce PSMC curves, adapting the *ms* command using a mutation rate of 1.5×10^{-8} [14], a recom-
221 bination rate of 0.7×10^{-8} per bp per generation [4], and a generation time of 25 years [2]. We produced

222 a (pseudo-observed) PSMC curve with PSMC [24] (flags -N 25 -t 15 -r 5 -p "4+25*2+4+6"). Altogether,
223 these pseudo-observed IICR and PSMC curves were used by SNIF as POD, and the inference steps were
224 done exactly as described in the previous section for the empirical PSMC curves.

225 **2.4 Integration of the four subspecies n -island models in a general tree model**

226 In the previous section, we inferred and validated demographic scenarios able to reproduce and fit the ob-
227 served PSMC curves for each subspecies independently. Here we asked whether it was possible to integrate
228 the four sub-subspecies into one unique demographic model that could explain the individual empirical
229 PSMC curves, while incorporating a splitting tree based on the relationships between the subspecies as in-
230 ferred by Prado-Martinez *et al.* [2] and the stepwise stationary n -island models within each branch of the
231 tree, instead of assuming a panmictic population or subspecies. We constructed a scenario where an ancestral
232 species is subdivided into n populations, and splits at time T_{CENW} into two branches which are themselves
233 subdivided in demes (Fig. 7). One of these branches will later divide into a set of demes representing the
234 ancestor of the Central chimpanzees and another set of demes corresponding to the Eastern chimpanzees'
235 ancestors. The other ancestral branch becomes the ancestor to Western and Nigeria-Cameroon chimpanzees
236 following a similar process. These splits thus generate the demes corresponding to the current four sub-
237 species, at T_{CE} and T_{NW} for Central/Eastern chimpanzees and Western/Nigeria-Cameroon chimpanzees,
238 respectively (see further, Figure 7).

239 SNIF cannot infer complex models involving both n -islands and tree models. Consequently, we built
240 a general scenario manually, using the arbitrary "average" scenario used for the validation step above as a
241 starting point. From the subspecies scenarios, we constructed a tree model where the subspecies n -island
242 models merge (backward in time) in a way similar to that used by Rodríguez *et al.* [30]. For instance,
243 the n -island models of Western and Nigeria-Cameroon chimpanzees were characterized by $n = 25$ and
244 $n = 13$ islands respectively, and we thus merged the two sets of islands so as to use the largest n number
245 for the ancestral species as suggested by Rodríguez *et al.* [30]. The same process was done for Central and
246 Eastern chimpanzees, and then again for the ancestral branches when they merged into the most ancestral
247 meta-population. Different values were tested for T_{CENW} , T_{NW} and T_{CE} to match the times at which the
248 PSMC curves of the sub-populations were merging backward in time, namely $T_{CENW} \in \{900, 800, 700\}$,
249 $T_{NW} \in \{900, 800, 700\}$ and $T_{CE} \in \{600, 500, 400\}$ in kya (thousands of years ago). For each scenario we
250 generated the IICR plots using a script developed by W. Rodríguez [29]. We used the script to simulate 10^6

251 T_2 values with ms , sampling two haploid individuals in one deme, repeating the process for each of the four
252 current meta-populations.

253 **2.5 Prediction of genomic diversity and differentiation statistics**

254 To test whether the general tree model (Figure 7) was able to predict genetic diversity and differentiation
255 statistics in addition to the IICR, we simulated 100 segments of 1 Mb under the four subspecies models and
256 under variations of the general model using ms [40], where we allowed for the splitting times (or joining
257 times, with time going backward) to take several values (see previous section). We used a mutation rate
258 of 1.5×10^{-8} per bp per generation [14] and a recombination rate of 0.7×10^{-8} per bp per generation
259 [4]. We estimated genetic diversity by computing the individual observed heterozygosity (H_o) in 10 diploid
260 individuals sampled in the present from one deme for each subspecies. We computed H_o as the number
261 of heterozygous sites divided by the total length of the simulated genomes (100*1Mb). We also computed
262 genetic differentiation (Hudson’s F_{ST}) between demes of the same subspecies and between demes from
263 different subspecies, sampling ten diploid individuals per deme. Pairwise F_{ST} were computed using original
264 scripts from Tournebize and Chikhi [38].

265 Empirical values of genetic diversity were retrieved from Prado-Martinez *et al.* [2] (from Suppl. Ta-
266 ble 12.4.1) and de Manuel *et al.* [6] (Table S4). Both studies used the same genomic data produced by
267 Prado-Martinez *et al.* [2] and computed observed individual heterozygosity. We reported in Figure 9 their
268 measures. Empirical values of F_{ST} were retrieved from Fischer *et al.* [22] (computed on autosomal se-
269 quences) and Lester *et al.* [18] (computed on microsatellites). Lester *et al.* [18] only published F'_{ST} , another
270 estimate of genetic distance derived from F_{ST} , and they kindly shared with us the original F_{ST} values (Hud-
271 son’s estimator).

272 **3 Results**

273 **3.1 Independent demographic history of the different subspecies**

274 We found that by using the parameter space described in Table 1 and applying SNIF to all individual PSMCs
275 with high enough coverage within each subspecies, we were able to produce IICR curves that were similar to
276 the observed PSMC plots, as displayed in Figure 2 for an example and Supplementary Figures S4, S5, S6, S7
277 for all inferences. The inferred parameters are displayed in Figure 3. Panels A and B show the distribution

278 of the inferred number of islands n and their size N (in number of diploid individuals), respectively (see
 279 also Table S2 and S3). The largest number of islands and the smallest deme size were inferred for Western
 280 chimpanzees, with a median n equal to 21 (50% of the inferred n values being between 17 to 31) and a
 281 median N equal to 305 (50% of the inferred N values between 239 and 335). The inferred number of
 282 islands was similar for Nigerian-Cameron and Eastern chimpanzees, with median values being 11 and 13,
 283 respectively and median N being 1154 and 800, respectively. Finally, for Central chimpanzees, 50% of the
 284 inferred n and N fall within 16-20 and 589-834, respectively.

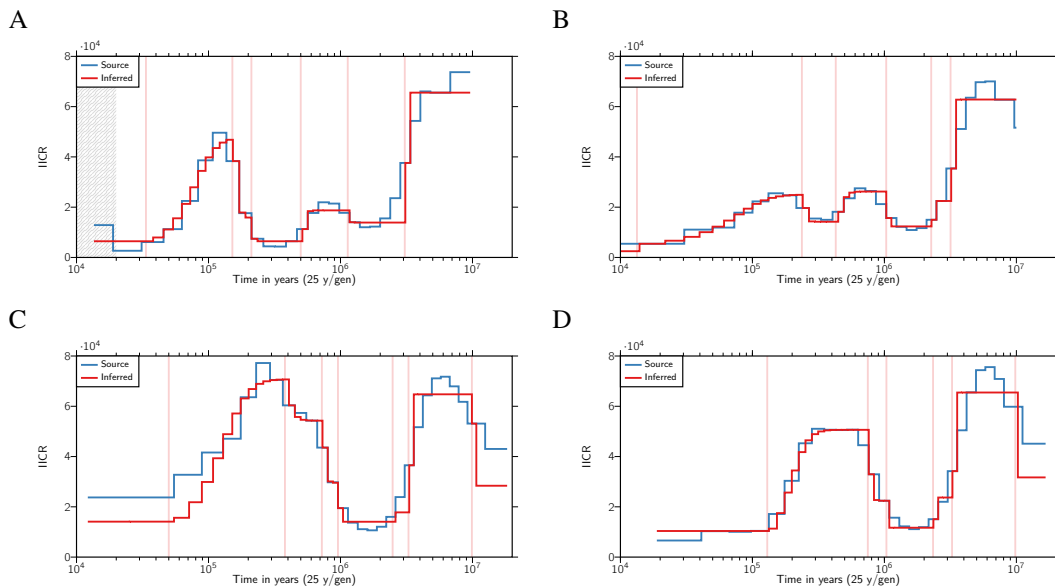


Figure 2: Inferred IICR curves and empirical PSMC curves for one individual per subspecies. The IICR curves are in red, and the empirical PSMC curves are in blue, and each panel corresponds to one individual from a different chimpanzee subspecies. Panel A . Western (Clint). Panel B. Nigerian-Cameron (Damian). Panel C. Central (Vaillant). Panel D. Eastern (Kidongo). only one repetition of SNIF is displayed. See Supplementary Figures S4, S5, S6 and S7 for all the inferences. The vertical red lines highlight the times at which there is an inferred change in migration rate and therefore delimit the SNIF components. The grey zone in panel A corresponds to a part of the source PSMC which was not taken into account in the fitting of the curve by SNIF (see Material and Methods).

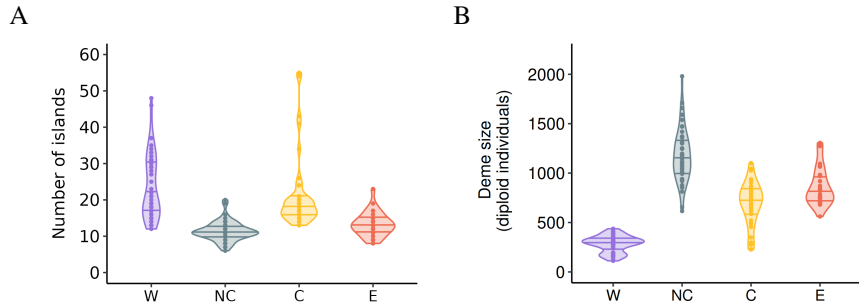


Figure 3: Distribution of the number and size of the demes inferred for the four chimpanzee subspecies. Panel A represents the inferred number of islands. Panel B represents the deme size (in number of diploid individuals). For both panels the results are plotted for each subspecies separately for Western (W), Nigeria-Cameroon (NC), Central (C) and Eastern (E) chimpanzees across the ten independent repetitions/inferences carried out per individual for all individuals, using the parameter space shown Table 1. Each dot corresponds to one repetition of SNIF done on one individual. The horizontal lines inside the violins correspond to the 25%, 50% (median) and 75% quantiles.

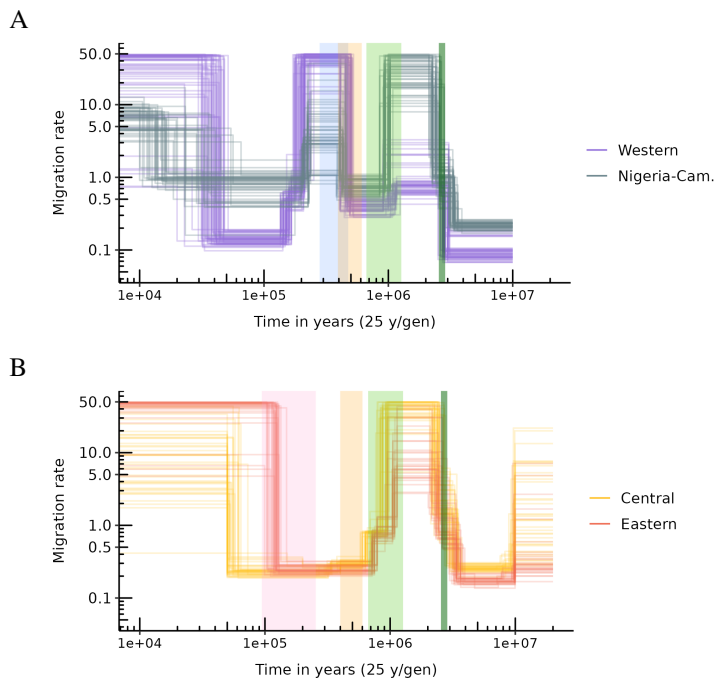


Figure 4: Connectivity graphs inferred by SNIF for the four chimpanzee subspecies. The y-axis represents scaled migration rates between demes (M_i), and the x-axis represents time in years on a logarithmic scale. Panel A shows connectivity for Western and Nigeria-Cameroon chimpanzees. Panel B shows the same for Central and Eastern chimpanzees. Each coloured curve corresponds to one inference (one repetition of SNIF) using one PSMC curve (or individual), giving therefore 50, 50, 40 and 30 curves in total for Western, Nigeria-Cameroon, Central and Eastern chimpanzees respectively. Backward in time, the vertical coloured intervals represent respectively: C-E divergence time (in pink, panel B), W-NC divergence time (in blue, panel A), C-E and W-NC ancestral populations (in yellow, both panels), the mid-Pleistocene transition (light green, both panels) and the Pliocene-Pleistocene transition (dark green, both panels).

285 The connectivity graphs (Figure 4) show the inferred migration rates ($M_i = 4Nm_i$) through time. For
286 the four subspecies, we observe a significant increase in connectivity (forward in time) between 2 and 3
287 Mya, with a higher support for the period 2.5-3 Mya, followed by a decrease around 1 Mya. This period of
288 increased connectivity is characterized by M_i values above 3 and up to 50 migrants per generation across the
289 n -island for Nigeria-Cameroon, Central and Eastern chimpanzees, while values for Western chimpanzees
290 are between 0.4 and 4. This period corresponds to a time when the four subspecies had a likely common
291 ancestor. For Western and Nigeria-Cameroon chimpanzees, we observe a second more recent increase in
292 connectivity between 500-600 kya and 200 kya, not observed in Central and Eastern chimpanzees, with M_i
293 values ranging between 0.8 and 50. Finally, in the more recent past, all subspecies exhibit an increase in
294 gene flow, occurring around 100-150 kya for Eastern chimpanzees, 50 kya for Central chimpanzees, 40 kya
295 for Western chimpanzees and between 70 and 10 kya for Nigeria-Cameroon chimpanzees.

296 While the connectivity graphs are rather robust across individuals from the same subspecies and for
297 more ancient periods for individuals from different subspecies, there is some variability in the inferred
298 scenarios, as expected from the fact that different individuals exhibit different PSMC plots (see next section).
299 We also observe variability in the number of islands or demes inferred for Western chimpanzees (extreme
300 values range: 12-48 islands), and in the deme size inferred for Nigerian-Cameroon chimpanzees (extreme
301 values range: 616-1980 diploid individuals). We also observe much variability in the most recent and most
302 ancient parts of the connectivity graphs. For instance, there is a great variability in M_i values for Central
303 chimpanzees in the last 50 kya and before 10 Mya, and in the M_i and t_i values for Nigeria-Cameroon
304 chimpanzees in the last 1 Mya.

305 **3.2 Validation step**

306 We simulated T_2 values from an average scenarios identified for each subspecies and obtained IICR curves
307 that were then analyzed using SNIF as a validation test of our inferential procedure (see Material and Meth-
308 ods). We were able to recover the original scenario with great precision, as shown in Figures 5 and 6. Black
309 dots and lines are the pseudo-observed data, and the coloured patterns are the values inferred by SNIF. The
310 inferred n and N are centered around the values that were used to generate the pseudo-observed IICRs,
311 suggesting that SNIF is able to infer the complex scenarios inferred from the real data. We observe some
312 variability in the inferences, as expected in any inference process and as we observed for the real data. Sim-
313 ilarly, the inferred connectivity graphs were generally very good, with nearly no variability in the inferred t_i

314 values, and slightly more variability in the larger M_i values. The shape of the inferred connectivity graphs is
 315 however perfectly inferred for the complex scenarios that had seven or eight components.

316 When we simulated genomic data under inferred scenarios, generated PSMC curves and provided them
 317 to SNIF as POD (Supp. Figure S10 and S11), we also recovered the original scenarios with good preci-
 318 sion, though SNIF inferred fewer and larger islands for Eastern chimpanzees, suggesting that we might be
 319 underestimating n and overestimating N for this particular subspecies. Inferred connectivity graphs were
 320 also generally good for the four subspecies, with higher variability in the inferred t_i and M_i values than for
 321 pseudo-observed IICRs computed on simulated T_2 , which approaches the variability observed when running
 322 SNIF on empirical data. Altogether these results confirm the ability to infer a complex history of changes in
 323 connectivity under the stepwise stationary n -island model.

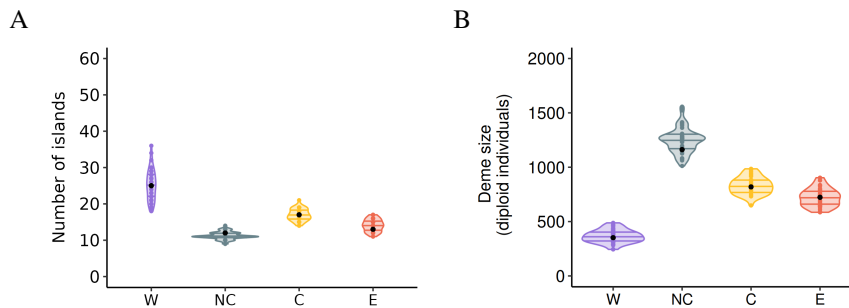


Figure 5: Distribution of the A. number of islands and B. deme size inferred by SNIF across the 10 repetitions per individual and all individuals for Western (W), Nigeria-Cameroon (NC), Central (C) and Eastern (E) common chimpanzees. Black dots are the pseudo-observed data.

324 3.3 General n -island model

325 The general tree model incorporating within its branches n -island models based on the inferences presented
 326 above for each subspecies is represented Figure 7. As explained in the Materials and Methods section, it
 327 was obtained by selecting for each subspecies an "average" inferred scenario for the different subspecies.
 328 The scenarios we kept had $n = 25$ islands of size $N = 352$ (diploid) individuals for Western chimpanzees, n
 329 $= 12$ islands of size $N = 1162$ individuals for Nigeria-Cameroon chimpanzees, $n = 17$ islands of size $N = 819$
 330 individuals for Central chimpanzees and $n = 13$ islands of size $N = 723$ individuals for Eastern chimpanzees.
 331 The sets of demes were then successively divided at times corresponding to the estimated split times for
 332 the pairs of subspecies. These split times are not known but can be approximated by using the times at
 333 which the different PSMC curves join. For instance, at time T_{CE} , the 17 demes of Central chimpanzees and

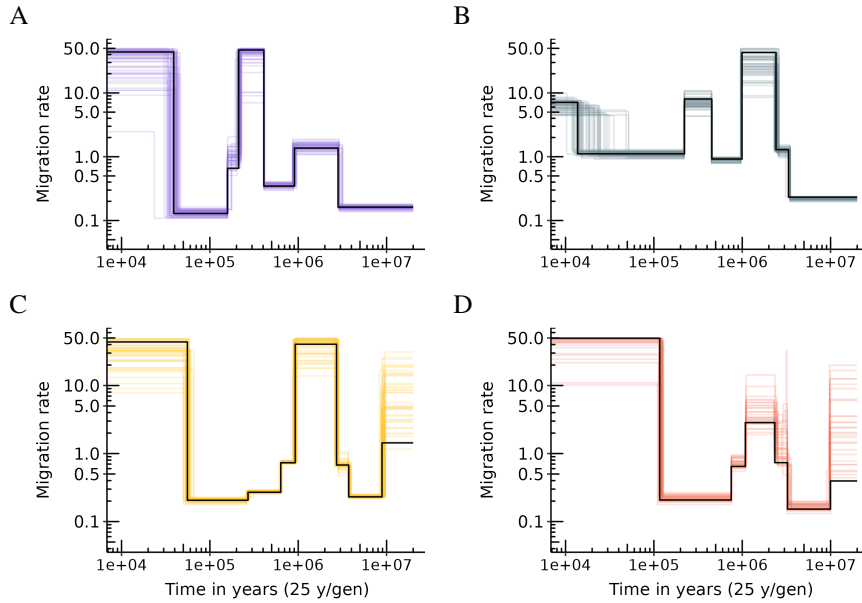


Figure 6: Inferred connectivity graph using a scenario inferred by SNIF as pseudo-observed data for each subspecies of common chimpanzee. A. Western chimpanzees, B. Nigeria-Cameroon chimpanzees, C. Central chimpanzees and D. Eastern chimpanzees. Black lines are the pseudo-observed data, and each colored line corresponds to one inference.

334 the 13 demes of Eastern chimpanzees are all assumed to derive (forward in time) from the demes of their
 335 ancestor. As noted in the Materials and Methods, this ancestor was assumed to have 17 demes as 17 is the
 336 largest of the two values of n . For simplicity, the 13 Eastern chimpanzee demes were assumed to derive
 337 from 13 demes rather than from all 17 demes of the ancestral meta-population. Similarly, at time T_{NW} , 12
 338 demes of Nigeria-Cameroon chimpanzees join backward in time. 12 (out of 25) demes of the ancestor they
 339 share with Western chimpanzees. Finally, at time T_{CENW} , the 17 islands of the ancestral meta-population of
 340 Central and Eastern chimpanzees join 17 (out of 25) islands of the ancestral meta-population of Western and
 341 Nigeria-Cameroon chimpanzees. Thus, the most ancestral meta-population is represented by 25 demes.

342 Several values for T_{CE} , T_{NW} , and T_{CENW} were tested as it is unclear how closely splitting times of meta-
 343 populations correspond to splitting times of IICR or PSMC curves (see for instance Rodríguez *et al.* [30] and
 344 Chikhi *et al.* [29]). Empirical and simulated IICR curves presented in Figure 8 were obtained for $T_{CE} = 600$
 345 kya, $T_{NW} = 800$ kya and $T_{CENW} = 900$ kya, which are the values that gave the best visual fit of the estimated
 346 IICR curve to the observed PSMC curves (in particular for Nigeria-Cameroon and Eastern chimpanzees,
 347 see below and Supp. Figure S12-S15). For each subspecies, the simulated IICR curve produced for a
 348 sample taken in a deme is represented and closely follows the corresponding observed PSMC. We found

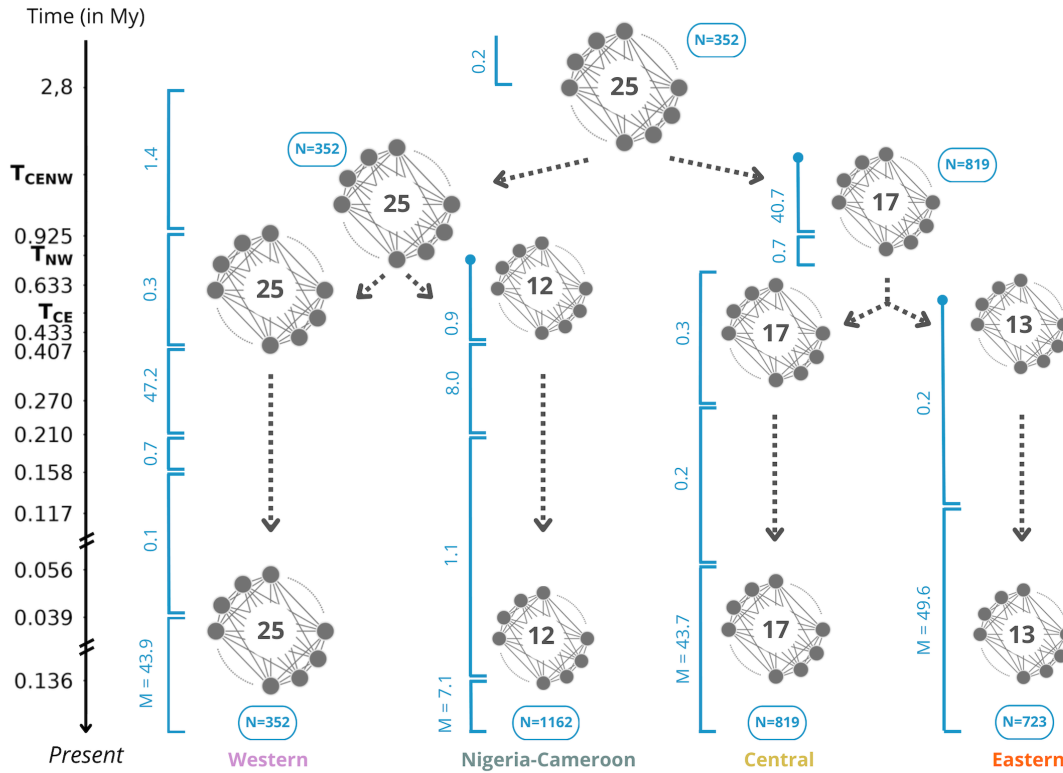


Figure 7: Proposed general n -island model for the history of the four subspecies of common chimpanzee. Dark full circles symbolize subpopulations structured in n -island, and the number in the middle corresponds to the number of demes n . Deme size N is given in number of diploid individuals. T_{CE} , T_{NW} and T_{CENW} correspond to the times at which two meta-populations join each other (backward in time), for Central/Eastern Chimpanzees, Nigeria-Cameroon/Western chimpanzees, and the two ancestral meta-populations respectively. In blue, along the vertical intervals, are the migration rates $M_i = 4Nm_i$.

349 that changing the splitting times (Supp. Figure S12-S15), and especially testing more recent values, did not
 350 significantly change the IICR curves, even though the estimated IICR could depart from the observed PSMC
 351 at the splitting time when the latter occurred too recently (see the case of Nigeria-Cameroon and Eastern
 352 chimpanzees in Supp. Figures S13 and S15 respectively). Altogether, we could construct a general model
 353 able to explain all the observed PSMC curves while incorporating both a tree model and intra-subspecies
 354 population structure, without any population size change within each branch.

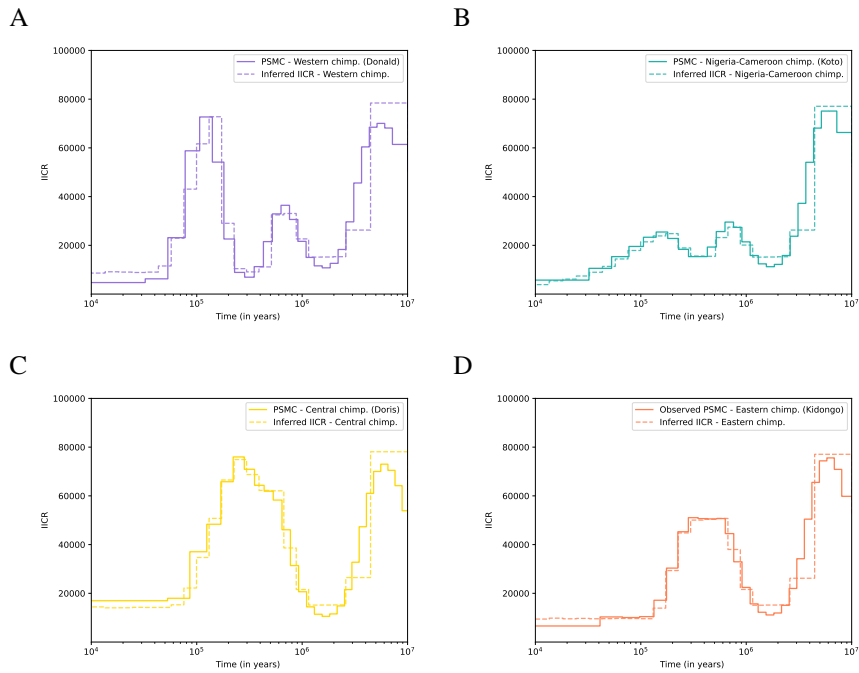


Figure 8: Empirical PSMC (solid line) and simulated IICR (dotted lines) for each subspecies of common chimpanzees under the n -island model displayed Figure 7, with $T_{CE} = 600$ Mya, $T_{NW} = 800$ Mya and $T_{CENW} = 900$ Mya. A. Western chimpanzees, B. Nigeria-Cameroon chimpanzees, C. Central chimpanzees and D. Eastern chimpanzees.

355 3.4 Prediction of other genomic statistics of diversity and differentiation

356 Though we stress that none of the models above (individual and global) should be taken at face value, the
 357 results obtained suggest that we were able to generate IICR plots that were similar to the observed PSMC
 358 plots under 1) n -island models for each subspecies independently and 2) a general model incorporating the
 359 four subspecies. We simulated genomic data under our general model and computed statistics representing
 360 genetic diversity and genetic differentiation to see if it could predict values close to empirical ones. As
 361 can be seen in Figure 9, we found that our simulated diversity measures were close to the observed values

362 computed by de Manuel *et al.* [6], and slightly lower than those computed by Prado-Martinez *et al.* [2]
 363 for Nigeria-Cameroon, Central and Eastern chimpanzees. We also found that our simulations recovered
 364 the ranking of genetic diversity for three subspecies, with Central chimpanzees being the most genetically
 365 diverse and Western chimpanzees harbouring the lowest level of genetic diversity, as observed empirically
 366 (Figure 9). However, the simulated Nigeria-Cameroon chimpanzees showed the same genetic diversity as
 367 Western chimpanzees, which is not consistent with what is found empirically [2]. These diversity estimates
 368 were identical across the different splitting times we tested.

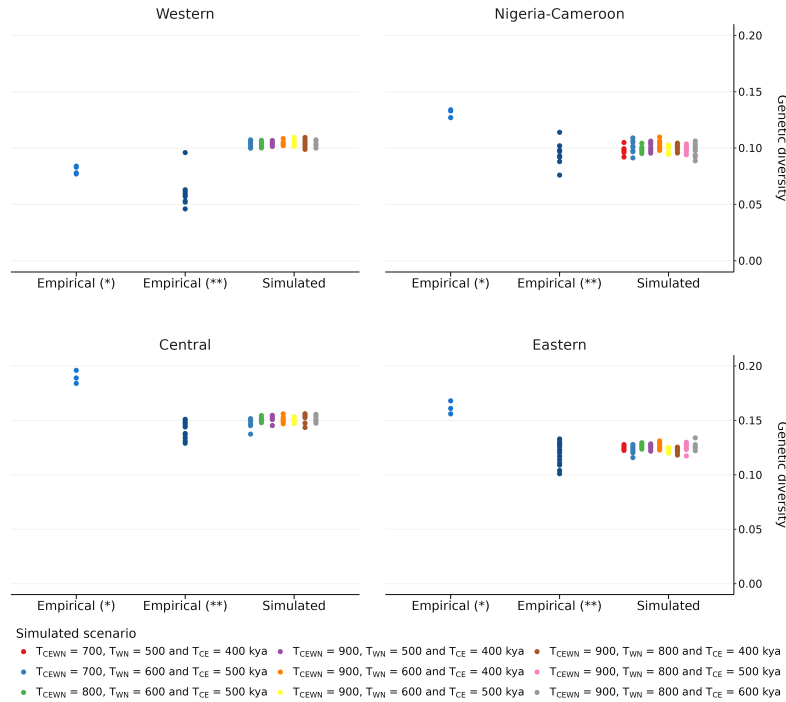


Figure 9: Genetic diversity of genomic data simulated under the model Figure 7 with several values for splitting times, sampling 10 diploid individuals in one deme. Empirical values were retrieved from (*) Prado-Martinez *et al.* [2] and (**) de Manuel *et al.* [6], each point corresponding to an estimate of individual observed heterozygosity.

369 Regarding the pairwise F_{ST} values, Figure 10 (and Supplementary Figures S16, S17, S18) shows that
 370 the general model predicts levels of within subspecies genetic differentiation that are within the empirical
 371 distribution, with the exception of Nigeria-Cameroon chimpanzees, a subspecies for which there are nearly
 372 no observed pairwise values. Figure 10 also shows that we strongly over-estimate between subspecies
 373 differences. As expected, the F_{ST} values between subspecies were sensitive to splitting times. For $T_{CE} = 600$
 374 kya, $T_{NW} = 800$ kya and $T_{CENW} = 900$ kya, the values of splitting times that follow most closely the empirical

375 PSMC (see Figure 8), our model overestimated genetic differentiation in all pairs of subspecies. The F_{ST}
376 values estimated from our model were three to five times higher than their respective empirical values for all
377 pairs of subspecies. For instance, the median of the empirical F_{ST}^{W-NC} was 0.12 whereas for the simulated
378 F_{ST}^{W-NC} it was 0.50. For the other pairs we had similar results (median empirical $F_{ST}^{W-C} = 0.10$ vs simulated
379 $F_{ST}^{W-C} = 0.40$, median empirical $F_{ST}^{W-E} = 0.14$ vs simulated $F_{ST}^{W-E} = 0.46$, median empirical $F_{ST}^{NC-C} =$
380 0.08 vs simulated $F_{ST}^{NC-C} = 0.41$, median empirical $F_{ST}^{NC-E} = 0.08$ vs simulated $F_{ST}^{NC-E} = 0.47$, median
381 empirical $F_{ST}^{C-E} = 0.08$ vs simulated $F_{ST}^{C-E} = 0.28$).

382 As expected we found that having more recent splitting times reduced our F_{ST} estimates which were
383 getting closer to empirical values, though they never reached them for the parameter values we tested and
384 which were selected to match the splitting times in the PSMC curves (Supplementary Figures S16, S17,
385 S18). Genetic differentiation between demes of the same subspecies was much lower than between demes
386 from different subspecies and were low and similar for three subspecies (Western, Central and Eastern) but
387 much higher value within the Nigeria-Cameroon subspecies.

388 As expected as well, our general model predicted lower F_{ST} values between Western and Nigeria-
389 Cameroon chimpanzees and between Central and Eastern chimpanzees than between other pairs of sub-
390 species. This what is empirically observed, but we note that this is the reason why the original authors
391 proposed the topology that we used. Finally, Eastern chimpanzees are the most differentiated subspecies to
392 both Western and Nigeria-Cameroon chimpanzees, and Nigeria-Cameroon chimpanzees are the most distant
393 subspecies to Central and Eastern chimpanzees, in both observed and simulated estimates.

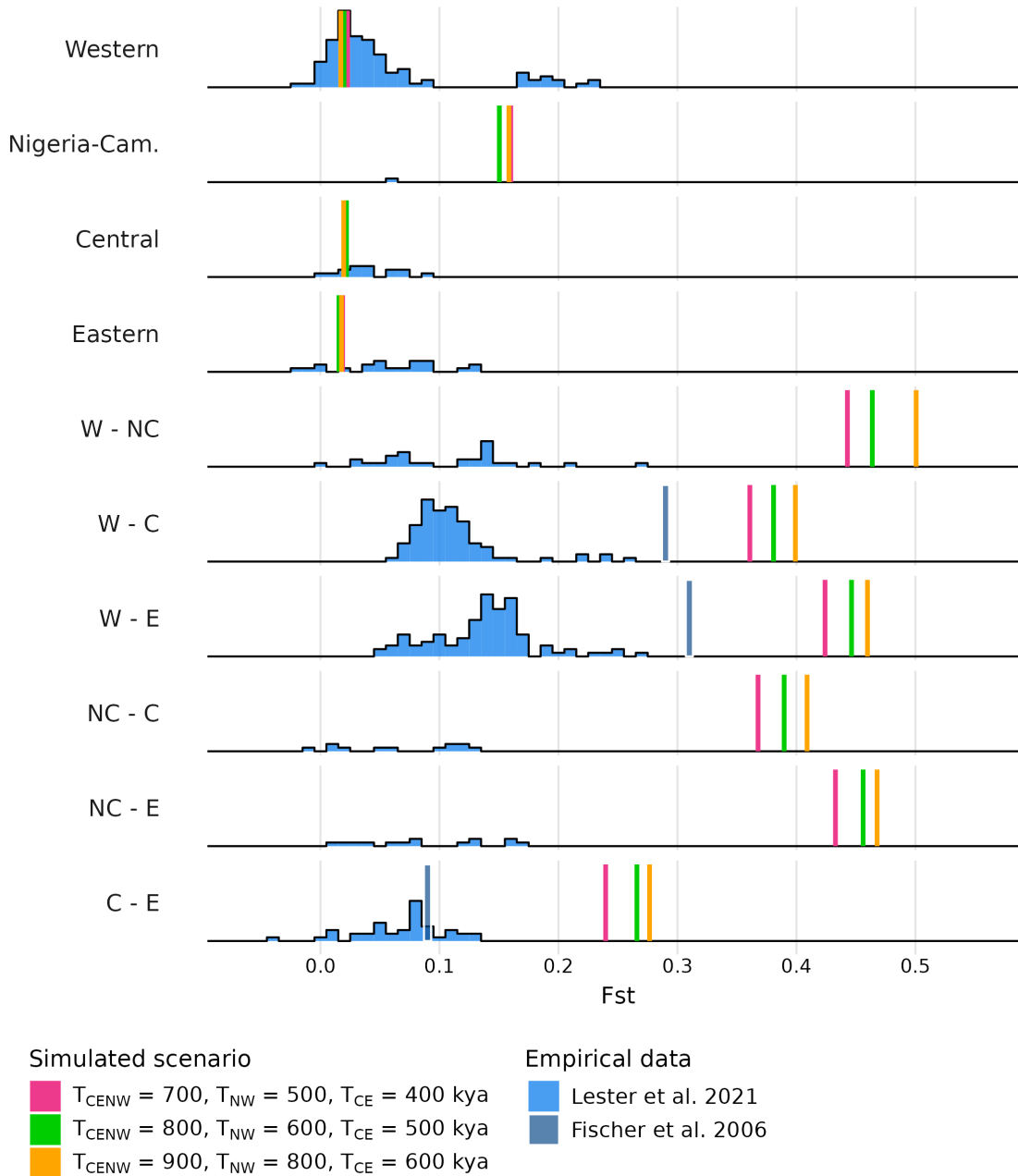


Figure 10: Genetic differentiation within and between subspecies. F_{ST} were computed on genomic data simulated under the model Figure 7 with $T_{CE} = 600$ kya, $T_{NW} = 500$ kya and $T_{CENW} \in \{700, 800, 900\}$ kya. See Supplementary Figures S16, S17, S18 for other splitting time values. In blue are the empirical values: histograms were retrieved from Lester *et al.* [18] (who used microsatellite data) and the blue vertical lines were retrieved from Fischer *et al.* [22] (who did not have samples of Nigeria-Cameroon chimpanzees in their study).

4 Discussion

Reconstructing the demographic history of species from genetic data is a complex endeavor and a major challenge because many factors have likely influenced the genetic patterns we observe today. These factors include population structure, changes in connectivity and in population size, selection, social structure (mating systems), among others [11, 41, 24, 42]. Major progress in human population genetics and genomics, including paleogenomics, have revolutionized our understanding of present-day and past genetic variation [43, 44]. Ideas and methods coming from human population genetics have influenced our understanding of the genetic diversity of other species [45, 46, 6, 14]. Here we propose to rather use what we know about other great apes to ask questions about ancient population structure and the evolutionary history of humans, and perhaps learn from such comparative analyses, as others have also suggested [47]. The work presented here is thus both an attempt at increasing our understanding of the ancient structure of chimpanzees but also on the evolutionary history of humans.

4.1 Towards a demographic history of chimpanzees incorporating population structure

We managed to explain patterns of genetic diversity within each subspecies of common chimpanzees with simple models of population structure and variable migration rates only, and we obtained demographic scenarios for each subspecies with shared periods of connectivity change. The validation step we applied (see Supplementary Material) suggests that if real genomic data had been generated under the inferred demographic scenarios, our method would have been able to infer them. While we do take inferred scenarios with a grain of salt, this validation step suggests that complex population structure can be inferred from single genomes. This is particularly notable because we recovered the simulated scenarios for each subspecies independently. Though this does not confirm that chimpanzees evolved under the inferred scenarios, it suggests that SNIF can infer different complex scenarios from the chimpanzee PSMC curves. A similar validation process is often applied in ABC studies [39, 48] but it is not that common in the literature, and we argue that it should be implemented more often to validate scenarios proposed on the basis of other inference methods.

Despite some variability in the inferences, we observed consistency across inferences within and between subspecies. We found that Western chimpanzees are characterized by a higher number of demes with a smaller size than the other three subspecies. This could be consistent with the fact that this subspecies

422 lives in a drier habitat, mostly in savanna [49], leading to a forest habitat that is more fragmented. However,
423 it is unclear if it was the case throughout the evolutionary history of Western chimpanzees, and thus drawing
424 strong conclusions is difficult at this stage. More generally, interpreting the number of islands and their
425 size is not trivial and relating these parameters to empirical observations is not straightforward, in the same
426 way that effective population size (N_e) values inferred in previous studies assuming panmixia are not easily
427 interpreted. We assumed for simplicity that the number of demes and their size were constant. Allowing for
428 the number of demes to vary would be more realistic but would also significantly increase the number of
429 parameters in the models. At this stage, the inferred values of n and N should thus be interpreted with care.

430 Our models suggest that the four subspecies share a similar history of connectivity until approximately
431 500 kya (forward in time). We found a period of high connectivity between 2.5 and 1 Mya, followed by
432 a decrease in connectivity until approximately 600-500 kya. The start of this period coincides with the
433 Pliocene-Pleistocene transition boundary dated to around 2.6 Mya, whereas the drop in connectivity around
434 1 Mya falls within the Middle Pleistocene transition thought to have occurred between 1.2 Mya and 700
435 kya [50]. A second and more recent period of high connectivity, between 600-500 and 200-150 kya is also
436 observed, although in Western and Nigeria-Cameroon chimpanzees only. The fact that only two chimpanzee
437 subspecies were affected by this increase in migration during the most recent Middle Pleistocene period
438 suggests that whichever environmental disturbances caused the genetic signal observed in the PSMC, these
439 disturbances were localised mostly in Western Africa. Interestingly, Mazet *et al.* [28] and Arredondo *et al.*
440 [31] also inferred high values of migration rates between 2.5 and around 1 Mya using PSMCs from humans,
441 but did not identify the more recent period of high connectivity found in Nigeria-Cameroon and Western
442 chimpanzees. This suggests that humans may share a common environmental history with Eastern and
443 Central African chimpanzees, rather than with Western and Nigeria Cameroon chimpanzees for this period,
444 at least. This also supports the idea that comparative analyses of genomic data from other vertebrates and
445 primates from Africa (Eastern and Western) could improve our understanding of the history of the genus
446 *Homo* in the last two millions of years.

447 We must however be careful in interpreting genomic data and environmental changes together, and more
448 work would be needed to validate these results since they are based on a simple interpretation of the PSMC
449 curves and on the assumption that PSMC curves infer the IICR with sufficient precision. At this stage we
450 still lack a clear demographic model that would integrate the Pliocene-Pleistocene and Middle Pleistocene
451 transitions and that can explain how environmental changes would have affected habitat connectivity (or

452 changes in effective population size), similarly impacting the PSMC curves in humans and chimpanzees.
453 Also, we must acknowledge that reconstructing paleo-environments and habitats is still a complex endeavour
454 [51, 52].

455 From a more technical point of view, we should also note that the inferred migration rates for Western
456 chimpanzees were lower than for the other three species (Figure 4). This is surprising since all subspecies
457 should provide similar values for the periods where there was one ancestral species to all four, and the PSMC
458 curves overlap. We currently have no simple interpretation, and this could be due to some specificity of the
459 Western subspecies, the quality of its genome, or the fact that we also inferred smaller deme sizes.

460 Similarly, we must note that the PSMC curves exhibit a large variance in the recent past with an apparent
461 increase (forward in time) in the recent past that is interpreted in the connectivity graph as an increase in
462 gene flow. We stress that this observed increase (forward in time) could also be due to a recent increase
463 in the deme size, or to an uncertainty in the inference of the IICR. Indeed, the large variance in PSMC
464 estimates in the recent past has been noted since the publication of the method of Li and Durbin [24]. Since
465 SNIF assumes models with constant size it cannot typically fit this section of the IICR without making
466 major changes in M . One must recall that under a model of constant size the IICR will necessarily stay at
467 a low value (corresponding to the deme size in the recent past). IICR theory also shows that the IICR will
468 "move up" quicker (backward in time) from the deme size to large values when M is large. Thus, under
469 the assumption of constant size, SNIF will infer large M values in the very recent past to allow the IICR to
470 move "up" rapidly from the inferred deme size, as explained by Mazet *et al.* [28]. At this stage, we thus
471 considered that the recent increase in migration rate inferred for all chimpanzees should be interpreted very
472 cautiously, if not ignored.

473 **4.2 The general model and the limits of tree models**

474 Using the demographic scenarios inferred for each subspecies of common chimpanzees, we successfully
475 integrated the results of SNIF for each subspecies within a general tree model inspired by previous research
476 on the four subspecies [2, 6, 14]. The difference with previous research was thus that we used n -island
477 models instead of panmictic populations within each of the branches of the phylogenetic tree. We found that
478 this model explained the PSMC curves of the four subspecies, and predicted well observed heterozygosity
479 within demes and genetic differentiation between demes from the same subspecies. However, even using
480 the shortest split times that would be consistent with the PSMC curves, the model led to an overestimation

481 of genetic differentiation between subspecies. This suggests that the statistics that depended on the SNIF
482 inference were generally better than those that depended on the tree model. This consequently implies that
483 using a tree topology without gene flow to define the relationships between the four subspecies and ignoring
484 possible gene flow between them may not be appropriate. Two recent studies identified IBD patterns across
485 the four subspecies considered as a single unit, suggesting that the four subspecies were part of a very large
486 spatial metapopulation with gene flow between neighbouring populations, including populations currently
487 attributed to different subspecies. Spatial models, instead of n -island models, might thus be necessary to
488 represent the evolutionary history of chimpanzees.

489 The idea that gene exchange may have taken place between subspecies has been present in the literature
490 [2, 14, 53, 6, 13, 11, 12, 10]. However, in most cases gene flow was seen as discrete events that could be
491 dated, or that were limited to a pair of subspecies, which were in some cases not in geographical contact.
492 Brand *et al.* [14] reviewed the literature on this question and found that at least 14 admixture events had
493 been identified by eight different studies (Figure 1 of Brand *et al.* [14]) including one admixture event from
494 a mysterious ghost species into the ancestors of bonobos [53]. Among these putative admixture events,
495 some were identified by only one study whereas others were identified by two to five. It also appeared that
496 some studies identified only one admixture event [7] whereas others identified as many as eight [13]. Brand
497 *et al.* [14] themselves used an inferential method (Legofit, [54]) and a model that allowed for up to seven
498 admixture events but only found support for two.

499 Altogether, this suggests that it has been difficult to find a consistent history of admixture or gene flow
500 among previous genetic studies. We must stress that these studies are not always easy to compare, and some
501 differences may arise from the fact that their sampling was different. For instance, several studies have
502 no sample from one or two chimpanzee subspecies, whereas in other cases, the authors used samples from
503 individuals with unknown geographic origin. However, one common feature of all these studies is that they
504 consider tree models that ignore population structure below the subspecies level. They usually assume that
505 the chimpanzee subspecies and the bonobos should be modelled as independent and panmictic lineages of
506 an evolutionary tree where the only gene flow allowed is through these discrete admixture events.

507 **4.3 The limits of the piecewise n -island model: towards spatial models**

508 The approach used throughout the manuscript follows the theoretical and simulation-based work of several
509 authors who found that structured stationary and non-stationary models can generate genetic signatures that

510 will be interpreted in terms of population size change when population structure is ignored [32, 55, 33, 56,
511 57, 28]. However, the n -island models we assumed with SNIF ignore spatial processes. As a consequence,
512 IBD patterns observed by [17] and [18] cannot be reproduced, and suggest that the different subspecies were
513 genetically connected in the recent past even if the chimpanzees's habitat is currently highly fragmented and
514 discontinuous.

515 A difficulty that could arise from the use of spatial models is that the parameter space may increase
516 significantly making the inference process more difficult. However, if we wish to improve our understanding
517 of the evolutionary history of great apes, including humans, we may have no choice but integrate spatial
518 models [58, 59]. As a simple test example and to illustrate the importance of spatial models, we developed
519 a simple 1D stepping-stone model inspired by the demographic model proposed by de Manuel *et al.* [6]
520 to study the demographic history of chimpanzees and bonobos. These authors assumed a tree model and
521 allowed for the possibility of admixture events between subspecies and between bonobos and chimpanzees.
522 They computed D-statistics and found evidence for admixture between bonobos and chimpanzees. Details of
523 our 1D stepping-stone models and most of the results can be found in the Supplementary Material, but here
524 we mainly wish to stress that we were able to reproduce the D-statistics with our spatial model without any
525 introgression between bonobos and chimpanzees. By changing gene flow and deme size in the structured
526 ancestral species, we found that we were recovering even higher D values than those observed today. This
527 suggests that the bonobo admixture signals detected in chimpanzees might be the simple result of both
528 ancient and recent population structure.

529 **5 Conclusions**

530 In this work, we showed that it is possible to propose a demographic model for common chimpanzees that
531 accounts for population structure and gives a coherent interpretation of PSMC curves produced by previous
532 studies. Although we stress that the general model we propose here should not be taken as face value, it
533 manages to explain several patterns of genetic diversity within subspecies despite the limits of the n -island
534 models (e.g. lack of spatial attributes). We noted the importance of using spatial models to account for
535 the genetic differentiation between the subspecies and also showed that spatial models might also explain
536 possibly spurious signatures of admixture with bonobos. This work is a first step towards more complex
537 models, though we recognise the difficulty of such endeavour. There is an increasing recognition that ig-

538 noring population structure and spatial processes may lead to the inference of events that may never have
539 happened during the evolutionary history of the species studied [33, 36, 37, 60, 38]. This has implications
540 for many species but also important consequences on the understanding of human evolutionary history.

541 **Ethics Statement**

542 Not applicable.

543 **Consent for Publication**

544 Not applicable.

545 **Availability of Data and Material**

546 All code used for this paper is available at <https://github.com/camillesteux/structurechimpanzees>.

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555 **Competing Interests**

556 Not applicable.

557 **Author Contributions**

558 Conceptualization: LC; Methodology: LC, CS, CC, AA, WR, OM, RT; Investigation: LC, CS; Visualiza-
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567 **Supplementary data**

568 Supplementary Information S1: On the validation step.

569 Supplementary Information S2: Spatial structure confounds ancient admixture estimates.

570 Table S1: Prior ranges for the t_i .

571 Table S2: Distribution of inferred n .

572 Table S3: Distribution of inferred N .

573 Figure S1: Model and statistics calculated under a no-admixture structured population model.

574 Figure S2: PSMC curves provided by Prado-Martinez *et al.*.

575 Figures S3-S6: Inferred IICR curves for each subspecies of chimpanzees.

576 Figure S7: Distribution of inferred n and N coloured by individual.

577 Figure S8: Inferred connectivity coloured by individual.

578 Figure S9: Pseudo-observed data given to SNIF for the validation step.

579 Figure S10: Results of the validation step when giving to SNIF simulated PSMC curves as pseudo-observed
580 data.

581 Figures S11-S14: Empirical PSMC and simulated IICR under the general tree model for each species of
582 chimpanzees.

583 Figures S15-S17: Genetic distances within and between subspecies computed on genomic data simulated
584 under the general tree model for different splitting times.

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Supplementary Information S1: On the validation process

The validation process that we applied in this study is similar to that used in ABC studies. We started with a PSMC curve for which we inferred ten scenarios corresponding to ten runs of SNIF, as explained in the Materials and Methods section. When these ten scenarios were similar we chose one of them, say scenario S^* , and generated a new IICR curve using the corresponding *ms* command. This IICR curve served as input to a new SNIF inference and we obtained ten newly inferred scenarios, $S_1^{**}, S_2^{**}, \dots, S_{10}^{**}$ from the ten independent runs. If these scenarios are different from each other, this may suggest that the optimization has not reached equilibrium and the number of iterations should be increased. Assuming now that the $S_1^{**}, S_2^{**}, \dots, S_{10}^{**}$ do not differ significantly from each other but differ from S^* , this suggests that the inferred scenario S^* should not be trusted at this stage since SNIF was not able to infer it despite using ten independent runs and reaching equilibrium. This was never the case with the chimpanzee data and we come back to this below.

In such a case where S^* should not be trusted, we suggest several solutions. One could explore more simple n-island models (with smaller c values for instance) to determine if S^* is too parameter-rich to be inferred by SNIF. If this fails too, it could also indicate that the real evolutionary history may be too complex to be approximated by a piecewise stationary n-island model such as S^* or simpler versions of S^* . In such a case, other demographic models should be explored, perhaps involving population size changes or spatial structure (stepping stone models for instance), or tree models.

If, on the contrary, S^* can be inferred reasonably well (i.e. the S_i^{**} scenarios are similar to S^*) as we observe with the chimpanzees, this could suggest that the scenario S^* is not only able to explain the original observed data but it can be inferred by SNIF if it were true. In other words, if the real species had evolved under S^* we would be able to infer S^* with SNIF. This does not prove that the species evolved under S^* but that S^* might be a reasonable approximation of reality to explain the PSMC computed for that species, at least until we find better alternatives.

These (or other) validation steps are fundamental and we suggest that they should be applied more often in demographic inference studies. It is more commonly applied in ABC studies, but there are still studies which infer a scenario without demonstrating that if real data had been generated under the inferred scenario, the authors would indeed be able to infer it back again, even approximately. While this validation process may be difficult to apply to some methods using genomic data, the current study shows that it is possible.

Supplementary Information S2: Spatial structure confounds ancient admixture estimates

Several studies have inferred ancient admixture events between lineages of the *Pan* genus [6, 13, 11, 21] (cf. Brand *et al.* [14] for a review). The mode and tempo of these putative events vary greatly with little consistency across studies (see the Discussion section in the main manuscript). This could suggest a complex admixture history involving the different subspecies and the bonobos, of which previous research works identified only some elements. Alternatively, the inferred admixture events might also be caused by the confounding effect of population structure (or other departures from model assumptions) which could generate different results across studies, depending on the models, statistics, samples, etc. used by the authors.

For instance, de Manuel *et al.* [6] inferred introgression between chimpanzees and bonobos using different approaches including the D -statistic [61], TreeMix method, and SFS -based demographic inference (Site Frequency Spectrum). However, like most previous studies, they assumed panmixia within each subspecies, and thus did not test for ancient population structure, which is an increasingly recognised confounder for the detection of admixture [61, 36, 37, 38].

Here, we implemented a simple linear stepping-stone model to test the hypothesis that population structure alone, without any gene flow between bonobos and chimpanzees, could replicate the observed D -statistics. We found that non-zero D -statistics could indeed be generated, following a gradient similar to what is observed on the empirical data. Noteworthy, our model not only predicted the empirical levels of D but it also predicted realistic values of the nucleotide diversity and the F_{ST} among chimpanzee subspecies. Altogether, this suggests that population structure can reproduce several signals of present-day genetic diversity, including purported admixture ones. It thus calls for more caution regarding the strength of the evidence favoring ancient admixture over population structure in the extant *Pan* genus, in a way that is similar to that suggested in recent research on the genus *Homo* [36, 37, 38].

793 S2.1 Methods

794 S2.1.1 Demographic model

795 We implemented a simple linear (one-dimensional) stepping-stone model (Fig. S1A), where each subspecies
796 of chimpanzee is treated as a "metapopulation" of five connected demes of respective size N_i diploids.
797 Bonobos are modelled in a similar way, except that no bonobo subspecies is currently recognised. We will
798 abbreviate henceforth: Western chimpanzees as "W", Nigeria-Cameroon as "NC", Central as "C", Eastern
799 as "E", and Bonobos as "P" (for *paniscus*). Thus, the full model is composed of five metapopulations of five
800 demes each.

801 For simplicity, we set the deme size in each metapopulation using the θ_W estimate produced by de
802 Manuel *et al.* [6] (Table S2 in the original article), with $N = \theta_W / (4n\mu)$, where n is the number of demes
803 we consider in this study for each metapopulation ($n = 5$). We used the same mutation rate as de Manuel
804 *et al.*, *i.e.* $\mu = 1.2 \times 10^{-8}$ per bp per generation. This led us to set $N_{NC} = 5,559$ diploids, $N_E = 6,498$,
805 $N_C = 9,462$. For Western chimpanzees, we found that the original θ (leading to $N_W = 3,475$) produced an
806 excess of nucleotide diversity compared to empirical values and we thus set it to a lower value ($N_W = 600$).
807 We fixed the deme size in bonobos to $N_P = 4,000$ (about half N_C [62]), in the absence of the θ_W estimate in
808 de Manuel *et al.* [6].

809 Within all metapopulations, demes are connected to their neighbours with a per-generation symmetric
810 migration rate of $m_w = 10^{-2}$ (*i.e.* $M_{i,j} = m_w N_i$ diploid individuals migrating from deme i to deme j at
811 each generation, backward). The different chimpanzee metapopulations are connected to the neighbouring
812 metapopulation by a low-level (symmetric) gene flow of $m_b = 8 \times 10^{-4}$. The migration rate within the
813 bonobo metapopulation was fixed at $m_{w,P} = 1.1 \times 10^{-4}$.

814 We acknowledge that several of these parameter values were fixed arbitrarily, since our purpose was
815 not to infer parameters. We intended to showcase how a simple model can explain empirical data (when
816 accounting for known population structure, without requiring unknown ancient admixture events), especially
817 in producing apparent signatures of putative ancient admixture events.

818 Metapopulations split times were implemented in the model using the average of the divergence times
819 reported in de Manuel *et al.* [6] (Figure 3 in the original article). Specifically, NC started to expand from
820 W at 250 kya; E from C at 160.5 kya, the two ancestral chimpanzee lineages at 588.5 kya, bonobos from
821 chimpanzees at 1.88 Mya. Each expansion is modelled, forward in time, by successive founding of each

822 within-metapopulation deme, every 200 years. We note that these founding events correspond exclusively
823 to the instantaneous creation of a deme of size N_i (*i.e.* no bottlenecks).

824 For the time period prior to the first split between chimpanzee metapopulations (588.5 kya), the deme
825 sizes in the ancestral chimpanzees were set to $N_{anc} = 7,000$ and the migration rate between the demes
826 of this ancestral metapopulation was set to the same value as the present-day bonobo migration rate (*i.e.*
827 $m_{anc} = m_{w,P} = 1.1 \times 10^{-4}$). All parameters for the remaining bonobo metapopulation were kept the same.

828 It should be clear that this model assumes that bonobos and chimpanzees never exchange gene flow at
829 any time of their history after they separated 1.88 Mya.

830 The total number of non-redundant parameters in our model is 15, making it less parameter-rich than
831 the panmictic model of de Manuel *et al.* [6]:

- 832 • 1 parameter for the number of demes per metapopulation (set to 5),
- 833 • 2 parameters for within-metapopulation migration rate in chimpanzees and bonobos (set to $m_w = 10^{-2}$
834 and 1.1×10^{-4} , respectively),
- 835 • 1 parameter for between-metapopulation migration rate in chimpanzees (set to $m_b = 8 \times 10^{-4}$),
- 836 • 5 parameters for deme sizes (N_i),
- 837 • 1 parameter for ancestral deme size (N_{anc}),
- 838 • 4 expansion times (*i.e.* the founding of the different metapopulations),
- 839 • 1 parameter for the delay between successive founding of demes (set to 200 years).

840 **S2.1.2 Simulations**

841 Using `msprime v1.1` with Hudson's coalescent algorithm [63, 64], we simulated genetic data for 20 chro-
842 mosomes of 20 Mbp each ($G = 400$ Mbp), sampling 15 diploid individuals in the central deme of each
843 metapopulation. This resulted in a total of 75 diploid genotypes per segregating site. Mutations were
844 generated using a binary model, with two flipping alleles, at a rate of 1.2×10^{-8} per bp per generation.
845 Recombination was assumed uniform, with rate 0.7×10^{-8} per bp per generation. We used a generation
846 time of 25 years for both chimpanzees and bonobos [6].

847 **S2.1.3 Statistics**

848 Based on the simulated biallelic genetic data, we calculated, using the `scikit-allel v1.3.5` package:

- 849 • The nucleotide diversity π for each population sample (average number of pairwise differences).
- 850 • The differentiation index F_{ST} (Hudson's formula based on expected heterozygosities) between all
851 pairs of chimpanzee populations.
- 852 • The D -statistic, as $D(X, Y; bonobo, outgroup)$ with X and Y being any chimpanzee population sample,
853 and $outgroup$ being a virtual diploid genotype homozygous for the ancestral allele. To calculate the
854 standard error (SE), we used a block-weighted jackknife with a typical block size of around 5 Mbp
855 [65]. Confidence intervals at 95% were calculated as $D \pm 1.96 \times SE$.

856 **S2.1.4 Observed data**

857 We retrieved the empirical statistical values from previously published papers:

- 858 • π (average pairwise differences): from Fischer *et al.* [22], calculated on 26 intergenic sequences
859 totalling 22.4 kbp for around 10 diploids in each sampled population.
- 860 • F_{ST} (Hudson's formula): from Fischer *et al.* [22], calculated on the same dataset as π .
- 861 • D -statistic: from de Manuel *et al.* [6], calculated as $D(X, Y, bonobo, humans)$ using whole-genome
862 sequences on a set of 68 *Pan* samples. We used the D values estimated by the authors when aligning
863 the *Pan* sequences on the human *hg19* assembly.

864 **S2.2 Results**

865 Our 1D stepping-stone structured population model replicated the observed gradient of D -statistics across
866 focal chimpanzee subspecies (Fig. S1D). It further predicted the empirical values of between-chimpanzee
867 F_{ST} (with the Central-Eastern being slightly underestimated in our simulations) (Fig. S1C), as well as the
868 nucleotide diversity, with a slight excess of diversity for Eastern chimpanzees (Fig. S1A) (which likely
869 results from the N_E value that we extracted from [6]).

870 In conclusion, these results show that the ancient admixture inferred in the *Pan* genus might not be ro-
871 bust to ancestral population structure.

872

873 We further investigated the variation of the D -statistic as a function of the ancestral connectivity, i.e.
874 the connectivity within the metapopulation ancestral to extant chimpanzees (and further, extant *Pan* species)
875 from 588.5 kya towards the past. To this end, we sampled $N_{anc}m_{anc}$ values from 10^{-3} to 10, every 0.2 on a
876 \log_{10} -scale. Keeping N_{anc} fixed at 7,000 (cf. previous model), we derived m_{anc} according to the composite
877 parameter $N_{anc}m_{anc}$. All other demographic and simulation parameters were kept the same as in the previous
878 model, except for genome size, restricted to 10×10 Mbp chromosomes for computational reasons. We
879 estimated D between present-day Central and Western chimpanzees: $D(C, W, bonobo, outgroup)$.

880 Our results (Fig. S2) show that the D -statistic values follow a sigmoid curve, "saturating" at zero for
881 the highest $N_{anc}m_{anc}$ values (towards the right). This is expected, since with such high connectivity, the
882 population model becomes nearly panmictic, and it does not incorporate admixture from bonobos into C
883 lineages. The curve also plateaus around 0.6 for the lowest $N_{anc}m_{anc}$ range. Interestingly, we note that the
884 D -statistic values start to become significant, in our model, around $N_{anc}m_{anc} = 1$ migrant per generation.
885 A steep variation in D is observed for connectivity values ranging between around 0.06 and 0.6 migrants
886 per generation. These results confirm that very significant values of the D -statistic can be produced under
887 a structured population model in the absence of admixture, and that they depend mostly on the level of
888 the ancestral connectivity within the metapopulation ancestral to the tested samples. We show that D can
889 reach very high values (0.6) compared to the empirical values reported here, confirming that the level and
890 significance of the D statistic cannot be used as indisputable evidence for admixture.

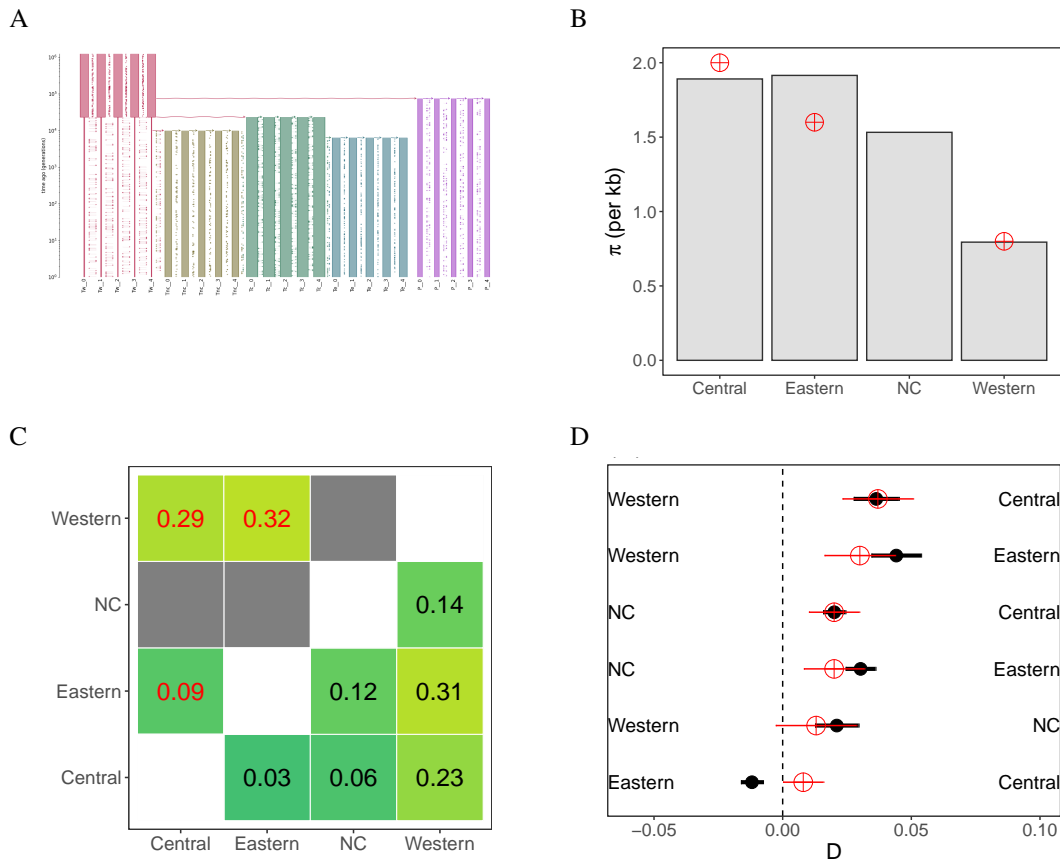


Figure S1: Model and statistics calculated under a no-admixture structured population model. A. Representation of the simulated demographic model. Each color corresponds to a chimpanzee subspecies or to the bonobos. Red: W, olive: NC, green: C, blue: E, purple: bonobos. B. Nucleotide diversity per kbp estimated for each population, for the data simulated under the structured population model (gray bars), and on the empirical data (red points). No NC samples were available in the [22] study. C. Pairwise F_{ST} obtained on the simulated data (lower-right triangle, black text) and on the empirical data (upper-left triangle, red text). We note that in the original article, the NC population was not studied [22], thus appearing here as empty gray cells. D. D -statistics from the simulated data (black points with 95% confidence interval) and empirical data (red points). The D -statistic values were calculated as $D(X, Y, P, O)$ with "P" the bonobos. On the plot, X populations are labeled on the right and Y on the left.

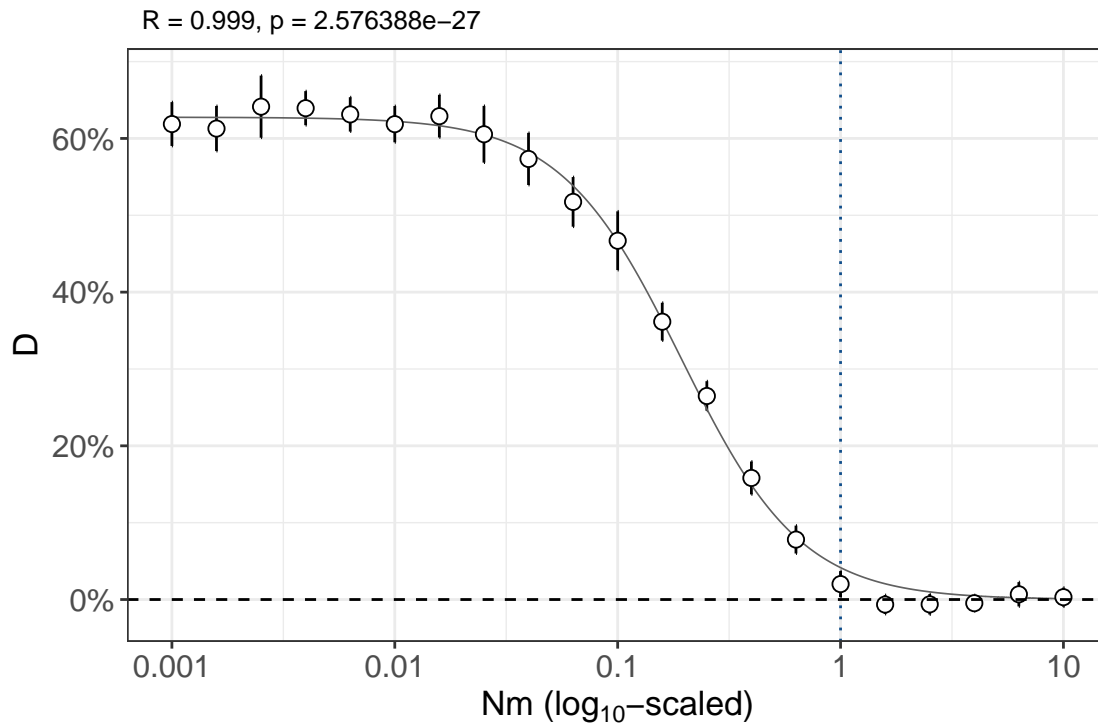


Figure S2: Distribution of the D -statistic as a function of ancestral migration rates. The D -statistic was computed as $D(C, W, P, O)$ for our no-admixture structured model, where we allowed the migration rate in the ancestral metapopulation to vary. This ancestral metapopulation corresponds to the period prior to 588.5 kya, *i.e.* before the foundation of the bonobos (cf. model description) We allowed $N_{anc} \times m_{anc}$ to vary from 10^{-3} to 10. The error bars represent the confidence intervals at 95%. The x -axis is \log_{10} -scaled. The vertical blue dotted line represents the first tested $N_{anc}m_{anc}$ value from decreasing order with significant D -statistics. The gray curve is a logistic fit to the empirical scatter plot. The Pearson's correlation coefficient representing the fit of the curve to the empirical data is reported in the title.

Table S1: Prior ranges of the t_i (times at which migrations rates are allowed to change, delimiting the components) given to SNIF for the final analysis. Note that here the times are given in years, but they have to be divided by the generation time when given to SNIF.

Subspecies	c	Priors of t_i (in years)
Western	7	(2e4, 1e5), (1e5, 3e5), (1e5, 3e5), (3e5, 7e5), (7e5, 1.5e6), (1.5e6, 5e6)
Nigeria-Cam.	7	(1e4, 1e5), (1.5e5, 3e5), (3.5e5, 5e5), (8e5, 1.1e6), (2e6, 3e6), (4e6, 7e6)
Central	8	(5e4, 2e5), (2e5, 4e5), (5e5, 2e6), (5e5, 2e6), (2e6, 5e6), (2e6, 5e6), (6e6, 1e7)
Eastern	7	(5e4, 2e5), (4e5, 1.5e6), (4e5, 1.5e6), (2e6, 6e6), (2e6, 6e6), (7e6, 1e7)

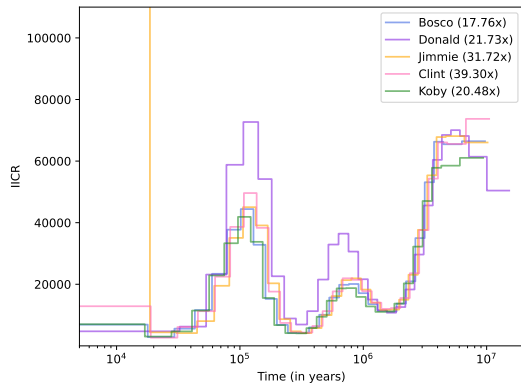
Table S2: Distribution of inferred n , the number of demes of the n -island models.

Subspecies	Min	25% quantile	Median	Mean	75% quantile	Max
Western	12	17	21	23	31	48
Nigeria-Cameroon	6	10	11	11	13	20
Central	13	16	18	21	20	55
Eastern	8	11	13	13	15	23

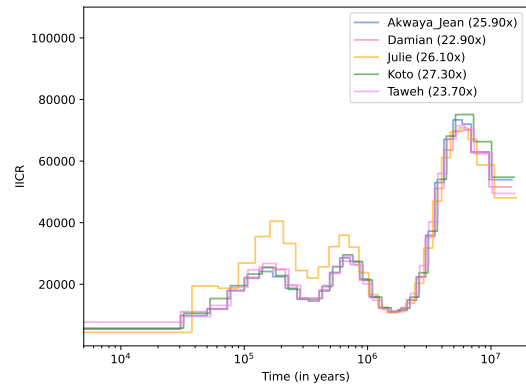
Table S3: Distribution of inferred N , the deme size of the n -island models (in number of diploids).

Subspecies	Min	25% quantile	Median	Mean	75% quantile	Max
Western	112	239	305	285	335	437
Nigeria-Cameroon	616	1009	1154	1174	1311	1980
Central	227	589	737	694	834	1101
Eastern	561	728	801	863	975	1306

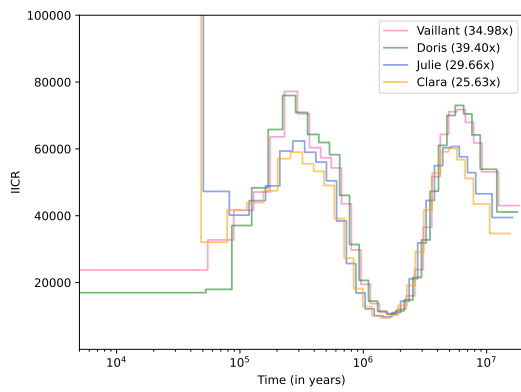
A



B



C



D

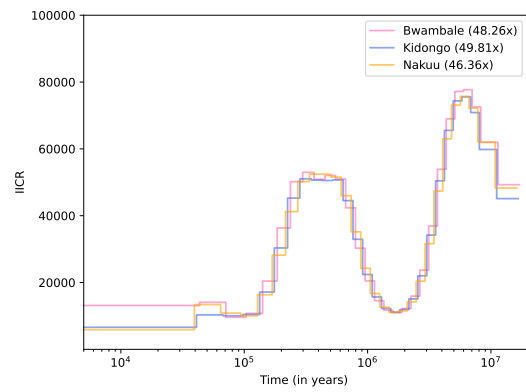


Figure S3: PSMC curves for A. Western chimpanzees, B. Nigeria-Cameroon chimpanzees, C. Central chimpanzees and D. Eastern chimpanzees, computed using PSMC files provided to us by Prado-Martinez *et al.* [2]

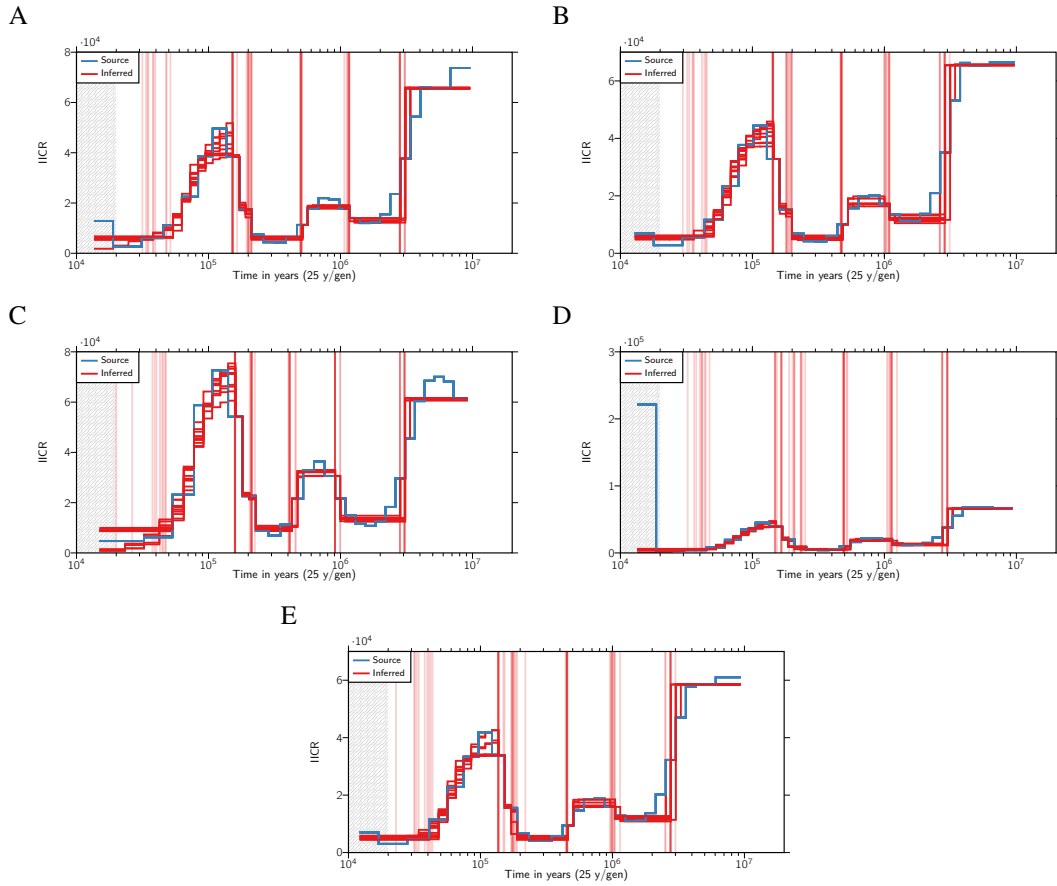


Figure S4: Inferred IICR curves (in red) and empirical PSMC (in blue) for the five Western common chimpanzees. Each red curve is a repetition of SNIF. The vertical red lines highlight the times at which there is an inferred change in migration rate and therefore delimit the components. A. Clint, B. Bosco, C. Donald, D. Jimmie and E. Koby. The grey zone corresponds to a part of the source PSMC which was not taken into account for the fitting of the curve by SNIF (see Material and Methods).

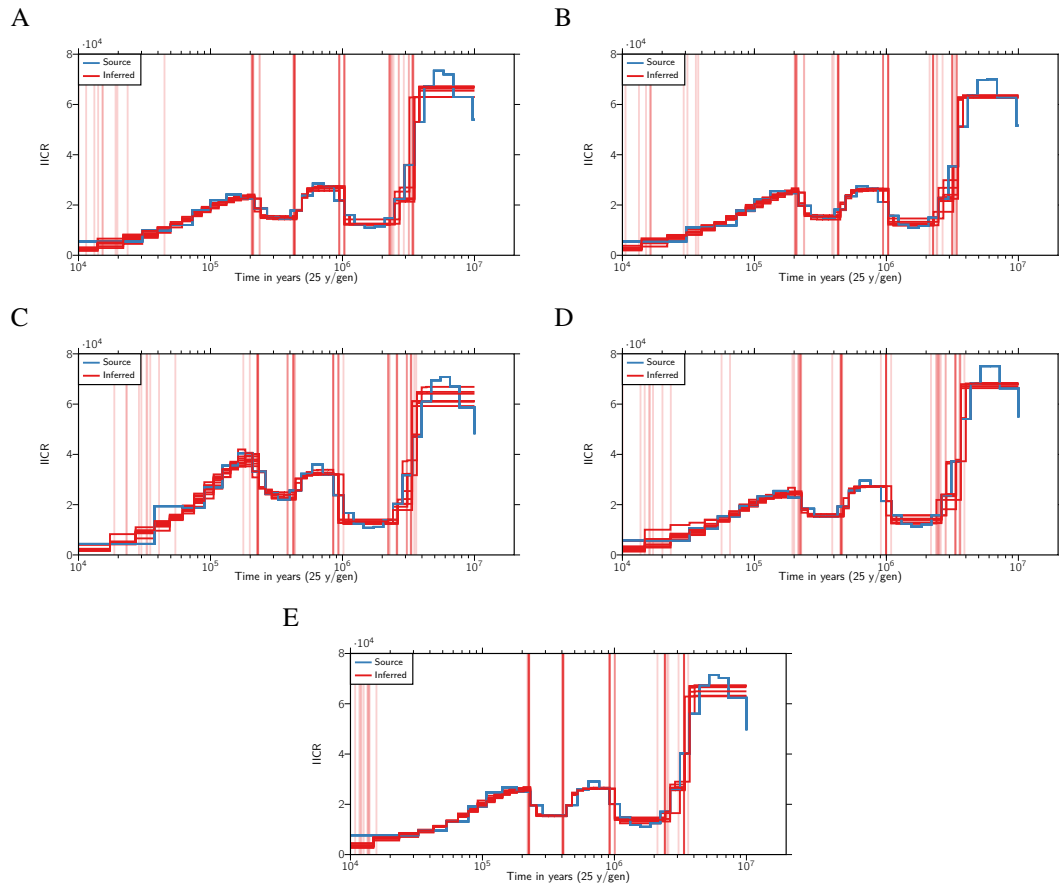


Figure S5: Inferred IICR curves (in red) and empirical PSMC (in blue) for the five Nigeria-Cameroon common chimpanzees. Each red curve is a repetition of SNIF. The vertical red lines highlight the times at which there is an inferred change in migration rate and therefore delimit the components. A. Akwaya-Jean, B. Damian, C. Julie, D. Koto and E. Taweh.

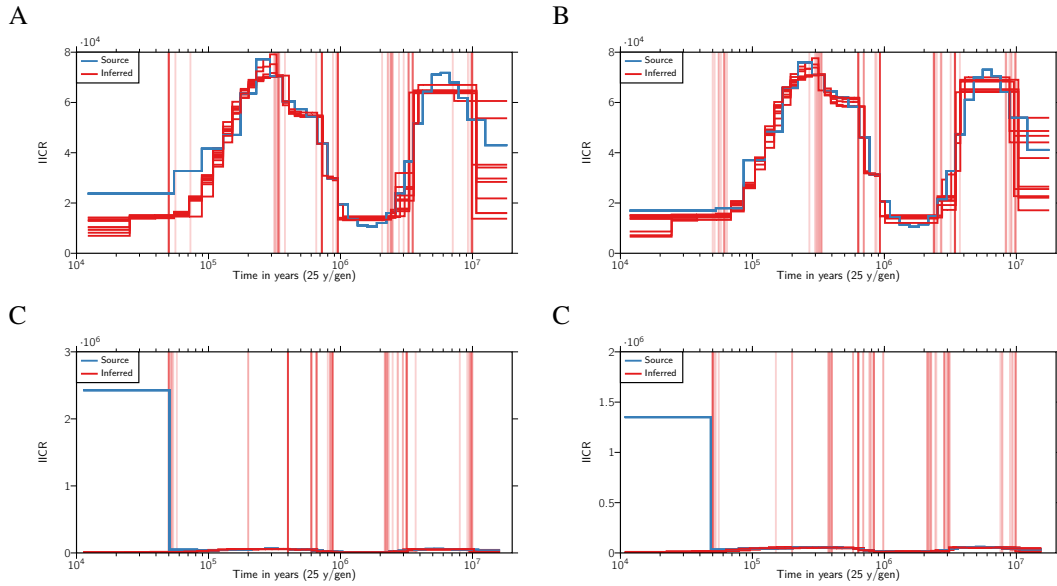


Figure S6: Inferred IICR curves (in red) and empirical PSMC (in blue) for the four Central common chimpanzees. Each red curve is a repetition of SNIF. The vertical red lines highlight the times at which there is an inferred change in migration rate and therefore delimit the components. A. Vaillant, B. Doris, C. Julie and D. Clara.

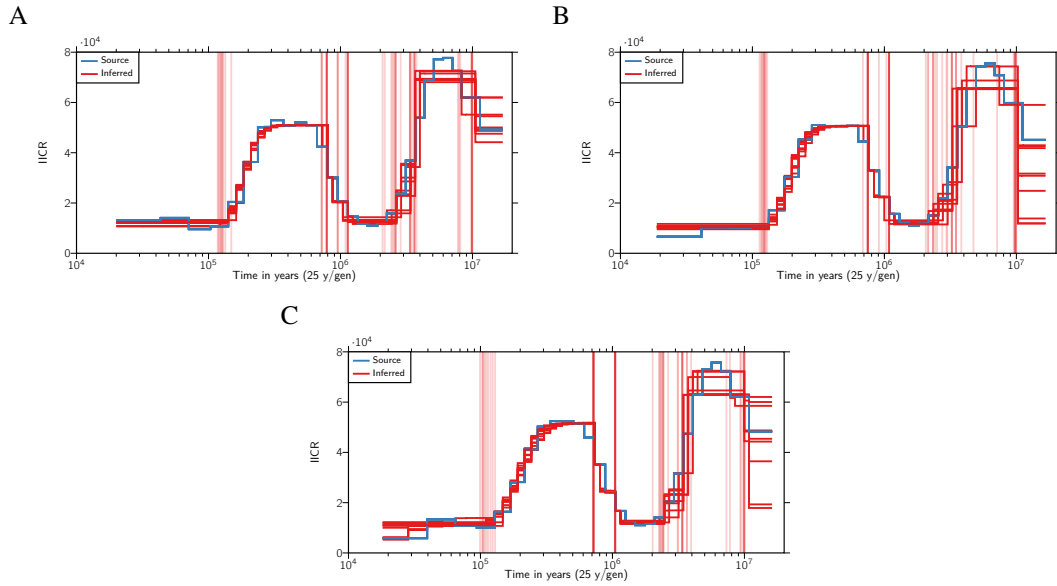


Figure S7: Inferred IICR curves (in red) and empirical PSMC (in blue) for the three Eastern common chimpanzees. Each red curve is a repetition of SNIF. The vertical red lines highlight the times at which there is an inferred change in migration rate and therefore delimit the components. A. Bwambale, B. Kidongo and C. Nakuu.

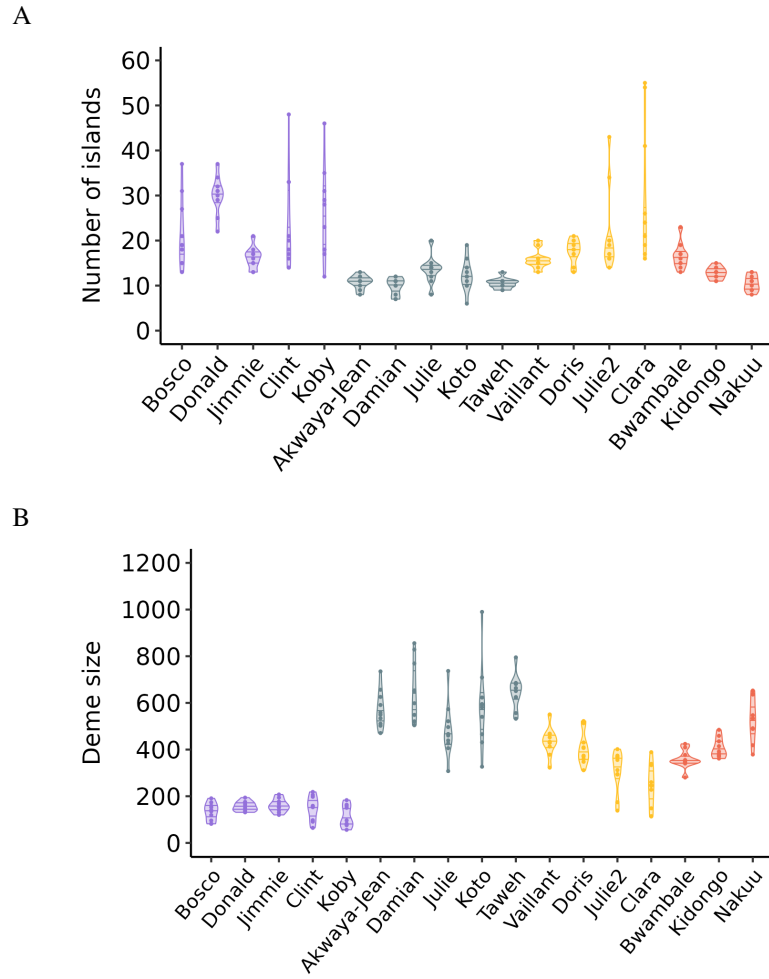


Figure S8: Distribution of the inferred A. number of islands and B. deme size (given in number of diploid individuals) across the 10 repetitions for each individual, using the parameter space shown Table 1. Horizontal lines in the violins represent the 25%, 50% (median) and 75% quantiles.

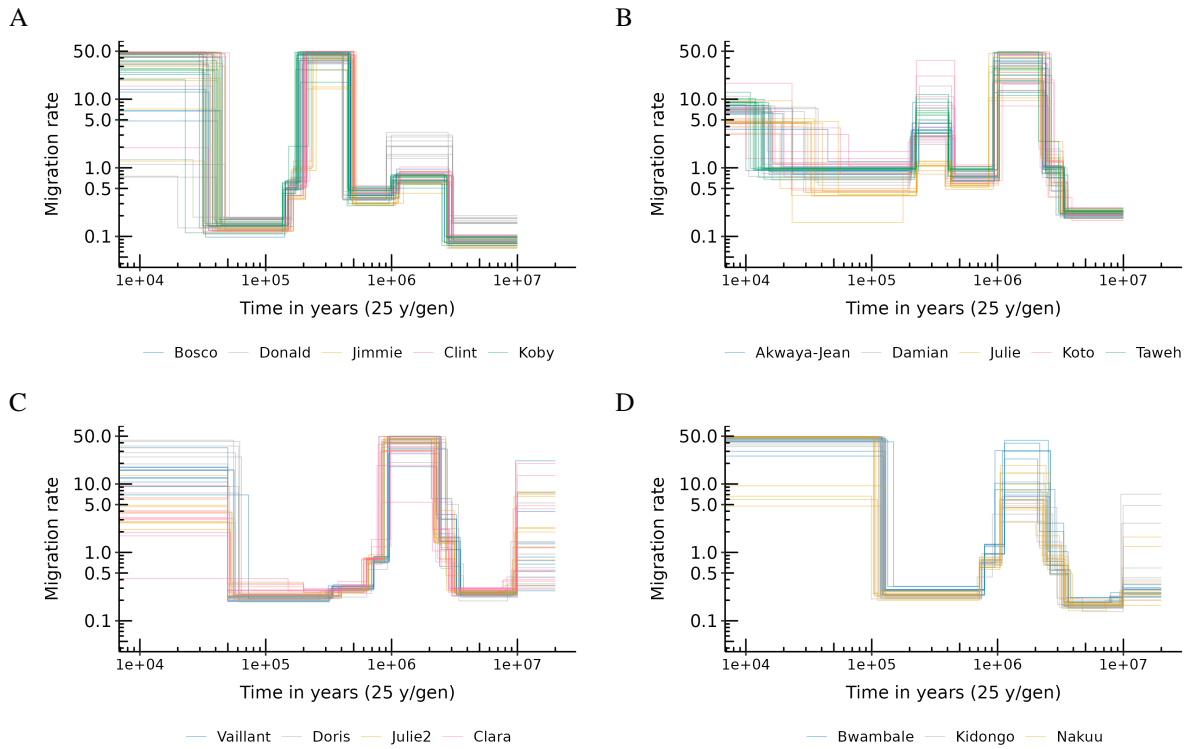


Figure S9: Connectivity graph (migration rates along successive time components) inferred by SNIF coloured by individual for A. Western, B. Nigeria-Cameroon, C. Central and D. Eastern chimpanzees. Each line corresponds to one inference (one repetition of SNIF) using one PSMC curve (or individual) as observed data.

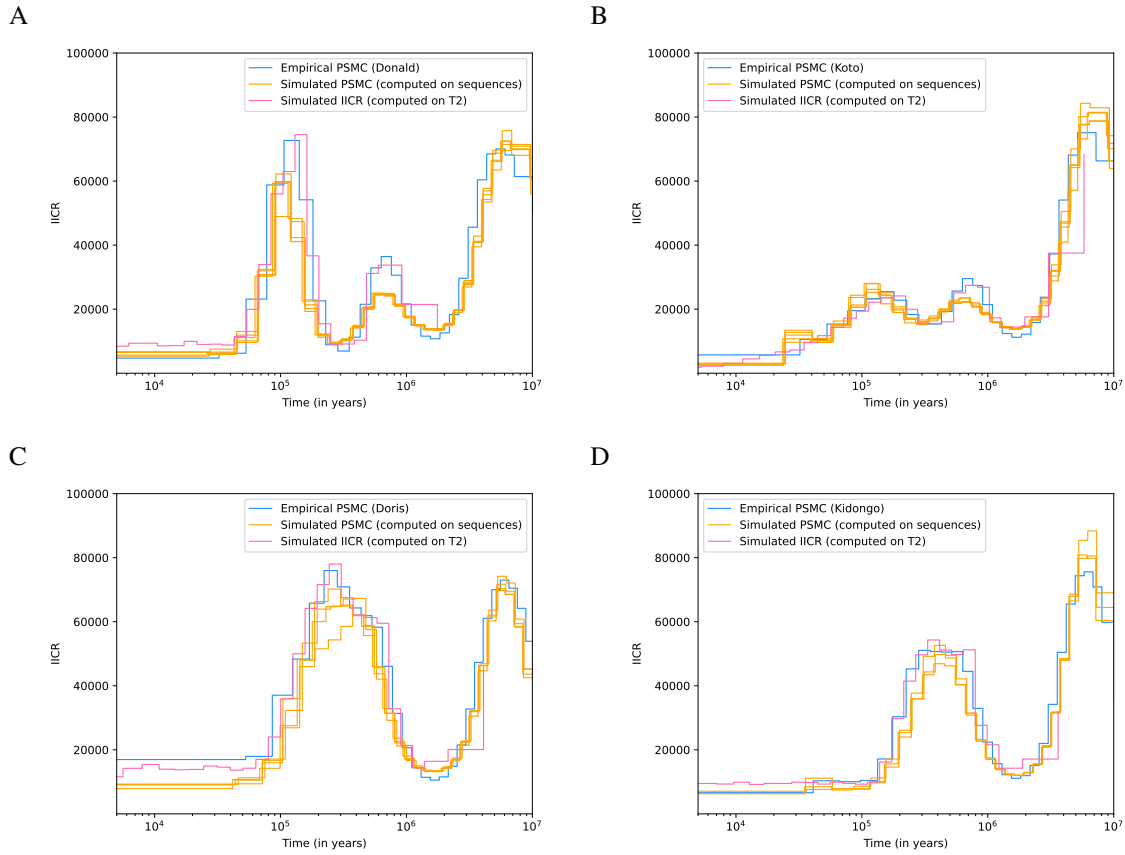


Figure S10: Simulated PSMC computed on simulated sequences (10x100Mb) (in blue) and simulated IICR computed on simulated coalescent times (T_2) (in orange), both given to SNIF as pseudo-observed data for the validation procedure. A. Western chimpanzees, B. Nigeria-Cameroon chimpanzees, C. Central chimpanzees and D. Eastern chimpanzees.

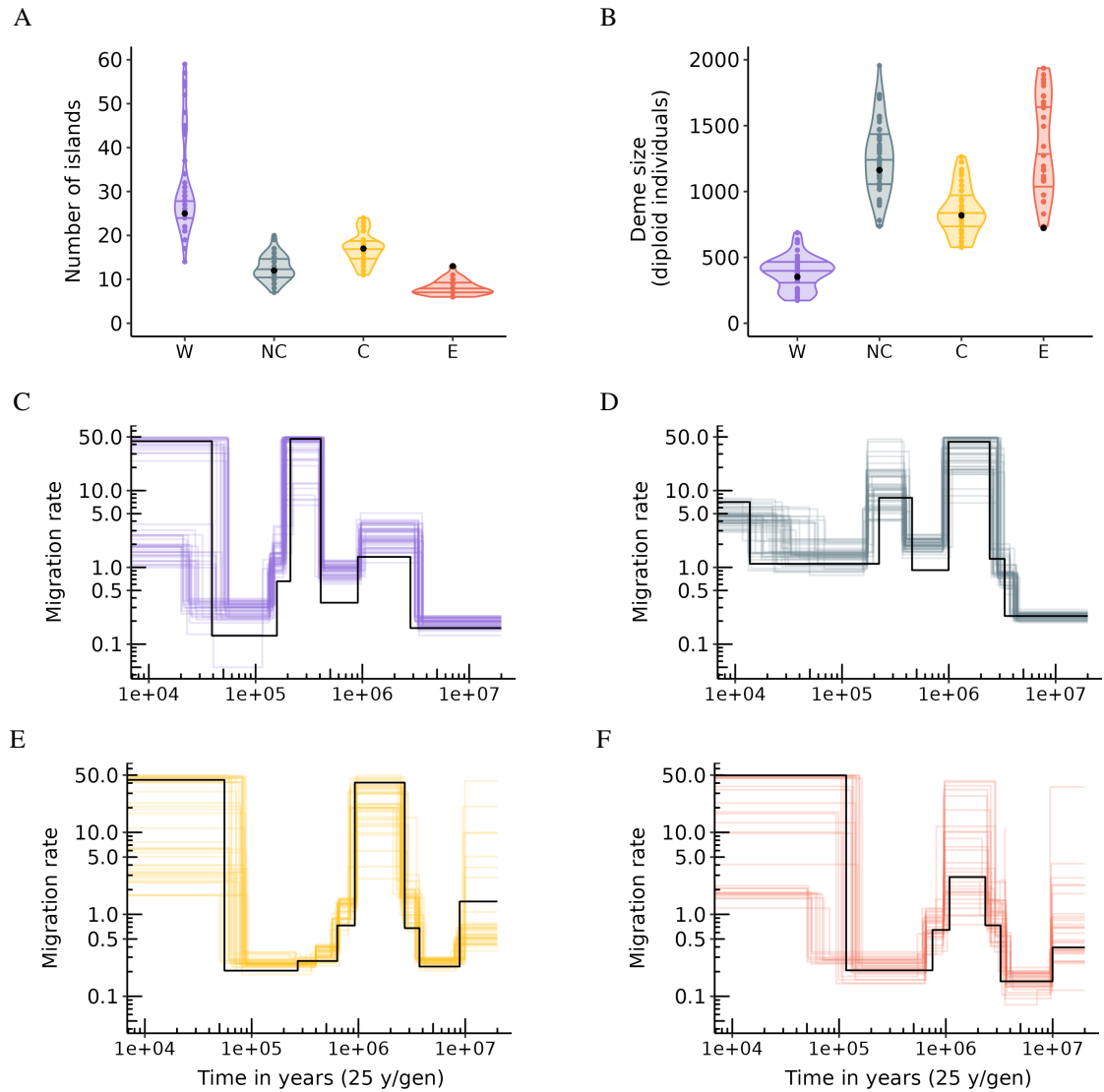
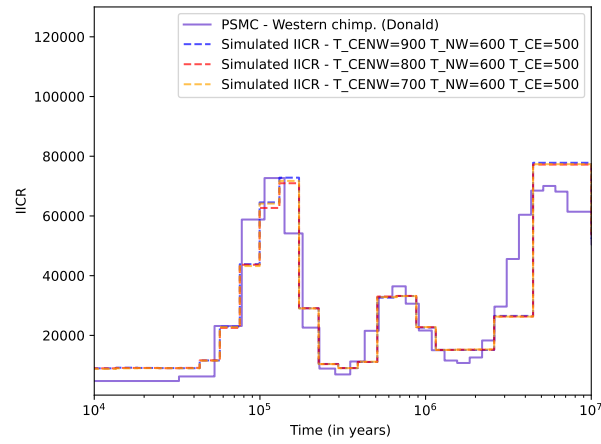


Figure S11: Results of the validation procedure when giving to SNIF simulated PSMC (see orange curves in Figure S10) as pseudo-observed data. A. Inferred number of islands (n), B. Inferred deme sizes (N), C. Inferred connectivity graph for Western chimpanzees, D. Inferred connectivity graph for Nigeria-Cameroon chimpanzees, E. Inferred connectivity graph for Central chimpanzees and F. Inferred connectivity graph for Eastern chimpanzees. Horizontal lines in the violins on panels A and B represent the 25%, 50% (median) and 75% quantiles.

A



B

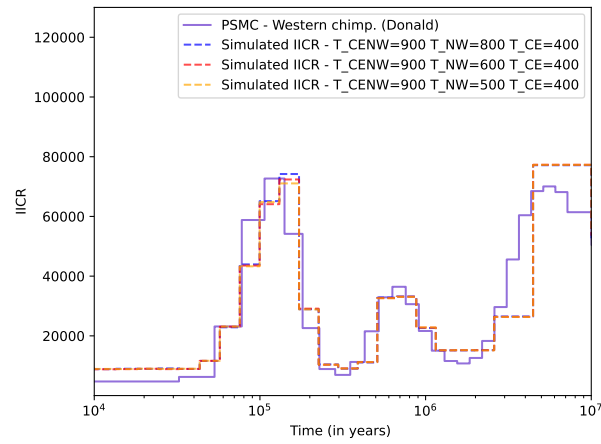
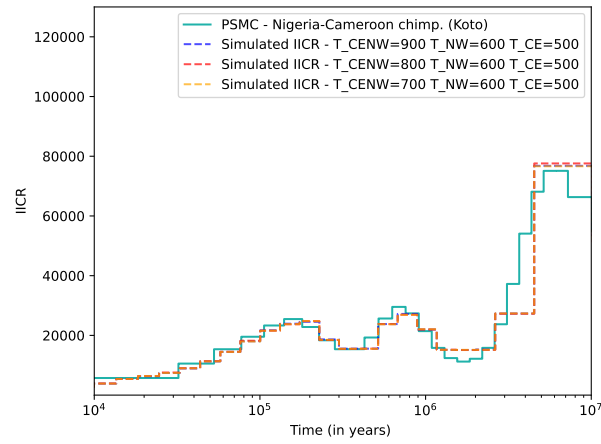


Figure S12: Empirical PSMC (solid line) and simulated IICR (dotted lines) for Western common chimpanzees under the general n -island model Figure 7 for different values of splitting times. (A) $T_{CENW} \in \{700, 800, 900\}$, $T_{NW} = 600$ and $T_{CE} = 500$ and (B) $T_{CENW} = 900$, $T_{NW} \in \{500, 600, 800\}$ and $T_{CE} = 400$ (in kya).

A



B

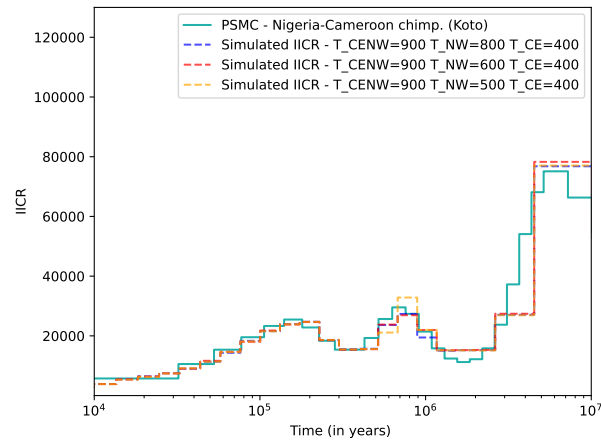
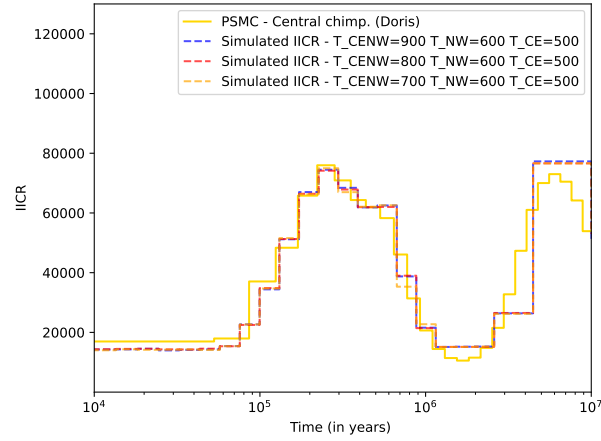


Figure S13: Empirical PSMC (solid line) and simulated IICR (dotted lines) for Nigeria-Cameroon common chimpanzees under the general n-island model Figure 7 for different values of splitting times. (A) $T_{CENW} \in \{700, 800, 900\}$, $T_{NW} = 600$ and $T_{CE} = 500$ and (B) $T_{CENW} = 900$, $T_{NW} \in \{500, 600, 800\}$ and $T_{CE} = 400$ (in kya)

A



B

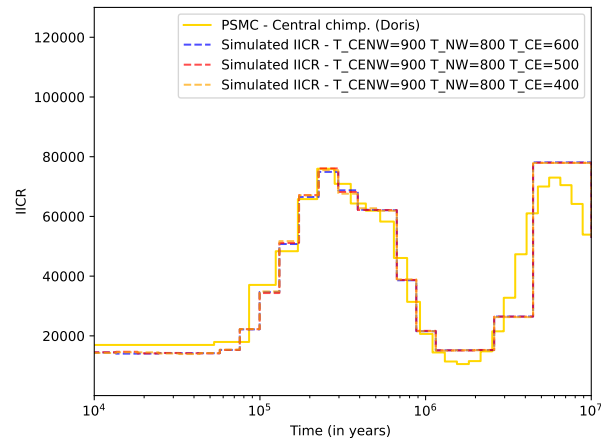
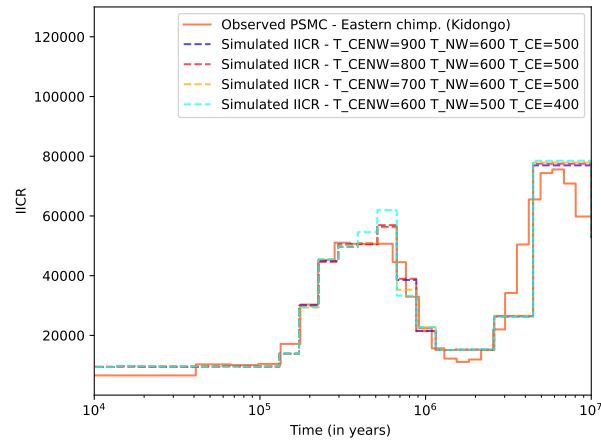


Figure S14: Empirical PSMC (solid line) and simulated IICR (dotted lines) for Central common chimpanzees under the general n-island model Figure 7 for different values of splitting times. (A) $T_{CENW} \in \{700, 800, 900\}$, $T_{NW} = 600$ and $T_{CE} = 500$ and (B) $T_{CENW} = 900$, $T_{NW} = 800$ and $T_{CE} \in \{400, 500, 600\}$ (in kya).

A



B

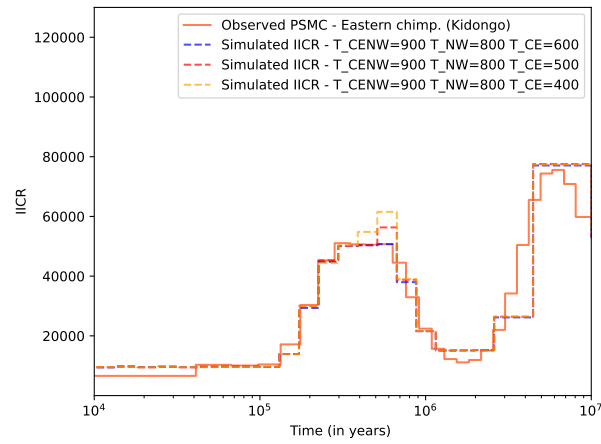


Figure S15: Empirical PSMC (solid line) and simulated IICR (dotted lines) for Eastern common chimpanzees under the general n-island model Figure 7 for different values of splitting times. (A) $T_{CENW} \in \{700, 800, 900\}$, $T_{NW} = 600$ and $T_{CE} = 500$ and (B) $T_{CENW} = 900$, $T_{NW} = 800$ and $T_{CE} \in \{400, 500, 600\}$ (in kya).

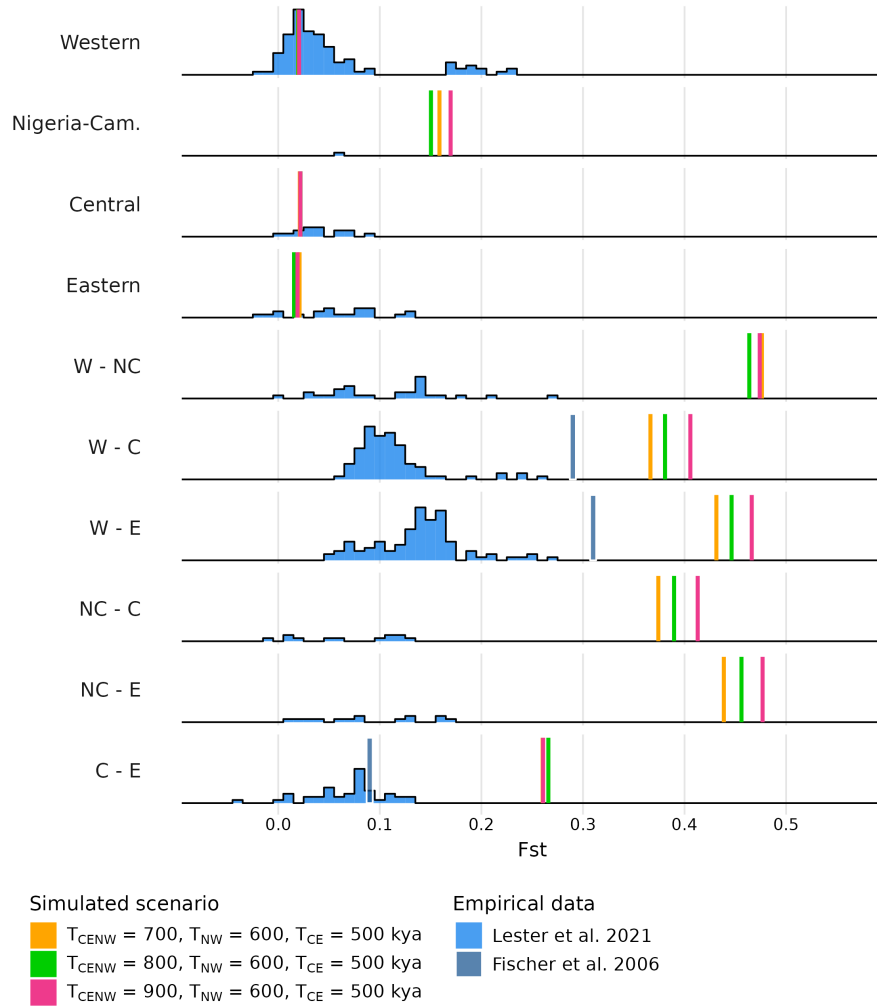


Figure S16: Genetic distance (F_{ST}) between demes of the same subspecies or between demes from different subspecies computed on genomic data simulated under the model Figure 7 with $T_{CE} = 500$ kya, $T_{NW} = 800$ kya and $T_{CENW} \in \{700, 800, 900\}$ kya. In blue are the empirical values: histograms were retrieved from Lester *et al.* [18] and the darker blue vertical lines were retrieved from Fischer *et al.* [22]

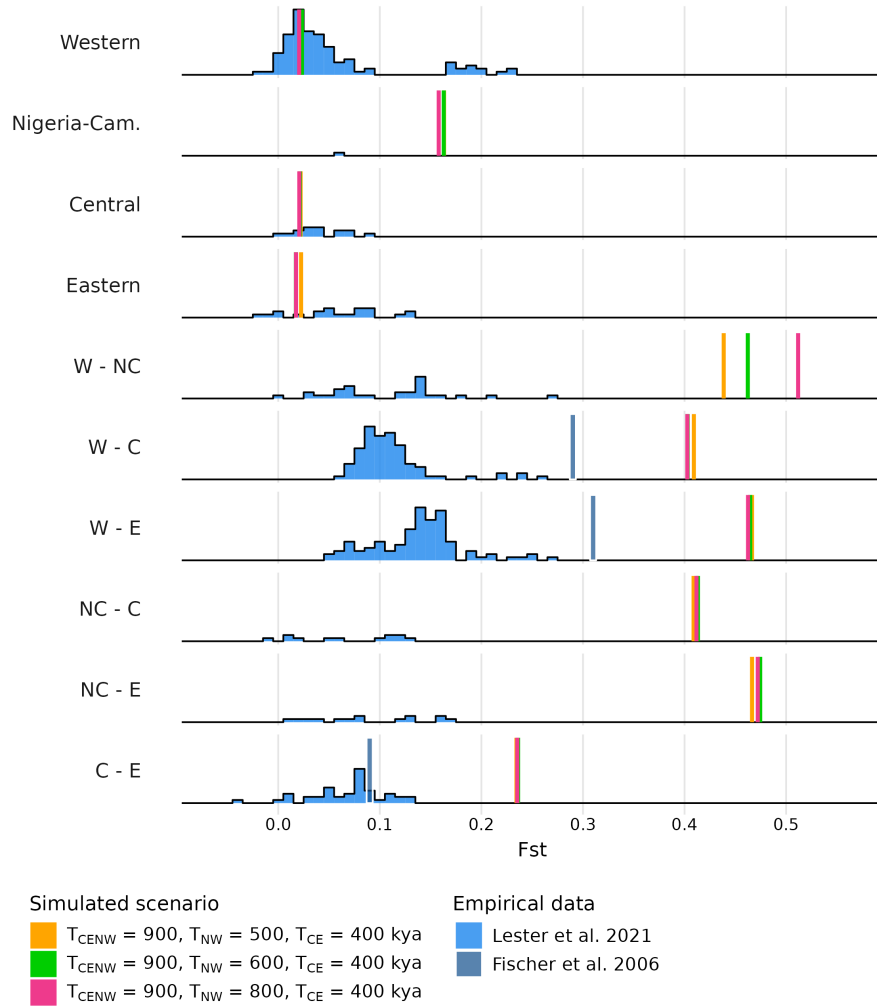


Figure S17: Genetic distance (F_{ST}) between demes of the same subspecies or between demes from different subspecies computed on genomic data simulated under the model Figure 7 with $T_{CE} = 500$ kya, $T_{CENW} = 900$ kya and $T_{NW} \in \{500, 600, 800\}$ kya. In blue are the empirical values: histograms were retrieved from Lester *et al.* [18] and the blue vertical lines were retrieved from Fischer *et al.* [22]

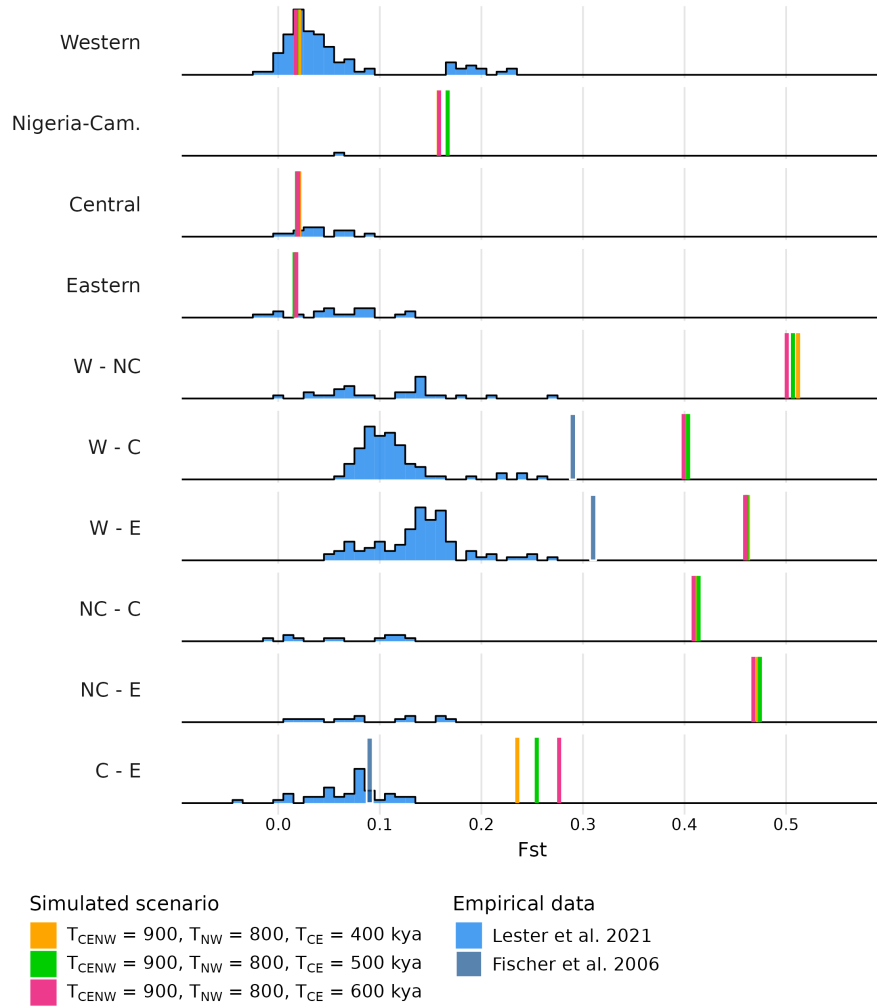


Figure S18: Genetic distance (F_{ST}) within and between subspecies computed on genomic data simulated under the model Figure 7 with $T_{CENW} = 900$ kya, $T_{NW} = 800$ kya and $T_{CE} \in \{400, 500, 600\}$ kya. In blue are the empirical values: histograms were retrieved from Lester *et al.* [18] and the blue vertical lines were retrieved from Fischer *et al.* [22]