Grains, trade and war in the multimodal transmission of Rice yellow mottle virus: an historical and phylogeographical retrospective

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Abstract

Rice yellow mottle virus (RYMV) is a major pathogen of rice in Africa. RYMV has a narrow host range limited to rice and a few related poaceae species. We explore the links between the spread of RYMV in East Africa and rice history since the second half of the 19th century. The phylogeography of RYMV in East Africa was reconstructed from coat protein gene sequences (ORF4) of 335 isolates sampled over two million square kilometers between 1966 and 2020. Dispersal patterns obtained from ORF2a and ORF2b, and full-length sequences converged to the same scenario. The following imprints of rice cultivation on RYMV epidemiology were unveiled. RYMV emerged in the middle of the 19th century in the Eastern Arc Mountains where slash-and-burn rice cultivation was practiced. Several spillovers from wild hosts to cultivated rice occurred. RYMV was then rapidly introduced into the adjacent large rice growing Kilombero valley. Harvested seeds are contaminated by debris of virus infected plants that subsist after threshing and winnowing. Long-distance dispersal of RYMV is consistent (i) with rice introduction along the caravan routes from the Indian Ocean Coast to Lake Victoria in the second half of the 19th century, (ii) seed movement from East Africa to West Africa at the end of the 19th century, from Lake Victoria to the north of Ethiopia in the second half of the 20th century and to Madagascar at the end of the 20th century, (iii) and, unexpectedly, with rice transport at the end of the First World War as a troop staple food from the Kilombero valley towards the South of Lake Malawi. Overall, RYMV dispersal was associated to a broad range of human activities, some unsuspected. Consequently, RYMV has a wide dispersal capacity, its dispersal metrics estimated from phylogeographic reconstructions are similar to those of highly mobile zoonotic viruses.

Author summary

Rice yellow mottle virus (RYMV) poses a major threat to rice production in Africa. We explored through a multidisciplinary approach the links between the history of rice in East Africa since the second half of the 19th century and the spread of RYMV. The results illuminate the causes of RYMV diffusion. We show the role of long-distance caravan trade, the impact of the First World War and the consequences of seed exchange in the dispersal of RYMV. The paradoxical role of seeds in the spread of RYMV - which is vector transmitted and not seed transmitted – is explained in the light of rice biology and agronomy. Overall, this study reveals the wide range of transmission ways, some unexpected, in the dispersal of plant viruses. It also highlights the role of human transmission of pathogens, even vector-borne, and sheds light on the risk of transmission of RYMV and of other plant viruses from Africa to other continents.

Introduction

Contact transmission is a major transmission pathway for plant viruses, yet it has largely been neglected [1]. Contact-transmitted viruses have particles that are stable outside the infected cells, remain infectious on contaminated surfaces, and reach high concentrations (titer) in infected plants. Owing to their virion stability and their high titer, Sobemoviruses, Tobamoviruses, Potexviruses and Tombusviruses are listed as candidates for contact and abiotic transmission [1]. The sobemovirus species differ from the three other genera by a narrow host range and by the mode of transmission, most often by beetles. Beetles are involved in the transmission of several genera [2].

Rice yellow mottle virus (RYMV) is a single-stranded RNA virus of the Sobemovirus genus [3]. RYMV is a major pathogen in all sub-Saharan African countries that grow rice [4]. Its host range is limited to the two cultivated rice species *Oryza sativa* and *O. glaberrima*, to the wild rice species and to a few related *Eragrostideae* species [5]. RYMV does not infect the seed embryo [6, 7, 8]. RYMV is transmitted by chewing insects, mainly beetles of the Chrysomelidae family, in a non-persistent mode and by leaf and root contact between infected and healthy plants [5]. RYMV reached high virus concentration within two to three weeks. It remains infectious in rice stubbles for months [5, 7], and after passage through the intestinal tract of mammals [9]. The spread of the disease was first attributed to vector transmission, although no clear link has been found between the size of the beetle populations and the incidence of the disease. Later, the role of mechanical transmission through leaf-to-leaf and root-to-root contact was established experimentally [10]. Contamination in the soil also occurred by contact of the roots of young seedlings with infected rice stubble present in the soil. This is referred to as soil transmission or soil contamination [1, 11, 12]. Soil contamination has several origins, infected rice residues buried in the soil after harvesting or after mammal consumption, and also by planting rice seeds contaminated by infected plant residues (see below). Due to the stability of

RYMV [7], soil transmission persists months after the infected rice residues have been buried. RYMV is disseminated by transplanting young infected seedlings from nurseries to fields sometimes located kilometers away [13]. Altogether, contact and soil transmission accounts for on-site survival of the virus and its local spread.

Yet, the long-distance transmission of RYMV has not been elucidated. Without experimental evidence, it has been tentatively ascribed to movements of beetles during tornadoes, transmission by more proficient flyer insects such as grasshoppers [5], or transmission by seeds in specific circumstances [14, 15]. The last of the three hypotheses, which posited transmission with seeds, relied on the following observations. RYMV is not present in the rice embryo but is detected in the glumes, and in the outer envelopes of the grain [8]. Rice threshing and winnowing does not eliminate all the outer husks and all the leaf and stem residues [16]. Accordingly, infected plant debris remain in bags of rice seeds. We referred to them as contaminated seeds to make the distinction with infected seeds [4, 17]. Rice seeds are transported between villages and across regions for food consumption and for agronomical purposes [18]. Rice planting with contaminated seeds as well as consumption of contaminated rice seeds by mammals (including humans) result in burying infected rice residues in the soil. Rice planted in a contaminated soil is infected through mechanical contact of the roots of the young seedlings with the infected residues. Based on these observations, it was hypothesized that RYMV was transported with bags of contaminated rice seeds to new areas, potentially far away from its sources [4, 17]. Accordingly, seed transport would be the primary mode, possibly the exclusive mode, of long distance dissemination of RYMV.

Nevertheless, long-distance transmission of plant viruses, be it by vectors or with seeds, has been difficult to establish [19, 20], and this is true for RYMV as well. None of the hypotheses put forward for long-distance transmission of RYMV has been experimentally validated. Phylogeography offers new perspectives through the reconstruction of the spatiotemporal

pattern of spread [21, 22]. It unveils the underlying processes that shape the dynamics of spread, including rare and past events, and leads to hypotheses on the modes of transmission and the impact of host biology and history. RYMV is a measurably evolving population [23], and the phylogeographic reconstructions are not affected by the time dependent rate phenomenon [24]. The relaxed random walk (RRW) model in continuous phylogeography allows for variation in dispersal rates across branches of the phylogeny [22]. This model provides flexibility to accommodate the different means of transmission when reconstructing the phylogenetic dispersal history of the virus.

In this study, the phylogeography of RYMV in East Africa was reconstructed from a comprehensive heterochronous sequence dataset. Given that RYMV has a narrow host range limited to rice and a few related species, it was expected that its dissemination has been shaped by rice history. Subsequently, we paid special attention to the history of rice in East Africa since the beginning of the 19th century. RYMV originates in East Africa but unlike in Madagascar and in West Africa, rice cultivation had remained localized until recently [25, 26, 27]. Rice had been cultivated along the Indian Ocean Coast for centuries but was confined to a few scattered coastal sites [26]. The sole documented case of large plantation at the beginning of the 19th century is the Kilombero valley, upstream of the mouth of the coastal river Rufiji, 300 km from the Indian Ocean [28]. By the end of the 19th century, rice supplies from the Rufiji flood plains had emerged as a sufficiently important source for that area to acquire the nickname “Little Calcutta” [29, 30]. In the middle of the 19th century, rice was introduced around the great lakes of East Africa (Lake Victoria, Lake Tanganyika and Lake Malawi) [31]. Rice cultivation became generalized at the end of the 20th century. Assessing the virus movements between these far apart rice-producing regions helps to identify the main modes of dissemination.

151 Dispersal statistics are increasingly used to characterise and quantify the spread of viruses [32,
152 33, 34]. We assessed the dispersal capacity of RYMV and compare it to a range of zoonotic
153 viruses [33]. Altogether, this study suggests that the transport of contaminated rice seed was
154 decisive in the long-distance dissemination of RYMV, not only within East Africa, but also in
155 the introduction of the virus from East Africa to West Africa and to Madagascar. It points the
156 most probable routes and modes of dissemination and unveils the links with rice history. It
157 further shows the likely role of a broad spectrum of human activities in RYMV dispersal, some
158 of them unsuspected. This explains why RYMV exhibits extensive dissemination capabilities,
159 similar to those of highly mobile zoonotic viruses.

160

161 **Results**

162 Temporal signal

163 BETS analyses indicate that the increase in sample size of heterochronous sequences lead to a
164 stronger temporal signal in West Africa (from 261 to 335 sequences) and in East Africa (from
165 240 to 335 sequences) (Table 1). The temporal signal was more pronounced in the set of West
166 African sequences (reflected by a higher Bayes factor). The temporal signal of the two datasets
167 was also tested using cluster randomization tests of the sampling dates. There was no overlap
168 of the credibility intervals of the substitution rate calculated with sampled dates and those with
169 randomized dates (data not shown). However, the differences obtained were more pronounced
170 with the WA335 dataset. The square of the correlation coefficient of the regression sampling
171 date vs. distance to the root obtained with TreeTime was 0.07 with the WA335 dataset vs. 0.01
172 with the EA335 dataset. Altogether, the temporal signal was more pronounced in the WA335
173 dataset than in the EA335 dataset. The stronger temporal signal of the West African dataset
174 probably results from a relatively uniform distribution of the sampling dates over the last thirty

175 years whereas that of East Africa isolates was concentrated over the last 15 years. Short
176 sampling periods are prone to unpurged transitory deleterious polymorphism leading to higher
177 and biased substitution rates [35]. Consistently, the weak temporal signal of the EA335 dataset
178 leads to a biased high substitution rate and correlatively to an inconsistent, obviously too recent,
179 age of the most recent common ancestor of the sampled sequences (tMRCA). Given the nested
180 position of the West African lineage within the East African lineages (see below), the tMRCA
181 in East Africa is expected to be substantially older than that in West Africa.

182 As the temporal signal from the East African corpus was not sufficient alone to allow a valid
183 reconstruction of the spatio-temporal dispersion of the RYMV in East Africa, a prior was set on
184 the substitution rate. The substitution rate estimates of the three datasets (WA261, WA335 and
185 Mg94) were similar (Table 1). The substitution rate of the Mg94 dataset indicates that a reliable
186 estimate was obtained from a dataset with a limited temporal signal after the integration of
187 another data source, in this instance epidemiological information derived from field surveys.
188 We selected as a prior the substitution rate of the WA335 dataset as its standard deviation was
189 the lowest. Accordingly, for the EA335 phylogeographic reconstructions, a prior was set on the
190 mean rate under the uncorrelated log-normal relaxed molecular clock (the "ucld.mean"
191 parameter), a normal distribution with a mean of $1.24\ 10^{-3}$ substitutions per site per year and
192 standard deviation of $1.16\ 10^{-4}$. A prior was also set on the standard deviation of the uncorrelated
193 log-normal relaxed clock (the "ucld.stdev" parameter), a normal distribution with a mean of
194 1.09×10^{-3} substitution per site per year and standard deviation of 2.87×10^{-4}.

195

196 <u>Phylogeny of RYMV in East-Africa</u>

197 The phylogeny of RYMV in East Africa reconstructed from 335 coat protein gene sequences is
198 made of three major lineages named, respectively, S4, S5 and S6 lineages (Fig. 1). The

199 phylogenetic group containing the S4 and S5 lineages does not have a strong bootstrap support.
200 Several strains are distinguished within the S4 and S6 lineages. The S4 lineage includes strains
201 S4lm, S4lv, S4ug and S4et named according to their geographical distribution (lm, Lake
202 Malawi; lv, Lake Victoria; ug, Uganda; et, Ethiopia). The S6 lineage includes strains S6a, S6b,
203 and S7 but was not supported by a strong bootstrap value. The S5 lineage consists of one strain
204 only.

205 The phylogeny of RYMV was also reconstructed from the full-length genomic sequences (with
206 recombination regions removed; see Materials and Methods) of 50 isolates representative of
207 the geographic and genetic diversity of RYMV in East Africa (Fig. 2). The same phylogenetic
208 pattern was observed at the lineage and strain levels, except that the S4lv and S4lm strains
209 belong to the same phylogenetic group in the reconstruction from the full-length sequences but
210 not from the coat protein gene sequences. Very few insertion-deletion events occurred in coding
211 regions. The basal insertion-deletion pattern at positions 19 and 60 in the ORF4 in the S4, S5
212 and S6 lineages was observed earlier [36]. An additional deletion occurred in the isolate Tz319
213 of the S5 strain at codon 432 in the ORF2a. It is the only insertion-deletion event found at a
214 terminal phylogenetic position (Fig. 2). All the insertion-deletion polymorphisms originated in
215 isolates of the Eastern Arc Mountains.

216

217 Phylogeography from 335 coat protein gene sequences

218 The spatio-temporal dispersal of RYMV lineages in East Africa was reconstructed from the
219 capsid protein gene sequences of 335 isolates (Figs. 3, 4, 5). The following periods are
220 distinguished.

221 (1) In the middle of the 19th century, RYMV emerged around the Great Ruaha Escarpment in
222 the Udzungwa mountains of the Eastern Arc Mountains north of the Kilombero Valley (Fig. 4);

223 (2) Within a few decades, RYMV dispersed to the adjacent Kilombero Valley (Fig. 4);

224 (3) Between the end of the 19th century and the beginning of the 20th century, RYMV reached
225 the south of Lake Victoria 400 km northward of the Kilombero Valley, the first long range
226 dispersal event (I) (lineage S4), and the Morogoro region 100 km eastward of the Kilombero
227 Valley (lineage S6) (Fig. 4);

228 (4) In the following decades, RYMV circulated at the east of Lake Victoria (Fig. 5);

229 (5) A second long range dispersal event (II) originated at the beginning of the 20th century in
230 the Kilombero valley to reach the south of Lake Malawi, 900km southward, 80 years later (Figs.
231 3. and 5);

232 (6) A third long range dispersal event (III) took place in the second half of the 20th century. It
233 originated at the east of Lake Victoria and reached northern Ethiopia, 1400 km northward, 50
234 years later (Figs. 3 and 5);

235 (7) During the last decades of the 20th century, RYMV dispersed eastward and northward from
236 the Kilombero Valley and the Morogoro region, and southward and westward from Lake
237 Victoria (Fig. 4). Recently, the virus became widespread in all rice-growing regions with an
238 increase in movements between adjacent localities (Figs. 3 and 5).

239 Altogether, the phylogeography of RYMV in East Africa reconstructed from the 335 coat
240 protein gene sequences was characterized by these three long-distance dispersal events along a
241 south-north axis from the middle of the 19th century to the second half of the 20th century. In
242 the past decades, a regular short distance dispersal eastward and westward became predominant.

243

244 <u>Phylogeography from full-length sequences and ORFs of 50 representative isolates</u>

245 The spatio-temporal dispersal of RYMV in East Africa was reconstructed from sequences of 50
246 isolates representative of the genetic and geographic diversity of the virus in East Africa: full-

247 length sequences (4468 nt, and excluding recombinant regions), sequences of ORF2a (including
248 protease and VPg; 459 codons), ORF2b (including polymerase; 540 codons) and ORF4 (capsid
249 protein, 240 codons). The differences in nucleotide diversity and in the selection pressure
250 among the ORFs are given in the Supplementary Table 5. No recombination events was detected
251 within the ORF2a, ORF2b and ORF4.

252 To make up for the weak temporal signal of these small datasets (50 sequences), a temporal
253 prior was applied to the root of each tree by using the tMRCA of the EA335 tree, following a
254 normal distribution with a mean 170 years and a standard deviation of 25 years. Regardless the
255 differences in sequence length, diversity and selection pressure between the ORFs
256 (Supplementary Table 5), the phylogeographic patterns were similar (Fig. 6), and consistent
257 with that reconstructed from the 335 sequences of the coat protein gene: (1) an emergence in
258 the Eastern Arc Mountains, (2) a rapid spread to the adjacent large rice growing valley of
259 Kilombero, (3-4) dispersal northward towards Lake Victoria, and eastward towards the
260 Morogoro region, (5) spread towards the south of Lake Malawi, (6) spread towards northern
261 Ethiopia, (7) generalized dissemination throughout East Africa.

262

263 Phylogeography of the three main lineages

264 The initial diversification of RYMV in East Africa resulted in the emergence of the three
265 lineages S4, S5 and S6 in the mid-19th century within or near the Kilombero valley. The
266 phylogeography of the three lineages is markedly different (Figs. 7a, 7b). The S4 lineage had
267 the greatest epidemic success. It was found south of Lake Victoria in the second half of the 19th
268 century (S4lv), and then circulated around Lake Victoria (S4ug) before dispersing northward
269 into Ethiopia (S4et), then southward to Malawi and finally westward to the Republic of Congo,
270 Rwanda and Burundi (S4lm). The S6 lineage remained confined to the Kilombero valley and

271 in the Morogoro region for several decades. In the last decades, it spread towards eastern
272 Tanzania, south-west Kenya and to the islands of Zanzibar and Pemba. The S7 strain split early
273 from the S6 lineage and was recovered recently in southern Malawi. The S5 lineage was found
274 exclusively in the Kilombero valley. The migration curve (Fig. 7c) illustrates the differences in
275 velocity among the lineages, with an early and rapid spread of the S4 lineage, a late but rapid
276 spread of the S6 lineage (except the early spread of the S7 strain), and a lack of dispersal for
277 S5. Interestingly, there was a slowdown in the dispersal rates the past decades within most
278 strains of the S4 and S6 lineages.

279 Additional sampling was performed from 2013 to 2017 at the Kilombero Rice Plantation (KPL)
280 rice intensification station, located within the Kilombero Valley, which covers 5 000 ha of rice.
281 A total of 75 isolates was collected in rice fields under intensifying schemes and in surrounding
282 traditional rice fields. The coat protein gene of these isolates was sequenced. Almost all of the
283 isolates belong to strain S6b already found in this region, one isolate of strain S6a, one S5
284 isolate and four S4lm isolates (data not shown). The absence of new strains and new variants
285 indicate that the diversity of the virus in the Kilombero valley was adequately represented in
286 the datasets used to reconstruct the phylogeography of RYMV in East Africa. The low
287 proportion of isolates, other than of the S6b strain, shows that the circulation of strains in the
288 Kilomobero rice valley was restricted, even in the present time.

289

290 <u>East African origin of the introduction of RYMV into West Africa and into Madagascar</u>

291 The phylogeny of RYMV was reconstructed from the full-length sequences of 101 isolates
292 representative of the genetic and geographic diversity of the virus in Africa: 50 isolates from
293 East Africa, 45 from West Africa and six sequences from Madagascar. A major split in the
294 phylogenetic network separates East Africa and Madagascar isolates from West Africa ones

295 (Fig. 8a). The phylogeny is characterized by the nested position of the West African lineage
296 within the East Africa lineage comprising the S4ug, S4mg and S4et strains (Fig. 8b). The S4mg
297 strain in Madagascar resulted from a recombination between the S4ug strain and an unidentified
298 minor parent 14]. The relationship between the West-African lineage and the S4et strain of this
299 lineage persist after excluding the S4mg and S4ug sequences (Fig. 8c). This confirms the earlier
300 assumptions, made on a restricted dataset, that RYMV in West Africa and in Madagascar
301 originated in East Africa [14, 15], and brings information on the source lineage of RYMV in
302 West Africa.

303 We detailed the East African origin of the introduction of RYMV into West Africa and into
304 Madagascar. Convergence of the analyses with the full dataset (AE335, WA335 and Mg94
305 dataset, i.e. a total of 784 coat protein gene sequences) was difficult to reach. So 50 isolates
306 representative of the diversity of the virus in West Africa and 15 isolates representative of that
307 in Madagascar were selected using PDA analyzer [37]. Then we reconstructed the
308 phylogeography of the collection of the coat protein gene of 335 isolates from East Africa, the
309 50 representative isolates from West Africa and the 15 representative isolates from Madagascar,
310 i.e. a total of 400 isolates. The phylogeographic model was that defined for the analysis of the
311 EA335 sequence dataset (see Materials and Methods). The split between the East and the West
312 African clades occurred in ca. 1868 (95% HPD 1831-1906) at the south of Lake Victoria (Fig.
313 9). The introduction of RYMV in the Niger Inner Delta in West Africa occurred in ca. 1892
314 (95% HPD, 1857-1909). The subsequent pattern of dispersion throughout West Africa and
315 toward Central Africa mirrored the findings from comprehensive surveys conducted in West
316 Africa [38, 39]. In Madagascar, RYMV was introduced in ca. 1980 (95% HPD 1975-1986) from
317 the northeast of Lake Victoria. The introduction of RYMV in the northwest of Madagascar
318 followed by the spread of the virus southward of the country is a scenario similar to that
319 obtained from the comprehensive dataset [14].

320

321 Comparative dispersal statistics of RYMV

322 For RYMV, variation in isolation-by-distance (IBD) signals among the three regions (East
323 Africa, West Africa and Madagascar) was apparent (from 0.35 to 0.56) (Table 2), yet it was less
324 pronounced than that of rabies virus lineages in different host species (from 0.09 to 0.74) [33].
325 The IBD index was higher in West Africa (0.52 and 0.56 for the two datasets) than in East Africa
326 (0.37) and in Madagascar (0.35) (Table 2). In East Africa, the recurrent long distance human-
327 mediated dispersal of RYMV in a wide range of directions revealed by this study is consistent
328 with a low IBD signal. The higher IBD signal estimated in West Africa may result from the
329 dominant eastward long-distance transmission events establishing more local transmission
330 chains [38, 39, 40]. The relatively low IBD signal estimated in Madagascar suggested that long-
331 distance human-mediated dispersal, which blurred the relationship between geographical and
332 genetic distances, is also frequent in a country where rice is widely grown. Diffusion
333 coefficients in the three regions ranged from 1100 to 1600 km^2 per year with overlapping 95%
334 HPD intervals. This indicates a similar dispersal capacity of the virus across the three regions
335 despite differences in IBD signal values, spatial scales, rice history and cultivation, and possibly
336 also in dispersal modes.

337 The diffusion coefficient of RYMV for East Africa, West Africa and Madagascar combined
338 (covering ca. 12 million km^2) was 2700 km^2/year, was twice that of each of three regions
339 reflecting the inclusion of the long distance dispersal from East Africa towards West Africa and
340 towards Madagascar (Table 2). The diffusion coefficient of RYMV was higher than that of
341 several animal viruses including rabies in various hosts, even when occasional rapid long-
342 distance dispersal events driven by human-mediated movements occurred [33]. Yet, the

343 diffusion coefficient of RYMV was lower by an order of magnitude than that of animal viruses
344 with long distance dispersal through animal trade or through migratory birds [33].

345

346 **Discussion**

347 The seven periods identified in the phylogeographic reconstructions of RYVM in East Africa
348 are interpreted as followed on the basis of the history of rice since the beginning of the 19th
349 century.

350 (1) The postulated emergence of RYMV in the Eastern Arc Mountains [41] was confirmed and
351 characterized in more details. The emergence of RYMV dates back to the mid-19th century. It
352 took place near the Great Ruaha Escarpment of the Udzungwa Mountains adjacent to the
353 Kilombero valley and close to the Morogoro region. Consistently, the insertion-deletion
354 polymorphism originated in isolates of this region. The original host(s) of RYMV were located
355 within the Eastern Afromontane biodiversity hotspot [15, 41]. Slash and burn rice cultivation
356 practiced in the mid-1800s near the Great Ruaha Escarpment of the Udzungwa Mountains [28,
357 31, 42, 43] resulted in spillovers from the primary hosts of the virus, presumably of the
358 Eragrostidae and related Poaceae families given RYMV host range, to cultivated rice. Primary
359 hosts may also include the cultivated finger millet, a possible alternative host of RYMV,
360 widespread in these mountains. This led to the introduction of RYMV in cultivated rice. The
361 basal split between the S4, S5 and S6 lineages and the insertion-deletion polymorphism suggest
362 (at least) three independent splillovers from the wild host(s) to cultivated rice. Strain specific
363 poaceae species such as Dactyloctenium aegyptium have been identified [44]. Specific
364 mutations of the S7 strain occurred at positions of the VPg under positive selection and
365 experimentally associated to host range [45, 46]. Further studies are necessary to understand
366 the genetic changes, if any, associated to host jumps and rice spillover.

367 (2) Within a few decades, RYMV spread to the large adjacent Kilombero Valley where rice had
368 been widely cultivated since the beginning of the 19th century [28]. This is consistent with the
369 movements of rice-growing populations between the Udzungwa Mountains and the Kilombero
370 Valley [28].

371 (3) Between the second half of the 19 th century and the beginning of the 20th century, RYMV
372 (lineage S4) spread to the south of Lake Victoria 400 km northward of the Kilombero Valley.
373 Its dispersal followed the introduction of rice into the interior of the continent along the caravan
374 routes linking the coastal strip to Lake Victoria [47, 48, 49]. There are indications that the
375 caravan routes crossed the Kilombero valley [31]. Interestingly, the migration pathways of
376 turnip mosaic virus (TuMV), a seed transmitted potyvirus, retraced some of the historical trade
377 arteries of the Silk Road [50]. So, both RYMV and TuMV illustrate the link between plant virus
378 dispersal and trade routes. During the same period, RYMV (lineage S6) was introduced in the
379 Morogoro region 100 km eastward of the Kilombero Valley.

380 (4) In the following decades, up to the middle of the 20th century, RYMV dispersed at the east
381 of Lake Victoria where rice had been introduced at the end of the 19th century, probably by
382 boat [51, 52]. Interestingly, the first field report of RYMV in East Africa was in 1966 near
383 Kisumu also at the east of Lake Victoria [5].

384 (5) At the beginning of the 20th century, RYMV was introduced from the Kilombero valley to
385 the south of Lake Malawi. This movement is parallel and concomitant to the movement of
386 military troops at the end of the First World War [53]. Feeding the troops was a major issue
387 [54], rice was the main staple food for soldiers, and the Kilombero valley was the main rice
388 production area. Accordingly, RYMV may have been dispersed through the transport of
389 contaminated seeds during the First World War. An alternative hypothesis, linking virus
390 dispersal to the Kilwa-Nyasa south caravan route, from Kiwa 300 km south of Zanzibar to the

south of Lake Malawi (formerly named Lake Nyasa), is less likely. First, there is no firm indication that rice had been introduced at the south of Lake Malawi along this caravan route [55, 56]. Second, the peak of activity along the Kilwa-Nyasa south caravan route occurred in the second half of the 19th century [55, 56] whereas the introduction of RYMV at the south of Lake Malawi occurred at the beginning of the 20th century.

(6) In the second half of the 20th century, RYMV was introduced into northern Ethiopia from the north of Lake Victoria. Large rice intensification schemes were established in the 1960s around Lake Victoria [5] and in the 1980s around Lake Tana in northern Ethiopia [57]. Seed exchanges between these intensification schemes were frequent and may have introduced RYMV in northern Ethiopia. The widespread cultivation of teff (Eragrostidae), a possible host of RYMV, in the Ethiopian highlands may have facilitated the dissemination.

(7) RYMV then spread eastward and northward from the Morogoro region (strain S6a) and from the Kilombero Valley (strain S6b), and southward and westward from the Lake Victoria region (strains S4). RYMV finally became widespread throughout East Africa. This spread accompanied the expansion of rice cultivation of the last decades of the 20th century and of the beginning of the 21st century. The slowdown in the dispersal rates of several strains of the S4 and S6 lineages over the past decades reflected a shift from an expansion phase to an endemic phase [32, 33] in RYMV epidemiology. This may be due to changes in the trade and market patterns [58] with a gradual change from long distance to local seed transport as rice became widely cultivated.

Altogether, the long-distance dispersal of RYMV was closely linked to rice movement in several regions, at different periods and under various circumstances. The dispersal of the RYMV was associated to rice introduction along the caravan routes from the Indian Ocean Coast to Lake Victoria in the second half of the 19th century, to rice transport as troop staple

415 food from the Kilombero valley towards the South of Lake Malawi at the end of the First World
416 War, to seed exchanges between Lake Victoria and Ethiopia in the second half of the 20th
417 century. Alternative hypotheses involving beetle dissemination of the virus are unlikely given
418 the paucity of rice cultivation and alternative hosts at these early periods between regions
419 located several hundreds of kilometers apart. Seed transport could also account for short
420 distance dispersal of the virus, in complement or as an alternative to beetle transmission, around
421 Lake Victoria in the first half of the 20th century and along the Indian Ocean in the past few
422 decades. Finally, the ongoing transport of contaminated seeds could also explain the current
423 generalized dispersal of RYMV throughout East Africa.

424 Early long-distance transport of contaminated seeds led to the dispersal of the main lineages in
425 different directions and environments. So, the contrasting epidemic characteristics of the S4,
426 S5 and S6 lineages resulted primarily from historical circumstances. In complement, the role
427 of genetic properties of the strains should be explored. For instance, positive selection at
428 positions of the VPg involved in the host range [45, 46] may have impacted the epidemiological
429 characteristics of the S7 strain. The S5 lineage remained confined to the Kilombero valley, yet
430 without becoming extinct, whereas the S4 lineage and later the S6 lineage were widely spread
431 throughout East Africa. In West Africa, strain dominance was observed in competition
432 experiments and by comparison of the virus titer of two strains [59]. Similar experiments with
433 S5 and S6 and S4 isolates were not conclusive (Pinel-Galzi A, Fargette D, Hébrard E,
434 unpublished results). Yet, these fitness tests may not encompass all the relevant traits involved
435 in epidemiological differences and should be refined accordingly.

436 Phylogenetic analyses indicate that the West African RYMV diversity is nested as a
437 monophyletic clade within the East African diversity, indicating an East African origin [15, 41].
438 The current phylogeographic study (i) confirms this hypothesis, (ii) brings information on the
439 date, the location and the lineage of the origin, (iii) provides clues on the means of introduction,

(iv) shows that the spread of RYMV throughout Africa can be reconstructed from a single RRW model. The origin of RYMV in East Africa was confirmed, based on a more representative dataset, by the nested phylogenetic position and the subset of insertion-deletion polymorphism of the West African clade. The phylogeography of RYMV throughout East Africa unveiled the role of rice transport in the long-distance movement of the virus. Similarly, the introduction of RYMV in West Africa may result from seed movements. Seed exchanges in Africa between agricultural stations, experimental farms, botanical and missionary gardens, even far apart, were frequent in the second half of the 19th century [60, 61]. The Niger Inner Delta was a major destination for seeds from a wide range of origins, including Madagascar, because of rice intensification in this region since the end of the 19th century [62, 63]. The origin of RYMV introduced in West Africa was located at the south of Victoria Lake at the end of the 19th century, in Tanzania, which was under German occupation at that time. Contacts between German scientists and agricultural stations of the Niger Inner Delta at the end of the 19th century are documented [61]. RYMV may have been introduced directly from this region, or indirectly through the Amani research station which was the main experimental station in East Africa [64]. The main trends of dispersal of RYMV throughout West Africa and Madagascar were captured within a single RRW model. This underlines the flexibility of the RRW models to reconstruct spatio-temporal dispersal when long-distance jumps, even transcontinental ones, occurred. The RRW that was used in this study is equivalent to a Cauchy process on a tree with rescaled branch lengths, which is a pure jump process allowing for long-distance dispersion events [65]. Our results also confirm the Ugandan origin of the Madagascar strain [14]. Increased seed exchanges between Madagascar and East African countries have occurred during the recent decades [66]. Transport of contaminated rice seeds may also account for this introduction.

464 RYMV dispersal through the transport of contaminated seeds shows the importance of this
465 neglected virus transmission pathway in plant virus epidemiology [1]. This study also unveils
466 the wide range of human activities, some of them unsuspected, involved in man-mediated
467 movements of a plant virus. Consequently, a plant virus like RYMV has wide dispersal
468 capacities, greater than or equal to that of most zoonotic viruses. Maize streak virus A (MSV-
469 A) causes another major cereal disease in Africa [67]. It is transmitted by leafhoppers and not
470 by seeds. Interestingly, introductions of MSV-A from Uganda to Madagascar and from Kenya
471 to Ethiopia have been reported. These movements, parallels to those of RYMV, were also
472 attributed to human-mediated introductions [66, 68]. It shows that the spread of RYMV and
473 MSV-A, two major vector borne viruses, does not necessarily, or even primarily, depend on
474 vector transmission.

475 An important pending question is why RYMV, given its wide dispersal capacities, is still
476 restricted to Africa and does not have a worldwide distribution, unlike several sobemoviruses
477 with similar biological properties. Long-distance movement of RYMV across the sea is possible
478 but is quite a rare event as indicated by the unique successful introduction of the virus in West
479 Africa. Rice was imported into America from West Africa in the 17th century and early 18th
480 centuries, at least a century before the introduction of RYMV in West Africa. In the 19th century,
481 rice exports from East Africa were limited and directed towards regions where rice was not
482 cultivated [30]. In the 20th century, rice was imported into Africa rather than exported from this
483 continent. Altogether, this explains why RYMV remained restricted to Africa. However, the risk
484 of accidental introduction of RYMV into other continents subsists, in particular through the
485 transfer of seeds for agronomical breeding which we have found to be a decisive means of long
486 distance dissemination of the virus in Africa. Incidentally, sequences of MSV-A from the
487 Philippines have recently been deposited on NCBI (PQ034624, OR983352 and eight others), a

488 possible illustration of such human-mediated trans-continental introductions of vector borne
489 plant viruses.

490

491 **Materials and Methods**

492 Datasets

493 A collection of 335 capsid protein gene sequences of East African isolates was built. The dataset
494 consists of 240 sequences retrieved from NCBI (2024-06-01) supplemented by 95 sequences
495 obtained in this study (Supplementary Table 1). The isolates originated from eight countries
496 (Burundi, Republic of Congo, Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda). The
497 sampling locations were distributed between latitudes 15.6° South and 11.9° North, and from
498 longitudes 28.8° West to 39.8° East, ca. 3 000 kilometers in latitude x 1 200 km in longitude,
499 i.e. a study area of ca. two million square kilometers. The isolates were sampled from 1966 to
500 2019 (54 years). A minor variant named S4ke recently identified in Kenya with a recombinant
501 event in the capsid protein [69] was considered in this study (see below) but not included in this
502 corpus.

503 A collection of full-length sequences of 101 isolates from Africa was set. This dataset consisted
504 of sequences of 50 isolates of East Africa and the East of Central Africa (referred to as the East
505 African dataset), 45 isolates of West Africa and the West of Central Africa (referred to as the
506 West African dataset) and six sequences of Madagascar. Among the 50 full-length sequences of
507 the East African dataset, 23 were sequenced for this study and 27 were retrieved from NCBI
508 (Supplementary Table 2). This sample is representative of the genetic and geographic diversity
509 of RYMV in East Africa, including the S4ke variant from western Uganda. No recombination
510 signal was detected within the ORF2a and ORF2b genes.

511 In complement, a collection of 335 capsid protein gene sequences from West African isolates,
512 was considered to estimate the substitution rate of RYMV (Supplementary Table 3). It consists
513 of sequences retrieved from NCBI (2024-06-01), 261 sequences used in a study of the
514 phylogeography in West Africa [38] complemented by 46 sequences of Ghana [39] and 28
515 sequences of Burkina Faso [40]. The 28 sequences from Burkina Faso were chosen from the
516 144 available on NCBI using the PDA software [37] in order to maximize the genetic diversity
517 of the sample. In total, the samples were collected in 15 countries (Benin, Burkina Faso,
518 Cameroon, Central African Republic, Chad, Gambia, Ghana, Guinea, Ivory Coast, Mali, Niger,
519 Nigeria, Senegal, Sierra Leone, Togo). They were sampled between 1975 and 2021 (47 years).

520 Another estimate of the substitution rate was made from the collection of 94 capsid protein gene
521 sequences of Malagasy isolates sampled between 1989 and 2017 (29 years) (Supplementary
522 Table 4) that had been used to reconstruct the phylogeography of RYMV in Madagascar [14].
523 A temporal prior was introduced on the date of emergence of RYMV in Madagascar, the disease
524 having been detected for the first time in the fields in the 1970s [14].

525

526 Phylogenetic reconstructions

527 Sequences were aligned using CLUSTAL X with default parameters [70]. Maximum-likelihood
528 (ML) phylogenetic trees were inferred using the PHYML-3.1 algorithm implemented in the
529 SEAVIEW version 4.7 software [71] under a HKY85 substitution model. The ML trees were
530 rooted at the point in the tree that minimizes the residual mean square of the root-to-tip
531 distances. The neighborNet phylogenetic network of the 101 fully sequenced isolates was
532 inferred [72] under an HKY85 distance model as implemented in SplitsTrees4. The
533 neighborNet phylogenetic network illustrates the genetic relationships between sequences
534 taking into account the conflicting phylogenetic signals that are possibly due to recombination

535 events. The full-length sequence alignment was screened for recombination signals using RDP5
536 [73]. The default settings were used for each of the seven recombination detection algorithms
537 that RDP incorporates, as was a Bonferroni corrected P-value cut-off of 0.05. Only
538 recombination events detected by more than four of the seven methods implemented in RDP
539 were considered. The phylogeny was reconstructed from recombinant-free alignments. This
540 was obtained by removing either the recombinant sequences or the recombinant regions. In the
541 latter case, it was checked that further recombination was excluded through the pairwise
542 homoplasy (PHI) test [74] implemented in SplitsTrees4 [72]. Total, synonymous, and non-
543 synonymous nucleotide diversity of ORF2a, ORF2b and ORF4 were assessed by DnaSP6 [75].
544 The ORF1, too short, too variable and with a low phylogenetic signal [76], was not considered.

545

546 Bayesian evolutionary inferences

547 RYMV is a measurably evolving population, yet its overall temporal signal is weak [14, 15].
548 The temporal signal of each data set was assessed through tip cluster-randomization tests in
549 BEAST [77] and by BETS [78] under a Bayesian statistical framework, and by TreeTime under
550 a likelihood framework [79].

551 We subsequently reconstructed time-calibrated phylogenies using a Bayesian statistical
552 framework implemented in BEAST version 1.10.4 software [80]. BEAST uses Markov Chain
553 Monte Carlo integration to average over all plausible evolutionary histories for the data, as
554 reflected by the posterior probability. All analyses were performed using the BEAGLE library
555 to enhance computation speed [81, 82]. We specified an HKY85 substitution model with a
556 discretized gamma distribution (four categories) to model rate heterogeneity across sites. To
557 accommodate lineage-rate variation, an uncorrelated relaxed molecular clock that models the
558 branch rate variation according to a lognormal distribution was specified [83]. The flexible

559 nonparametric demographic skygrid prior was selected to accommodate for variation in the rate
560 of coalescence through time [84]. Stationarity and mixing (e.g. based on effective sample sizes
561 > 200 for the continuous parameters) were assessed using Tracer version 1.7 [85]. Consensus
562 trees deriving from the phylogenies sampled during the MCMC analysis were obtained using
563 TreeAnnotator version 1.10.4 [80].

564 To study the geographical spread of RYMV in continuous space in East Africa and to quantify
565 its tempo and dispersal, we fitted a continuous phylogenetic diffusion model to the East African
566 dataset, modelling the changes in coordinates (latitude and longitude) along each branch in the
567 evolutionary history as a bivariate normal random deviate [22]. As a more realistic alternative
568 to homogeneous Brownian motion, we adopted a "Cauchy" RRW extension that models
569 variation in dispersal rates across branches by independently drawing branch-specific rate
570 scalers of the RRW precision matrix from a gamma distribution with shape and scale equal to
571 1/2 to relax the assumption of a constant spatial diffusion rate throughout the whole tree [22].
572 Bayesian inference using continuous diffusion models yields a posterior distribution of the
573 phylogenetic trees, each having ancestral nodes annotated with location estimates. The EA335
574 dataset was used to reconstruct the dispersal of RYMV throughout East Africa. A spatial jitter
575 of 0.1° in latitude and in longitude (i.e. ca 10 km) was applied to the locations of the isolates.
576 This degree of noise for identical coordinates was needed to avoid improper posteriors under
577 the RRW model and associated inference problems [22, 86]. Evolaps2 was used to visualize the
578 continuous phylogeographic reconstruction of the dispersal history of RYMV lineages [87, 88].
579 The phylogeography of RYMV in East Africa was reconstructed from the coat protein gene
580 sequences of the full dataset (335 isolates), from the full genome and different ORFs of a
581 subsample of the 50 isolates representative of the genetic and geographic diversity of the virus.

582

583 Comparative dispersal statistics of RYMV

584 The phylogeography of RYMV has been reconstructed in East Africa (this study), in West
585 Africa [38] and in Madagascar [14]. The dispersal capacity and dynamics in the three regions
586 was compared through the weighted diffusion coefficient (km^2/year) [15] and the isolation-by-
587 distance (IBD) signal metric, two metrics identified as robust (to sampling intensity in
588 particular) and measuring complementary aspects of the overall dispersal pattern [33]. The
589 diffusion coefficient is an estimate of the dispersal capacity of the lineages. The IBD signal
590 metric quantifies how the dispersal is spatially structured, i.e. the tendency of phylogenetically
591 closely related tip nodes to be sampled from geographically close locations. An IBD signal was
592 apparent through the relationships between geographic and genetic pairwise distances in a
593 restricted dataset of sequences from East and West Africa [89]. The diffusion coefficient of
594 RYMV virus over the three regions combined was also estimated. Then, the dispersal capacity
595 of this plant virus was compared to that of a range of animal viruses in various host species
596 [33].

597

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827

828

829

830 **Tables**

831 Table 1. Temporal signals in the datasets assessed by BETS.

Datasets	Log marginal likelihood*		Bayes factor
	isochronous	dated	
West-Africa			
WA261	-10495	-10409	86
WA335	-13546	-13379	167
East-Africa			
EA240	-11294	-11246	48
EA335	-14634	-14539	95
Madagascar			
Mg94	-3701	-3671	30

832 *estimated under a strict molecular clock model.

833

834 Table 2: Dispersal metrics of RYMV in East Africa, West Africa, Madagascar and the three

835 regions combined[1]

Dataset	Weighted diffusion coefficient (km^2/year)	IBD signal (rP)[2]	Number of samples	Study area (km^2)[3]	Reference
East Africa	1081 [897, 1257]	0.37 [0.30, 0.45]	335	~2 103 000	this study
Madagascar	1246 [622, 1876]	0.35 [0.28, 0.44]	94	~446 000	Rakotomalala et al. (2019)
West Africa	1603 [1159, 2166]	0.56 [0.45, 0.64]	210	~2 979 000	Dellicour et al. (2018)
West Africa and the Niger Valley	1258 [953, 1585]	0.52 [0.44, 0.62]	261	~3 087 000	Issaka et al. (2021)
East Africa, West Africa and Madagascar combined	2718 [2259, 3379]	0.39 [0.24, 0.60]	400	~12 522 000	this study

836 [1] For each dataset and metric, we report both the posterior median estimate and the 95% highest posterior density

837 (HPD) interval.

838 [2] The isolation-by-distance (IBD) signal has been estimated by the Pearson correlation coefficient (rP) between

839 the patristic and log-transformed great-circle geographic distances computed for each pair of virus samples.

840 [3] The extent of the study areas were approximated by the inland area of the minimum convex hull polygon
841 surrounding all the sampling.

842

843 **Figure captions**

844 Figure 1. Phylogeny of RYMV in East Africa reconstructed from the coat protein gene
845 sequences of 335 isolates through the maximum likelihood method under a HKY85 model and
846 mid-point rooting. The names of the lineages and of the strains are given. The bootstrap support
847 (> 0.70) is indicated at the node of the lineages and of the strains.

848 Figure 2. Phylogeny of RYMV in East Africa reconstructed from the full-length genome (with
849 recombination regions removed; see Materials and Methods) of 50 isolates representative of
850 the geographic and genetic diversity through a maximum likelihood method under a HKY85
851 model and mid-point rooting. The names of the lineages and of the strains are given. The
852 insertion-deletion polymorphism of the lineages and of the isolate Tz319 are framed in green
853 as followed: "+", presence ; "-", absence of an amino acid at position 432 of the ORF2a, 19
854 and 60 of the ORF4 successively.

855 Figure 3. Continuous phylogeographic reconstruction of the spatiotemporal dispersal of RYMV
856 lineages in East Africa from 1850 to 2020 based on the coat protein gene sequences of 355
857 isolates collected from 1966 to 2019. The maximum clade credibility (MCC) tree and the 95%
858 highest posterior density (HPD) regions reflecting the uncertainty related to the
859 phylogeographic inference were mapped. The phylogeographic scenario is displayed with
860 temporal gradients linked to line thickness, curvature, opacity, and color. These gradients match
861 the depth of the nodes in the phylogenetic tree, ranging from ancient to recent: path thickness
862 ranges from wide to narrow, curvature varies from high to low, opacity shifts from light to

strong, and color transitions from light to deep brown. The three long range dispersal events were indicated (I, II, III) and the RYMV emergence zone was figured by a dotted frame.

Figure 4. Visualization of the continuous phylogeographic reconstruction of RYMV lineages in East Africa from 1875 to 1920. Transitions associated with the category 'parent node selected/child node not selected' are highlighted in red to distinguish the ongoing migrations from the completed ones highlighted in blue and associated to the category 'parent node selected/child node selected'. The location of the ancestral states (open red circle) is indicated alongside the location of the sampled isolates (full blue circles). The first long range dispersal event was indicated (I) and the RYMV emergence zone was visualized by a dotted frame.

Figure 5. Visualization of the continuous phylogeographic reconstruction of RYMV lineages in East Africa from 1930 to 2020 at stages that capture the major dispersal events. Transitions associated with the category 'parent node selected/child node not selected' are highlighted in red to distinguish the ongoing migrations from the completed ones highlighted in blue and associated to the category 'parent node selected/child node selected'.

Figure 6. Continuous phylogeographic reconstructions of the spatiotemporal dispersal of RYMV lineages in East Africa from 1850 to 2020 based on the non-recombinant full-length sequences (a), ORF2a (b) and ORF2b (c) and ORF4 (d) of 50 representative isolates of the genetic and geographic diversity. The recombinant regions were removed from the full-length sequences (see Materials and Methods). The phylogeographic scenario is displayed with temporal gradients linked to line thickness, curvature, opacity, and color. These gradients match the depth of the nodes in the phylogenetic tree, ranging from ancient to recent: path thickness ranges from wide to narrow, curvature varies from high to low, opacity shifts from light to strong, and color transitions from light to deep brown.

886 Figure 7 (a) Continuous phylogeographic reconstruction of the spatiotemporal dispersal of the
887 three main lineages of RYMV in East Africa from 1850 to 2020 based on the coat protein gene
888 sequences of 355 isolates collected from 1966 to 2019. The three lineages were distinguished
889 by their colors: S4 (green), S6 (brown), S5 (pink). Note that the S5 lineage, confined to the
890 Kilombero valley, is masked by the S6 lineage that has a broader distribution. The strains are
891 indicated close to their emergence area (S4lv, S4lm, S4et, S4ug, S6a, S6b, S7). (b) Maximum
892 credibility tree reconstructed from the dataset and used to generate the spatio-temporal dispersal
893 (same color code for each lineage). (c) Migration curves over time (preorder transversal of the
894 phylogenetic tree) for each parent/child node pair: X-axis = cumulative branch length (as dates
895 in years), Y-axis= cumulative great-circle distances knowing latitudes and longitudes.

896 Figure 8. NeighborNet phylogenetic network of the 101 fully sequenced isolates of RYMV
897 from East Africa and West Africa (purple) under a HKY85 distance model (8a). Maximum
898 likelihood phylogeny tree reconstructed under a HKY85 model and mid-point rooting of the
899 recombination-free full sequences obtained after removing the recombinant regions (8b), and
900 after removing the recombinant sequences (8c).

901 Figure 9. Dispersion of RYMV from East Africa (green, brown and pink for S4, S6 and S5
902 lineages, respectively) to West Africa (purple) and to Madagascar (blue) between 1850 and
903 2020 reconstructed from the ORF4 sequences of 335 isolates from East Africa, 50 isolates from
904 West Africa and 15 isolates from Madagascar. The phylogeographic scenario are displayed with
905 gradients linked to line thickness, curvature, opacity, and color. These gradients match the depth
906 of the nodes in the phylogenetic tree, ranging from ancient to recent: path thickness ranges from
907 wide to narrow, curvature varies from high to low, opacity shifts from light to strong, and color
908 transitions from light to deep yellow. Inlet: Maximum credibility tree reconstructed from the
909 dataset and used to generate the spatio-temporal dispersal (same lineage color code).

910

911 **Supporting information**

912 Supplementary Table 1. Name and accession number of the 335 isolates from East Africa.

913 Supplementary Table 2. Name and accession number of the 101 fully sequenced isolates from
914 West Africa, East Africa and Madagascar.

915 Supplementary Table 3. Name and accession number of the 335 isolates from West Africa.

916 Supplementary Table 4. Name and accession number of the 94 isolates of Madagascar.

917 Supplementary Table 5. Length, diversity and selection pressure of the ORF of Rice yellow
918 mottle virus.

Figure 1

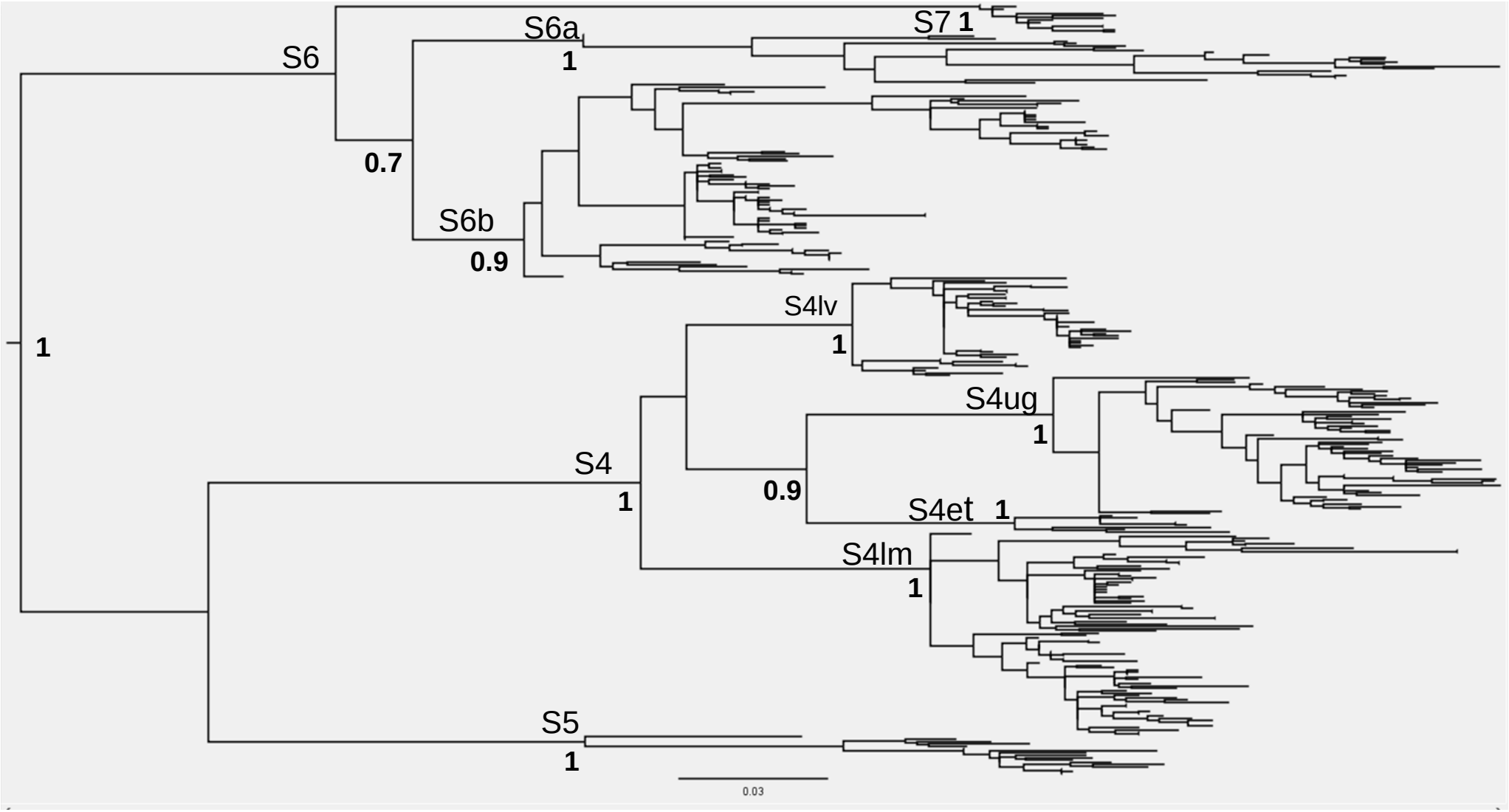


Figure 2

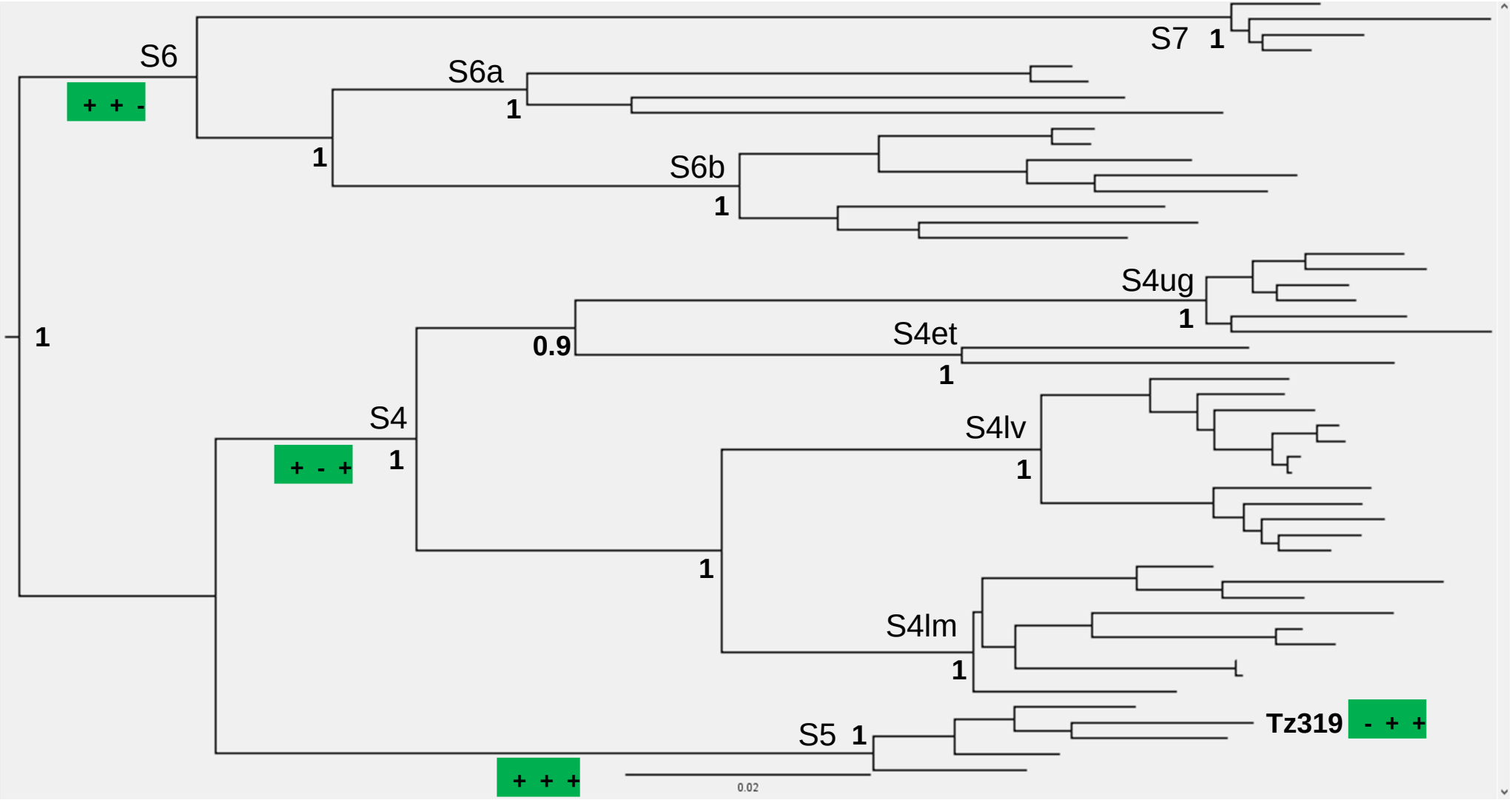

S6
+ + -
S7 1
S6a
1
1
S6b
1
S4ug
1
1
0.9
S4et
1
S4
1
+ - +
S4lv
1
1
S4lm
1
S5 1
Tz319
- + +
+ + +
0.02

Figure 3

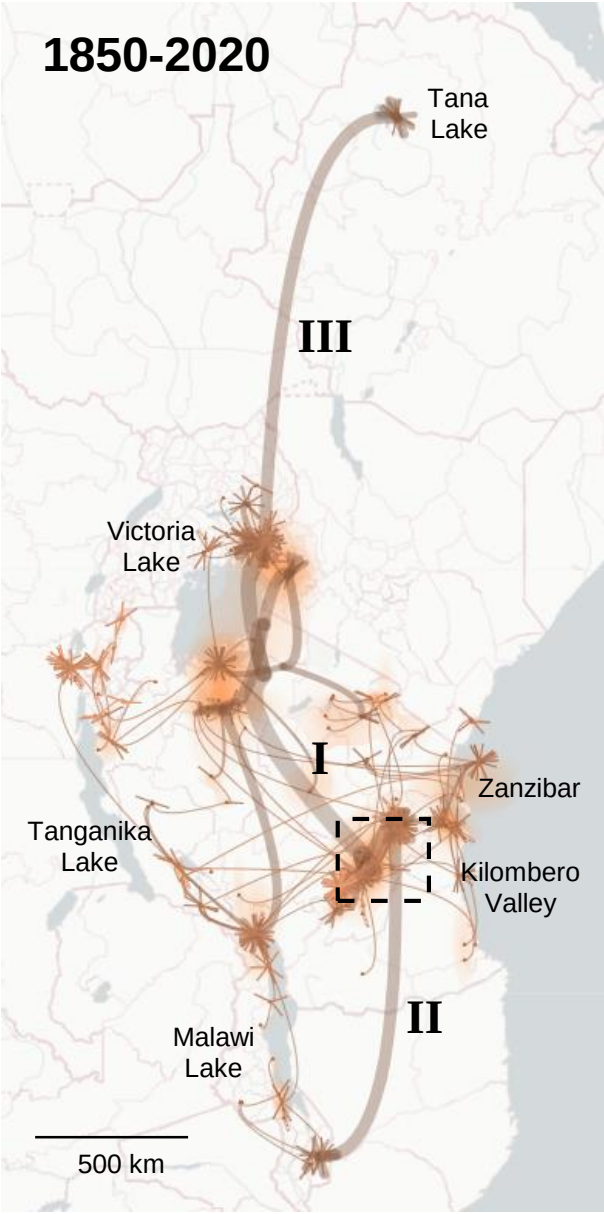

1850-2020
Tana
Lake
III
Victoria
Lake
I
Zanzibar
Tanganika
Lake
Kilombero
Valley
II
Malawi
Lake
500 km

Figure 4

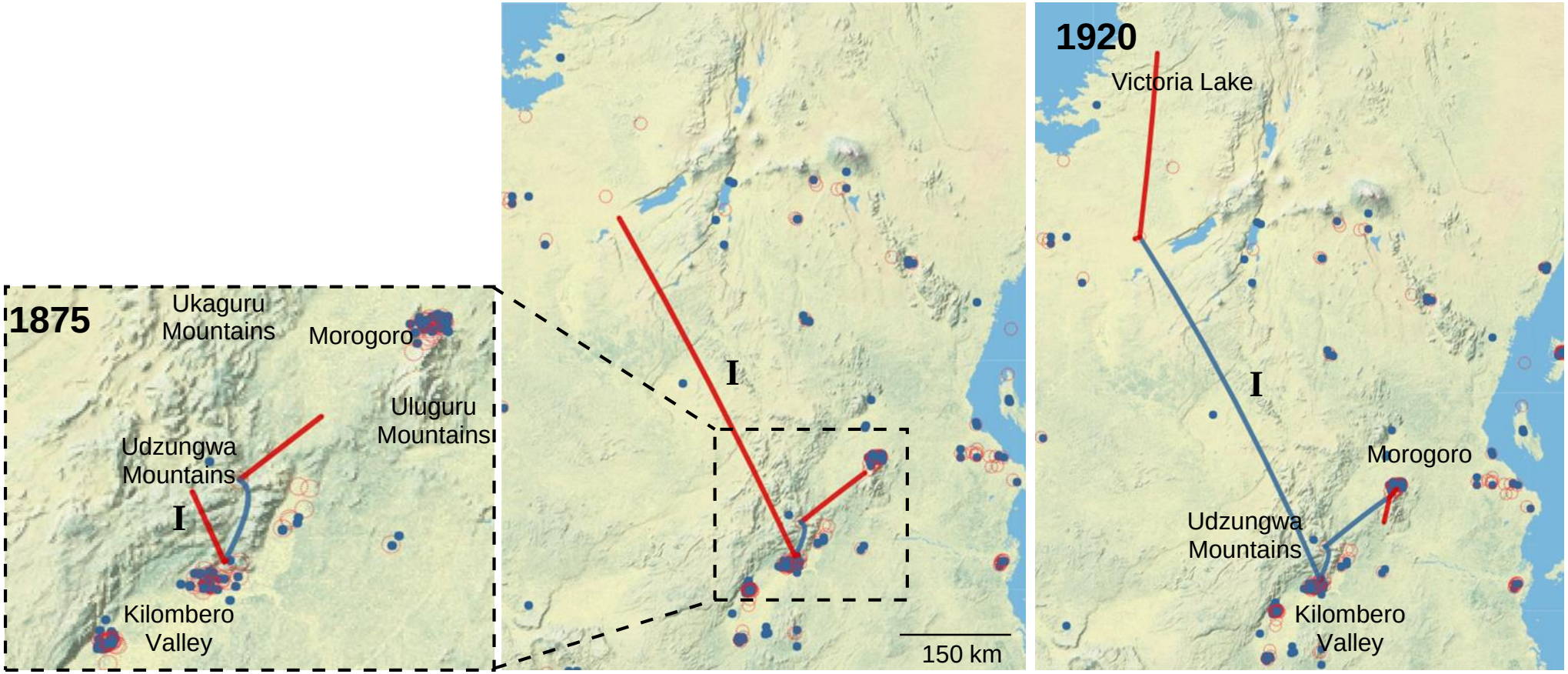

1875
Ukaguru Mountains
Morogoro
Uluguru Mountains
Udzungwa Mountains
I
Kilombero Valley
I
150 km
1920
Victoria Lake
I
Morogoro
Udzungwa Mountains
Kilombero Valley

Figure 5

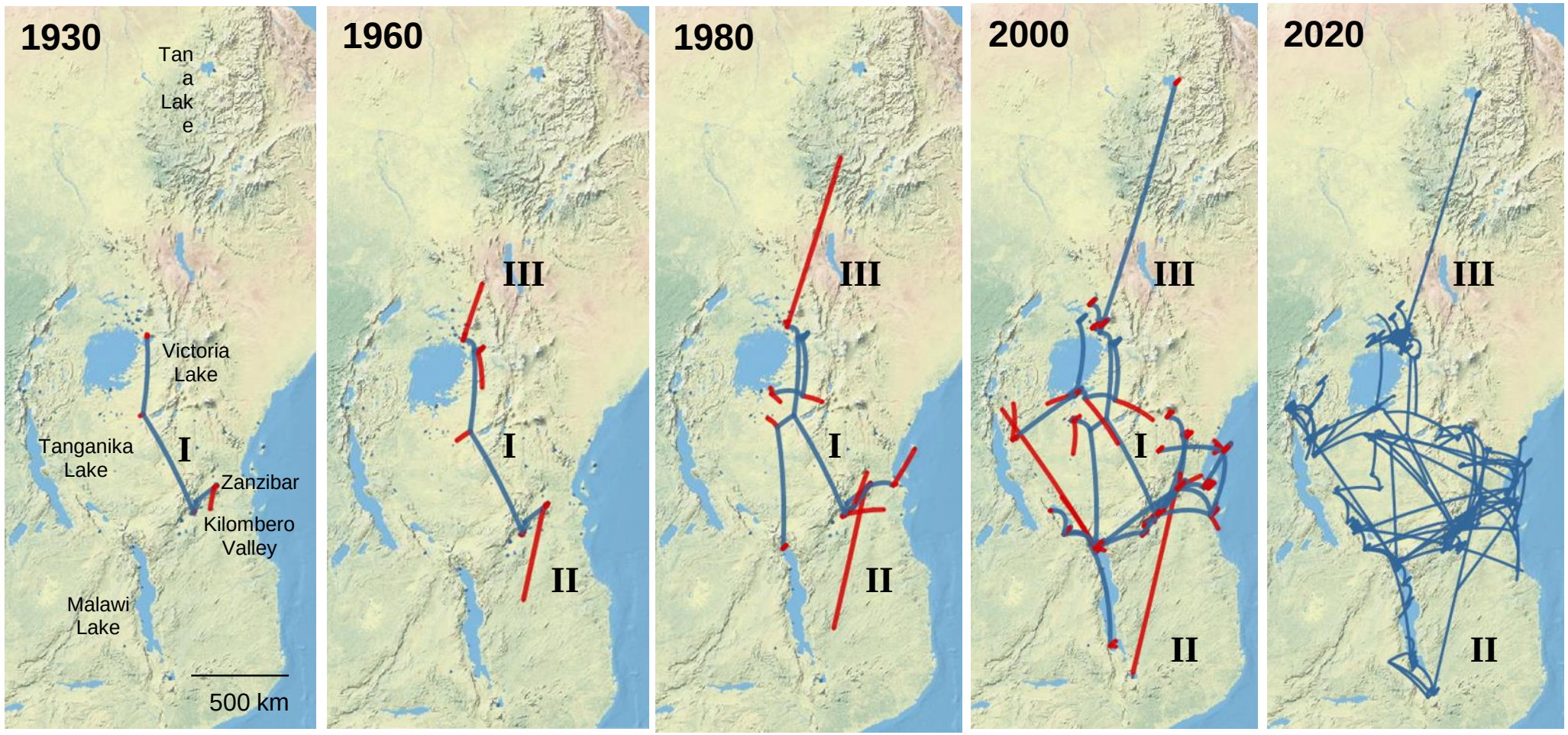

1930
Tan
a
Lak
e
Victoria
Lake
Tanganika
Lake
I
Zanzibar
Kilombero
Valley
Malawi
Lake
500 km
1960
III
I
II
1980
III
I
II
2000
III
I
II
2020
III
II

Figure 6

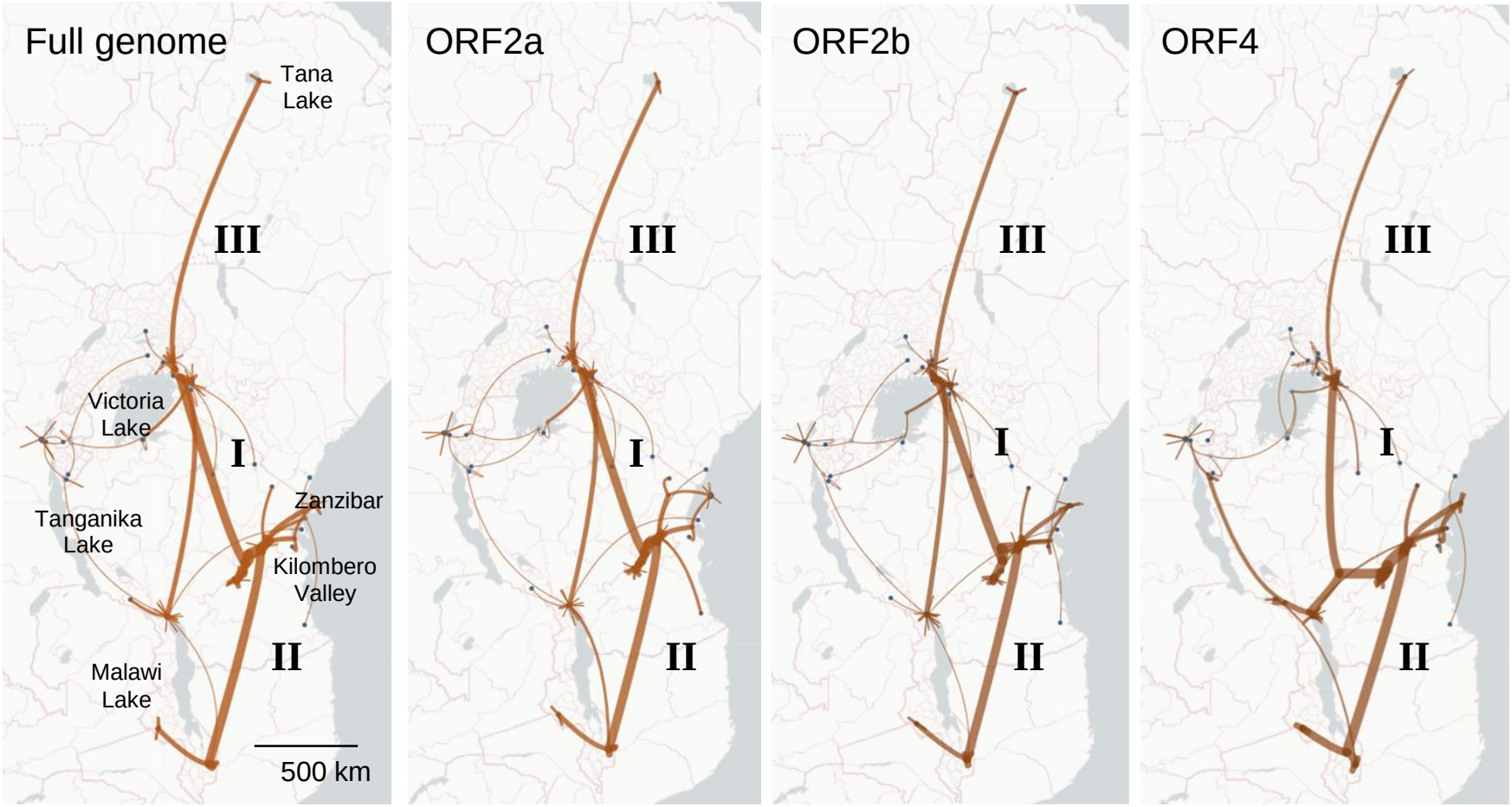

Full genome
Tana Lake
III
Victoria Lake
I
Zanzibar
Tanganika Lake
Kilombero Valley
II
Malawi Lake
500 km
ORF2a
III
I
II
ORF2b
III
I
II
ORF4
III
I
II

Figure 7

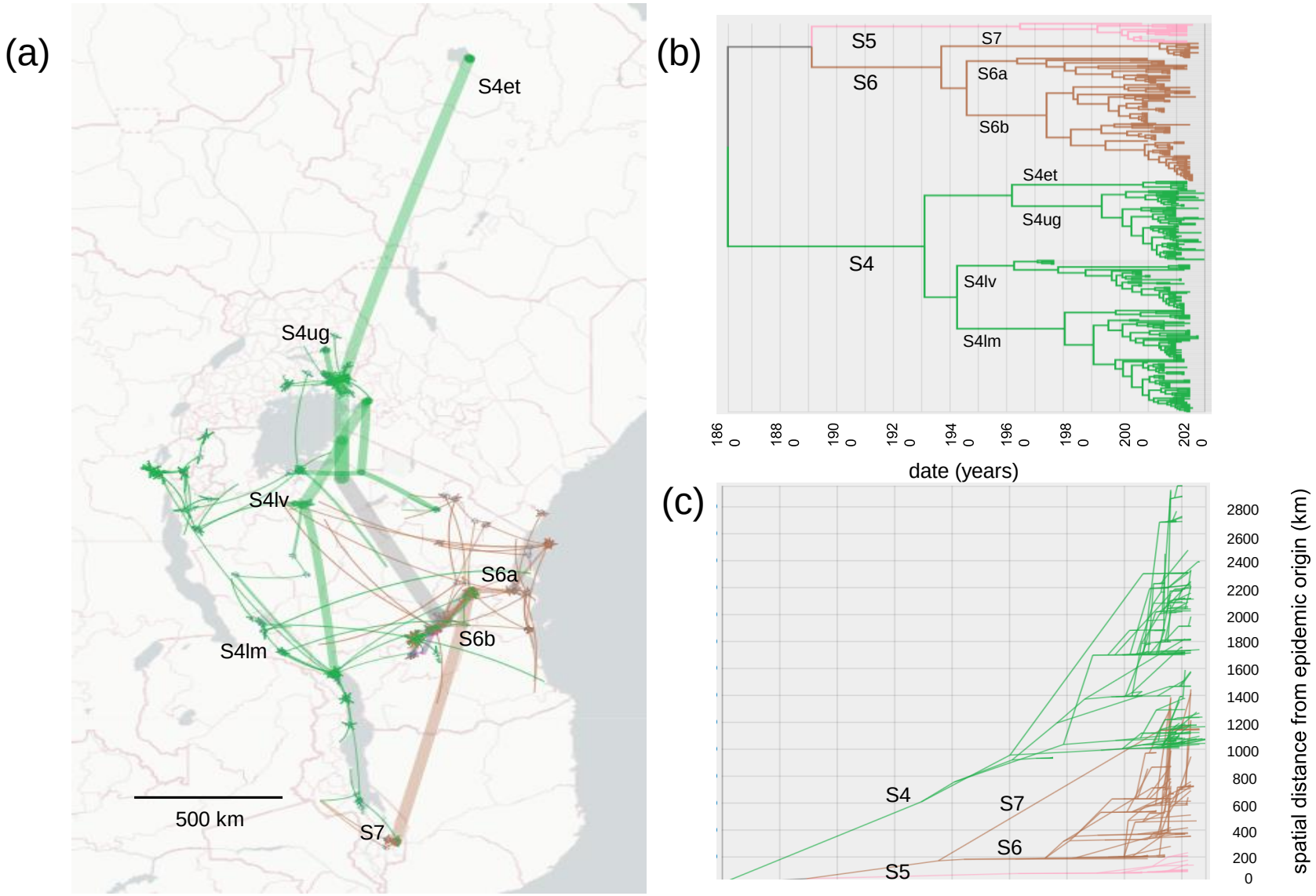

(a)
S4et
S4ug
S4lv
S6a
S6b
S4lm
500 km
S7
(b)
S5
S7
S6
S6a
S6b
S4et
S4ug
S4
S4lv
S4lm
1860
1880
1900
1920
1940
1960
1980
2000
2020
date (years)
(c)
S4
S7
S6
S5
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
spatial distance from epidemic origin (km)

Figure 8

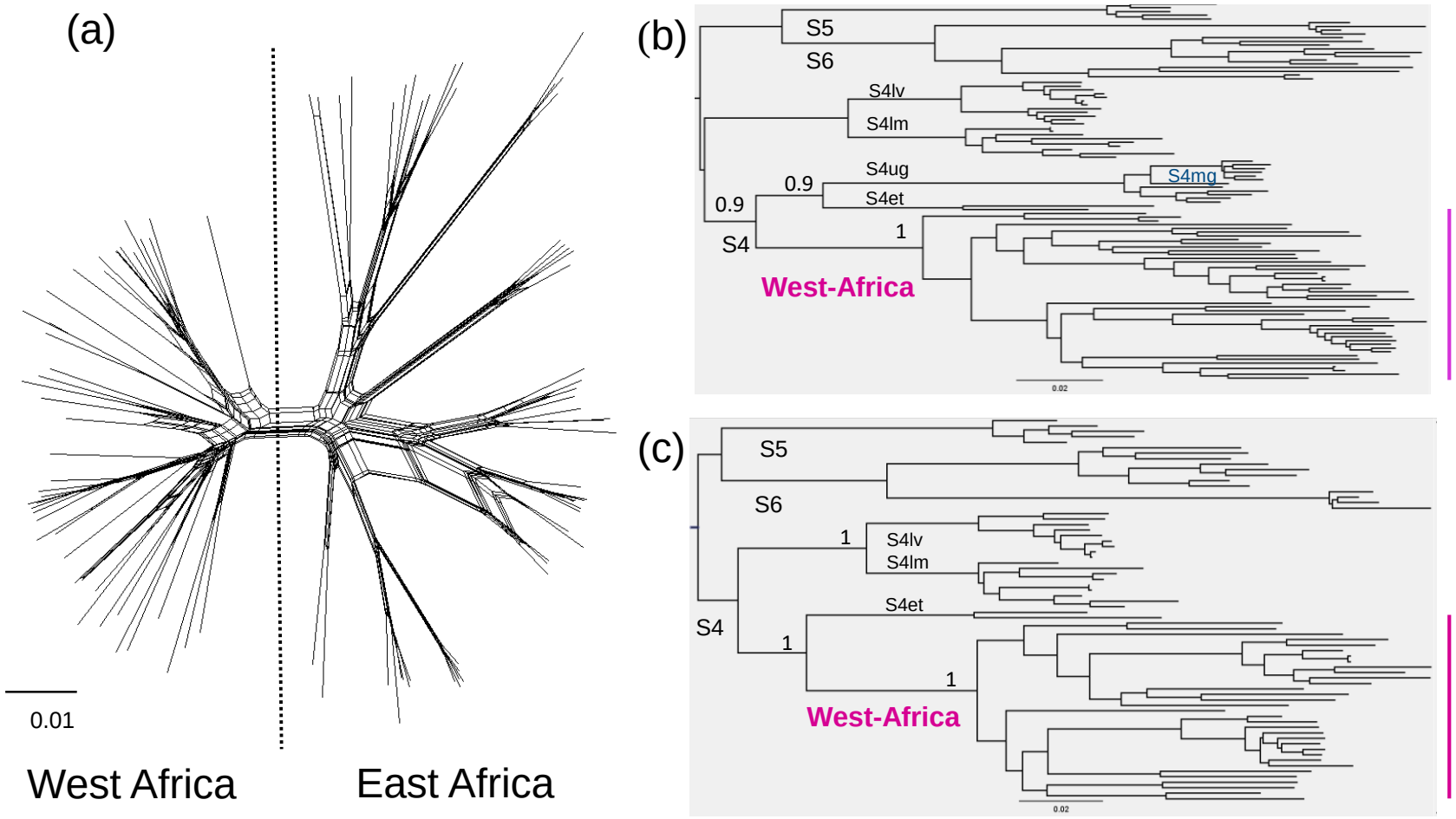
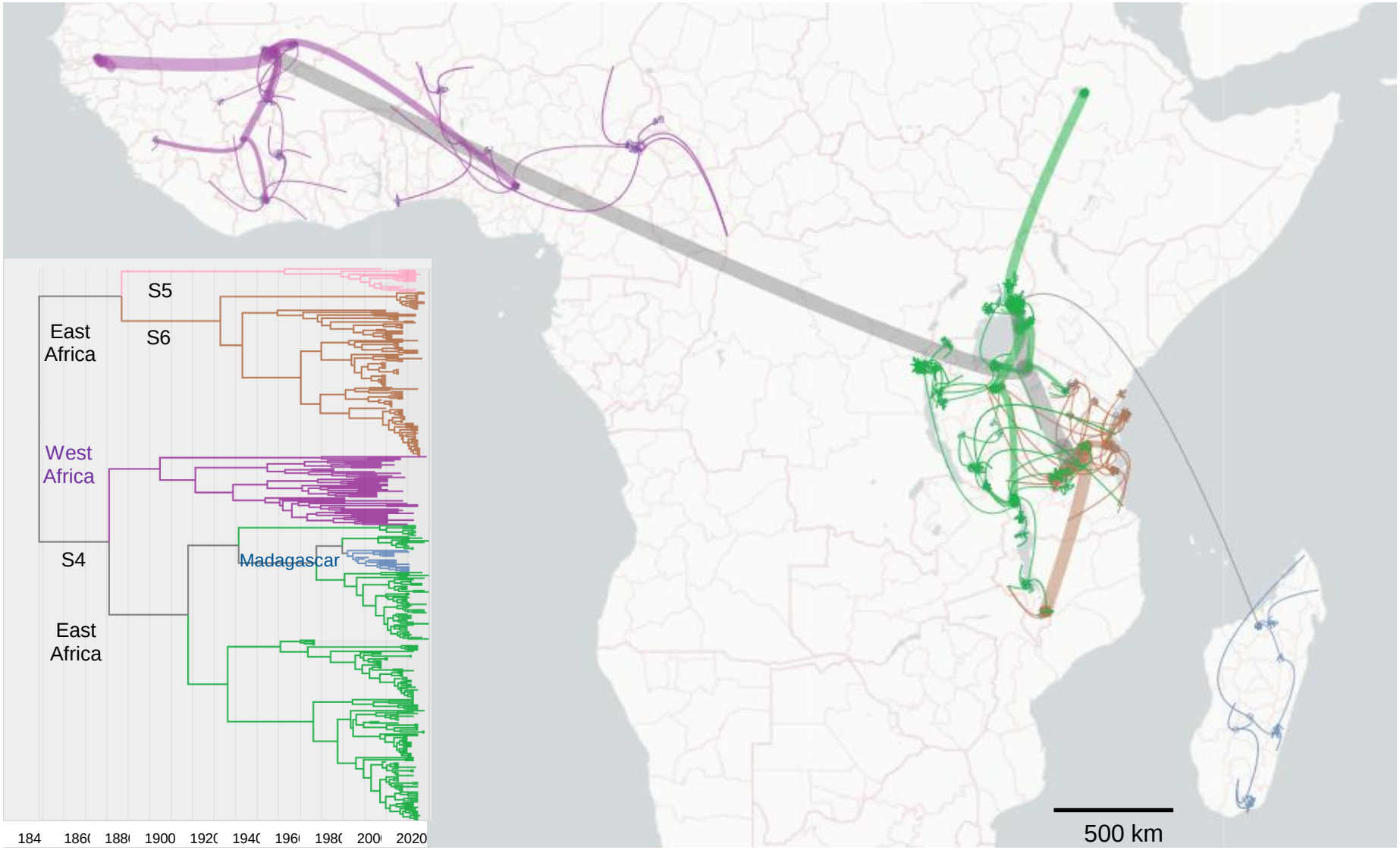

(a)
0.01
West Africa
East Africa
(b)
S5
S6
S4lv
S4lm
S4ug
S4mg
0.9
S4et
0.9
1
S4
West-Africa
0.02
(c)
S5
S6
1
S4lv
S4lm
S4et
S4
1
1
West-Africa
0.02

Figure 9


S5
S6
East Africa
West Africa
S4
East Africa
Madagascar
184
186
188
1900
192
194
196
198
200
2020
500 km