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 sequences, and from 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 of them unsuspected. Consequently, RYMV has a wide dispersal capacity, its dispersal metrics estimated from phylogeographic reconstructions are similar to those of highly mobile zoonotic viruses.

Introduction

Contact transmission is a major transmission pathway for plant viruses, yet it has largely been neglected (Jones, 2018). 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 (Jones, 2018). 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 (Peters et al, 2024).

Rice yellow mottle virus (RYMV) is a single-stranded RNA virus of the Sobemovirus genus (Sõmera et al, 2021). RYMV is a major pathogen in all sub-Saharan African countries that grow rice (Abo et al, 1997). 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 (Bakker, 1974). RYMV does not infect the seed embryo (Allarangaye et al, 2006; Fauquet and Thouvenel, 1977; Konaté et al, 2021). 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 (Bakker, 1974). RYMV reached high virus concentration within two to three weeks. It remains infectious in rice stubbles for months (Bakker, 1974; Fauquet and Thouvenel, 1977), and after passage through the intestinal tract of mammals (Sarrah and Peters, 2003). 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 (Traoré et al, 2009).

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 (Cooper and MacCallum, 1984; Jones, 2018; Teakle, 1986). 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 (Fauquet and Thouvenel, 1977), soil transmission persists months after the infected rice residues had been buried. RYMV is disseminated by transplanting young infected seedlings from nurseries to fields sometimes located kilometers away (Traoré et al, 2006). Altogether, contact and soil transmission accounts for on-site survival of the virus and for 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 (Bakker, 1974), or transmission by seeds in specific circumstances (Rakotomalala et al, 2019; Trovão et al, 2015). 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, in the outer envelopes of the grain (Konaté et al, 2001). Rice threshing and winnowing does not eliminate all the outer husks and all the leaf and stem residues (Abé, 2007). Accordingly, infected plant debris remain in bags of rice seeds. We referred to them as contaminated seeds to make the distinction with infected seeds (Abo, 1998; Banwo et al, 2004). Rice seeds are transported between villages and across regions for food consumption and for agronomical purposes (Richards, 1986). 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 original sources (Abo, 1998; Banwo et al, 2004). 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 (Pedgley, 1982; Thresh, 1983), 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 (Lemey et al, 2009; 2010). It unveils the underlying processes that shape the dynamics of spread, including rare and past events, and lead to hypotheses on the modes of transmission and the impact of host biology and history. RYMV is a measurably evolving population (Fargette et al, 2008), and the phylogeographic reconstructions are not affected by the time dependent rate phenomenon (Ghafari et al, 2024). The relaxed random walk (RRW) model in continuous phylogeography allows for variation in dispersal rates across branches of the phylogeny (Lemey et al, 2010). 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 (Carpenter, 1978; Gilbert, 2016; Portères, 1971). Rice had been cultivated along the Indian

Ocean Coast for centuries but was confined to a few scattered coastal sites (Gilbert, 2016). The sole documented case of large-size 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 (Jatzold and Baum, 1968). 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 of "Little Calcutta" (Alpers, 1984; 2009). In the middle of the 19th century, rice was introduced around the great lakes of East Africa (Lake Victoria, Lake Tanganyika and Lake Malawi) (Iliffe, 1979). 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.

Dispersal statistics are increasingly used to characterise and quantify the spread of viruses (Bastide et al, 2024; Dellicour et al, 2024; Pybus et al, 2012). We assessed the dispersal capacity of RYMV and compare it to a range of zoonotic viruses (Dellicour et al, 2024). Altogether, this study suggests that the transport of contaminated rice seed was decisive in the long-distance dissemination of RYMV, not only within East Africa, but also in the introduction of the virus from East Africa to West Africa and to Madagascar. It points the most probable routes and modes of dissemination and unveils the links with rice history. It further shows the likely role of a broad spectrum of human activities in RYMV dispersal, some of them unsuspected. This explains why RYMV has such a wide dispersal capacity, similar to that of highly mobile zoonotic viruses.

Materials and Methods

Datasets

A collection of 335 capsid protein gene sequences of East African isolates was built. The dataset consists of 240 sequences retrieved from NCBI (2024-06-01) supplemented by 95 sequences obtained in this study (Supplementary Table 1). The isolates originated from eight countries (Burundi, Republic of Congo, Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda). The sampling locations were distributed between latitudes 15.6° South and 11.9° North, and from longitudes 28.8° West to 39.8° East, ca. 3 000 kilometers in latitude x 1 200 km in longitude, i.e. a study area of ca. two million square kilometers. The isolates were sampled from 1966 to 2019 (54 years). A minor variant named S4ke recently identified in Kenya with a recombinant event in the capsid protein (Adego et al, 2018) was considered in this study (see below) but not included in this corpus.

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

In complement, a collection of 335 capsid protein gene sequences from West African isolates, was considered to estimate the substitution rate of RYMV (Supplementary Table 3). It consists of sequences retrieved from NCBI (2024-06-01), 261 sequences used in a study of the phylogeography in West Africa (Issaka et al, 2021) complemented by 46 sequences of Ghana (Omiat et al, 2023) and 28 sequences of Burkina Faso (Billard et al, 2023). The 28

sequences from Burkina Faso were chosen from the 144 available on NCBI using the PDA software (Chernomor et al, 2015) in order to maximize the genetic diversity of the sample. In total, the samples were collected in 15 countries (Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Gambia, Ghana, Guinea, Ivory Coast, Mali, Niger, Nigeria, Senegal, Sierra Leone, Togo). They were sampled between 1975 and 2021 (47 years).

Another estimate of the substitution rate was made from the collection of 94 capsid protein gene sequences of Malagasy isolates sampled between 1989 and 2017 (29 years) (Supplementary Table 4) that had been used to reconstruct the phylogeography of RYMV in Madagascar (Rakotomalala et al, 2019). A temporal prior was introduced on the date of emergence of RYMV in Madagascar, the disease having been detected for the first time in the fields in the 1970s (Rakotomalala et al, 2019).

Phylogenetic reconstructions

Sequences were aligned using CLUSTAL X with default parameters (Thompson, et al 1994). Maximum-likelihood (ML) phylogenetic trees were inferred using the PHYML-3.1 algorithm implemented in the SEAVIEW version 4.7 software (Gouy et al, 2010) under a HKY85 substitution model. The ML trees were rooted at the point in the tree that minimizes the residual mean square of the root-to-tip distances. The neighborNet phylogenetic network of the 101 fully sequenced isolates was inferred (Bryant and Moulton, 2004) under a HKY85 distance model as implemented in SplitsTrees4. The neighborNet phylogenetic network illustrates the genetic relationships between sequences taking into account the conflicting phylogenetic signals that are possibly due to recombination events. The full-length sequence alignment was screened for recombination signals using RDP5 (Martin et al, 2020). The default settings were used for each of the seven recombination detection algorithms that RDP incorporates, as was a Bonferroni corrected P-value cut-off of 0.05. Only recombination events detected by more than four of the seven methods implemented in RDP were considered. The phylogeny was reconstructed from recombinant-free alignments. This was obtained by removing either the recombinant sequences or the recombinant regions. In the latter case, it was checked that further recombination was excluded through the pairwise homoplasy (PHI) test (Bruen et al, 2006) implemented in SplitsTrees4 (Bryant and Moulton, 2004). Total, synonymous, and non-synonymous nucleotide diversity of ORF2a, ORF2b and ORF4 were assessed by DnaSP6 (Rozas et al, 2017). The ORF1, too short, too variable and with a low phylogenetic signal (Pinel-Galzi et al, 2009), was not considered.

Bayesian evolutionary inferences

RYMV is a measurably evolving population, yet its overall temporal signal is weak (Trovão et al, 2015; Rakotomalala et al, 2019). The temporal signal of each data set was assessed through tip cluster-randomization tests in BEAST (Murray et al, 2016) and by BETS (Duchêne et al, 2020) under a Bayesian statistical framework, and by TreeTime under a likelihood framework (Sagulenko et al, 2018).

We subsequently reconstructed time-calibrated phylogenies using a Bayesian statistical framework implemented in BEAST version 1.10.4 software (Suchard et al, 2018). BEAST uses Markov Chain Monte Carlo integration to average over all plausible evolutionary histories for the data, as reflected by the posterior probability. All analyses were performed using the BEAGLE library to enhance computation speed (Ayres et al, 2012; Suchard and Rambaut, 2009). We specified an HKY85 substitution model with a discretized gamma

distribution (four categories) to model rate heterogeneity across sites. To accommodate lineage-rate variation, an uncorrelated relaxed molecular clock that models the branch rate variation according to a lognormal distribution was specified (Drummond et al, 2006). The flexible nonparametric demographic skygrid prior was selected to accommodate for variation in the rate of coalescence through time (Gill et al, 2013). Stationarity and mixing (e.g. based on effective sample sizes > 200 for the continuous parameters) were assessed using Tracer version 1.7 (Rambaut et al, 2018). Consensus trees deriving from the phylogenies sampled during the MCMC analysis were obtained using TreeAnnotator version 1.10.4 (Suchard et al, 2018).

To study the geographical spread of RYMV in continuous space in East Africa and to quantify its tempo and dispersal, we fitted a continuous phylogenetic diffusion model to the East African dataset, modelling the changes in coordinates (latitude and longitude) along each branch in the evolutionary history as a bivariate normal random deviate (Lemey et al, 2010). As a more realistic alternative to homogeneous Brownian motion, we adopted a "Cauchy" RRW extension that models variation in dispersal rates across branches by independently drawing branch-specific rate scalers of the RRW precision matrix from a gamma distribution with shape and scale equal to 1/2 to relax the assumption of a constant spatial diffusion rate throughout the whole tree (Lemey et al, 2010). Bayesian inference using continuous diffusion models yields a posterior distribution of the phylogenetic trees, each having ancestral nodes annotated with location estimates. The EA335 dataset was used to reconstruct the dispersal of RYMV throughout East Africa. A spatial jitter of 0.1° in latitude and in longitude (i.e. ca 10 km) was applied to the locations of the isolates. This degree of noise for identical coordinates was needed to avoid improper posteriors under the RRW model and associated inference problems (Fernandez and Steel, 2000, Lemey et al, 2010). Evolaps2 was used to visualize the continuous phylogeographic reconstruction of the dispersal history of RYMV lineages (Chevenet et al, 2021; 2024). The phylogeography of RYMV in East Africa was reconstructed from the coat protein gene sequences of the full dataset (335 isolates), from the full genome and from different ORFs of a subsample of the 50 isolates representative of the genetic and geographic diversity of the virus.

Comparative dispersal statistics of RYMV

The phylogeography of RYMV has been reconstructed in East Africa (this study), in West Africa (Issaka et al, 2021) and in Madagascar (Rakotomalala et al, 2019). The dispersal capacity and dynamics in the three regions was compared through the weighted diffusion coefficient (km^2/year) (Trovão et al, 2015) and the isolation-by-distance (IBD) signal metric, two metrics identified as robust (to sampling intensity in particular) and measuring complementary aspects of the overall dispersal pattern (Dellicour et al, 2024). The diffusion coefficient is an estimate of the dispersal capacity of the lineages. The IBD signal metric quantifies how the dispersal is spatially structured, i.e. the tendency of phylogenetically closely related tip nodes to be sampled from geographically close locations. An IBD signal was apparent through the relationships between geographic and genetic pairwise distances in a restricted dataset of sequences from East and West Africa (Abubakar et al, 2003). The diffusion coefficient of RYMV virus over the three regions combined was also estimated. Then, the dispersal capacity of this plant virus was compared to that of a range of animal viruses in various host species (Dellicour et al, 2024).

Results

Temporal signal

BETS analyses indicate that the increase in sample size of heterochronous sequences lead to a stronger temporal signal in West Africa (from 261 to 335 sequences) and in East Africa (from 240 to 335 sequences) (Table 1). The temporal signal was more pronounced in the set of West African sequences (reflected by a higher Bayes factor). The temporal signal of the two datasets was also tested using cluster randomization tests of the sampling dates. There was no overlap of the credibility intervals of the substitution rate calculated with sampled dates and those with randomized dates (data not shown). However, the differences obtained were more pronounced with the WA335 dataset. The square of the correlation coefficient of the regression sampling date vs. distance to root obtained with TreeTime was 0.07 with the WA335 dataset vs. 0.01 with the EA335 dataset. Altogether, the temporal signal was more pronounced in the WA335 dataset than in the EA335 dataset. The stronger temporal signal of the West African dataset probably results from a relatively uniform distribution of the sampling dates over the last thirty years whereas that of the East Africa isolates was concentrated over the last 15 years. Short sampling periods are prone to unpurged transitory deleterious polymorphism leading to higher and biased substitution rates (Pybus et al, 2007). Consistently, the weak temporal signal of the EA335 dataset leads to a high substitution rate and correlatively to a recent age of the most recent common ancestor of the sampled sequences (tMRCA), similar to that in West Africa. This estimate is inconsistent as obviously too recent. Given the nested position of the West African lineage within the East African lineages (see below), the tMRCA in East Africa is expected to be substantially older than that in West Africa.

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

Phylogeny of RYMV in East-Africa

The phylogeny of RYMV in East Africa reconstructed from 335 coat protein gene sequences is made of three major lineages named, respectively, S4, S5 and S6 lineages (Fig. 1). The phylogenetic group containing the S4 and S5 lineages does not have a strong bootstrap support. Several strains are distinguished within the S4 and S6 lineages. The S4 lineage includes strains S4lm, S4lv, S4ug and S4et named according to their geographical distribution (lm, Lake Malawi; lv, Lake Victoria; ug, Uganda; et, Ethiopia). The S6 lineage includes strains S6a, S6b, and S7 but was not supported by a strong bootstrap value. The S5 lineage consists of one strain only.

The phylogeny of RYMV was also reconstructed from the full-length genomic sequences (with recombination regions removed; see Materials and Methods) of 50 isolates representative of the geographic and genetic diversity of RYMV in East Africa (Fig. 2). The same phylogenetic pattern was observed at the lineage and strain levels, except that the S4lv and S4lm strains belong to the same phylogenetic group in the reconstruction from the full-length sequences but not from the coat protein gene sequences. Very few insertion-deletion events occurred in coding regions. The basal insertion-deletion pattern at positions 19 and 60 in the ORF4 in the S4, S5 and S6 lineages was that observed earlier (Fargette et al, 2004). An additional deletion occurred in the isolate Tz319 of the S5 strain at codon 432 in the ORF2a. It is the only insertion-deletion event found at a terminal phylogenetic position (Fig. 2). All the insertion-deletion polymorphism originated in isolates of the Eastern Arc Mountains.

Phylogeography from 335 coat protein gene sequences

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

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

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

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

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

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

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

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

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

Phylogeography from full-length sequences and ORFs of 50 representative isolates

The spatio-temporal dispersal of RYMV in East Africa was reconstructed from sequences of 50 isolates representative of the genetic and geographic diversity of the virus in East Africa: full-length sequences (4468 nt, and excluding recombinant regions), sequences of ORF2a (including protease and VPg; 459 codons), ORF2b (including polymerase; 540 codons) and ORF4 (capsid protein, 240 codons). The differences in nucleotide diversity and in the selection pressure among the ORFs are given in the Supplementary Table 5. No recombination events was detected within the ORF2a, ORF2b and ORF4.

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

Phylogeography of the three main lineages

The initial diversification of RYMV in East Africa resulted in the emergence of the three lineages S4, S5 and S6 in the mid-19th century within or near the Kilombero valley. The phylogeography of the three lineages is markedly different (Figs. 7a, 7b). The S4 lineage had the greatest epidemic success. It was found south of Lake Victoria in the second half of the 19th century (S4lv), and then circulated around Lake Victoria (S4ug) before dispersing northward into Ethiopia (S4et), then southward to Malawi and finally westward to the Republic of Congo, Rwanda and Burundi (S4lm). The S6 lineage remained confined to the Kilombero valley and in the Morogoro region for several decades. In the last decades, it spread towards eastern Tanzania, south-west Kenya and to the islands of Zanzibar and Pemba. The S7 strain split early from the S6 lineage and was recovered recently in southern Malawi. The S5 lineage was found exclusively in the Kilombero valley. The migration curve (Fig. 7c) illustrates the differences in velocity among the lineages, with an early and rapid spread of the S4 lineage, a late but rapid spread of the S6 lineage (with the exception of the early spread of the S7 strain), and a lack of dispersal for S5. Interestingly, there was a slowdown in the dispersal rates the past decades within most strains of the S4 and S6 lineages.

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

East African origin of the introduction of RYMV into West Africa and into Madagascar

The phylogeny of RYMV was reconstructed from the full-length sequences of 101 isolates representative of the genetic and geographic diversity of the virus in Africa: 50 isolates from East Africa, 45 from West Africa and six sequences from Madagascar. A major split in the phylogenetic network separates East Africa and Madagascar isolates from West Africa ones (Fig. 8a). The phylogeny is characterized by the nested position of the West African lineage within the East Africa lineage comprising the S4ug, S4mg and S4et strains (Fig. 8b). The S4mg strain in Madagascar resulted from a recombination between the S4ug strain and an unidentified minor parent (Rakotomalala et al, 2019). The relationship between the West-African lineage and the S4et strain of this lineage persist after excluding the S4mg and S4ug sequences (Fig. 8c). This confirms the earlier assumptions, made on a restricted dataset, that RYMV in West Africa and in Madagascar originated in East Africa (Rakotomalala et al, 2019; Trovão et al, 2015), and brings information on the source lineage of RYMV in West Africa.

We detailed the East African origin of the introduction of RYMV into West Africa and into Madagascar. Convergence of the analyses with the full dataset (AE335, WA335 and Mg94 dataset, i.e. a total of 784 coat protein gene sequences) was difficult to reach. So 50 isolates representative of the diversity of the virus in West Africa and 15 isolates representative of that in Madagascar were selected using PDA analyzer (Chernomor et al, 2015). Then we reconstructed the phylogeography of the collection of the coat protein gene of 335 isolates from East Africa, the 50 representative isolates from West Africa and the 15 representative isolates from Madagascar, i.e. a total of 400 isolates. The phylogeographic model was that defined for the analysis of the EA335 sequence dataset (see Materials and Methods). The split between the East and the West African clades occurred in ca. 1868 (95% HPD 1831-1906) at the south of Lake Victoria (Fig. 9). The introduction of RYMV in the Niger Inner Delta in West Africa occurred in ca. 1892 (95% HPD, 1857-1909). The subsequent pattern of dispersion throughout West Africa and toward Central Africa mirrored the findings from comprehensive surveys conducted in West Africa (Issaka et al, 2021; Omiat et al, 2023). In Madagascar, RYMV was introduced in ca. 1980 (95% HPD 1975-1986) from the northeast of Lake Victoria. The introduction of RYMV in the northwest of Madagascar followed by the spread of the virus southward of the country is a scenario similar to that obtained from the comprehensive dataset (Rakotomalala et al, 2019).

Comparative dispersal statistics of RYMV

For RYMV, variation in isolation-by-distance (IBD) signals among the three regions (East Africa, West Africa and Madagascar) was apparent (from 0.35 to 0.56) (Table 2), yet it was less pronounced than that of rabies virus lineages in different host species (from 0.09 to 0.74) (Dellicour et al, 2024). The IBD index was higher in West Africa (0.52 and 0.56 for the two datasets) than in East Africa (0.37) and in Madagascar (0.35) (Table 2). In East Africa, the recurrent long distance human-mediated dispersal of RYMV in a wide range of directions revealed by this study are consistent with a low IBD signal. The higher IBD signal estimated in West Africa may result from the dominant eastward long-distance transmission events establishing more local transmission chains (Billard et al, 2023; Issaka et al, 2021; Omiat el al, 2023). The relatively low IBD signal estimated in Madagascar suggested that long distance human-mediated dispersal, which blurred the relationship between geographical and genetic distances, are also frequent in a country where rice is widely grown. Diffusion coefficients in the three regions ranged from 1100 to 1600 km^2 per year with overlapping 95% HPD intervals. This indicates a similar dispersal capacity of the virus across the three regions

despite differences in IBD signal values, spatial scales, rice history and cultivation, and possibly also in dispersal modes.

The diffusion coefficient of RYMV for East Africa, West Africa and Madagascar combined (covering ca. 12 million km^2) was 2700 km^2/year, was twice that of each of three regions reflecting the inclusion of the long distance dispersal from East Africa towards West Africa and towards Madagascar (Table 2). The diffusion coefficient of RYMV was higher than that of several animal viruses including rabies in various hosts, even when occasional rapid long-distance dispersal events driven by human-mediated movements occurred (Dellicour et al, 2024). Yet, the diffusion coefficient of RYMV was lower by an order of magnitude than that of animal viruses with long distance dispersal through animal trade or through migratory birds (Dellicour et al, 2024).

Discussion

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

(1) The postulated emergence of RYMV in the Eastern Arc Mountains (Pinel-Galzi et al, 2015) was confirmed and characterized in more details. The emergence of RYMV dates back to the mid-19th century. It took place near the Great Ruaha Escarpment of the Udzungwa Mountains adjacent to the Kilombero valley and close to the Morogoro region. Consistently, the insertion-deletion polymorphism originated in isolates of this region. The original host(s) of RYMV were located within the Eastern Afromontane biodiversity hotspot (Pinel-Galzi et al, 2015; Trovao et al, 2015). Slash and burn rice cultivation practiced in the mid-1800s near the Great Ruaha Escarpment of the Udzungwa Mountains (Iliffe, 1979; Jatzold and Baum, 1968; Paul, 2003; Raison, 1994) resulted in spillovers from the primary hosts of the virus, presumably of the Eragrostidae and related Poaceae families given RYMV host range, to cultivated rice. Primary hosts may also include the cultivated finger millet, a possible alternative host of RYMV, widespread in these mountains. This led to the introduction of RYMV in cultivated rice. The basal split between the S4, S5 and S6 lineages and the insertion-deletion polymorphism suggest (at least) three independent splillovers from the wild host(s) to cultivated rice. Strain specific poaceae species such as Dactyloctenium aegyptium have been identified (Allarangaye et al, 2007). Specific mutations of the S7 strain occurred at positions of the VPg under positive selection and experimentally associated to host range (Ndikumana et al, 2017; Poulicard et al, 2012). Further studies are necessary to understand the genetic changes, if any, associated to host jumps and rice spillover.

(2) Within a few decades, RYMV spread to the large adjacent Kilombero valley where rice had been widely cultivated since the beginning of the 19th century (Jatzold and Baum, 1968). This is consistent with the movements of rice-growing populations between the Udzungwa Mountains and the Kilombero valley (Jatzold and Baum, 1968).

(3) Between the second half of the 19 th century and the beginning of the 20th century, RYMV (lineage S4) spread to the south of Lake Victoria 400 km northward of the Kilombero Valley. Its dispersal followed the introduction of rice into the interior of the continent along the caravan routes linking the coastal strip to Lake Victoria (Finch et al, 2017; Roberts, 1970; Wynne-Jones and Croucher, 2007). There are indications that the caravan routes crossed the Kilombero valley (Iliffe, 1979). Interestingly, the migration pathways of turnip mosaic virus (TuMV), a seed transmitted potyvirus, retraced some of the historical trade arteries of the Silk

Road (Kawakubo et al, 2021). So, both RYMV and TuMV illustrate the link between plant virus dispersal and trade routes. During the same period, RYMV (lineage S6) was introduced in the Morogoro region 100 km eastward of the Kilombero Valley.

(4) In the following decades, up to the middle of the 20th century, RYMV dispersed at the east of Lake Victoria where rice had been introduced at the end of the 19th century, probably by boat (Leclercq, 1913; Tosh, 1970). Interestingly, the first field report of RYMV in East Africa was in 1966 near Kisumu also at the east of Lake Victoria (Bakker, 1970).

(5) At the beginning of the 20th century, RYMV was introduced from the Kilombero valley to the south of Lake Malawi. This movement is parallel and concomitant to the movement of military troops at the end of the First World War (Von Lettow-Vorbeck, 1920). Feeding the troops was a major issue (Anderson, 2016), rice was the main staple food for soldiers, and the Kilombero valley was the main rice production area. Accordingly, RYMV may have been dispersed through the transport of contaminated seeds during the First World War. An alternative hypothesis, linking virus 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 (Alpers, 1975; Biginagwa and Mapunda, 2017). Second, the peak of activity along the Kilwa-Nyasa south caravan route occurred in the second half of the 19th century (Alpers, 1975; Biginagwa and Mapunda, 2017) 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 (Bakker, 1974) and in the 1980s around Lake Tana in northern Ethiopia (Alemu et al, 2018). 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 (Bastide et al, 2024; Dellicour et al, 2024) in RYMV epidemiology. This may be due to changes in the trade and market patterns (Meillassoux, 1971) 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 food from the Kilombero valley towards the South of Lake Malawi at the end of the First World War, to seed exchanges between Lake Victoria and Ethiopia in the second half of the 20th century. Alternative hypotheses involving beetle dissemination of the virus are unlikely given the paucity of rice cultivation and alternative hosts at these early periods between regions located several hundreds of kilometers apart. Seed transport could also account for short distance dispersal of the virus, in complement or as an alternative to beetle transmission, around Lake Victoria in the first half of the 20th century and along the Indian Ocean the past

few decades. Finally, the ongoing transport of contaminated seeds could also explain the current generalized dispersal of RYMV throughout East Africa.

Early long-distance transport of contaminated seeds led to the dispersal of the main lineages in different directions and environments. So, the contrasting epidemic characteristics of the S4, S5 and S6 lineages resulted primarily from historical circumstances. In complement, the role of genetic properties of the strains should be explored. For instance, positive selection at positions of the VPg involved in host range (Ndikumana et al, 2017; Poulicard et al, 2012) may have impacted the epidemiological characteristics of the S7 strain. The S5 lineage remained confined to the Kilombero valley, yet without becoming extinct, whereas the S4 lineage and later the S6 lineage were widely spread throughout East Africa. In West Africa, strain dominance was observed in competition experiments and by comparison of the virus titer of two strains (N'Guessan et al, 2000). Similar experiments with S5 and S6 and S4 isolates were not conclusive (Pinel-Galzi A, Fargette D, Hébrard E, unpublished results). Yet, these fitness tests may not encompass all the relevant traits involved in epidemiological differences and should be refined accordingly.

Phylogenetic analyses indicate that the West African RYMV diversity is nested as a monophyletic clade within the East African diversity, indicating an East African origin (Pinel-Galzi et al, 2015; Trovão et al, 2015). The current phylogeographic introduction (i) confirms this hypothesis, (ii) brings information on the 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, even far apart, were frequent in the second half of the 19th century (Bonneuil, 1997). 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 (Viguier, 1939; Portères, 1950). 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 (Tourte, 2019). 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 (Blais, 2023). 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 (Bastide and Didier, 2023). Our results also confirm the Ugandan origin of the Madagascar strain (Rakotomalala et al, 2019). Increased seed exchanges between Madagascar and East African countries have occurred during the recent decades (Oyeniran, 2022). Transport of contaminated rice seeds may also account for this introduction.

RYMV dispersal through the transport of contaminated seeds shows the importance of this neglected virus transmission pathway in plant virus epidemiology (Jones, 2018). This study also unveils the wide range of human activities, some of them unsuspected, involved in man-mediated movements of a plant virus. Consequently, a plant virus like RYMV has wide

dispersal capacities, greater than or equal to that of most zoonotic viruses. Maize streak virus A (MSV-A) causes another major cereal disease in Africa (Shepherd et al, 2010). It is transmitted by leafhopper and not by seeds. Interestingly, recent and repeated introductions of MSV-A from Uganda to Madagascar and from Kenya to Ethiopia have been reported. These movements, parallels to those of RYMV, were also attributed to human-mediated introductions (Ketsela et al, 2022; Oyeniran, 2022). It shows that the spread RYMV and MSV-A, two major vector borne viruses, do not depend only - or even primarily - on vector transmission.

An important pending question is why RYMV, given its wide dispersal capacities, is still restricted to Africa and does not have a worldwide distribution, unlike several sobemoviruses with similar biological properties. Long distance movement of RYMV across the sea is possible but is quite a rare event as indicated by the unique introduction of the virus in West Africa. Rice was imported into America from West Africa in the 17th century and early 18th centuries, at least a century before the introduction of RYMV in West Africa. In the 19th century, rice exports from East Africa were limited and directed towards regions where rice was not cultivated (Alpers, 2009). In the 20th century, rice was imported in Africa rather than exported from this continent. Altogether, this explains why RYMV remained restricted to Africa. However, the risk of accidental introduction of RYMV into other continents subsists, in particular through the transfer of seeds for agronomical breeding which we have found to be a decisive means of long distance dissemination of the virus in Africa. Incidently, sequences of MSV-A from the Philippines have recently been deposited on NCBI (PQ034624, OR983352 and eight others), a possible illustration of such human-mediated trans-continental introductions of vector borne plant viruses.

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Legends

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

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

Figure 3. Continuous phylogeographic reconstruction of the spatiotemporal dispersal of RYMV lineages in East Africa from 1850 to 2020 based on the coat protein gene sequences of 355 isolates collected from 1966 to 2019. The maximum clade credibility (MCC) tree and the 95% highest posterior density (HPD) regions reflecting the uncertainty related to the phylogeographic inference were mapped. 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 yellow. 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 are indicated (open red circle) 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 yellow.

Figure 7 (a) Continuous phylogeographic reconstruction of the spatiotemporal dispersal of the three main lineages of RYMV in East Africa from 1850 to 2020 based on the coat protein gene sequences of 355 isolates collected from 1966 to 2019. The three lineages were distinguished by their colors: S4 (green), S6 (brown), S5 (blue). Note that the S5 lineage, confined to the Kilombero valley, is masked by the S6 lineage that has a broader distribution. The strains are indicated close to their emergence area (S4lv, S4lm, S4et, S4ug, S6a, S6b, S7). (b) Maximum credibility tree reconstructed from the dataset and used to generate the spatio-

temporal dispersal (same lineage color code). (c) Migration curves over time (preorder transversal of the phylogenetic tree) for each parent/child node pair: X-axis = cumulative branch length (as dates in years), Y-axis= cumulative great-circle distances knowing latitudes and longitudes.

Figure 8. NeighborNet phylogenetic network of the 101 fully sequenced isolates of RY 2020MV under a HKY85 distance model (8a). Maximum likelihood phylogeny tree reconstructed under a HKY85 model and mid-point rooting of the fully sequenced isolates after removing the recombinant regions (8b), or after removing the recombinant sequences (8c).

Figure 9. Dispersion of RYMV from East Africa to West Africa and to Madagascar between 1850 and 2020 reconstructed from the ORF4 sequences of 335 isolates from East Africa, 50 isolates from West Africa and 15 isolates from Madagascar. The phylogeographic scenario are displayed with 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 yellow. Inlet: Maximum credibility tree reconstructed from the dataset and used to generate the spatio-temporal dispersal (same lineage color code).

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

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

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

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

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

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Figure 1

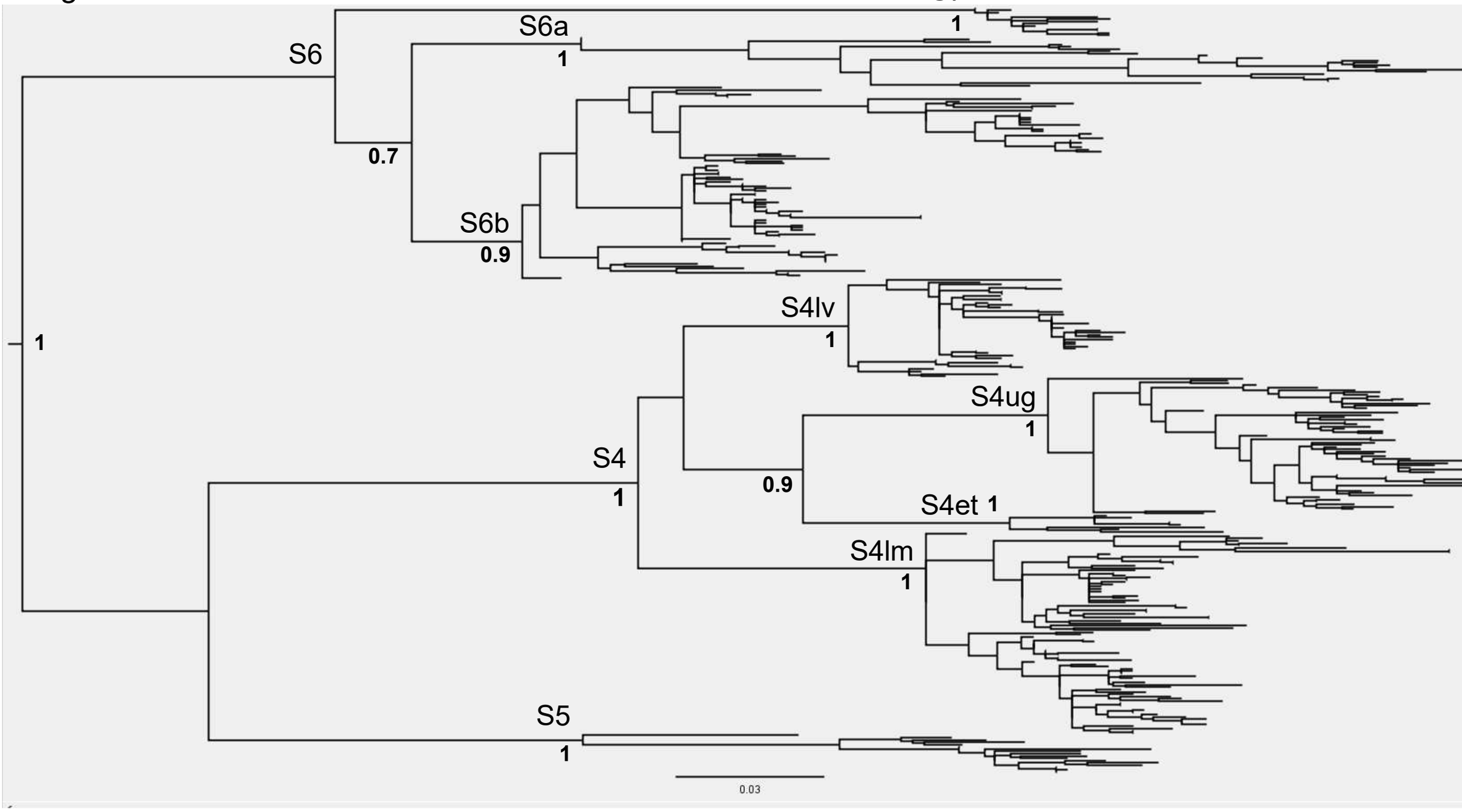


Figure 2

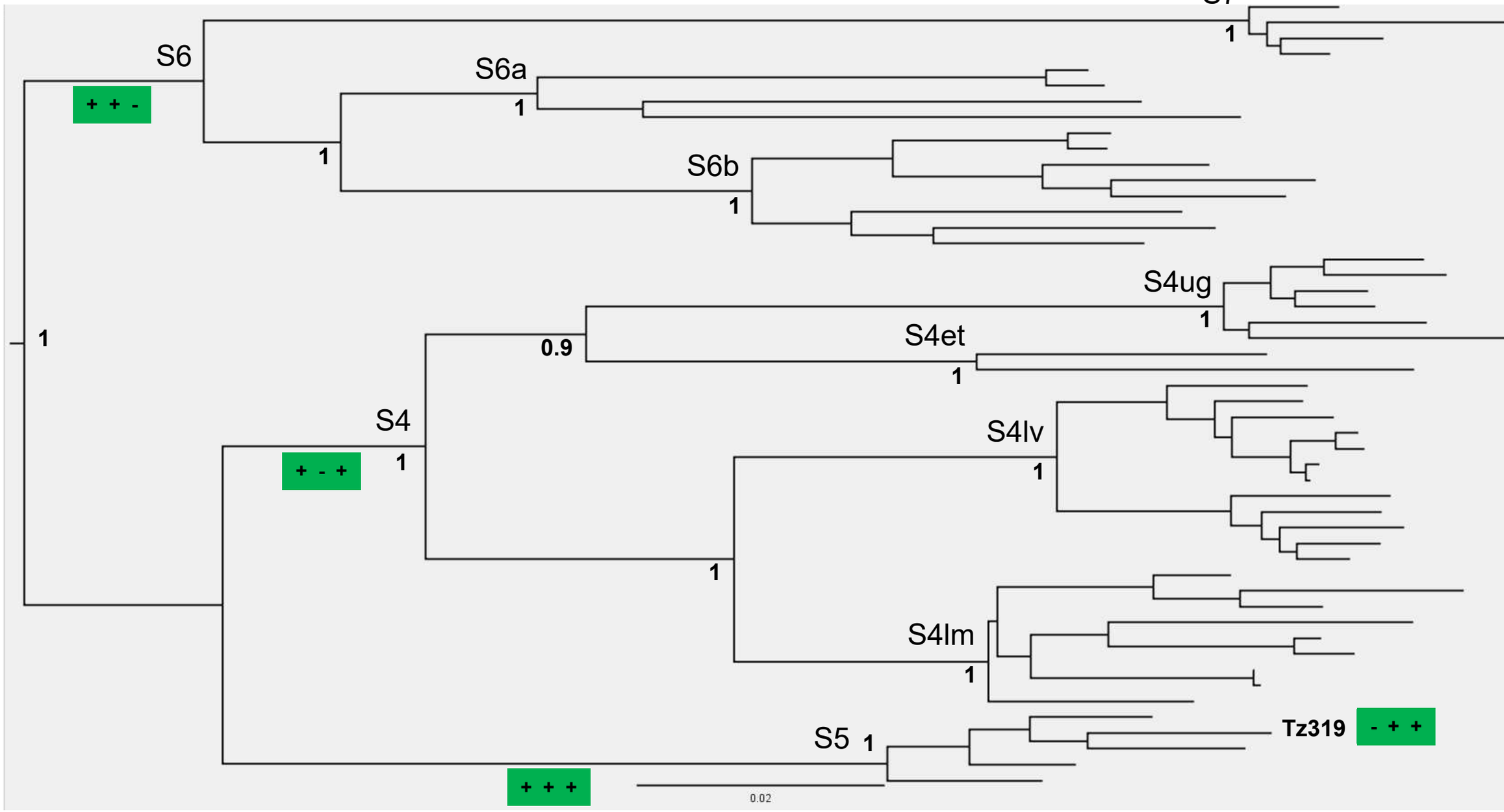

S7
1
S6
+ + -
S6a
1
1
S6b
1
S4ug
1
1
0.9
S4et
1
S4
1
+ - +
S4lv
1
1
S4lm
1
S5
1
Tz319
- + +
+ + +
0.02

Figure 3

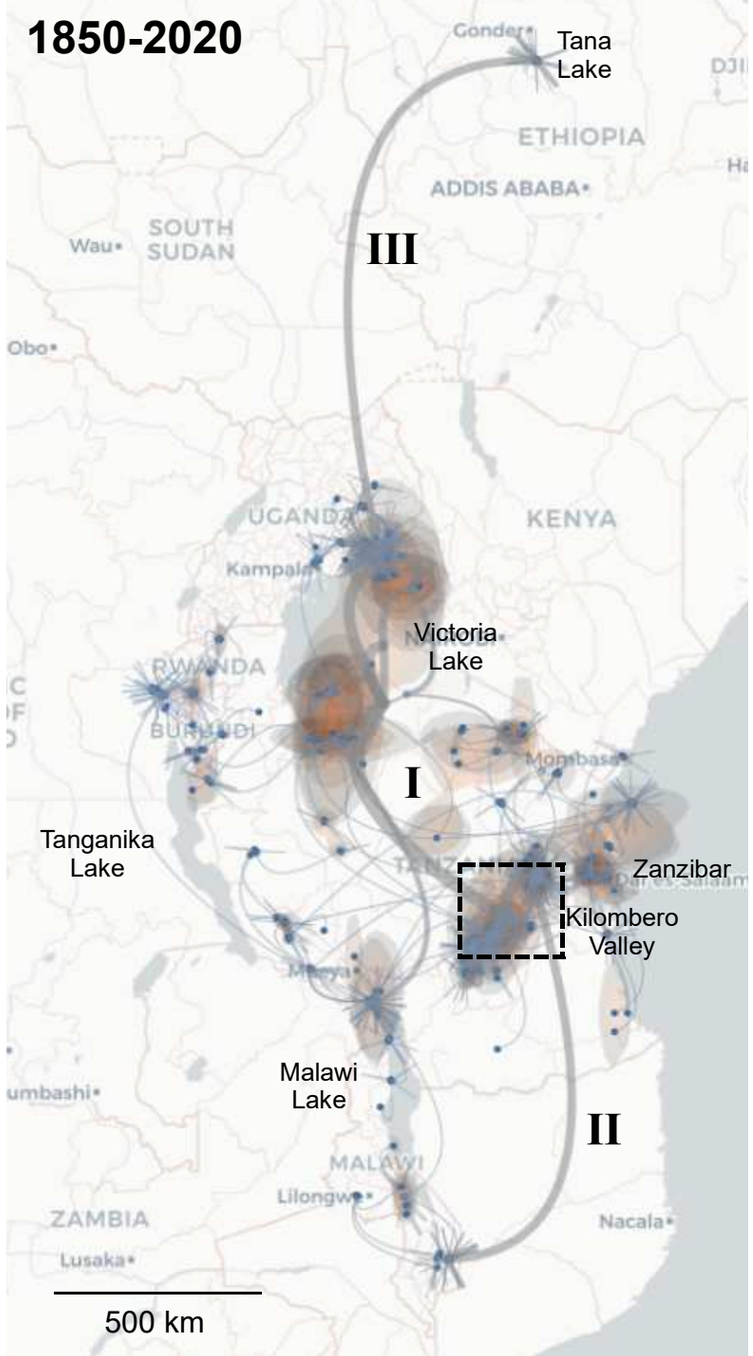

1850-2020
Tana Lake
ETHIOPIA
ADDIS ABABA
SOUTH SUDAN
Wau
III
Obo
UGANDA
KENYA
Kampala
Victoria Lake
RWANDA
BURUNDI
Mombasa
I
Tanganika Lake
Zanzibar
Kilombero Valley
Malawi Lake
II
MALAWI
Lilongwe
ZAMBIA
Nacala
Lusaka
500 km

Figure 4

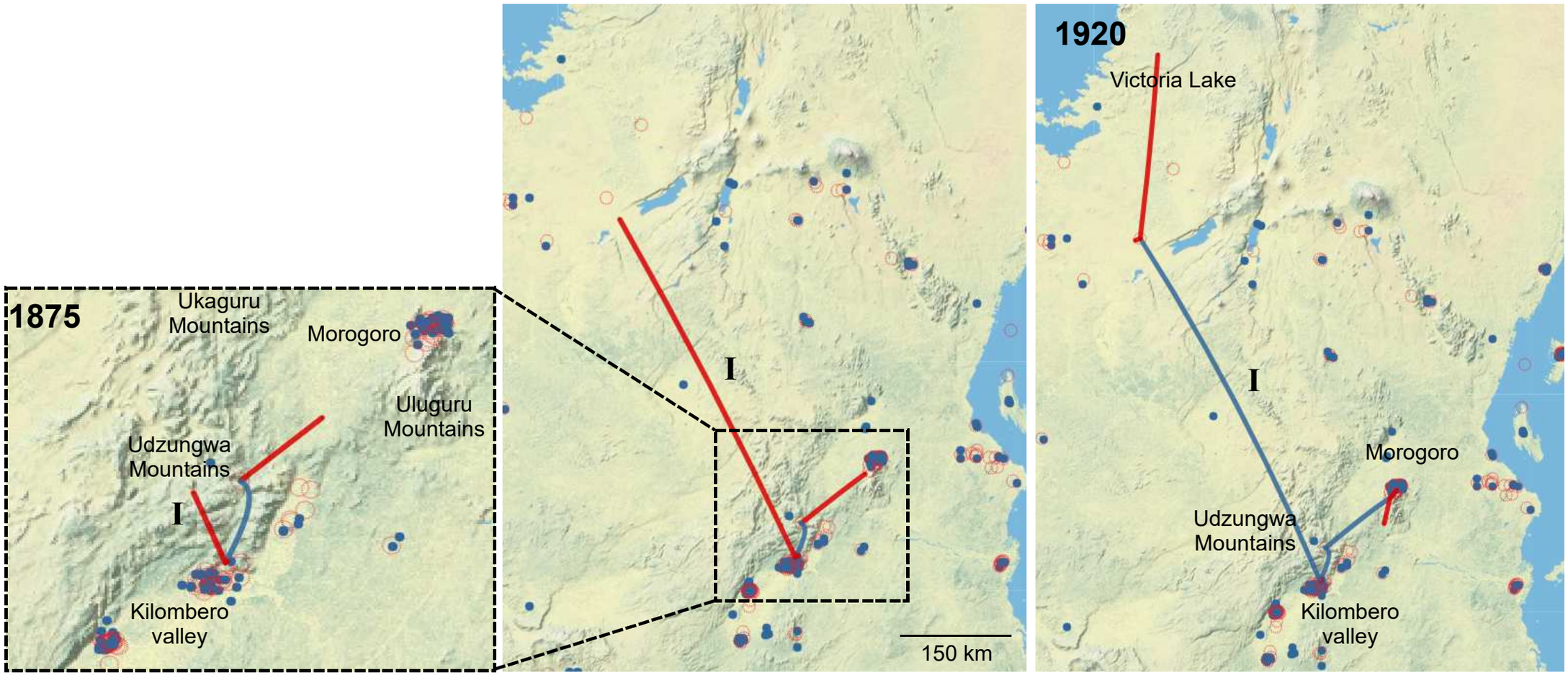

1875
Ukaguru Mountains
Morogoro
Uluguru Mountains
Udzungwa Mountains
I
Kilombero valley
I
150 km
1920
Victoria Lake
I
Morogoro
Udzungwa Mountains
Kilombero valley

Figure 5

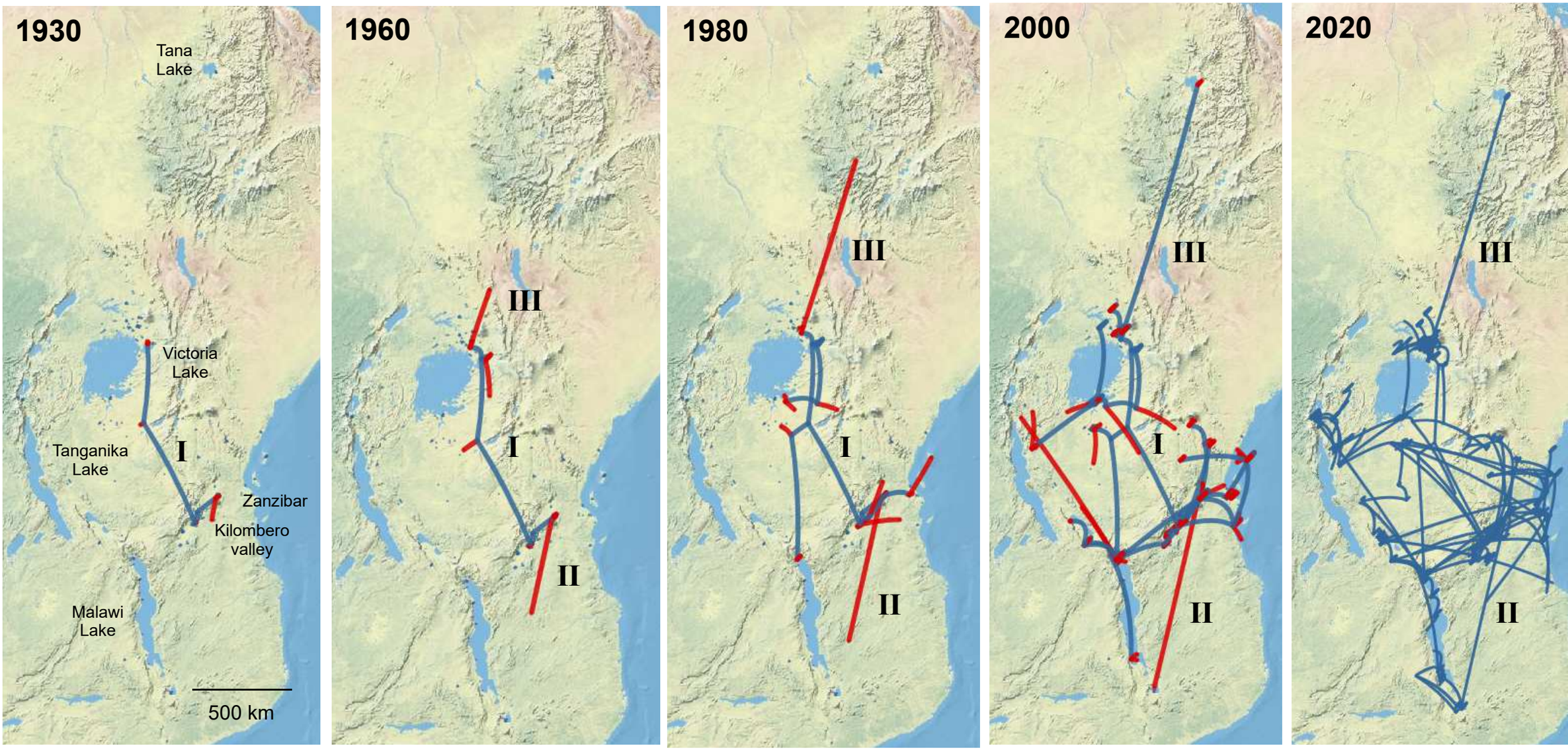

1930
Tana Lake
Victoria Lake
Tanganika Lake
I
Zanzibar
Kilombero valley
Malawi Lake
500 km
1960
III
I
II
1980
III
I
II
2000
III
I
II
2020
III
II

Figure 6

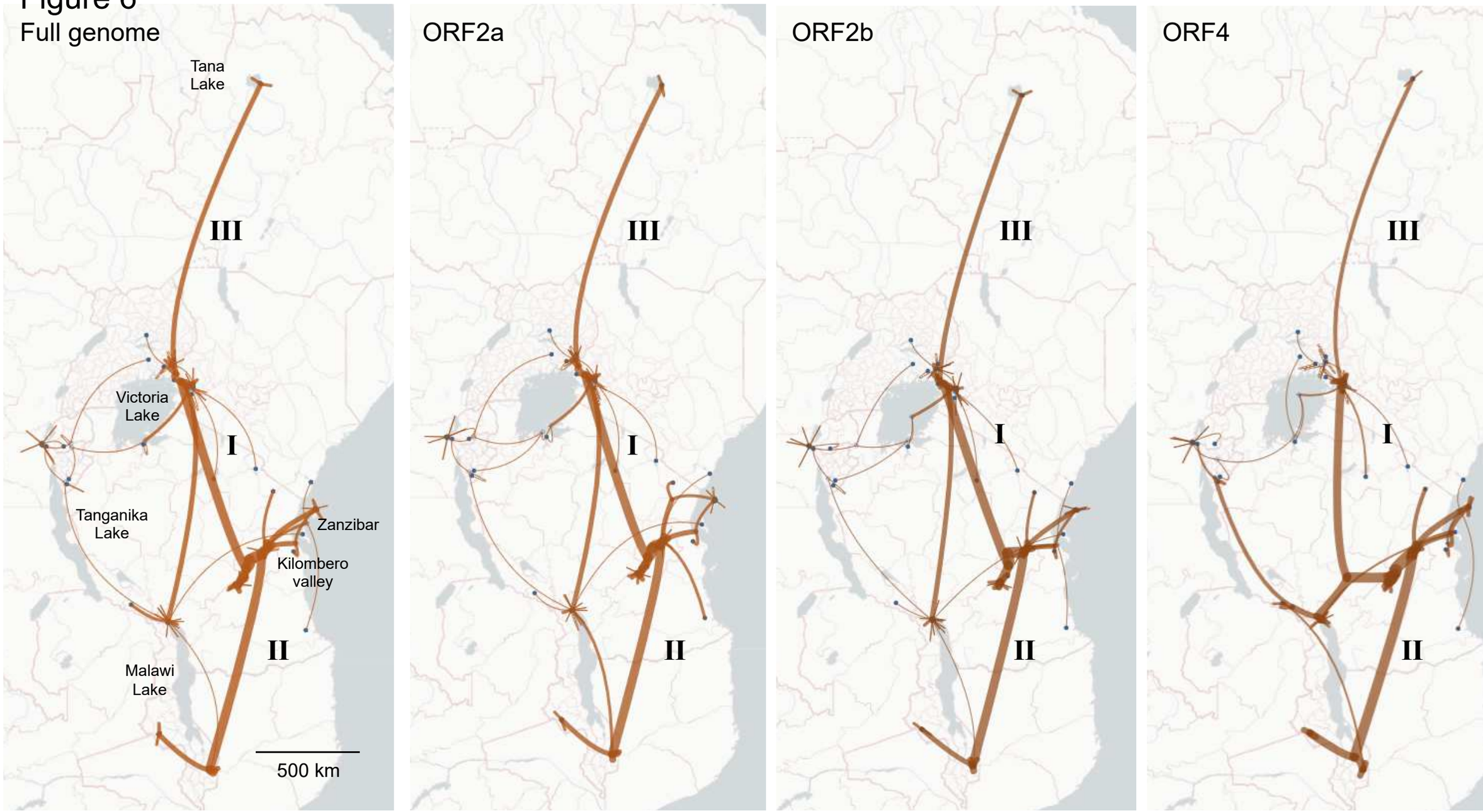

Full genome
ORF2a
ORF2b
ORF4
Tana Lake
Victoria Lake
Tanganika Lake
Zanzibar
Kilombero valley
Malawi Lake
I
II
III
500 km

Figure 7

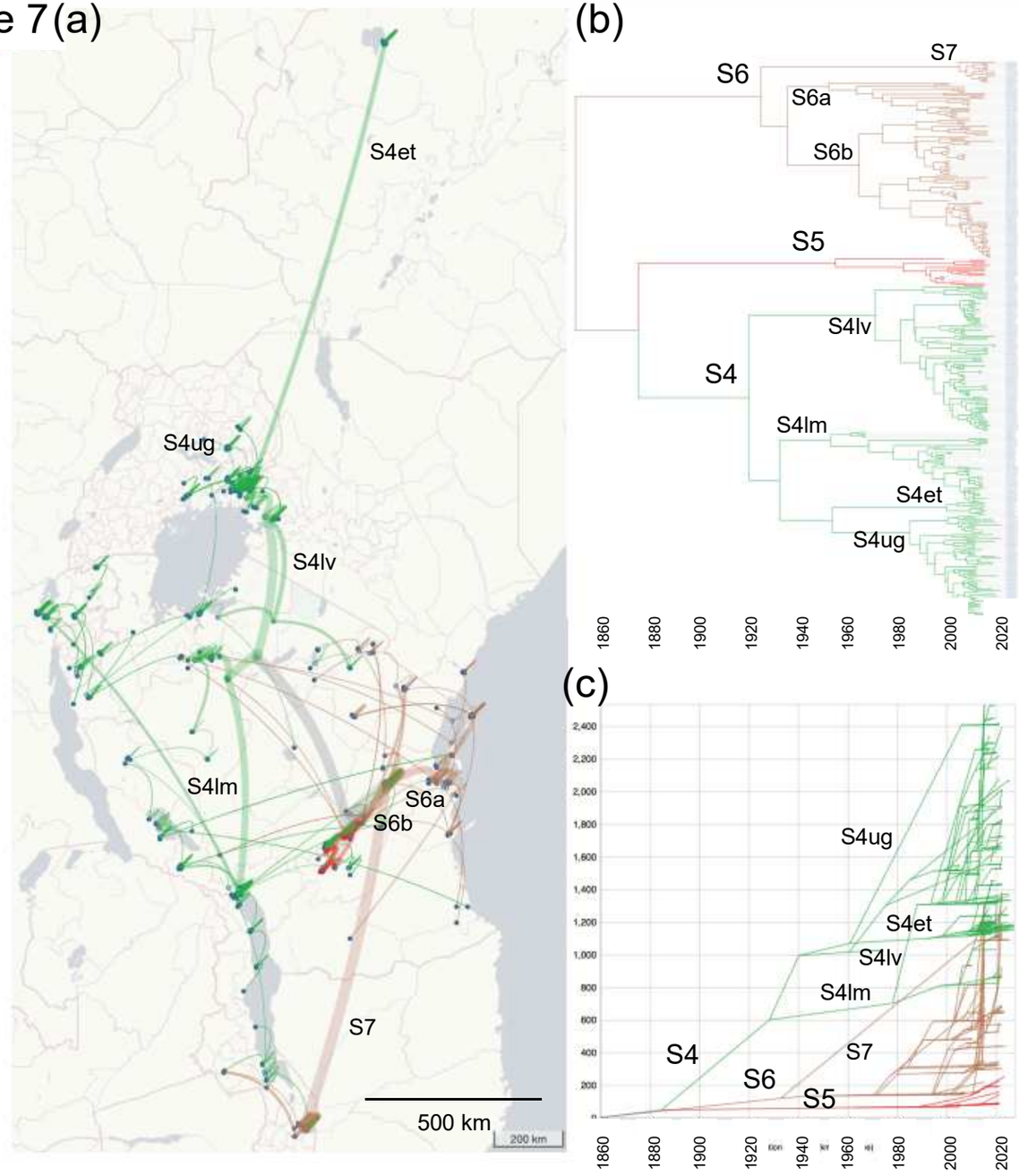
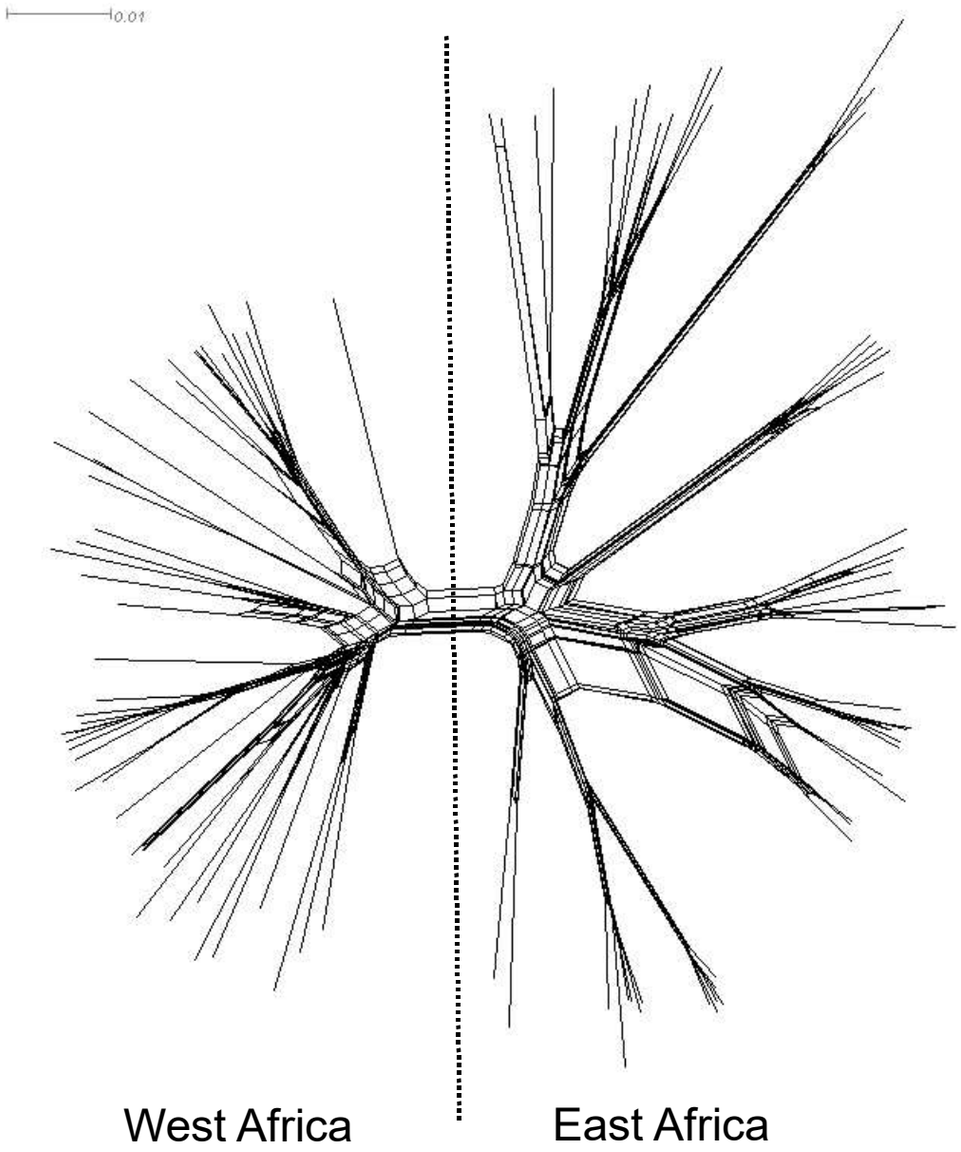
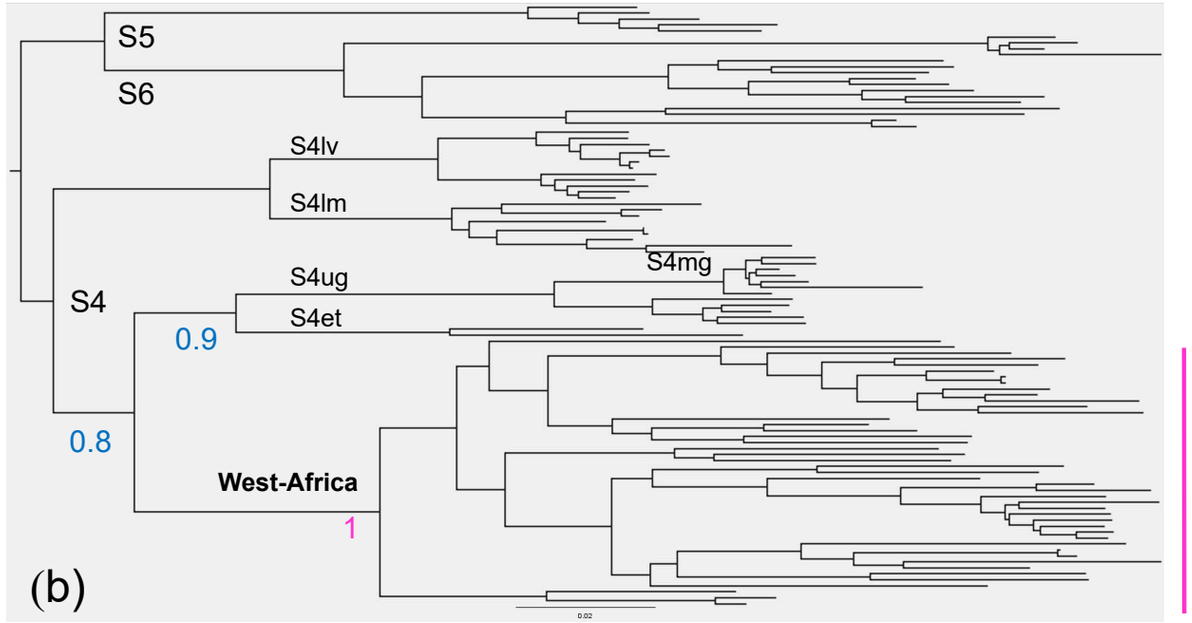

(a)
S4et
S4ug
S4lv
S4lm
S6a
S6b
S7
500 km
(b)
S7
S6
S6a
S6b
S5
S4lv
S4
S4lm
S4et
S4ug
1860
1880
1900
1920
1940
1960
1980
2000
2020
(c)
2,400
2,200
2,000
1,800
1,600
1,400
1,200
1,000
800
600
400
200
S4ug
S4et
S4lv
S4lm
S4
S6
S7
S5
1860
1880
1900
1920
1940
1960
1980
2000
2020

Figure 8 (a)


0.01
West Africa
East Africa


S5
S6
S4lv
S4lm
S4mg
S4ug
S4
S4et
0.9
0.8
West-Africa
1
(b)

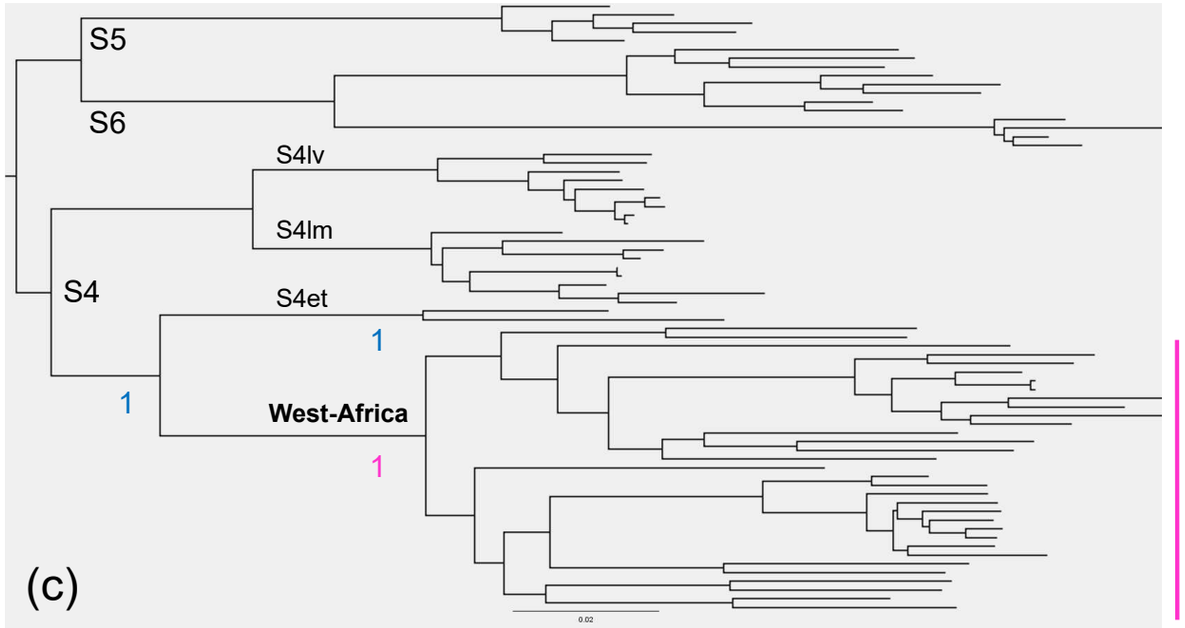

S5
S6
S4lv
S4lm
S4
S4et
1
1
West-Africa
1
(c)

Figure 9

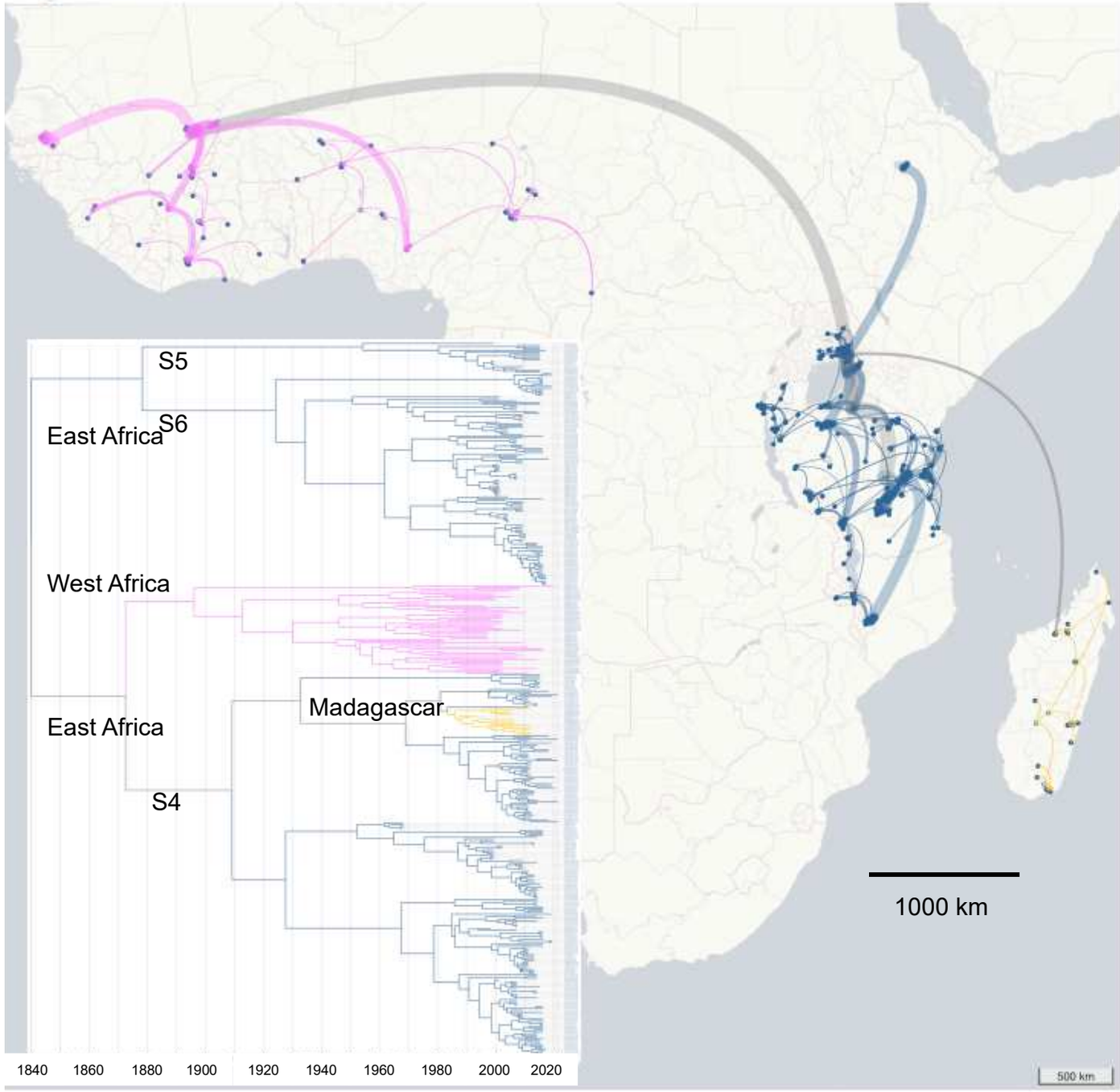

S5
S6
East Africa
West Africa
Madagascar
East Africa
S4
1840
1860
1880
1900
1920
1940
1960
1980
2000
2020
1000 km
500 km

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

*estimated under a strict molecular clock model.

Table 2: Dispersal metrics of RYMV in East Africa, West Africa, Madagascar and the three regions combined[1].

Dataset	Weighted diffusion coefficient (km2/year)	IBD signal (rP)[2]	Number of samples	Study area (km2)[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

[1] For each dataset and metric, we report both the posterior median estimate and the 95% highest posterior density (HPD) interval.

[2] The isolation-by-distance (IBD) signal has been estimated by the Pearson correlation coefficient (rP) between the patristic and log-ransformed great-circle geographic distances computed for each pair of virus samples

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