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ELEPHANT GENOTYPES REVEAL THE SIZE AND CONNECTIVITY OF TRANSNATIONAL IVORY TRAFFICKERS

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Elephant genotypes reveal the size and connectivity of transnational ivory traffickers

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Transnational ivory traffickers continue to smuggle large shipments of elephant ivory out of Africa, yet prosecutions and convictions remain few. We identify trafficking networks on the basis of genetic matching of tusks from the same individual or close relatives in separate shipments. Analyses are drawn from 4,320 savannah (*Loxodonta africana)* and forest (*L. cyclotis)* elephant tusks, sampled from 49 large ivory seizures totalling 111 t, shipped out of Africa between 2002 and 2019. Network analyses reveal a repeating pattern wherein tusks from the same individual or close relatives are found in separate seizures that were containerized in, and transited through, common African ports. Results suggest that individual traffickers are exporting dozens of shipments, with considerable connectivity between traffickers operating in different ports. These tools provide a framework to combine evidence from multiple investigations, strengthen prosecutions and support indictment and prosecution of transnational ivory traffickers for the totality of their crimes.

Transnational criminal organizations (TCOs) are well-organized criminal networks operating across countries. TCOs in the illicit ivory trade have been smuggling large volumes of ivory out of Africa for decades, severely impacting remaining elephant populations. About 100,000 African elephants were lost between 2007 and 2015[1]. Percentage wise, forest elephant (*Loxodonta cyclotis*) populations were more heavily impacted[2] due to Southeast Asian market preference for their higher density tusks[3]. However, savannah elephant (*L. africana*) populations have also experienced heavy declines since 2007[1].

Roughly 70% of ivory seizures are in individual shipments that exceed 0.5 t (ref. [4]). TCOs consolidate and containerize these large volumes of raw ivory for export, commonly out of a different African country from where the elephants were poached[5,6]. Most ivory shipments are transported out of Africa on marine cargo ships, allowing TCOs to conceal their contraband among the nearly 1 billion shipping containers moved around the world annually[6]. We contend that the most effective way to disrupt and dismantle this criminal enterprise is to target the TCOs exporting these large volumes of ivory out of Africa. Targeting TCOs could substantially reduce the amount of ivory entering transit, where it becomes far more difficult and expensive to trace. It would also eliminate the principal source of income to poachers and the middlemen who move the ivory up the illicit supply chain before consolidation.

Here, we provide DNA-based tools that connect individual TCOs to multiple large ivory seizures of forest and savannah elephants, while also showing connections between TCOs operating out of different ports. These connections are based on genetic matches between tusks from the same elephant (exact match, EM) or from close relatives (half-siblings or closer) found in separate large ivory seizures and the correspondence of these matches to the ports where the ivory shipments originated.

Forest elephants currently comprise about 6% of the remaining African elephant population[1]. They inhabit humid forest in West Africa and the Congo Basin, with the highest remaining densities in Gabon and Republic of the Congo. Roughly 23% of seizures examined contained primarily forest elephant ivory, with an average weight of 2.86 t per seizure. The most heavily poached areas were in Gabon and Republic of the Congo[5].

Savannah elephants inhabit grassy plains and bushlands. The savannah elephant range essentially wraps around the forest elephant range, including a narrow band north of the forest range in West and Central Africa and virtually all of East and Southern Africa. Their highest densities occur in the Kavango-Zambezi (KAZA) Transfrontier Conservation Area of southern Africa, followed by Tanzania, Zimbabwe and Kenya[1]. About 77% of the large ivory seizures we examined between 2002 and 2019 consisted of savannah elephant ivory, with an average weight of 2.24 t per seizure. The largest proportion of tusks in these seizures were from elephants poached in Tanzania, followed by northern Mozambique and southern Kenya[5], although several recent seizures contained a predominance of tusks poached in the KAZA Transfrontier Conservation Area[7].

Our previous research[6] linked multiple large ivory shipments to one another by genetically identifying EMs between tusks from the same elephant, exported in separate shipments. Tusks from the same elephant commonly get separated as they move up the supply chain from poacher to where they are consolidated for shipment[6]. Multiple lines of evidence suggested that separated tusks are still obtained by the same small number of TCOs dominating exports at a given port. Whenever separate shipments contained EMs, the two shipments were always exported from the same port, close in time and with high overlap in the assigned origins of their tusks[6]. This suggests that tusk matching between shipments is a powerful tool to link multiple shipments to the same TCO.

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Three major TCOs operating in Africa were identified on the basis of EMs: one TCO was operating in Mombasa, Kenya, a second in Kampala, Uganda, and a third in Lomé, Togo[6]. These three TCOs also appeared to be connected to varying degrees[6]. However, additional lines of evidence led us to suspect that many links between shipments were being missed due to the low probability of sampling both tusks. Both shipments containing the matching tusks needed to be sampled; even then, not all tusks in a seizure could be cost-effectively genotyped. These constraints led us to expand comparisons between tusks in separate shipments to also include familial searches[8], identifying genetic matches among tusks from close relatives (that is, parent–offspring, full- and half-siblings).

Matches among close relatives should be far more common than EMs, providing more opportunities to link together shipments and better delineate the reach of these TCO networks. This use of familial searches presumes that (1) female elephants stay in the same family group for life, (2) male elephants leave their natal herd but most still tend to stay in the same or a nearby subpopulation/protected area and (3) seizure pairs sharing large numbers of close-relative matches are derived primarily from poachers targeting the same localized population over time. Multiple seizures are probably trafficked by the same TCO when the seizures (1) share large numbers of tusks with exact and/or close-relative matches, (2) share ports of containerization and (3) when containerized inland, transit through shared seaports.

Given a pair of sampled genotypes, we consider the evidence that these genotypes originated from one of the following relationships: an exact match (genotypes from a single individual or from identical twins, although twin elephants seldom survive); close relatives; or unrelated individuals. We use likelihood ratio (LR) statistics to assess the strength of evidence for a particular relationship[9], while allowing for inclusion of the population structure parameter θ. Pairs with $\log_{10}(\mathrm{LR}) > 2$ for any close relationship were considered potential matches. We then applied a correction for false positives generated by the large number of comparisons. We incorporate these exact and close-relative matches in network analyses[10,11] to show the connectivity between seizures. Shared physical evidence connecting the same seizures (for example, common port of containerization, transit port, exporter, importer, cell phone data, cover load and transporter within Africa) is also examined, illustrating how genetic and physical evidence corroborate connections to the same TCO.

Results show that the three criminal networks originally identified in Kenya, Uganda and Togo[6] are involved with many more seizures and more connected to each other than previously discovered. Although genetic matches are limited by sample access, the composite of genetic matches among representatively sampled seizures[5] provides a basis to strengthen investigations and prosecutions. It enables law enforcement to connect evidence from multiple independent investigations and supports indictments and prosecutions of transnational ivory traffickers for the totality of their crimes. It also expands the links that can be pursued to uncover financial connections among shipments that can be tied back to the same TCO.

Results

Familial searches. Close-relative matches between seizures were inferred from 2,450,546 comparisons between savannah elephant tusks and 241,117 comparisons between forest elephant tusks. Simulation of unrelated elephants showed that false-positive rates were extremely low (Table 1). Nevertheless, the large number of comparisons made would still be expected to generate numerous false positives. We correct for false positives by weighting matches on the basis of probabilities derived from our simulation data (Table 1). The weight of each exact match was then multiplied by five (Methods) to account for the greater evidentiary value of an exact match; while two poachers working for independent TCOs could potentially take related elephants, the two tusks of the same elephant necessarily arise from a single poaching event.

The maximum number of weighted matches between any two seizures was 21.9. We detected 603.0 weighted close-relative matches (later filtered to 567.1 to remove between-seizure links of weight <1) and 27 EMs (Supplementary Table 1). This preponderance of close-relative matches was expected for two reasons: an elephant has only two tusks but may have many relatives and tusks from separate individuals, potentially poached at different times, are more likely to wind up in separate shipments. Previously studied EMs were seized no more than 13 months apart[6,12]. Familial matches were more distant in time, with 75% of weighted matches in savannah elephants and 59% in forest elephants between seizures separated in time by 13 months or more and a maximum time difference of 11 yr (Supplementary Table 2).

Network results. Figure 1 introduces the geographical span of the data and the country-specific colour codes for the ports where seizures were containerized. These country-specific colour codes are used in all subsequent figures.

Figure 2 displays how the pattern of connectedness among all analysed seizures emerges through time, on the basis of shared genetic and physical evidence. The few seizures in our database before 2009 consist predominantly of savannah elephant ivory containerized in Tanzania, Malawi and Zambia (key, Fig. 1), with ivory originating from southern Tanzania, northern Mozambique and Zambia[5]. A single forest elephant ivory seizure is also seen, containerized in Cameroon, with ivory originating from Gabon and the Republic of the Congo[5]. Connections are only seen among seizures made within Tanzania and between Malawi and Zambia, up through 2009. By 2012, we begin to see interconnected seizures containerized in Kenya and a small number of seizures containerized in Uganda. All of these seizures are connected to one another and to the Tanzania seizures, with most tusks still originating from Tanzania and northern Mozambique[5]. The beginnings of connections between East and West Africa can also be seen. This pattern expanded dramatically by 2015, with a disproportionate increase in seizures containerized in Uganda, containing ivory predominantly originating in Tanzania and southern Kenya[5] and numerous connections within and between the Uganda, Kenya and Tanzania containerized seizures. A growth in connections between East and West Africa is also apparent. This expansion continued through our most recent data in 2019 but with the addition of interconnected seizures containerized in the Democratic Republic of the Congo (DRC) and Angola.

Figures 3 and 4 take a closer look at seizure connectedness. Figure 3 details genetic matches (Fig. 3a) and shared physical evidence (Fig. 3b) among 16 representative seizures (on the *y* axis) containerized in Uganda or Kenya. The 16 seizures were selected because they share large numbers of genetic matches to one another and to additional seizures not among the 16 (*x* axis). All 49 seizures are numbered and presented in chronological order. Matches between seizures on the *x* and *y* axes are illustrated by a solid-coloured circle, indicating the port where the seizure in that column was containerized (see Fig. 1). The shared patterns of genetic matches among the 16 seizures to all seizures along the *y* axis is indicated by the number of solid-coloured circles within and between columns (Fig. 3a). Figure 3b shows the patterns of shared physical evidence among the same seizures, as well as the consistency in patterns between genetic and physical evidence. Figure 4a,b similarly illustrate representative seizures containerized in West Africa. Genetic matches and shared physical evidence among all seizures in our dataset are illustrated in Extended Data Fig. 1 for genetic matches and Extended Data Fig. 2 for shared physical evidence.

Ten of the 16 seizures in Fig. 3a include tusks with EMs in other seizures (Supplementary Table 1). Most seizures with genetic

Table 1 | Calculation of weights on the basis of observed matches and expected false positives

	Forest				Savannah			
$\log_{10}$(LR) category	False-positive rate	Observed matches	Expected false positives	Match weight	False-positive rate	Observed matches	Expected false positives	Match weight
2.0–2.5	1.8×10^{-4}	73	44.08	0.396	6.6×10^{-4}	2,084	1,615.12	0.225
2.5–3.0	4.2×10^{-5}	24	10.24	0.573	1.9×10^{-4}	558	467.11	0.163
3.0–3.5	9.5×10^{-6}	6	2.29	0.618	5.6×10^{-5}	172	137.17	0.203
3.5–4.0	4.1×10^{-6}	7	0.98	0.860	1.6×10^{-5}	58	39.43	0.320
4.0–4.5	1.0×10^{-6}	2	0.24	0.875	4.6×10^{-6}	19	11.24	0.408
4.5–5.0	1.4×10^{-7}	1	0.03	0.967	1.4×10^{-6}	14	3.47	0.752
5.0–5.5	1.4×10^{-7}	1	0.03	0.967	2.2×10^{-7}	5	0.54	0.892
5.5+[a]	1.4×10^{-7}	6	0.03	0.994	9.4×10^{-8}	39	0.23	0.994

[a]The highest bin includes all identified EMs.

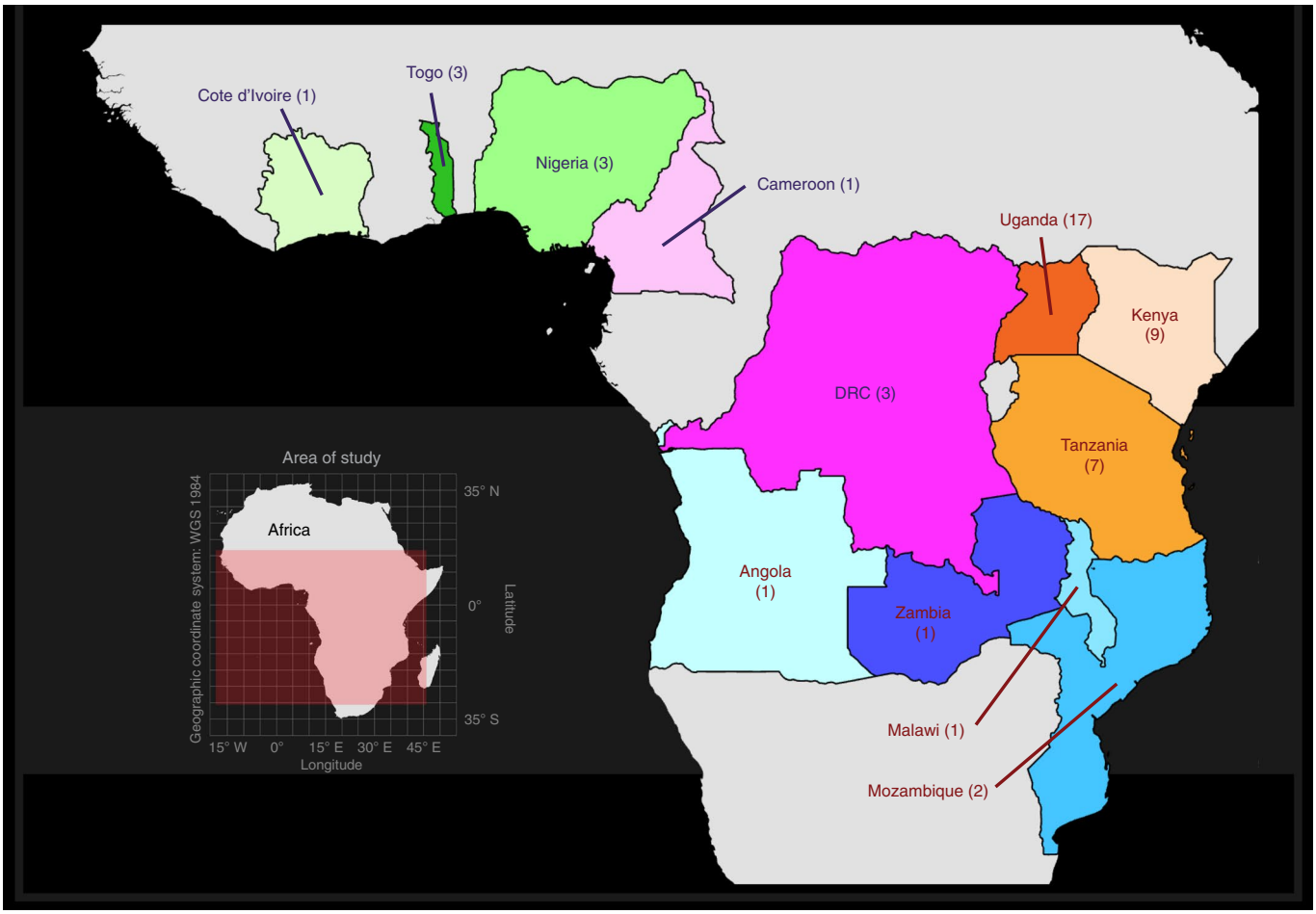

Fig. 1 | Geographical span and colour code scheme for ports of containerization used for all consequent figures. Number of seizures per port is shown in panrentheses. Map displayed using the World Geodetic System (WGS) 1984 geographic co-ordinate system. Country boundary data are from Esri, Garmin International, US Central Intelligence Agency and National Geographic Society. World Countries (Generalized) (feature class). ArcGis Living Atlas of the World. April 2021.

matches in Fig. 3 were containerized in Uganda (dark orange) but transited Kenya (Supplementary Table 3) when not seized in Uganda (Supplementary Table 3). The temporal shifts described in Fig. 2 can also be observed in Fig. 3 by the colour changes in the columns moving from left to right (Extended Data Fig. 1). The earliest seizures were containerized in Tanzania (light orange circles), followed by a disproportionate increase in seizures containerized in Kenya (tan circles) between 2010 and early 2013. The predominance of seizures containerized in Uganda (dark orange circles) began mid-2013. A more recent shift to containerization in DRC (purple circles) and Angola (cyan circles) began in 2016 (Extended Data Fig. 1).

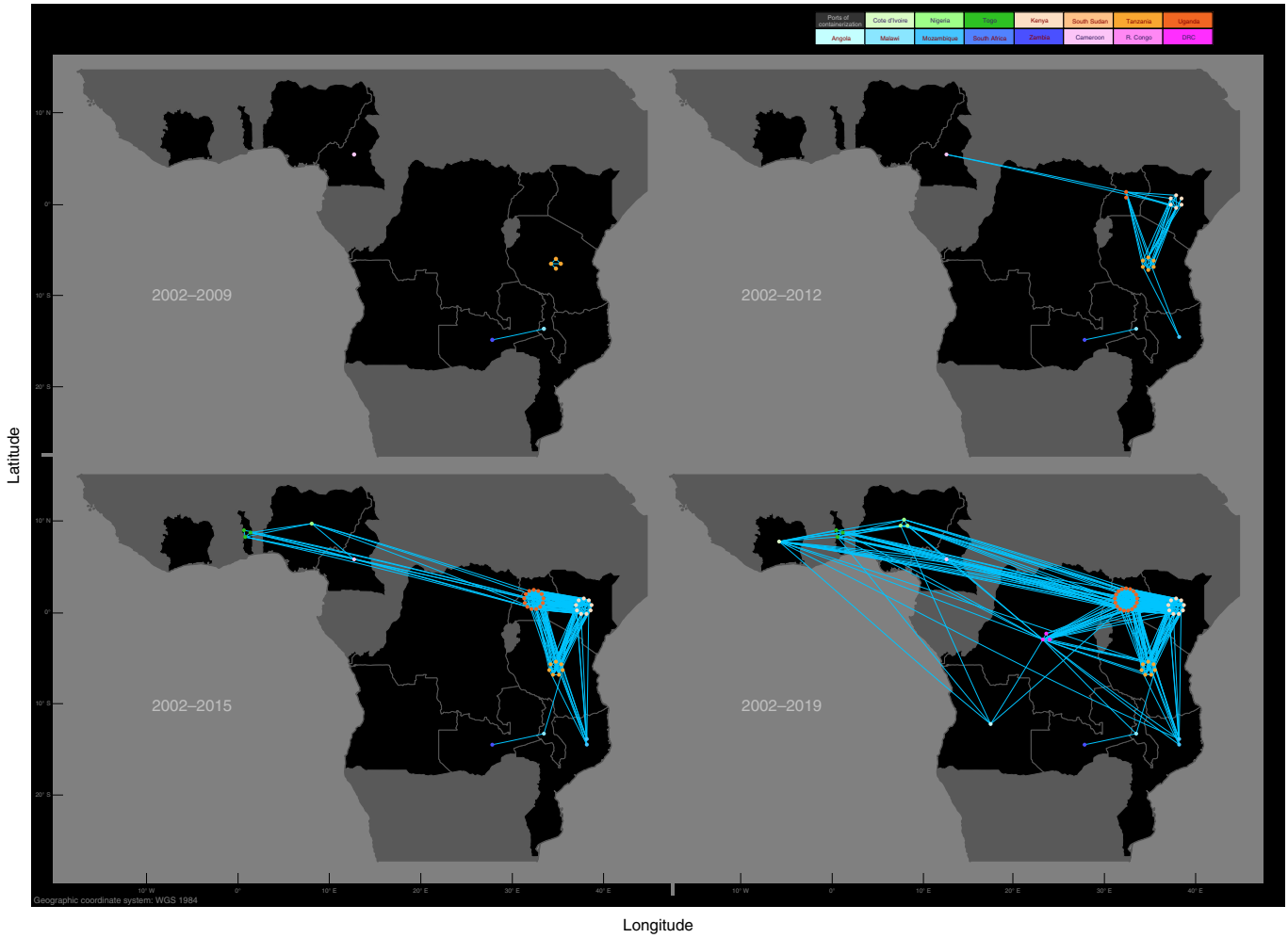

Fig. 2 | Temporal progression in the major ports of containerization and their connectivity, based on genetic matches and shared physical evidence between seizures. Each seizure is represented by a solid point with the port of containerization indicated by the colour of that point as per the colour scheme in Fig. 1. A blue line connecting any two seizures indicates one or more genetic matches and/or shared physical evidence between them. Points are centred around country centroids and arranged in circles for ease of visualization, with circle area being proportional to the number of points in a given country. Early seizures of savannah elephant ivory were containerized in Tanzania, Zambia and Malawi but shifted to Kenya (2010–2012) and then Uganda (2013–2015). Containerization next shifted to western Central Africa (DRC and Angola) (2016–2019). Connectivity within and between all of these shipments grew with the number of new seizures. Similarly, ports of containerization of forest elephant ivory shifted from Togo (2013–2014) to Nigeria (2016–2019) along with connections to each other but also to multiple seizures containerized in East and western Central Africa. Country boundary data are from the same source as Fig. 1. Map displayed using the WGS 1984 co-ordinate system. R. Congo, Republic of the Congo.

The MYS, 12-12, 6.0 t seizure in Fig. 3a (no. 18, fourth seizure from the top) is termed a connector seizure, defined as a seizure with genetic matches to multiple other seizures exported from widely separated ports. It connects 21 seizures made in, or exported from, East Africa to four seizures made in, or exported from, West Africa. Seizure no. 18 was either recontainerized or simply added to in Togo after initial containerization in Kenya (Supplementary Table 3) and has EMs of savannah elephant tusks to four separate seizures (Supplementary Table 1): two containerized in Togo (nos. 27 and 32) and two containerized in Uganda that were seized in, or transited through, Kenya (nos. 14 and 29) (Supplementary Table 3). Seizure no. 27 consisted entirely of forest elephant ivory[5] and had an exact match to a West African forest elephant tusk in seizure no. 18 (Supplementary Table 1). All but two tusks analysed in seizure 32 were forest elephant ivory but its two savannah elephant tusks were EMs to East African savannah elephant tusks in seizure no. 18 (Supplementary Table 1). Seizure no. 18 also had close-relative matches to seizures of savannah ivory exported from East Africa (Fig. 3a) and forest elephant ivory exported from West Africa (Fig. 4a). The latter included a 7.2 t shipment containerized in Nigeria (no. 44), seized in Hong Kong 5 yr after seizure no. 18 was seized (Supplementary Table 3). Seizure no. 18 was the first to indicate a connection between TCOs operating in East and West Africa[5].

The focal seizure in the last row of Fig. 3 (no. 49: SGP, 07-19, 8.8 t) is the most recent seizure in our dataset and, at 8.8 t, among the largest ivory seizure on record; it also contained 12 t of pangolin scales. Seizure no. 49 is another connector seizure. It was containerized in Kinshasa, DRC, and transited through Pointe Noire, Congo, before being seized in Singapore (Supplementary Table 3). Of 196 analysed tusks from no. 49, 172 were inferred to originate in the KAZA Transfrontier Conservation Area[7], reportedly a newly emerging poaching hotspot inhabited by 230,000 of the 400,000 remaining elephants in Africa[5,13]. Seizure no. 49 was linked by close-relative matches to seizure no. 47 (containerized in Luanda, Angola) and seizure no. 40 (containerized in Kinshasa, DRC), both inferred to have been poached in the KAZA[7]. However, it is a close-relative

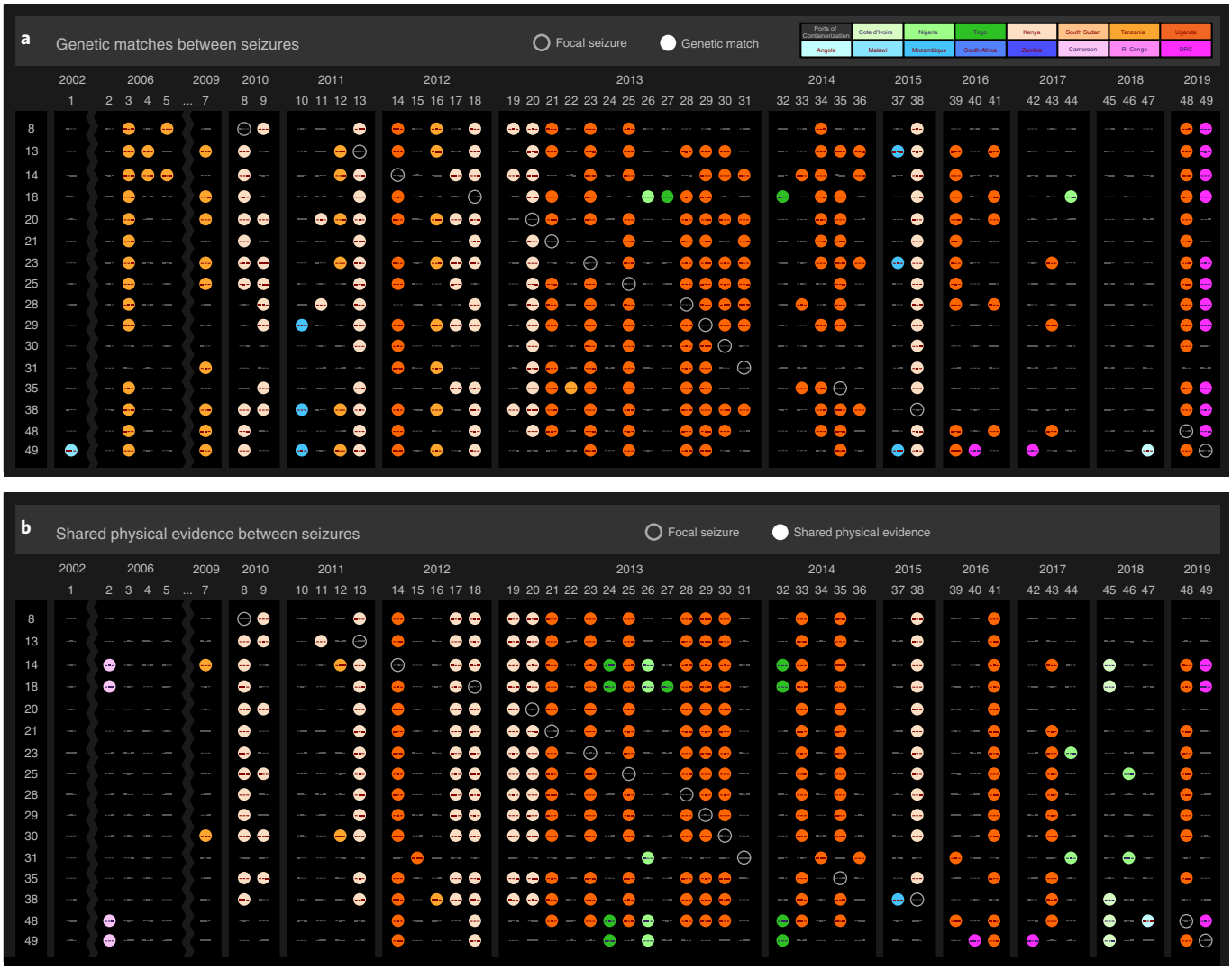

Fig. 3 | Genetic and physical-evidence matches between tusks in representative ivory seizures containerized in East Africa and all other seizures in our dataset. a,**b**, Genetic matches (**a**) and shared physical evidence (**b**) between the corresponding seizures on the *x* and *y* axes are illustrated by a solid-coloured circle, with the circle colour indicating the port where the seizure in that column was containerized (see colour key and Fig. 1). Each row represents a single focal seizure (listed in the left-hand column of the row and displayed with open grey circle). The ordering of the matched seizures from left to right is chronological, on the basis of seizure date. The seizures on the left-hand side of the figure were all containerized in Kenya or Uganda and were chosen as focal seizures for their high connectivity in genetic matches to one another. Some seizures along the *y* axis are missing because they had no genetic matches or shared physical evidence to the seizures on the *x* axis. The consistency in patterns of connectivity among seizures on the *x* axis is easily seen by the number of solid circles shared within and between columns. The predominance of seizures containerized in Uganda and the shift from containerization in Tanzania (light orange columns), to Kenya (tan columns), Uganda (dark orange columns) and DRC is illustrated by the respective changes in columns of circles from orange, to tan, dark orange and purple. Seizure number key: 1, SGP, 06-02, 6.5 t; 2, HKG, 05-06, 3.9 t; 3, HKG, 07-06, 2.6 t; 4, TWN, 07-06, 1.2 t; 5, TWN, 07-06, 3.0 t; 6, SGP, 03-07, 0.5 t; 7, PHL, 06-09, 4.9 t; 8, VNM, 04-10, 2.2 t; 9, KEN, 08-10, 1.5 t; 10, THA, 01-11, 0.33 t; 11, KEN, 05-11, 1.3 t; 12, MYS, 09-11, 1.1 t; 13, KEN, 12-11, 1.5 t; 14, LKA, 05-12, 1.5 t; 15, UGA, 09-12, *X* t;16, HKG, 10-12, 1.9 t A; 17, HKG, 10-12, 1.9 t B; 18, MYS, 12-12, 6.0 t; 19, HKG, 01-13, 1.3 t; 20, KEN, 01-13, 3.8 t; 21, ARE, 05-13, 1.5 t; 22, MWI, 05-13, 2.6 t; 23, KEN, 06-13, 1.5 t; 24, HKG, 07-13, 2.0 t; 25, KEN, 07-13, 3.3 t; 26, HKG, 08-13, 2.2 t; 27, TGO, 08-13, 0.7 t; 28, KEN, 10-13, 2.0 t; 29, KEN, 10-13, 2.9 t; 30, UGA, 10-13, 2.9 t; 31, UGA, 12-13, 1.4 t; 32, TGO, 01-14, 3.9 t; 33, SGP, 03-14, 1.0 t; 34, UGA, 05-14, 1.8 t; 35, KEN, 06-14, 2.2 t; 36, UGA, 07-14, 0.6 t; 37, MOZ, 05-15, 1.2 t; 38, SGP, 05-15, 4.6 t; 39, SSD, 06-16, 0.5 t; 40, MYS, 07-16, 0.89 t; 41, KEN, 12-16, 1.0 t; 42, MYS, 01-17, 0.85 t; 43, UGA, 02-17, 1.3 t; 44, HKG, 07-17, 7.2 t; 45, CIV, 01-18, 0.5 t; 46, SGP, 03-18, 3.3 t; 47, AGO, 06-18, 1.8 t; 48, UGA, 01-19, 3.3 t; 49, SGP, 07-19, 8.8 t. Country ISO codes as described in the ISO 3166 international standard: AGO, Angola; ARE, United Arab Emirates; CIV, Cote d'Ivoire; HKG, Hong Kong; KEN, Kenya; LKA, Sri Lanka; MOZ, Mozambique; MWI, Malawi; MYS, Malaysia; PHL, Philippines; SGP, Singapore; SSD; South Sudan; TGO, Togo; THA, Thailand; TWN, Taiwan; UGA, Uganda; VNM, Vietnam. 1.9 t A and 1.9 t B designate separate seizures. *X* t, weight unknown.

match to 17 seizures poached and containerized in East Africa (nos. 3, 7, 8, 12, 13, 14, 16, 18, 23, 25, 28, 29, 35, 38 and 48; Fig. 3a).

Figure 4 shows a similar pattern of multiple genetic matches among seizures containerized in West Africa as well as a temporal shift in the major port of containerization. Most of these seizures were containerized in Togo or Nigeria, carrying forest elephant ivory originating from protected areas bordering Gabon, Republic of the Congo, Central African Republic and Cameroon[5,6]. There

Fig. 4 | Seizures containerized in West Africa. a,**b**, Genetic (**a**) and physical-evidence (**b**) matches between tusks in ivory seizures containerized in West Africa and all other seizures in our dataset. Linear format is as in Fig. 3. The shift from Togo (dark green) to Nigeria (light green) as the dominant port of containerization is also shown.

were numerous genetic matches among those shipments. Earlier seizures were largely containerized in Togo (nos. 24, 27 and 32) or recontainerized in Togo (no. 18) (Supplementary Table 3) but shifted to Nigeria in 2017. The Cote d'Ivoire seizure (no. 45, CIV, 01-18, 0.5 t) in Fig. 4 was also sourced to Nigeria through court testimony from the trafficker who was arrested in possession of the ivory (Supplementary Table 3). Seizure no. 45 had genetic matches to three other seizures containerized in Nigeria, including an exact match to the 3.3 t Singapore seizure (no. 46) and close-relative matches to that seizure and the 7.2 t Hong Kong seizure (no. 44), Fig. 4a. A financial investigation facilitated by DNA results further revealed that the same TCO that paid for seizure no. 45 also paid for seizure no. 49, the 8.8 t connector seizure containerized in DRC, adding support for the connector status described for seizure no. 49. Seizure no. 45 had physical-evidence links to East Africa as well (Fig. 4b), like the connector seizures nos. 18 and 49. The apprehended trafficker for seizure no. 45 had paper copies of the Bill of Lading for a Mombasa shipment that he had presented to freight forwarders to indicate where to send the Cote d'Ivoire container. Additionally, the ivory in seizure no. 45 was packed in hollowed hardwood beams, embedded in paraffin. Five other seizures shared that same modus operandi, including a second seizure containerized in Cote d'Ivoire (not analysed) and four others containerized in East Africa (two of which, seizures nos. 41 and 48, were analysed).

Cluster analyses. A network of all genetic matches between seizures is shown in Fig. 5a. We performed two types of network structure detection on these data. A Louvain clustering approach[14], grouping seizures with high interconnectivity, identified five clusters (Fig. 5b). A structural equivalence approach[11], grouping seizures on the basis of similarities in their patterns of connection, identified six clusters (Fig. 5c). We primarily interpret the Louvain network (left) but some groupings appear better resolved by the equivalence network (right). Note that the spatial layout of nodes is optimized to prevent overlap and is not driven solely by the genetic data. Thus, nodes that appear close together but have no connections are not necessarily associated.

Both methods see a distinctive cluster of seizures (group D: nos. 45, 26, 44, 27 and 32) containerized in West Africa (Nigeria, Togo or Cote d'Ivoire) between 2012 and 2018. The Louvain analysis also includes seizure no. 18 in this group, despite its strong connections to many East African seizures (groups A, B, C and E), consistent with information that seizure no. 18 was recontainerized or added to in Togo. The equivalence analysis places seizures nos. 18 and 46 together in a unique group D-2, calling attention to their connector status between this network and the remainder of the graph. All the seizures in group D are focal seizures in Fig. 4.

The Louvain analysis divides the remaining seizures into four additional groups. Groups A, B and C are tightly connected to one another, so much so that the equivalence network merged all three groups into two (groups F and G). Group E, while not connected enough for the equivalence network to merge it with the other three groups, still has connections to them. Both genetic and physical evidence strongly connect the four seizures in group E that are most proximal to group B (nos. 3, 13, 14 and 38) to the other groups. Seizure no. 3 was not included among the focal seizures in Fig. 3 but has familial matches to 14 of the 16 focal seizures in Fig. 3a. The remaining three were focal seizures and have 14, 12 and 15 out of 15 possible matches, respectively, to the other focal seizures in Fig. 3a. All the seizures in groups A, B, C and the listed subset of E were containerized in Uganda or Kenya in East Africa, with the exception of seizure no. 3, which was among the earliest seizures we analysed (made in 2006) and was containerized in Tanzania.

Group A contains four seizures (nos. 39, 41, 43 and 48), all of which included ivory with Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) inventory markings indicating they were taken from the Burundi government ivory stockpile (Supplementary Table 3). Two of those seizures

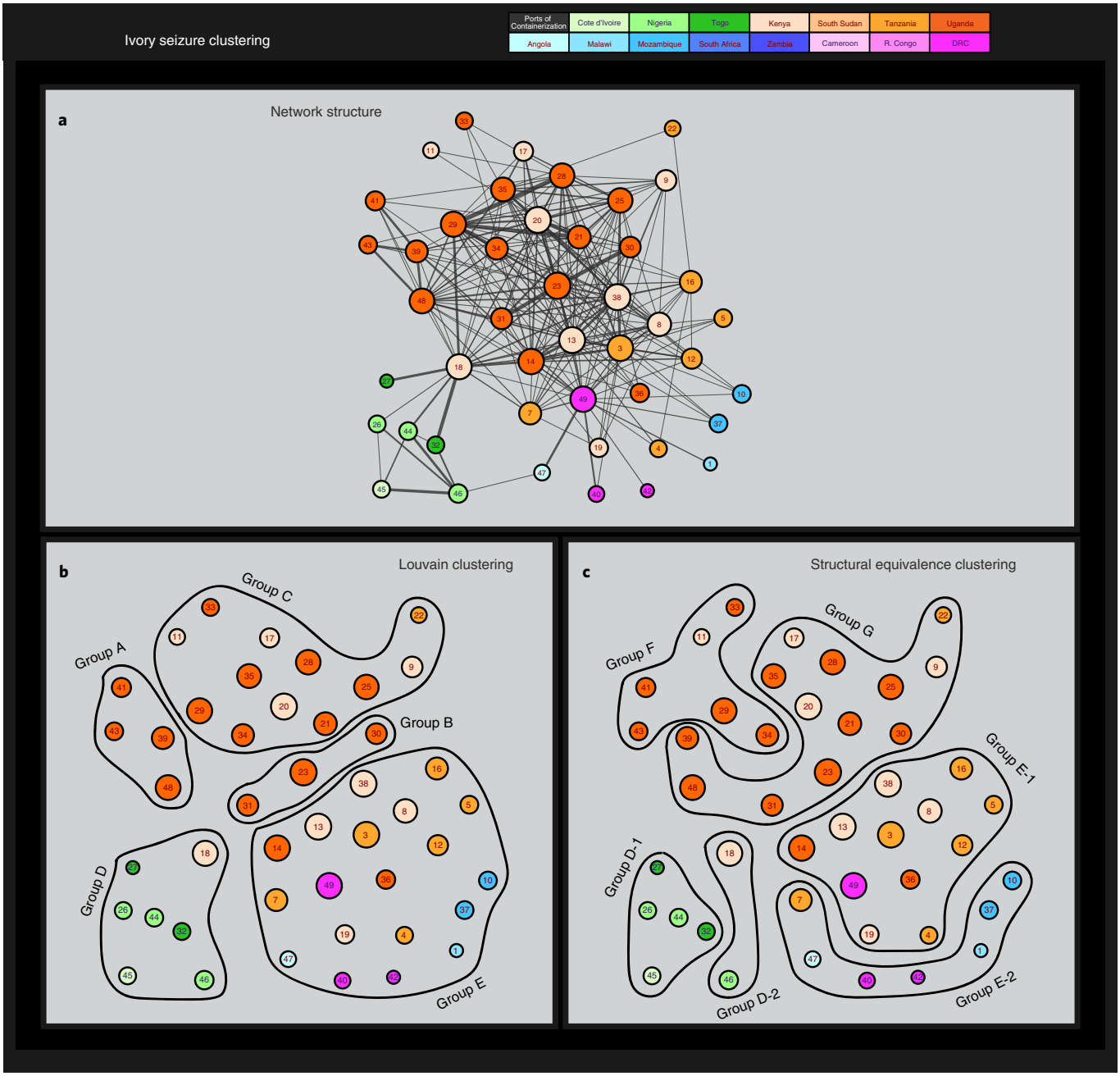

Fig. 5 | Network of all genetic matches between seizures. a,**b**, Network of genetic matches between ivory seizures (**a**) and cluster groups within that network based on Louvain (**b**) and structural equivalence (**c**) clustering. Louvain clustering emphasizes density of within-group connections. Structural equivalence clustering emphasizes similarity of connection patterns (Methods). Each solid circle represents a seizure (node), coloured to correspond to the port where the shipment originated in Africa (Fig. 1) and numbered corresponding to the seizure name (Fig. 3). The size of each node is proportional to the sum of all weighted matches that node shares with all other seizures. Links connecting nodes represent genetic matches with line thickness corresponding to the weighted genetic matches between seizures, based on their $\log_{10}$(LR) bin (Table 1). Orientation of nodes is based on the Louvain clustering to facilitate comparison between clusters A and B. Each of the five (Louvain) and six (structural equivalence) network clusters are circled and identified by groups A–G.

(nos. 41 and 48) had their ivory concealed in hollowed teak logs embedded in paraffin, as did seizure no. 45 in group D (Supplementary Table 3). All four seizures in group A were containerized in Uganda and were relatively new, made between 2016 and 2019 (seizure 45 also occurred in that interval).

Group B contains three seizures (nos. 23, 30 and 31); all were containerized in Uganda in 2013 and have tight genetic links to one another, as well as to groups A, C and the four aforementioned seizures in group E. Seizure no. 23, which was seized while transiting Kenya from Uganda (Supplementary Table 3), has 14 matches to the other 15 focal seizures in Fig. 3a. All three seizures in group B and 7 out of the 12 seizures in group C are focal seizures in Fig. 3.

Group E is comprised of 19 seizures. It includes all but the most recent seizure (no. 22) containerized in Tanzania (nos. 3, 4, 5, 7, 12 and 16), seizures containerized in Kenya and Uganda (nos. 8, 13, 14, 19, 36 and 38), including the three tightly linked seizures previously

mentioned and southern containerized seizures (nos. 1, 10, 37, 40, 42, 47 and 49). Here, the equivalence network is useful in subdividing this group: it calls out group E-2 consisting of seizures containerized in southern West Africa (DRC and Angola), containing ivory primarily poached in the KAZA Transfrontier Conservation Area[7], as well as seizures poached and containerized in the southern part of eastern Africa (Mozambique and Malawi). However, the previously mentioned connector seizure no. 49 remains in group E-1, supporting its links to the East African network in E-1 as well as the more southern African networks in E-2.

Discussion

While our method is powerful, the following limitations should be kept in mind. (1) Despite low false-positive rates per comparison (Table 1), the large number of comparisons will generate many false positives. Weighting of matches compensates for this in general but random clustering of false positives could generate spurious links between seizures. Nevertheless, the major conclusions of our study are supported by multiple high-weight matches between seizures and in many cases by EMs, which are very unlikely to be false positives (Table 1). (2) A proportion of putative relative matches will be individuals from the same local population but not half-sibling or closer. While technically false positives, these matches do indicate repeated poaching from the same local group. (3) Only a subset of tusks from a seizure can be cost-effectively genotyped and not all genuine relative matches can be detected among genotyped tusks. Absence of a link between two seizures may therefore reflect limited detection power rather than genuine independence. (4) Presence of related elephants in separate seizures suggests, but does not prove, that they were trafficked by the same or related organizations. It is possible that two independent organizations could take animals from the same herd or restricted local group. However, the concordance between physical and genetic evidence supports the suggestion that related elephants appear in related seizures.

Matching of tusks from close relatives found in separate seizures shows that most large ivory seizures made over the past decade or more resulted from repeated poaching of the same localized elephant populations. The consistency of genetic matches among large numbers of shipments containerized in, and transiting through, the same African port implies that a very small number of TCOs are responsible for the bulk of these shipments, even when shipments are containerized in separate nearby countries. The TCOs operating in Mombasa, Kenya, and Kampala, Uganda, may in fact, represent a single large network as was suggested by a report based on over 400 contacts from the Uganda TCO's phones, covering many countries and continents, most notably in East Africa and Southeast Asia[15].

The notion of one big operative is also supported by the abrupt temporal shifts in port of containerization in East Africa from Tanzania, to Kenya to Uganda. Major competition between these TCOs would be expected to result in a more mosaic-like transition. Presumably, these shifts resulted from TCOs trying to evade increased law enforcement pressure at these ports. Consolidating the ivory in the inland container depots of Uganda before shipping to Mombasa by truck or rail reduces chances of the container being searched by authorities in Mombasa. This strategy is made effective by broader economic efforts to maintain open borders for free trade in East Africa, reducing the likelihood that containers in transit will be searched. The West African Togo and Nigeria exports[5,6] similarly appear to have abruptly shifted to Nigeria as the major hub of export operations in West Africa by 2017.

We also identified connector seizures linking TCOs operating across Africa. Both genetic matches and shared physical evidence connected seizure no. 18 to major TCOs operating in East and West Africa (Figs. 3–5), as did physical evidence from seizure no. 45 (Supplementary Table 3). Seizures 46 and 47 similarly connected TCOs operating in Nigeria and Angola. Seizure no. 49 connected TCOs in Kinshasa, DRC, and Luanda, Angola, moving multiple seizures (nos. 40, 42 and 47) of ivory largely poached in a newly emerging hotspot in the KAZA[7], to the major TCOs operating in Kenya and Uganda (Figs. 3 and 5) moving ivory primarily poached in East–Southeast Africa[5,6]. The latter connection suggests that TCOs operating in East Africa may be attempting to reduce growing law enforcement pressure on them by taking advantage of the multiple porous borders with DRC as well as the relative weak rule of law in that country[16]. These collective findings point to the ability of TCOs to shift operations across the continent, which makes vital open and direct international collaboration among law enforcement, the scientific community, NGOs and the private sector to combat internationally collaborating TCOs.

The connections made by combining geographic assignment, genetic matching and shared physical evidence among large ivory seizures can greatly empower investigations and prosecutions. They provide a means to connect evidence from multiple investigations, uncovering the extent and connectivity of major TCO networks. These connections also provide a roadmap to guide financial investigations by the US Department of Homeland Security, Homeland Security Investigations (HSI). Financial investigations of these TCOs identify money laundering operations used to facilitate their illegal shipments and launder their proceeds. Following the money can lead directly to the bank accounts of TCO members. If any of the TCO's financial transactions involve US currency, the traffickers are in violation of multiple US statutes, including money laundering and wire fraud. This enables law enforcement to disrupt these TCOs by seizing their assets and, if necessary, seeking extradition for these otherwise untouchable criminals to face prosecution in the United States[17]. Financial investigations facilitated by genetic links between seizures also exposes TCO networks through discovery of shared illicit funding sources.

More broadly, our findings have important implications for how major TCOs are being prosecuted across Africa and Southeast Asia. Most prosecutions tend to focus on a single seizure[18], failing to acknowledge the linkages of individual TCOs to numerous transnational shipments. Too often, these cases are treated as a simple possession crime, instead of prosecuting the TCO for all the associated crimes they committed. Failure to acknowledge the seriousness and breadth of these transnational wildlife crimes during courtroom prosecutions too often results in serious trafficking prosecutions, sometimes lasting years in duration, being repeatedly re-assigned to new or inexperienced prosecutors who are not conversant with the complexities or depth of these cases. This lack of continuity or experience commonly results in defendants receiving minimal sentences, acquittals or dismissals of the case[18]. All of this is well exemplified in the case against the perpetrator of seizure no. 35.

The perpetrator initially convicted for seizure no. 35 had his conviction quashed 2 years into his 20-yr sentence due to Appeal Court's findings of trial irregularities, constitutional concerns and insufficient evidence. Wasser et al.[6] suggested this TCO had broader connections to multiple shipments, despite an absence of EMs between seizure 35 and other presumed associated seizures. In fact, a major incentive for pursuing familial searches was the suspicion that many links between shipments were missed when relying solely on EMs due to the low probability of sampling both tusks and that familial searches might help uncover those broader connections. Familial matches demonstrated the strength of this perpetrator's connections to the entire network of seizures in Figs. 3 and 5, among others.

Seizure no. 38, a 4.6 t seizure made in Singapore in 2015, connected to 24 other seizures containerized in Uganda, Kenya or Tanzania, including seizure no. 35 (Fig. 3) and a variety of physical evidence also linked seizure no. 38 to the major trafficker indicted for shipping seizure no. 35 (Supplementary Table 3). Wasser et al.[6] reported nine seizures (nos. 14, 17, 21, 23, 25, 28, 29, 33 and 35) seized in, or transited through, Mombasa, Kenya, after containerization in Kampala, Uganda, plus two more containerized and seized

in Uganda (nos. 30 and 31), presumed to be on route to Mombasa (Supplementary Table 3). All 12 seizures had high spatial and temporal overlap in addition to common ports of containerization. However, only three of the nine had EMs to one another. A fourth (no. 23) only had EMs to the two seizures containerized and seized in Uganda (nos. 30 and 31). Physical evidence (Supplementary Table 3) linked seizure no. 23 to seizures nos. 25 and 35 but there were no EMs between them. All of these seizures are now shown to have numerous close-relative matches to one another, including to seizure no. 35 (Fig. 3a).

The four seizures (nos. 41, 39, 43 and 48) containing tusks stolen from the 1989 Burundi government ivory stockpile, including two seizures (nos. 41 and 48) concealed in high value, hollowed out teak logs, also link back to the perpetrator initially convicted for seizure no. 35. These four seizures collectively reflect an enormous time investment in obfuscation, as well as connections to corrupt government officials to gain access to the Burundi stockpiles. The Burundi ivory was kept in seven shipping containers secured in a government military compound and was audited by CITES in 2004[19]. Eight other seizures, including seizure no. 45 and seven others (not yet analysed) exported out of East and West Africa during late 2016, had the same hollowed log modus operandi. Genetic and physical evidence (Figs. 3 and 4 and Supplementary Table 3) link these seizures to the connector seizure no. 18 and more broadly to the large Kenya–Uganda network(s) on the East African side (Fig. 3) and to the Nigeria TCO network on the West African side (Fig. 4). Evidence obtained from seizure no. 43, which also has EMs to seizures nos. 39 and 48 (Extended Data Fig. 1 and Supplementary Table 3), led to another seizure in Nairobi Kenya (not yet analysed). One of the six perpetrators arrested for seizure no. 43 called the trafficker indicted for seizure no. 35 while the trafficker was still in prison before his acquittal.

These combined findings could have reduced the likelihood of this perpetrator's conviction being overturned had they been available during his trial.

Linking genetic and physical evidence from multiple independent investigations, as described in this paper, can build stronger cases by strengthening evidentiary connections. Ideally, this approach will encourage the appointment of special prosecutors who can use this combined evidence to prosecute TCOs for their involvement in multiple illegal ivory shipments. This could, in turn, increase chances of conviction on multiple charges resulting in stiffer penalties.

Since TCOs are increasingly diversifying, our approach also has direct relevance to combatting other transnational crimes. For example, pangolins have become one of the most poached animals in the world and ~25% of large pangolin seizures are comingled with large ivory seizures[20]. Both ivory and pangolin shipments increasingly include timber as their cover load; much of that timber is illegally harvested, in a growth industry that annually brings in US$50–150 billion in illegal sales[21].

Applying familial searches and other forms of genetic analysis to different types of comingled contraband will provide insights into the larger strategies used by these TCOs, including how they are acquiring multiple species of contraband with diverse natural histories. These methods could also help combat other transnational organized crimes. Major TCOs smuggling wildlife increasingly move less traceable forms of contraband, including narcotics and weapons. These shipments are not necessarily comingled with wildlife products but TCOs tend to move them through the same criminal supply chain from exporters to shippers and importers. The high traceability of wildlife populations separated over space and time, compared to farmed, manufactured, or synthesized contraband, has already helped inform law enforcement about trafficker strategies for moving these other, less traceable, forms of contraband[22].

Methods

Tusks were sampled as in Wasser et al.[5,6], to increase the probability of sampling just one of the two tusks per elephant, while capturing the geographical diversity of tusks in each seizure. One tusk of each identifiable pair was removed; the remaining 'singletons' were grouped by features suggesting that they came from a common location and tusks were then randomly selected for DNA analysis in proportion to the relative number of tusks per group. A piece of ivory was cut from the hollow base of each sampled tusk (3–5 cm in diameter and 0.3–1 cm thick) using an electric circular saw with a fine-toothed blade and then shipped to our laboratory for analysis. All ivory samples were imported following the rules of the Convention on International Trade in Endangered Species, including CITES import and export permits and USFWS clearance upon arrival.

DNA was extracted in duplicate from tusks using methods described in Mailand and Wasser[23] and further optimized by Winters et al.[24] and then amplified for 16 microsatellite DNA loci. Amplification for 16 microsatellite DNA loci was split into six multiplexes with a minimum of four amplifications per locus (two per extract). Positive and negative PCR controls were included in all analyses. Primers (Supplementary Table 4) included the sets published in Nyakaana and Arctander[25] and Comstock et al.[26,27] and were multiplexed according to the conditions described in the Supplementary Information and Supplementary Table 5. PCR products were subjected to fragment analysis on an ABI 3730 capillary array genetic analyser. Following the forensic analysis protocol in Wasser et al.[5], allele sizes were scored using GeneMarker v.2.4–v.3.0.0. Confirmation of a homozygous locus required that the one allele be observed in a minimum of three replicates with no other allele observed at that locus in more than one replicate. Confirmation of a heterozygous locus required the two different alleles to be observed in a minimum of two replicates with no other allele observed at that locus in more than one replicate. Loci that failed to meet either of those criteria were not confirmed. Only samples with ten or more of the 16 loci confirmed were included in further analysis.

The probability that each seizure or reference individual was an interspecific hybrid was assessed with EBhybrids[28] and individuals with hybrid probability >50% were removed from further analysis, as the relevant reference allele frequencies for familial matching of hybrids cannot be determined. Individuals with fewer than ten successfully amplified loci were also removed from analysis. This procedure yielded 1,548 reference samples from savannah elephants and 630 from forest elephants.

Reference samples were collected in the field, while avoiding collection of samples closer than 1 km apart[29,30]. This served to reduce chances of sampling individuals from the same family, while still providing a simple protocol that could be understood by a wide range of sample collectors. The 1 km threshold also helped assure that sufficient sample sizes would be acquired from small populations. Hybrids and samples with fewer than ten successfully amplified loci were removed from analysis.

Origin assignments were conducted for each sample by comparing its genotype to the allele frequencies in its species-specific (forest or savannah) DNA reference map, using the continuous assignment method implemented in SCAT2 v.2.1 (ref. [29]) with Voronoi tessellation-based postprocessing implemented in Voronoi v.1.0 (ref. [30]). Only tusks and reference samples that amplified for a minimum of ten out of 16 microsatellite loci were included in origin assignment.

For validation purposes, we sequenced a 600 bp fragment of the mitochondrial DNA (mtDNA) control region D-loop from 11 putative EMs and 193 putative full sibling matches following the protocol of Nyakaana and Arctander[25], using the primers Laf CR1 and Laf CR2 (ref. [31]). PCR products were enzymatically purified and sent to GeneWiz for sequencing. The reads were then assembled using Sequencher v.5.4.6 (genecodes.com), aligned in MAFFT[32] and pairwise distances calculated using PAUP* (ref. [33]).

Likelihood ratio calculation of exact and close-relative matches. Given a pair of genotype profiles S_1 and S_2, we consider the proposal that they originated from one of the following relationships: an EM; parent–offspring (PO); full-siblings (FS); half-siblings (HS) or equivalent relationships such as uncle/nephew; or unrelated individuals (UN). To assess the strength of evidence for a particular relationship, we use the LR statistics

$$\mathrm{LR\,(EM)} = \frac{\prod_{k=1}^{K} \Pr[S_{1k}, S_{2k}|\mathrm{EM}]}{\Pr[S_{1k}, S_{2k}|\mathrm{UN}]},$$

$$\mathrm{LR\,(PO)} = \frac{\prod_{k=1}^{K} \Pr[S_{1k}, S_{2k}|\mathrm{PO}]}{\Pr[S_{1k}, S_{2k}|\mathrm{UN}]},$$

$$\mathrm{LR\,(FS)} = \frac{\prod_{k=1}^{K} \Pr[S_{1k}, S_{2k}|\mathrm{FS}]}{\Pr[S_{1k}, S_{2k}|\mathrm{UN}]},$$

$$\mathrm{LR\,(HS)} = \frac{\prod_{k=1}^{K} \Pr[S_{1k}, S_{2k}|\mathrm{HS}]}{\Pr[S_{1k}, S_{2k}|\mathrm{UN}]},$$

where the loci, indexed by $k = \{1,\ldots,K\}$, are assumed to be independent.

To compute these LR statistics, we require joint genotype probabilities at each locus. To compute the genotype probabilities, we use standard expressions[6], which allow for inclusion of the population structure parameter θ. These equations depend on the relatedness vector κ, where κ_j denotes the probability of the two individuals sharing j IBD (identical-by-descent) alleles. For an EM relationship, the relatedness vector is $\kappa=(0,0,1)$; for PO it is $\kappa=(0,1,0)$; for FS it is $\kappa=(0.25,0.5,0.25)$; for HS it is $\kappa=(0.5,0.5,0)$; and for UN it is $\kappa=(1,0,0)$.

We used the estimates $\theta=0.059$ for forest elephants and $\theta=0.047$ for savannah elephants, based on the results of Wasser et al.[6]. Allele frequencies were determined per subpopulation as described below. Some of the analysed genotypes included alleles that were absent from the reference data. In the case of one novel allele, we introduced the novel allele at frequency θ and multiplied all other allele frequencies by $1-\theta$. In the case of two novel alleles, we introduced each at a frequency of θ and multiplied all other allele frequencies by $1-2\theta$.

Division into subpopulations. The close-relative matching calculations require local allele frequencies. In whole-species analysis, both forest and savannah samples violated Hardy–Weinberg expectations, indicating local population structure which could yield false positives. We therefore divided the forest range into two subpopulations (West and Central) and the savannah range into four subpopulations (Northeast, Northwest, East and South) and compared only samples inferred to fall into the same subpopulation, using that subpopulation's reference allele frequencies. The above subpopulations are consistent with the divisions of the African Elephant Specialist Group[1] for forest elephants but add northwest and northeast divisions for savannah elephants due to their genetic distinctiveness from eastern and southern savannah elephants[28,29]. Reference samples were assigned to subpopulations on the basis of their inferred species from EBhybrids[28] and their location, while seizure samples were assigned to subpopulation using the subregional inference option of SCAT2 v.3.0.0 (ref. [29]). We tested the accuracy of subpopulation assignment by using SCAT2 to infer the subpopulation of the location-known reference samples and found 99.2% accuracy in forest and 78.7% accuracy in savannah elephants (Supplementary Table 6).

An mtDNA analysis was used to check accuracy of relationship assignments. We found that EMs were accurately identified, with 1/1 putative EMs in forest and 10/10 in savannah showing identical mtDNA. However, putative full-siblings were often discordant for mtDNA (4/12 forest pairs and 110/181 savannah pairs) indicating that the approach cannot distinguish full-sibling pairs from parent/offspring or half-sibling pairs, as also seen in simulated data (below). We therefore group all relationship categories as 'close relatives' for this study.

Simulation studies. The performance of this approach was assessed using a simulation of unrelated pairs to estimate false-positive rates and a simulation of related pairs to assess false negatives.

Unrelated pairs. We used SCAT2 v.3.0.0 (ref. [29]) to estimate allele frequencies in each sampling location (for example, protected areas) on the basis of reference samples from that location and nearby locations, weighted by distance. For simulation purposes we did not use sampling locations with fewer than ten samples, although their data were still incorporated into allele frequencies for other locations. We simulated 3,000 unrelated individuals per subpopulation, divided as evenly as possible among sampling locations, by random independent draws from the sampling location allele frequencies. We estimated the proportion of missing data for each of the 16 microsatellite loci, separately for forest and savannah elephants, in our seizure data. We then randomly marked loci as missing in the simulated data at the corresponding rate. We performed familial matching analysis on all pairs that came from different simulated sampling locations, discarding pairs with fewer than 13 non-missing loci in common. To improve precision, we repeated the simulation process twice. Table 1 shows the false-positive rates calculated from matches found among simulated unrelated individuals from different sampling locations, tabulated by $\log_{10}$(LR) category. The lower false-positive rate of close-relative matching in forest elephants is apparently due to higher genetic diversity in the forest population as reflected in its higher θ value.

False-positive rates were higher in comparisons among simulated individuals from the same sampling location, indicating that some population structure is not captured by the division into subpopulations. We have chosen to use different-location false-positive rates in our analysis, on the grounds that matches between individuals taken from the same park or reserve, even if they are not in fact close relatives, probably indicate activity of the same poachers.

Relative pairs. We simulated family groups consisting of three parents (P1, P2 and P3) and an unrelated fourth individual (U) by choosing a sampling location and drawing from its inferred allele frequencies as above. We then simulated two offspring of P1 and P2 (yielding a full-sib pair) and one offspring of P1 and P3 (which formed two half-sib pairs with the previous two offspring). Our data for each family group consisted of P1, P3, U and the three offspring (P2 was not used to maintain independence of comparisons). We simulated 100 such family groups per subpopulation, divided as evenly as possible across sampling locations with ten or more samples. Missing data were imposed as above. We then performed a familial matching analysis and tabulated the results on the basis of the true (simulated) relationships among individuals, separately for forest and savannah elephants, using a $\log_{10}$(LR) cutoff of 2.0. Results are shown in Supplementary Table 7. Close-relative matching was more powerful in forest elephants, presumably due to higher genetic diversity; over half of the simulated parent–offspring and full-sib pairs could be detected in forest elephants, whereas only about one-third could be detected in savannah elephants. Half-sib relationships were seldom detectable.

Genetic matching analysis. Within each subpopulation, we performed all possible pairwise LR calculations for EM, PO, FS and HS relationships for pairs of samples that shared at least 13 successfully typed loci. This resulted in 241,117 comparisons between forest elephants and 2,450,546 comparisons between savannah elephants. If $\log_{10}(LR)>2$ for PO, FS and/or HS, we consider the genetic evidence as favouring close relatedness.

As the hypotheses of close relationship and no relationship are non-nested, standard LR tests are not possible here. We therefore used simulation to assess significance of our results. Even though the false-positive rates were low in our simulations (Table 1), with the large number of comparisons being made numerous false positives would be expected. We used the estimated false-positive rates in Table 1 to weight observed matches on the basis of their $\log_{10}$(LR) bin. We tabulated matches in each bin across the entire forest or savannah elephant dataset and computed the number of expected false positives in that bin on the basis of the simulated data and the number of comparisons made. The weight of a match was then calculated as (observed matches – expected false positives)/observed matches. This approach treats the estimated false positives as if they were actual false positives and calculates the proportion of total matches that exceed the estimated false positives and are therefore putative true positives (the number of total matches was greater than the number of estimated false positives in all cases). These weights are shown in Table 1.

We modified this procedure in the case of EMs. We had previously published[7] EMs inferred by taking into account the possibility of allelic dropout, rather than requiring a perfect match at every locus. It was not feasible to include allelic dropout in our familial searches as the computational time was prohibitive. We therefore added EMs that had been previously published or, for seizures analysed after that study, determined using CERVUS[34], to those detected by the current method. EMs detected by the familial matching algorithm were invariably in the highest $\log_{10}$(LR) bin, so we placed EMs detected by other methods in this bin as well.

EMs between two seizures were considered stronger evidence of connection than a close-relative match, as the former represents possession of two tusks or tusk segments from the same elephant, which have almost surely passed through the same hands. We therefore applied a multiplier of five to the weight when scoring an EM. This multiplier is somewhat arbitrary since its quantification would require samples known to be from the same as well as different TCOs, which are unavailable. We tested whether this multiplier would impact the structure of our networks and found its effect to be negligible (see Seizure clustering below).

Network analyses. Linear network visualizations (Figs. 3 and 4 and Extended Data Figs. 1 and 2) were created in Jupyter Notebook using the NetworkX module[35,36]. They were then exported as JSON files and sent to RStudio, where they were visualized using the visNetwork package in a Shiny application we created specifically for viewing the networks[37,38]. High-quality screen captures were taken of the visualizations from the Shiny application and compiled into composite figures with Adobe Illustrator.

Separate visualizations were created on the basis of genetic matches (Figs. 3a, 4a and 5) and shared physical evidence (Figs. 3b and 4b). Genetic match links were formed if exact and/or close-relative matches with a combined weight of 1.0 or greater existed between two seizures. A weighted match of 1.0 indicates that our best estimate of the number of matches connecting two seizures is 1. We deemed weaker matches not to be solid evidence of connection. If a link contained both savannah and forest elephant matches, the link was maintained as long as the sum of the matches was 1 or greater.

Physical evidence was compiled by our law enforcement colleagues and included information from open-source data, bills of lading and other shipping documents, records of phone data analysis, court files and confidential sources. We considered 12 seizure traits:

(1) Port of origin (that is, where the shipment was assumed to be containerized)
(2) First transit location in Africa
(3) Whether the port of origin of one seizure matched the first African transit location of another seizure
(4) Shipment cover load
(5) Importer
(6) Exporter
(7) Transporter
(8) Clearing agent
(9) Ivory markings
(10) Phone data
(11) Nationalities of the accused
(12) Links between accused in different seizures, such as the same driver transporting both shipments or payments made by the same individual to multiple traffickers

If two seizures shared at least one of these 12 traits, we considered the seizures to be connected and formed a physical-evidence link.

For visualization, seizures were numbered chronologically on the basis of the date each seizure occurred. Seizures were then arranged in a linear layout on the basis of seizure ID number, with blank spaces and vertical divider lines added to delineate changes in seizure year. The position of the focal seizure in this linear format is identified by a grey open circle. Seizures with one or more genetic matches (Figs. 3a and 4a) or physical-evidence matches (Figs. 3b and 4b) to the focal seizure are indicated by a solid circle. The colours of these circles represent the countries where each ivory shipment originated, assumed to be where the ivory was containerized for export (see Fig. 1 for colour key).

Seizure clustering. Two methods, Louvain and structural equivalence analysis, were used to cluster seizures within the network on the basis of exact and close-relative matches only. In both cases, links with a weight <1 were removed before analysis. Louvain clusters were made using the Louvain-community module in NetworkX[36]; weighted matches were supplied as link weights. Louvain clustering sequentially clusters groups of nodes with a high density of connections between them and low density of connections with other groups; the number of clusters is chosen by the algorithm.

Structural equivalence clusters were made using the statnet, cluster and ClassDiscovery R packages[39–41]. Two seizures are structurally equivalent to one another to the degree that they share the same relationship to all other seizures. In other words, if one were to swap out one seizure for another, connections to all other seizures would remain the same if the swapped seizures are structurally equivalent. We calculated structural equivalence using Pearson's correlation because it only focuses on the pattern of connections (rather than the mean and variance) and takes into account the strength of the connection between each seizure[9]. From the output correlation values, we calculated correlation distance and ran a hierarchical cluster analysis on the distance matrix.

After the analysis, we determined the number of clusters (k) present in the networks on the basis of the silhouette coefficient at various values of k (ref. [42]). The silhouette coefficient is a value between −1 and 1 that indicates whether seizures are placed into the correct cluster. Negative values suggest that a seizure is placed in an incorrect cluster while positive values confirm a seizure is assigned its proper cluster. A value of 0 indicates that a seizure exists between two clusters and could fit into either of them equally well. In choosing the number of clusters, we aimed to maximize the average silhouette coefficient for the genetic networks. We chose six clusters even though there were higher-scoring values of k because the higher values of k produced clusters made up of relatively uninformative dyads.

After deciding on six clusters, we examined the silhouette coefficient for each individual seizure. We refined the clustering manually, placing misclassified seizures into their nearest neighbour cluster. This refinement resolved the misclassifications and slightly increased the average silhouette coefficients.

Layout was then performed using the SFDP algorithm in graph-tools using the Louvain categories to guide layout and then hand-optimized to improve visibility of connections. Link thicknesses were proportional to weighted matches with a power parameter of 0.4. As in the linear networks, seizure nodes were coloured on the basis of the countries where each ivory shipment originated. Clusters were circled on the basis of their classification for both the Louvain and structural equivalent approaches. Both networks were displayed with the same layout and similar clusters were labelled with the same name to facilitate comparison.

Finally, we tested whether our arbitrarily assigning a weight of 5× to EMs relative to close-relative matches impacted the structure of these networks. We repeated both the Louvain and structural equivalence analyses with weights for an EM ranging from 1× to 10× the weight of a relative match. The weights resulted in negligible change in number of clusters or cluster composition, indicating that the choice of 5× weight was not impacting our network results.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

DNA sequences have been deposited in GenBank (accession numbers OK382584–OK382941; http://www.ncbi.nlm.nih.gov/nucest?term=OK382584:OK2941). Data related to this paper may be requested from the authors. However, ivory samples and genetic data derived from them are subject to restricted access (see https://obamawhitehouse.archives.gov/the-press-office/2014/02/11/fact-sheet-national-strategy-combating-wildlife-trafficking-commercial-b and https://obamawhitehouse.archives.gov/the-press-office/2014/02/11/fact-sheet-national-strategy-combating-wildlife-trafficking-commercial-b for the US regulatory conditions currently governing trade in ivory, which may also apply to availability of samples). Software used in this study is available on GitHub: EBhybrids, https://github.com/stephenslab/EBhybrids; familial matching, https://github.com/cwolock/elephant_fam_match; SCAT, https://github.com/stephens999/scat; VORONOI, https://github.com/stephens999/voronoi; ivory, analysis, pipeline, https://github.com/mkkuhner/ivory_pipeline.

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Author contributions

The idea for the study was conceived by S.K.W. Sampling was conducted by S.K.W., J.E.B., A.W., C.J.F. and M.Y.O. Laboratory analyses were conducted by Y.H., Z.A.K., E.J. and K.H. Familial searches and analyses were conducted by C.J.W., M.K.K. and B.S.W. Network analyses were conducted by R.H. and M.K.K. Physical evidence was compiled by J.E.B., C.M. and S.K.W. Manuscript preparation was by S.K.W., M.K.K., C.J.W., J.E.B., C.M. and R.H. Manuscript edits were by S.K.W., C.J.W., J.E.B., C.M., R.H., M.K.K. and B.S.W.

Competing interests

The authors declare no competing interests.

Additional information

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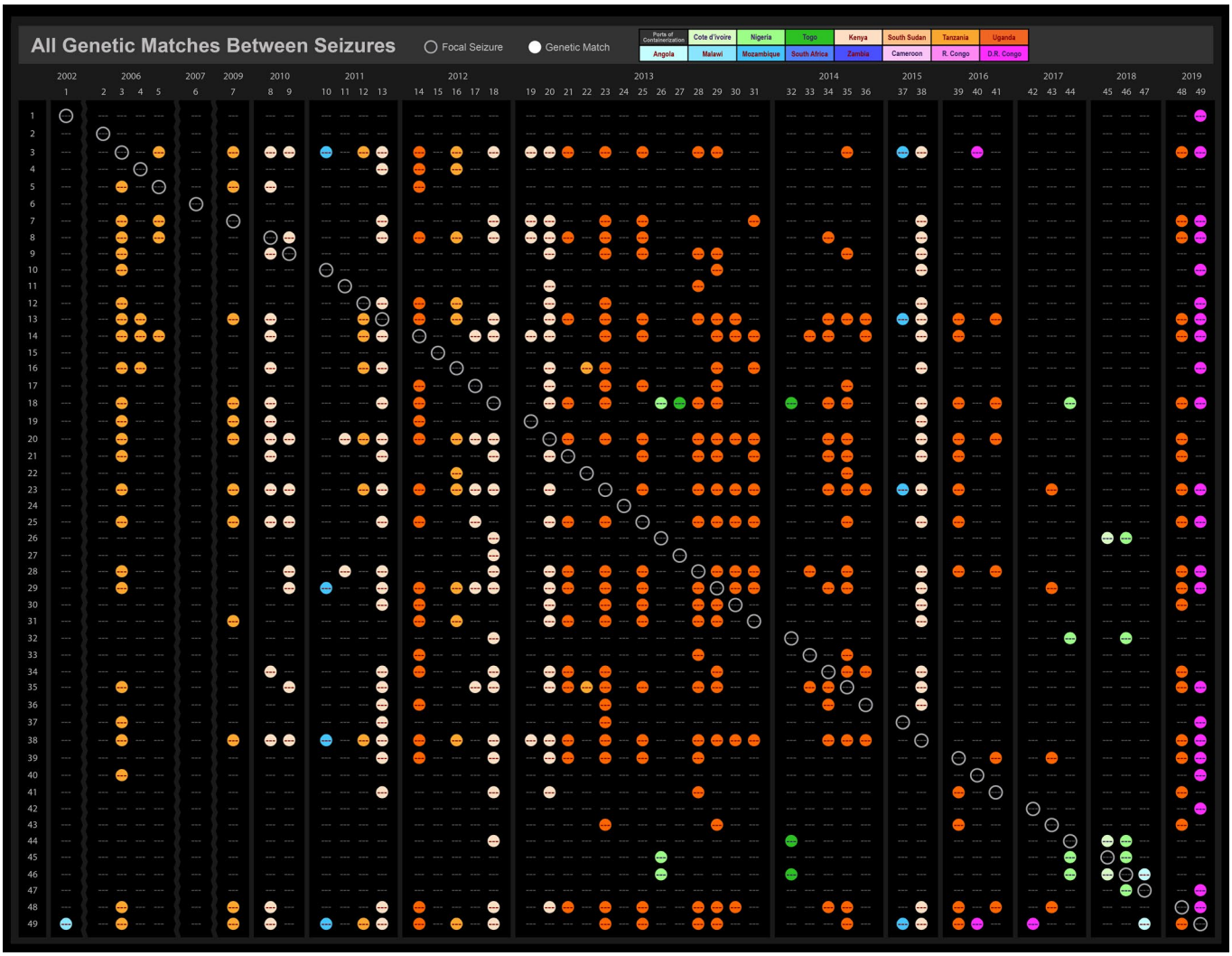
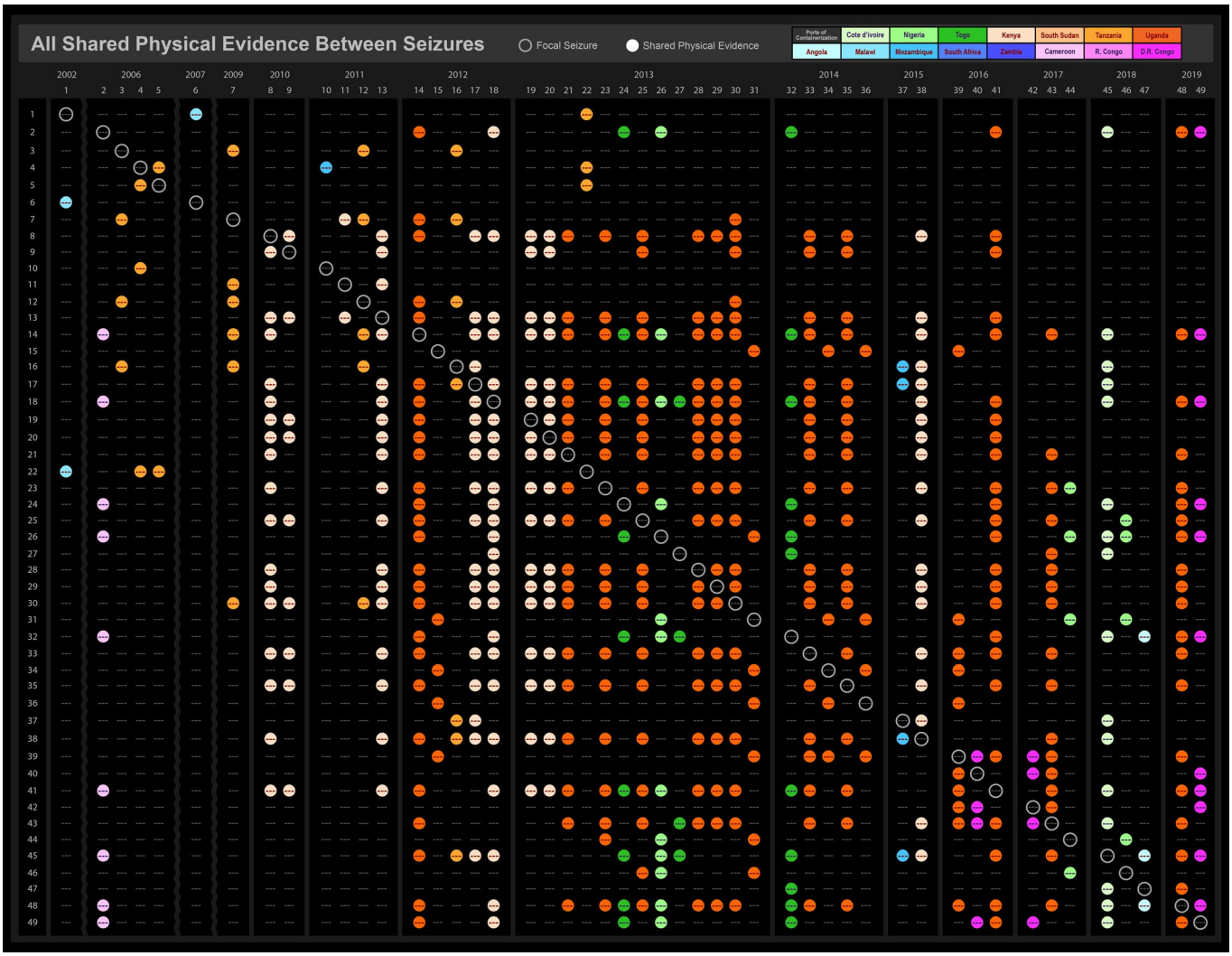


Extended Data Fig. 1 | Genetic matches between tusks found in separate ivory seizures. Format is the same as in Fig. 3a. Seizure number key: 1 = SGP, 06-02, 6.5t; 2 = HKG, 05-06, 3.9t; 3 = HKG, 07-06, 2.6t; 4 = TWN, 07-06, 1.2t; 5 = TWN, 07-06, 3.0t; 6 = SGP, 03-07, 0.5t; 7 = PHL, 06-09, 4.9t; 8 = VNM, 04-10, 2.2t; 9 = KEN, 08-10, 1.5t; 10 = THA, 01-11, 0.33t; 11 = KEN, 05-11, 1.3t; 12 = MYS, 09-11, 1.1t; 13 = KEN, 12-11, 1.5t; 14 = LKA, 05-12, 1.5t; 15 = UGA, 09-12, Xt,;16 = HKG, 10-12, 1.9tA; 17 = HKG, 10-12, 1.9tB; 18 = MYS, 12-12, 6.0t; 19 = HKG, 01-13, 1.3t; 20 = KEN, 01-13, 3.8t; 21 = ARE, 05-13, 1.5t; 22 = MWI, 05-13, 2.6t; 23 = KEN, 06-13, 1.5t; 24 = HKG, 07-13, 2.0t; 25 = KEN, 07-13, 3.3t; 26 = HKG, 08-13, 2.2t; 27 = TGO, 08-13, 0.7t; 28 = KEN, 10-13, 2.0t; 29 = KEN, 10-13, 2.9t; 30 = UGA, 10-13, 2.9t; 31 = UGA, 12-13, 1.4t; 32 = TGO, 01-14, 3.9t; 33 = SGP, 03-14, 1.0t; 34 = UGA, 05-14, 1.8t; 35 = KEN, 06-14, 2.2t; 36 = UGA, 07-14, 0.6t; 37 = MOZ, 05-15, 1.2t; 38 = SGP, 05-15, 4.6t; 39 = SSD, 06-16, 0.5t; 40 = MYS, 07-16, 0.89t; 41 = KEN, 12-16, 1.0t; 42 = MYS, 01-17, 0.85t; 43 = UGA, 02-17, 1.3t; 44 = HKG, 07-17, 7.2t; 45 = CIV, 01-18, 0.5t; 46 = SGP, 03-18, 3.3t; 47 = AGO, 06-18, 1.8t; 48 = UGA, 01-19, 3.3t; 49 = SGP, 07-19, 8.8t. ISO Key: AGO = Angola, ARE = United Arab Emirates, CIV = Cote d'Ivoire, HKG = Hong Kong, KEN = Kenya, LKA = Sri Lanka, MOZ = Mozambique, MWI = Malawi, MYS = Malaysia, PHL = Philippines, SGP = Singapore, SSD = South Sudan, TGO = Togo, THA = Thailand, TWN = Taiwan, UGA = Uganda, VNM = Vietnam.



Extended Data Fig. 2 | Physical-evidence matches between tusks found in separate ivory seizures. Format is the same as in Fig. 3b.

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DNA sequences have been deposited in GenBank (accession numbers OK382584 - OK382941).

Data related to this paper may be requested from the authors. However, ivory samples and genetic data derived from them are subject to restricted access (see www.whitehouse.gov/thepress-office/2014/02/11/fact-sheet-nationalstrategycombating-wildlife-trafficking-commercial-b for the U.S. regulatory conditions currently governing trade in ivory, which may also apply to availability of samples).

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	n/a
Research sample	Sample are microsatellite DNA profiles from singleton ivory tusks (one tusk per elephant), representatively sampled.
Sampling strategy	We attempted to acquire all large ivory seizures we could find. However, access was country dependent. Sampling begin with visually excluding one of the two tusks from the same elephant when detected, dividing the remaining singleton tusks into groups based on physical characteristics that suggest they might have been in the same place at the same time (e.g., tusks cut into sections versus whole, white tusks versus orange tusks colored from being buried in the same soil, tusks with handwriting on them). We then selected up to 200 tusks per seizure, selected randomly from each group in proportion to the group size.
Data collection	All features of the tusk were recorded directly on an Excel spreadsheet, including weight, diameter at base and any distinguishing features on the tusk (e.g., color, hand-writing on tusk)
Timing and spatial scale	Sampling occurred from 2005-2019, whenever ivory seizures could be accessed.
Data exclusions	In network construction, only sample pairs with 13+ shared non-missing loci were used. In familial matching, only pairs with 10+ shared non-missing loci were used. Samples with ≥ 50% probability of being a hybrid elephant were excluded. When both tusks from the same elephant were in the dataset, one of the two was excluded.
Reproducibility	n/a
Randomization	We attempted to acquire all large ivory seizures we could find. However, access was country dependent. Sampling begin with visually excluding one of the two tusks from the same elephant when detected, dividing the remaining singleton tusks into groups based on physical characteristics that suggest they might have been in the same place at the same time (e.g., tusks cut into sections versus whole, white tusks versus orange tusks colored from being buried in the same soil, tusks with handwriting on them). We then selected up to 200 tusks per seizure, selected randomly from each group in proportion to the group size.
Blinding	n/a

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Sampling occurred in secure government facilities where the ivory was stored.
Location	Various countries throughout Africa and Asia
Access & import/export	All samples were imported with CITES import and export permits, cleared and stamped by customs in the course country and by US Fish and Wildlife Service upon arrival in the USA
Disturbance	n/a

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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