

CONSERVATION

Genomic analyses reveal poaching hotspots and illegal trade in pangolins from Africa to Asia

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The white-bellied pangolin (*Phataginus tricuspis*) is the world's most trafficked mammal and is at risk of extinction. Reducing the illegal wildlife trade requires an understanding of its origins. Using a genomic approach for tracing confiscations and analyzing 111 samples collected from known geographic localities in Africa and 643 seized scales from Asia between 2012 and 2018, we found that poaching pressures shifted over time from West to Central Africa. Recently, Cameroon's southern border has emerged as a site of intense poaching. Using data from seizures representing nearly 1 million African pangolins, we identified Nigeria as one important hub for trafficking, where scales are amassed and transshipped to markets in Asia. This origin-to-destination approach offers new opportunities to disrupt the illegal wildlife trade and to guide anti-trafficking measures.

Overexploitation is one of the greatest threats to biodiversity worldwide (1). In particular, the illegal wildlife trade is accelerating the extinction of thousands of species globally (2, 3). Determining where animals are poached is a major challenge in curbing this exploitation, especially for internationally trafficked species such as pangolins (4–7). Pangolin scales are used as an ingredient in traditional medicines, despite no evidence of their efficacy (8). The largest markets for these products are in China (9–11). As populations of the Asian species of pangolins have declined, smugglers have begun importing African pangolins to meet demand (5, 12–14). Consequently, the white-bellied pangolin (*Phataginus tricuspis*), which occurs throughout Western and Central Africa, from Guinea to Zambia, is now the most trafficked mammal in the world (11, 15–19).

Given the extensive geographic range of white-bellied pangolins and many other trafficked species, identifying poaching hotspots at a scale

that is useful to law enforcement is crucial for conservation efforts. Without genetic data to reveal the true geographic origins of poached animals or products, seizures by law enforcement agencies offer limited information about their sources. For example, pangolin scales arriving in China from Nigeria may have originated there or been amassed and transshipped from other countries (5, 20). Determining the precise origins of animals involved in the global wildlife trade is an urgent priority (3, 21).

Here, we report an origin-to-destination approach for understanding where pangolins are harvested, amassed, shipped, and consumed. First, we mapped geographically and genetically distinct populations of white-bellied pangolin using 111 samples collected from wild pangolins at known localities across their range. We then used this spatially explicit genomic map to assign 643 confiscated scales to their previously unknown geographic origins (22). By sampling 32 confiscations seized between 2012 and 2018, representing over 100,000 trafficked pangolins,

we mapped pangolin poaching hotspots and documented changes in poaching pressure over time. Next, we analyzed data on pangolin trafficking incidents to connect poaching hotspots with common trafficking routes to markets. Our approach enables the monitoring of changes in poaching in near real-time, allowing for targeted and more effective anti-poaching measures.

Building a spatially explicit genomic map for white-bellied pangolins

We obtained 551 georeferenced samples from wild white-bellied pangolins. These samples included blood dots, muscle, and scales donated by pangolin hunters and recent tissue specimens from natural history collections (see materials and methods and data S1). To ensure fine-scale resolution for the map, we only included samples whose locality data were collected with a GPS unit. We excluded samples from urban and suburban bush meat markets, which may have obtained their pangolins through regional supply chains.

We extracted DNA that yielded high-quality genome sequences from 111 samples, which were used to construct the white-bellied pangolin genomic map (Fig. 1). The analyzed genomes contained over 4 million single-nucleotide polymorphisms (SNPs). We used principal component analysis and ADMIXTURE (23) to visualize genetic variation and identify distinct genetic clusters (fig. S1). We identified five distinct population groups that were strongly associated with distinct geographic regions (Fig. 1).

Genotyping confiscated scales to reveal poaching hotspots

We used the genomic variation detected in wild populations to generate a panel of 96 diagnostic SNPs for assigning unknown samples to their geographic origins (data S2). We tested the accuracy and precision of the SNP genotyping assay using the 111 mapped samples by first assigning them to distinct genetic clusters using the program rubias (24) and then predicting the geographic location of samples using OriGen (25). Rubias assigned 110 samples to the correct genetic cluster (99% accuracy), and our assay correctly localized 87.4% of these samples using OriGen (defined as within 500 km of

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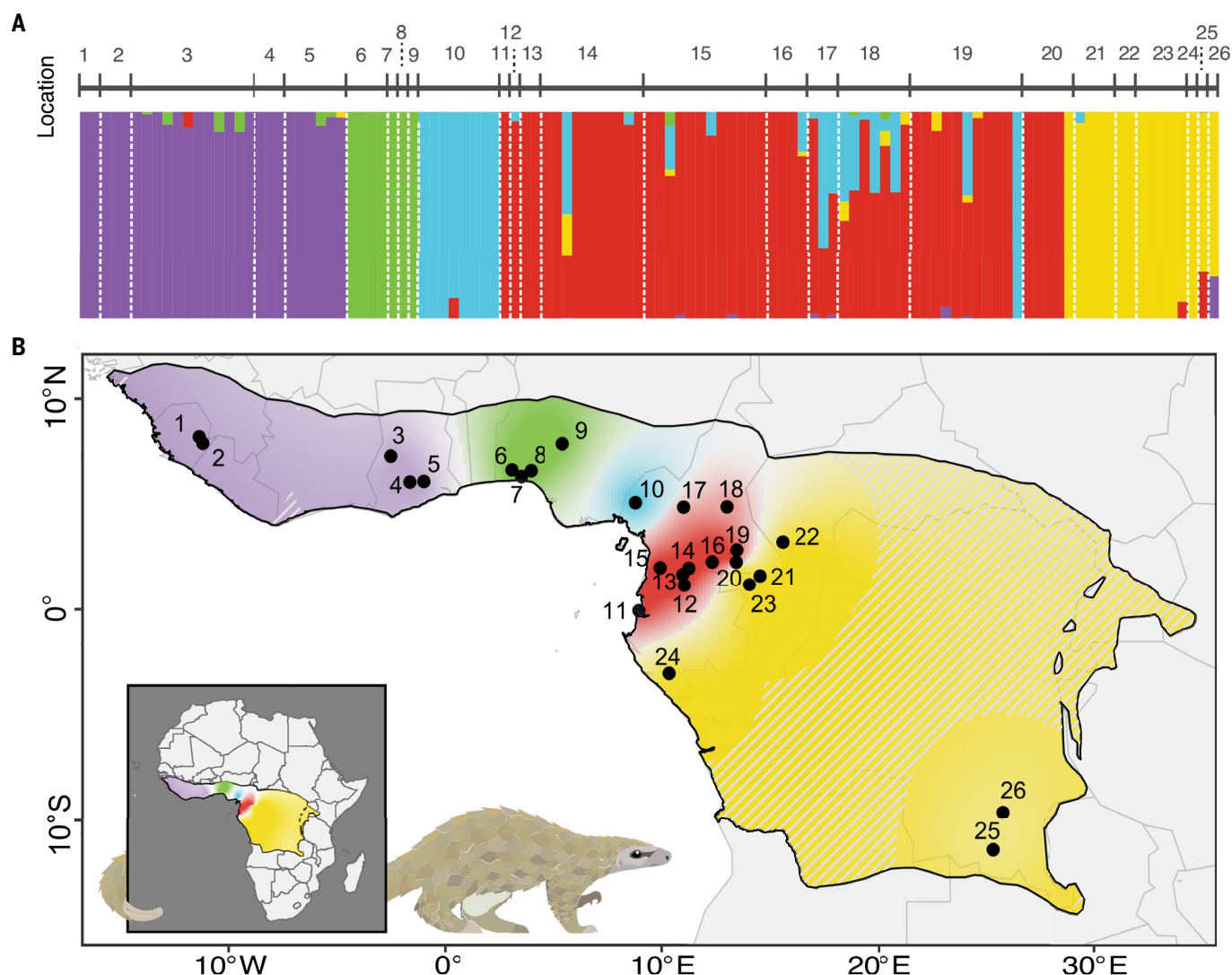


Fig. 1. Map of genomically identified white-bellied pangolin population clusters. (A) ADMIXTURE plot based on whole genomic data. The colored bars represent each sample's probability of assignment to genetically distinct population clusters. **(B)** Map of population clusters. Black dots indicate the 26 locations of the 111 samples included in the construction of the map. The intensity of the color represents the interpolation model's confidence that the indicated cluster occurs in that location. Areas more than 500 km away from a sampled locality are striped, showing more extensive interpolation, and will likely reveal subpopulation structure with additional sampling (fig. S1). [Pangolin illustration by S. McCabe]

their known origin; fig. S2). The 97 correct localizations had a median error of 63.5 km (mean, 126.0 km). Of the 14 incorrectly localized samples, 13 were still assigned to the correct genetic cluster. Median error for all scale location assignments was 72.2 km; mean error was 236.1 km.

Assignment errors were not randomly distributed across population clusters, either in magnitude or in frequency (fig. S2 and tables S1 to S3). We achieved the best resolution in the population clusters where sampling was densest. Incorrect localizations happened in clusters of populations spanning large geographic areas with fewer samples. For instance, the assay predicted that two individuals from southeastern Democratic Republic of the Congo (DRC) originated closer to the Central African Republic (fig. S2).

Additional sampling likely will resolve subpopulations within the five major population clusters (Fig. 1). This might also reduce the frequency and magnitude of misassignment errors, especially in the West African and Congo Basin clusters. Until the SNP assay is refined to include data from undersampled regions, OriGen-generated coordinates that fall within those ranges or plot far outside of densely sampled areas should be treated with caution (25).

We SNP genotyped 656 confiscated white-bellied pangolin scales. Authorities in Hong Kong SAR, China, seized these scales from 32 shipments, arriving from at least seven separate transit routes, between 2012 and 2018 (data S3). These seizures weighed a collective 38 tonnes and represented an estimated minimum of 105,447 dead pangolins. We successfully

genotyped 647 of these scales and assigned 643 (98%) to one of five distinct pangolin genetic clusters with >80% posterior probability. We then estimated their geographic origins (fig. S3).

Genotyping confiscated white-bellied pangolin scales revealed two major pangolin poaching hotspots. The vast majority of the 643 genotyped scales originated along Cameroon's southern border with Equatorial Guinea and Gabon, and from western Cameroon, near the border with Nigeria (Fig. 2 and data S4).

Comparing genomics with data on pangolin seizures

To compare genetically determined pangolin origins to those available from extant data sources, and to identify the trafficking routes used to smuggle scales to markets, we developed

a database of pangolin seizures (data S5). We found data on 3097 seizures of pangolins from January 1981 through December 2022 (fig. S4), at least 999 of which included African species. Using published scale-mass-to-individual conversion metrics (16, 20), we estimated that these seizures represented at least 986,894 poached African pangolins.

Network mapping of African pangolin seizures identified Nigeria as the highest-volume transit hub in Africa, where traffickers amass pangolin scales before shipping them overseas (Fig. 3 and fig. S5) (20, 26). Nigeria's seizures are more comparable to those of non-African transit locations, such as Hong Kong SAR, China, and Turkey (table S4). However, data from public records of illegal activity are subject to major biases such as law enforcement effort and media interest in large seizures (27). We investigated whether these reports could provide a reliable picture of where pangolins are poached.

The seizures database rarely indicated non-Nigerian origins for pangolins that transited through Nigeria (95.1% of seized animals have no recorded source other than Nigeria). By contrast, our genetic assay results show that only 4.2% of pangolins shipped from Nigeria originated there. Most of the pangolins in our samples that transited through Nigeria originated in southern Cameroon, mainland Equatorial Guinea, and Gabon (Fig. 3). For example, a 2018 seizure consisted of 7.1 tonnes of scales shipped by cargo container from Nigeria to Hong Kong SAR, China (#613/2018, data S3). However, the pangolins in our sample of this seizure originated in Cameroon, Equatorial Guinea, Gabon, and the Republic of the Congo (fig. S6; data S4).

Our results reveal the importance of using genetic data to understand pangolin poaching. Reports by law enforcement officials and anti-trafficking nongovernmental organizations such as those in the seizures database can show

major shipping routes (figs. S7 to S9) and guide the interception of shipments already in progress, but they cannot reliably identify where pangolins are harvested (Fig. 3).

Conversely, genetic assignments of scales do not reveal the intermediate stops that they take to market. Taken together, genetic analyses and seizure data show a major origin-to-destination trafficking route for white-bellied pangolins. Results suggest that the samples that we analyzed were harvested in southern Cameroon, Equatorial Guinea, and Gabon; amassed in Nigeria; transported to intermediate destinations in southeast Asia, often by sea; and ultimately used in southeastern provinces of mainland China, particularly Guangdong and Guangxi (Fig. 4).

Tracking poaching over time

Our results provide a geographically explicit understanding of where global trafficking networks threaten white-bellied pangolins most. However, our study and past work suggest that these routes will likely change over time, and continuous monitoring is necessary to detect changes in trafficking patterns (18).

Indeed, testing seizures confiscated over just 7 years (2012–2018) enabled us to detect changes in the origins of trafficked pangolins. Early on, poaching activity was confined to West Africa before shifting to Central Africa more recently (Fig. 5). These changes in trafficking patterns could represent (i) a response to increased enforcement; (ii) declining pangolin populations in West Africa; or (iii) taking advantage of new, convenient trade routes, or a combination thereof (14, 16). With over half a million African pangolins seized from the illegal wildlife trade in that time frame (fig. S4), unsustainable exploitation seems all but certain. We believe this number probably represents a gross underestimate of the trade in African species, because most confiscations in Asia do not document species or origin information. Further, many shipments are never detected at all (16).

Unsustainable harvest of the West African population of white-bellied pangolin has shifted pressure onto two geographically restricted populations (Figs. 1 and 5). Their limited range and high levels of exploitation make them some of the most threatened populations of white-bellied pangolins. Moreover, the threats that these populations face will likely increase with the construction of new ports, roads, and rail lines in the region (28–30). For example, the rapidly growing Kribi Deepwater Port facility and associated road network in southwestern Cameroon could easily provide transport for pangolins poached in the southern hotspot that we identified (Fig. 2). As a result, populations in southern Cameroon, northern Equatorial Guinea, and Gabon are at particularly high risk of overexploitation (30–32).

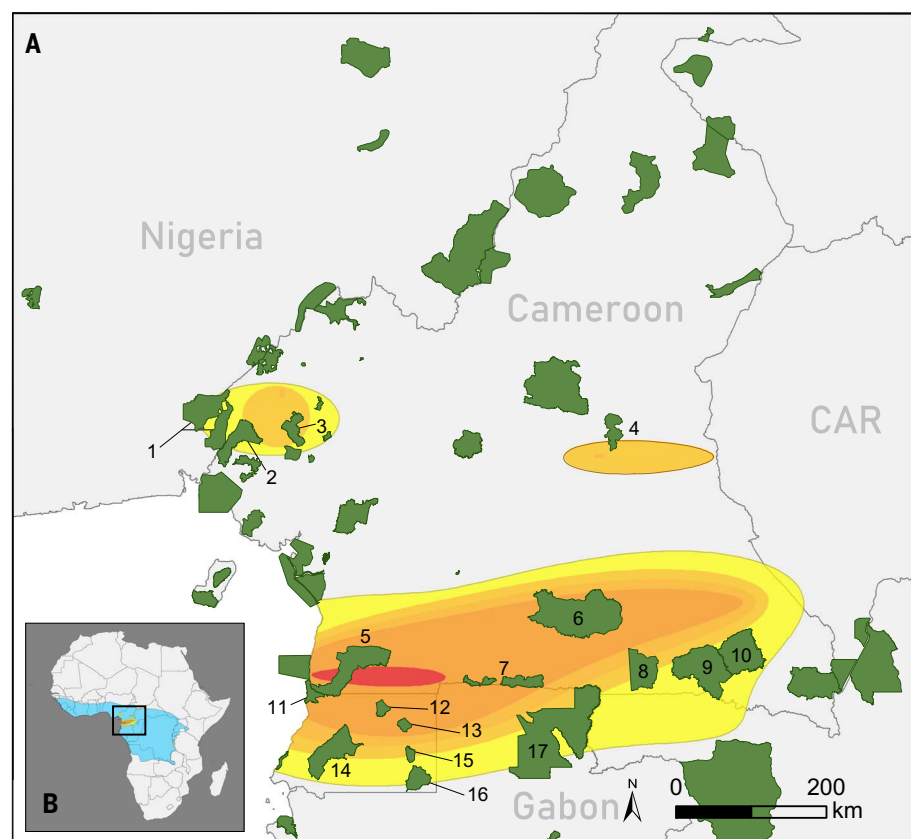


Fig. 2. Pangolin poaching hotspots. (A) Hotspots were derived from scales confiscated in Hong Kong SAR, China, between 2012 and 2018. Warm colors indicate areas where the bulk of scales in our sample originated, and warmer colors indicate an even greater density of scales originating there. Protected areas (in green) associated with poaching hotspots are (1) Cross River National Park, Nigeria; (2) Korup National Park, Cameroon; (3) Bayang Mbo Wildlife Sanctuary, (4) Deng Deng National Park, (5) Campo Ma'an National Park, (6) Dja Faunal Reserve, (7) Mengame Gorilla Sanctuary, (8) Ngoyla Faunal Reserve, (9) Nki National Park, (10) Boumba Bek National Park, and (11) Rio Campo Nature Reserve, Equatorial Guinea; (12) Monte Temelón Nature Reserve, (13) Piedra Bere Natural Monument, (14) Monte Alén National Park, (15) Piedra Bere Natural Monument, (16) Altos de Nsork National Park, and (17) Minkébé National Park, Gabon. Protected Area was defined as any conservation landscape falling into IUCN Protected Area Categories I–IV (UNEP-WCMC and IUCN 2022). (B) Location of hotspots in relation to the range of the white-bellied pangolin (in blue) (33).

Fig. 3. Network model of the flow of African pangolins and a comparison of genetic and report-based data. (A) Line widths indicate the relative quantity of pangolins shipped along each route, and line colors indicate the origin country. Only routes with a total greater than 10,000 pangolins and/or individual-equivalents by weight shipped are shown. (B) The origins of smuggled pangolins that transited through Nigeria, as indicated by traditional data from seizures reports and as determined using genomics. Percentages are also presented in tables S5 and S6.

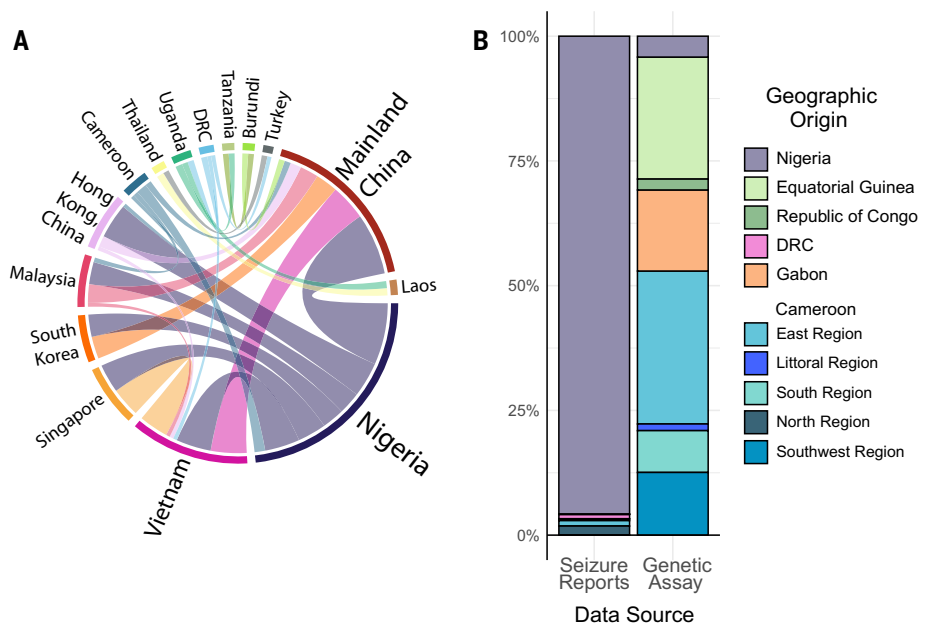
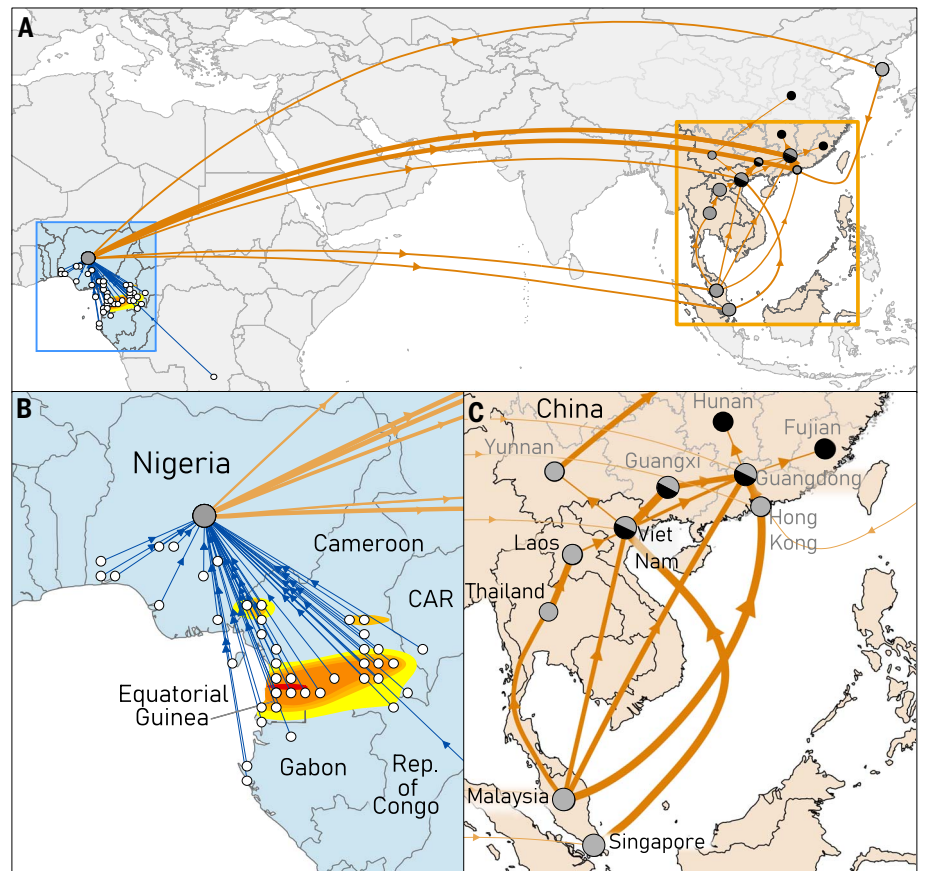


Fig. 4. An origin-to-destination map of pangolin trafficking. A combination of genomics (blue lines) and publicly reported data on pangolin seizures (orange) reveal major trafficking routes. This map focuses on pangolins that transited through Nigeria. White dots represent estimated pangolin origins, transit locations are gray, and market or consumption locations are black. Line widths reflect the quantity of pangolins smuggled along a route. These lines represent possible routes between known stops, not the actual paths taken by trafficked scales. (A) Transcontinental routes for trafficking African pangolins to Asia. CAR, Central African Republic. (B) A zoomed-in look at source localities for African pangolins transited through Nigeria. We picked a central point in Nigeria for visualization—most of these scales left the country via seaport. (C) Routes taken by African pangolins once they arrive in Southeast Asia.



When wildlife traffickers encounter increased enforcement, they typically move their operations (18). The genetic assay presented here will allow for near real-time monitoring of shifts in poaching hotspots. Our assay can localize most samples within 100 km of their geographic origin (median error: 72.2 km across

all samples). This is very precise, considering that the white-bellied pangolin's distribution covers roughly 6 million km² (33, 34). Large confiscations of white-bellied pangolin scales often represent multiple individuals poached in different locations. If sampled forensically, these seizures could give us a snap-

shot of poaching activity across West and Central Africa, complementing and extending data available from elephant ivory seizures (6, 7, 34). Given the discovery of novel severe acute respiratory syndrome (SARS)-related coronaviruses in Asian pangolin seizures (35), our assay could also provide spatial insights

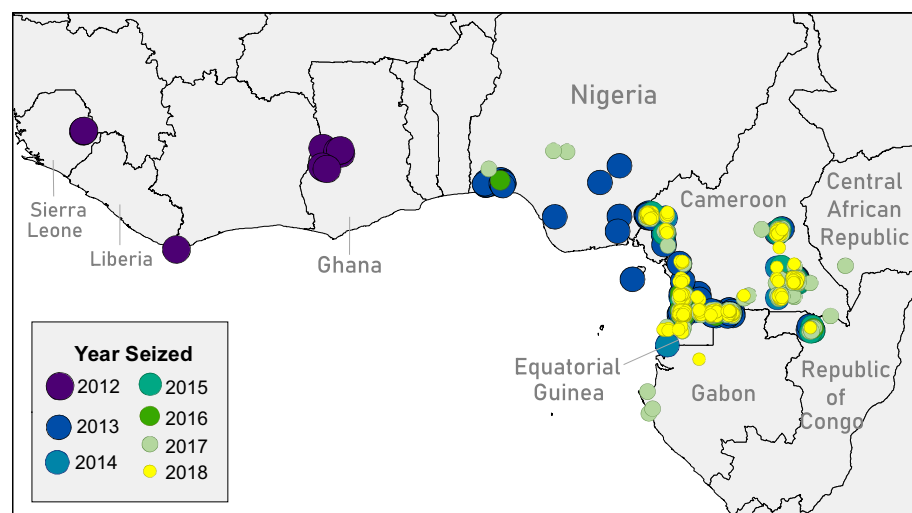


Fig. 5. Changes in pangolin poaching over time. A map of the predicted origins of 643 confiscated white-bellied pangolin scales. Authorities in Hong Kong SAR, China, confiscated these scales in 32 shipments originating from Nigeria, Cameroon, Egypt, Cote d'Ivoire, and Kenya (data S3). One scale, which originated in southeastern DRC and was seized in 2017, is not pictured. The precise location of the scales that were assigned to the West African population cluster (purple), should be treated with caution, as the SNP assay currently experiences relatively high rates of localization error in that cluster. Even so, given the diversity of genotypes observed in the scales from 2012, it seems likely that there were multiple geographic sources within the West African cluster.

into zoonotic disease risk. Compared with traditional law enforcement investigations, the genetic assay reduces the time lag between intercepting wildlife products, tracing an international supply chain to its origins, and reactive enforcement. This approach can dynamically guide preventive efforts by revealing poaching hotspots, representing an important step forward in conserving this highly trafficked species.

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SUPPLEMENTARY MATERIALS

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