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Role of transit countries in global illegal wildlife trade

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Abstract

Illegal wildlife trade is an important branch of global environmental crime. It relies heavily on transit countries to promote the cross-border movement of illegal wildlife products by boosting markets, laundering services, processing and packaging products, and concealing routes. However, transit countries' strategic role is not well understood. We constructed a dataset of 15 years of illegal wildlife seizure cases from the Center for Advanced Defense Studies (C4ADS) air seizure database and Wildlife Trade Portal database. From the dataset, we determined transnational illegal wildlife trade routes with complete supply chain information. There were 84 transit countries, and the organisms involved in trade included mammals, birds, reptiles, marine species, amphibians, and arthropods. We identified that about 40% of illegal wildlife trade routes crossed one or multiple countries. Species being moved along these routes originated mainly from Africa and were transported through African, European, or Asian countries to East Asia or Southeast Asia. Transit countries for illegal wildlife products tended to be geographically close to and have a high trade volume of legal biological products with both the origin and destination countries and had advanced airport infrastructure. Transit countries were associated with 39.7% more individual animal products being illegally traded, particularly ivory, pangolin products, and rhinoceros horn, and served as key bridges among economically underdeveloped and geographically distant countries with weak trade links in legal biological products. These findings highlight the importance of monitoring and enforcement in transit countries and suggest that transit hubs be targeted based on location, trade in legal biological products, and transport infrastructure.

KEYWORDS
high-value species, transit hub, transnational routes, wildlife crime, wildlife trafficking

INTRODUCTION

The illegal wildlife trade is an important branch of global environmental crime, has become the fourth largest black market industry after drug trafficking, human trafficking, and arms trafficking, and has an annual transaction value up to $20 billion (INTERPOL, 2023; UNODC, 2020). This vast amount of illegal activity severely threatens biodiversity (Benitez-Lopez et al., 2017; Hughes et al., 2023; Morton et al., 2021). Nearly 6000 wildlife species are involved, which has led to an unprecedented decline in the populations of iconic species, such as elephants, rhinoceros, pangolins, and tigers (UNODC, 2020), accelerated species invasions (Reino et al., 2017), and the spread of zoonotic diseases (Daszak et al., 2000; Xiao et al., 2020). Illegal wildlife trade often coincides with corruption, armed violence, and money laundering activities (INTERPOL, 2023; UNODC, 2020), which can fuel the spread of drug trafficking, arms trafficking, and human trafficking (Avis, 2017; South & Wyatt, 2011). Although illegal wildlife trade has received high levels of attention by international organizations, such as the International Union for Conservation of Nature, the United Nations Office on Drugs and Crime, and the World Wide Fund for Nature, and led to the establishment of governance frameworks through international agreements, such as the Convention on International Trade in Endangered Species (CITES), the scale of illegal wildlife trade is alarmingly high (UNODC, 2024).

The illegal wildlife trade has a highly complex transnational supply chain that involves origin, transit, and destination countries (Keskin et al., 2023; TRAFFIC, 2015). Currently, 162 countries are involved in illegal wildlife trade (UNODC, 2024). Illegal wildlife products are transported from origin countries, either directly to the destination countries or through one or

multiple transit countries, before reaching their final destination (UNODC, 2024). Although the scale, driving factors, and impacts of illegal wildlife trade in the origin and destination countries have been studied extensively (Liang et al., 2023; Tinsman et al., 2023; van Uhm & Wong, 2021; Wasser et al., 2007; Wittemyer et al., 2014), little is known about the role of the transit countries. This imbalance is reflected in the existing international policy frameworks (such as CITES Conference of the Parties resolutions), which mainly focus on the origin and destination countries (CITES, 2024). Studies of illicit activities, such as human trafficking and environmental crimes, suggest that transit countries provide a convenient and low-risk conduit for illicit activities by concealing trafficking routes (Perrin, 2010; UNODC, 2013), reprocessing and packaging products (Runhovde, 2017; UNODC, 2024), laundering illegal transactions (Elliott, 2012), and brokering cross-border and large-scale trade (Runhovde, 2017). However, the strategic role of transit countries in the illegal wildlife supply chain remains unclear.

Only a few studies have focused on transit countries, particularly on those involved in trafficking high-value species in specific regions. Germany and Myanmar are important transit hubs for pangolin smuggling (Heinrich et al., 2019; Nijman et al., 2016; Zhang et al., 2017), and Kenya, Thailand, and China are key transit points for the trafficking of ivory, rhinoceros horn, and tiger products (Patel et al., 2015). South Africa and Uganda have become transit hubs for African ivory flowing to Asian markets due to their favorable geographic locations, good infrastructure, and weak governance (Runhovde, 2017; Warchol et al., 2003). The illegal wildlife trade represents a complex global network that includes numerous transit nodes that extend far beyond specific regions, and the involved species are not limited to high-value wildlife. To our knowledge, no one has systematically analyzed the characteristics of transit countries and their role in the supply chain at a global scale.

Research on the operational mechanisms of the illegal wildlife trade supply chain has focused mostly on its connection with other trade supply chains. Criminals often hide illegal wildlife trading behind legitimate trading operations to reduce detection risks (Duensing et al., 2023), and the routes and modes of transportation for wildlife trafficking often overlap with those of other illicit activities, such as human trafficking, drug trafficking, and arms smuggling, and these activities are often linked to money laundering and barter trade (Avis, 2017; van Uhm et al., 2021). However, existing studies lack in-depth exploration of the interaction between the various actors in the illegal wildlife supply chain, particularly between transit countries and the origin and destination countries. A better understanding of the full scope of illegal wildlife trade can promote the development of targeted and effective policies and enforcement actions.

To fill these knowledge gaps, we applied the framework of metacoupling (e.g., human–nature interactions, such as illegal wildlife trade, across origin, transit, and destination countries [Liu, 2023]) to systematically explore the role of transit countries in the supply chain from a global and multispecies perspective. To reveal the structural characteristics linking transit countries with upstream and downstream trade nodes (i.e., the preceding and following countries in the trade chain) and demonstrate the critical roles of transit countries in cross-border wildlife trade, we mapped transnational trafficking routes for multiple illegally traded species based on origin, transit, and destination country information. We sought to go beyond supply-and-demand relationships between origin and destination countries to provide new insights into the underlying mechanisms that sustain the high incidence of global illegal wildlife trade. We also aimed to gather information that could be used to identify and target key nodes in the illegal wildlife trade network.

METHODS

Data and measures

We obtained illegal wildlife trade data from the Center for Advanced Defense Studies (C4ADS) air seizure database (C4ADS, 2023) and the Wildlife Trade Portal database (TRAFFIC, 2023), which are compiled from public resources, such as news reports, academic and statistical reports, and social media. The C4ADS air seizure database covers the trade routes through airports from 2009 to 2021 of products associated with elephants (ivory), rhinoceroses (horn), pangolins, birds, reptiles, other mammals, marine species, arthropods, and amphibians and includes the origin, transit, and destination countries of the products. The Wildlife Trade Portal database covers seized wildlife, plants, and fungi transported through air, land, and water from 1994 to the present. We selected 15 years (2009–2023) of illegal wildlife seizure data from the 2 databases. We excluded duplicate incidents, instances of domestic trade, routes with missing origin or destination information, and unclear routes that involved multiple origin or destination countries within a single route. Because we traced all the countries connected with seizure records, our dataset also included many countries where the seizure did not occur.

We compiled socioeconomic data from the World Bank (2023), the United Nations Conference on Trade and Development (2023), and the Uppsala Conflict Data Program (2023). The socioeconomic data covered the following indices: gross domestic product (GDP), GDP per capita, population density, governance index, trade volume of biological products, merchandise exports, airport infrastructure status, distances between countries, presence of armed conflict, and number of trade partners. Detailed information on these indices is provided in Appendix S1.

Statistical analyses

Because we could obtain data on only reported illegal wildlife trade, we assessed whether the sample adequately captured the diversity of transit countries with the species accumulation curves created with the R package vegan. To construct the accumulation curve, this method simulated the sequential addition of samples and recorded the cumulative number of observed transit countries. The plateauing of the curve indicated that most of the transit countries were accounted for. We then used the

Chao1 richness estimator to estimate the total number of transit countries.

We employed a general linear model to analyze the relationship between transit countries and the volume of illegal wildlife trade. Given that the seized items were recorded either by weight (in kilograms) or by count (number of individuals), we developed separate models for weight-based seizures (Equation 1) and count-based seizures (Equation 2):

$$\log\left(\text{weight}\right)_{it} = \beta_0 + \beta_1 \text{transit}_{it} + \beta_2 x_{it} + \beta_3 \gamma_t, \quad (1)$$

$$\log\left(\text{count}\right)_{it} = \beta_0 + \beta_1 \text{transit}_{it} + \beta_2 z_{it} + \beta_3 \gamma_t, \quad (2)$$

where $\log(\text{weight})_{it}$ is the logarithm of the species weight for the ith route in the tth year, $\log(\text{count})_{it}$ is the logarithm of the species count, transit_{it} is whether transit countries are involved (1, yes; 0, no), and γ_t is the year fixed effect.

We analyzed the relationship between transit countries and the trade volume of ivory, rhinoceros horn, and pangolins based on weight and that of other species based on count. We used a random forest algorithm from the R package randomForest to separately select 5 control variables with the highest information content and pairwise correlation below 0.6 for both the weight-based and count-based models, denoted as x_{it} and z_{it}, respectively. These control variables were selected from a list of variables that included governance index, GDP, GDP per capita, population density, number of trade partners, armed conflict, airport infrastructure status, trade volume of biological products, merchandise exports for both the origin and destination countries, differences in these metrics, and the geographic distance between the origin and destination countries (Appendix S1). The differences were measured as the absolute logarithmic ratio of the variables between the origin and destination countries.

To assess whether the trafficking of high-value species or products, such as ivory, rhinoceros horn, and pangolins, relies more on multiple transit countries, we used a Poisson regression model:

$$\text{transit count}_{it} \sim \text{Poisson}(\exp(\beta_0 + \beta_1 \text{high value}_{it} + \beta_2 X_{it} + \beta_3 \gamma_t), \quad (3)$$

where $\text{transit count}_{it}$, the dependent variable, is the number of transit countries along each route (range 0–4) and high value_{it}, the independent variable, is a species-type dummy that equals 1 when the trafficked item is ivory, rhinoceros horn, or pangolin and 0 for other products or species. Control variables (X_{it}) were chosen based on the random forest algorithm.

We constructed a panel dataset that contained all the countries in the world from 2009 to 2023 to determine the differences in the number of transit events of illegal wildlife trade among different countries. Because the number of transit events was a count variable that exhibited overdispersion (i.e., its variance exceeded its mean) and the Hausman test ($p = 0.557$) indicated that the random effects model was more appropriate, we employed a random effects negative binomial model for the analyses:

$$\log\left(y_{jt}\right) = \alpha_{jt} + \beta x_{jt} + \mu_j + \varepsilon_{jt}, \quad (4)$$

where y_{jt} is the number of transit events of illegal wildlife trade within country j in year t. After excluding variables with correlations >0.6, the final predictor variables included the governance index, GDP, population density, number of trade partners, armed conflict, and airport infrastructure status, which are represented as x_{it}. These variables were standardized. μ_j is the country-specific random effects, and ε_{jt} is the random disturbance term.

We used a logit model to study the characteristics of origin and destination countries that depend on transit countries:

$$\text{logit}(\text{transit}_{it}) = \beta_0 + \beta_1 x_{it} + \beta_2 \gamma_t, \quad (5)$$

where transit_{it} is whether transit countries are involved in the ith route in the tth year. The predicting variables included the governance index, GDP, GDP per capita, population density, number of trade partners, armed conflict, airport infrastructure status, trade volume of biological products, merchandise exports for both the origin and destination countries, and the differences in these metrics and the geographic distance between the origin and destination countries. We selected variables with correlations <0.6 (Table 1), which are denoted as x_{it}.

We examined the characteristics of transit countries with the logit models (Equation 5). We conducted 3 regression analyses for the transit nodes from the routes with only one transit country, for the first transit node, and for the subsequent transit nodes in the routes that involved multiple transit countries. Here, transit_{it} equals 1 if the transit country is involved in the ith route during the tth year and 0 for other transit countries of the tth year. The x_{it} is the distance and trade volume of biological products between each pair of countries (e.g., origin and transit, transit and transit, and transit and destination) and the airport infrastructure status of the transit countries. These variables were standardized. To validate the robustness of the results, we extended the analyses to include the transit countries in each year and the transit countries before and after the corresponding year, which resulted in consistent findings (Appendix S2).

RESULTS

Patterns of global illegal wildlife trade

From a total of 3688 complete supply chain records, we identified 2622 transnational illegal wildlife trade routes that involved 84 transit countries across six continents (Appendix S3). These routes included 730 for ivory, 206 for rhinoceros horn, 243 for pangolins, 269 for birds, 508 for reptiles, 296 for other mammals, 337 for marine species, 21 for arthropods, and 12 for amphibians. Air transport, land transport, water transport, other types of transport, and unknown trans-

TABLE 1 Relationship between the use of transit countries and the characteristics of the origin (O) and destination (D) countries in the illegal trade in wildlife products.

Characteristic	Coefficient	SE
O gross domestic product (GDP) per capita	−0.300[a]	0.082
D GDP per capita	−0.414[a]	0.086
O population density	−0.208	0.179
D population density	−0.078	0.093
O airport infrastructure status	0.157[c]	0.082
D airport infrastructure status	0.289[a]	0.078
O armed conflict	0.111	0.131
D armed conflict	0.346[b]	0.160
O number of trade partners	0.198[c]	0.108
D number of trade partners	−0.092	0.072
O × D GDP per capita difference	0.120	0.080
O × D population density difference	0.008	0.069
O × D governance index difference	0.018	0.072
O × D merchandise exports difference	−0.059	0.097
O × D airport infrastructure difference	0.238[a]	0.068
O × D trade volume of biological products	−0.249[a]	0.095
O × D distance	0.966[a]	0.070
Constant	−0.261	0.256
Year fixed effect	Yes	
Number of observations	2062	

[a]Significance level 1%.
[b]Significance level 5%.
[c]Significance level 10%.

port accounted for 77.99%, 8.58%, 4.12%, 0.38%, and 8.92% of these routes, respectively. The species accumulation curve showed a clear flattening, and the Chao1 estimator projected a total of 106 transit countries (95% CI 82–130) (Appendix S4), which suggests that we included most of the transit countries.

The trade in rhinoceros horn, pangolins, and ivory was primarily concentrated in Africa, Asia, and Western Europe. Africa was the main origin region (72.1% of the total trade from all origin regions), followed by Southeast Asia (13.5%). East Asia (55.0% of the total trade to all destinations) and Southeast Asia (32.2%) were the major destinations. The trade in birds, reptiles, marine species, arthropods, amphibians, and other mammals was more geographically dispersed. Key origin regions included Africa (24.8%), Southeast Asia (24.7%), South Asia (11.8%), and South America (6.0%), and major destinations included East Asia (32.6%), Southeast Asia (18.2%), and North America (9.3%) (Appendix S5). In trade that involved transit countries, Africa was the origin region for 93.0% of the trade in rhinoceros horn, pangolins, and ivory, and 48.3% of the trade for other products and species. Southeast Asia was the destination for 42.0% of the trade in rhinoceros horn, pangolins, and ivory, and East Asia was the destination for 43.6% of the trade for other species (Appendix S5). Therefore, African countries and East and Southeast Asian countries relied heavily on transit countries for illegal wildlife trade.

About 40% of the illegal wildlife trade involved up to 4 transit countries, and 88% of this trade involved only one transit country. Among routes that involved only one transit country for rhinoceros horn, pangolins, and ivory, most of them originated from Africa and were transported through Western Europe (25.3%), Africa (14.2%), or Western Asia (7.0%) to reach the East Asian market or through other African countries (11.5%), Western Asia (10.0%), or Southeast Asia (5.7%) to reach the Southeast Asian market (Figure 1a; Appendix S6). Other species from Africa were transported through Western Europe (21.3%), other African countries (4.4%), or Southeast Asia (1.3%) to reach East Asia, transported through other African countries (5.1%) or Western Europe (1.5%) to reach Southeast Asia, or transported and sold within African countries (2.3%). In addition, other species from Southeast Asia were mainly transported within Southeast Asia and ultimately entered East Asia (2.3%) (Figure 1b; Appendix S7).

Along routes that involved multiple transit countries, rhinoceros horn, pangolins, and ivory from African countries were transported through other African countries and Southeast Asia to reach the Southeast Asian market (23.0%), through Western Asia and Southeast Asia to reach Southeast Asia (17.24%), and through other African countries and Western Asia to reach East Asia (8.05%) (Figure 1a; Appendix S8). The trafficking routes for other species or products were more diverse. Other species or products from European countries were transported through other European countries to reach Asia (12.1%). Other species or products from Asian countries were transported and sold within Asia (12.1%). Other species or products from African countries were transported either through African and Asian countries to reach Asia (18.2%) or through African and European countries to reach Europe (6.1%) (Figure 1b; Appendix S9).

Characteristics of transit countries

High-frequency transit countries in illegal wildlife trade typically featured well-developed airport infrastructure ($p < 0.05$), weak governance ($p < 0.05$), high population density ($p < 0.1$), a large number of trade partners ($p < 0.1$), and high GDP ($p < 0.1$). Among these factors, airport infrastructure development, governance quality, and the number of trade partners had the most influence on the frequency of being a transit country (Appendix S10).

Transit countries in the routes that involved only one transit country tended to be geographically close to ($p < 0.01$) and have a high volume of trade in legal biological products ($p < 0.01$) with both the origin and destination countries and possessed advanced airport infrastructure ($p < 0.05$) (Figure 2a). For the routes that involved multiple transit countries, the role of these factors varied among different transit countries. In the upstream stage of supply chains (from the origin country to the first and second transit countries), the distances from the first transit country to both the origin country and the second

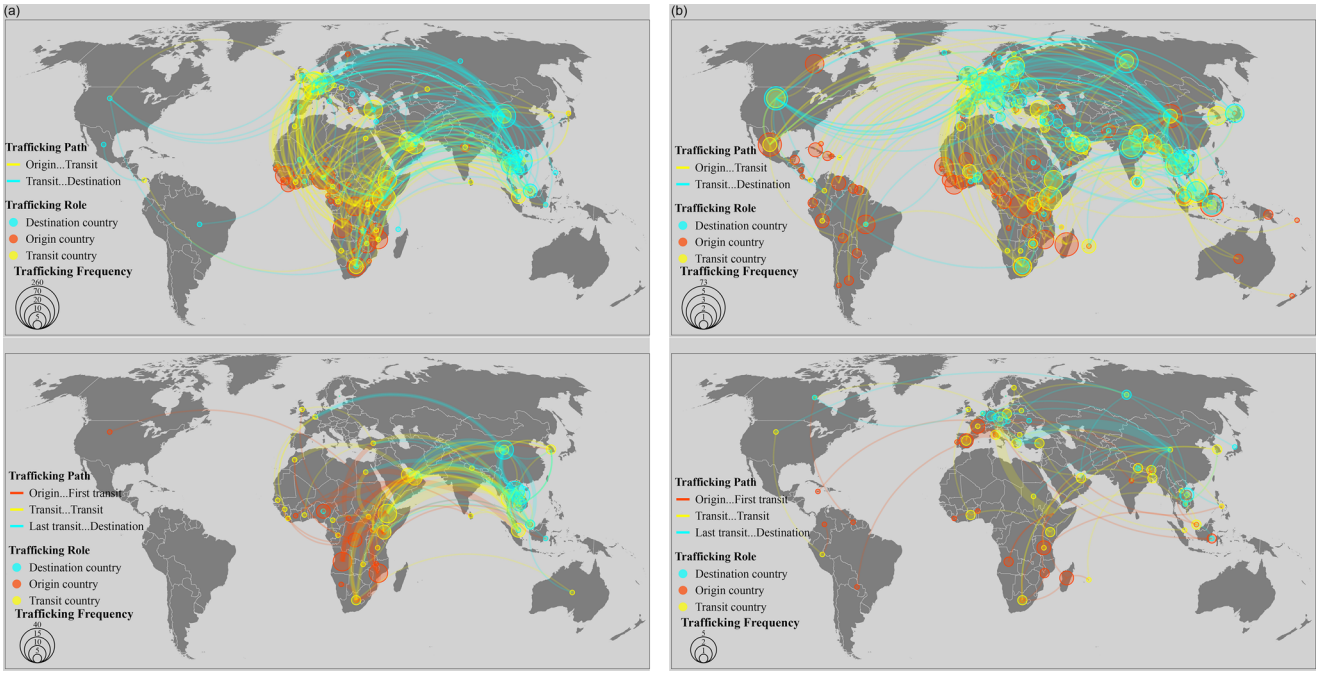

FIGURE 1 Routes in the illegal trade in (a) ivory, rhinoceros horn, and pangolins and (b) products from species other than those in (a) through transit countries (maps on the top, routes with one transit country; maps on the bottom, routes with multiple transit countries).

transit country were more important than the trade volume of biological products in determining the first transit country. Air transportation did not play a role in determining the first transit country (Figure 2b). For subsequent transit countries, their presence along the route was primarily determined by the trade volume in legal biological products and the distance to the next node (either the next transit country or the destination); distance to and trade volume with the preceding node (the prior transit country) were less important (Figure 2c).

Characteristics of countries that relied on transit countries

The adoption of transit countries was significantly correlated to the economic status, airport infrastructure, and geopolitical conditions of both the origin and destination countries. Origin countries that had low GDP per capita, poor airport infrastructure, and a high number of trade partners and destination countries that had low GDP per capita, poor airport infrastructure, and armed conflict were more likely to adopt transit countries ($p < 0.1$). Furthermore, transit countries were more likely to be adopted when there were large geographic distances, small trade volume of biological products, and substantial gaps in airport infrastructure between the origin and destination countries ($p < 0.01$) (Table 1). Geographically, origin countries that heavily relied on transit countries (i.e., transit countries involved in more than 50% of the trade) were mainly concentrated in Central and southern Africa (Figure 3a); destination countries that relied heavily on transit countries included Laos, Cambodia, Russia, Vietnam, and Thailand (Figure 3b).

TABLE 2 Relationship between the number of transit countries on trade routes and the trafficking of high-value illegally traded species based on a Poisson regression model.

Variable[a]	Coefficient (SE)
High-value species or products	0.188[c] (0.076)
Constant	−1.305[b] (0.185)
Number of observations	2218

[a]Control variables and year fixed effect included in the model.
[b]Significance level 1%.
[c]Significance level 5%.

Transit countries for high-value species

Transit countries were highly involved in the illegal trade of 3 high-value species or products: rhinoceros horn, pangolins, and ivory. About 56.3%, 47.3%, and 47.0% of the trade cases for rhinoceros horn, pangolins, and ivory involved transit countries, respectively (Appendix S11). The trafficking of rhinoceros horn, pangolins, and ivory was significantly and positively associated with the number of transit countries along a route ($p < 0.05$), which suggests that the illegal trade of these high-value species relied more on multiple transit countries and complex trafficking networks than that of other species (Table 2). Both the weight- and count-based models showed that transit countries were significantly associated with the global volume of illegal wildlife trade ($p < 0.1$). The trade volume of ivory, rhinoceros horn, and pangolins through transit countries was 87.0% greater ($p < 0.01$), and the trade volume of other species through transit countries was 40.5% greater ($p < 0.1$), than that without transit countries (Table 3).

TABLE 3 Relationship between the scale of wildlife trafficking and the use of transit countries based on a general linear model.

Variable[a]	All species or products		Ivory, rhinoceros, pangolins	Other species
	log weight (SE)	log count (SE)	log weight (SE)	log count (SE)
Transit	0.350[d] (0.193)	0.334[c] (0.143)	0.626[b] (0.194)	0.340[d] (0.178)
Constant	4.968[b] (0.574)	3.201[b] (0.411)	4.743[b] (0.576)	3.536[b] (0.496)
Number of observations	1019	1676	887	1140

[a]Control variables and year fixed effect included in the model.
[b]Significance level 1%.
[c]Significance level 5%.
[d]Significance level 10%.

DISCUSSION

We constructed over 2000 complete illegal wildlife trade routes that involved 84 transit countries, 138 origin countries, and 113 destination countries. We comprehensively explored, for the first time, trafficking patterns that involve transit countries and the characteristics and role of transit countries in the illegal wildlife trade. Transit countries were widely distributed across 6 continents, and those most active typically possessed well-developed airport infrastructure, many trade partners, and weak governance. About 40% of the illegal wildlife trade routes involved up to 4 transit countries. In the routes that involved only a single transit country, transit countries tended to be geographically close to and have a high volume of trade in legal biological products with both the origin and destination countries and possessed advanced airport infrastructure. For the routes that involved multiple transit countries, the role of these factors varied among different transit countries along the supply chain. Transit countries were heavily relied on for the trafficking of high-value products, such as ivory, pangolins, and rhinoceros horn, and significantly increased the volume of this trade. Additionally, transit countries acted as crucial bridges between economically underdeveloped nations, geographically distant countries, and countries with weak trade links in legal biological products. Our results support international organizations' focus on and monitoring of transit countries to more effectively curb the illegal trade.

A range of characteristics—extensive trade partner networks, robust airport infrastructure, high GDP, high population density, and low governance index—explained why some countries served as active transit points in the illegal wildlife trade. The extensive trade partner network indicated that active transit countries had signed numerous free trade agreements and created a vibrant international trade environment. High population density and GDP signaled these countries possessed significant market potential and favorable consumption environments. Well-developed airport infrastructure highlighted the strategic geographical location of these countries and the technical support for rapid transshipment. A lower governance index typically suggested problems, such as corruption, lack of accountability mechanisms, and weak law enforcement, that create governance gaps and facilitate illegal activities.

Geographically, transit country hubs were mainly concentrated in Southeast Asia, Western Europe, East Africa, Southern Africa, and North America. These countries often play multiple roles in wildlife trade: intermediaries, origin or destination countries of illegally traded wildlife (Appendix S12), and trade hubs for legal wildlife (Scheffers et al., 2019). This multifaceted role suggests that within these countries, there may be a large supply–demand market for wildlife, which provides fertile ground for the proliferation of illegal wildlife trade. Of greater concern is the overlap between these transit countries and those used for human trafficking (Derluyn & Broekaert, 2005; Içduygu, 2004; Mattar, 2005) and drug smuggling (UNODC, 2013). This suggests that organized crime groups may have established bases in these countries and are engaging in various types of illegal trafficking activities through shared transportation routes (South & Wyatt, 2011; van Uhm et al., 2021).

The transit countries were typically geographically close to the origin and destination countries, had high trade volume of legal biological products, and possessed developed airport infrastructure. Short distances between transit countries and the origin and destination countries reduce transportation costs and risk of exposure. A high level of trade in wildlife products provides a natural shield for concealing illegal wildlife products because traffickers can mix illegal wildlife products with legal goods. This camouflage strategy can reduce the risk of detection by law enforcement agencies. Moreover, the development of airport infrastructure in transit countries ensures efficient logistics and transfer capabilities. These characteristics indicate that trafficking routes are determined by existing trade networks, transport conditions, and geographic location, which constrain traffickers to operating within a limited set of feasible pathways.

In supply chains that involved a single transit country, the geographic proximity and existing legal trade networks between the origin and transit countries played a key role in determining the trafficking routes. In supply chains that involved multiple transit countries, the distance to adjacent nodes largely determined the first transit country, which suggests that traffickers prioritize moving products quickly out of the origin country. Subsequent transit countries were adopted primarily based on the trade volume of products and distance to the next node, which indicated the importance of concealment and accessibility to the final destination in trafficking. Overall, tran-

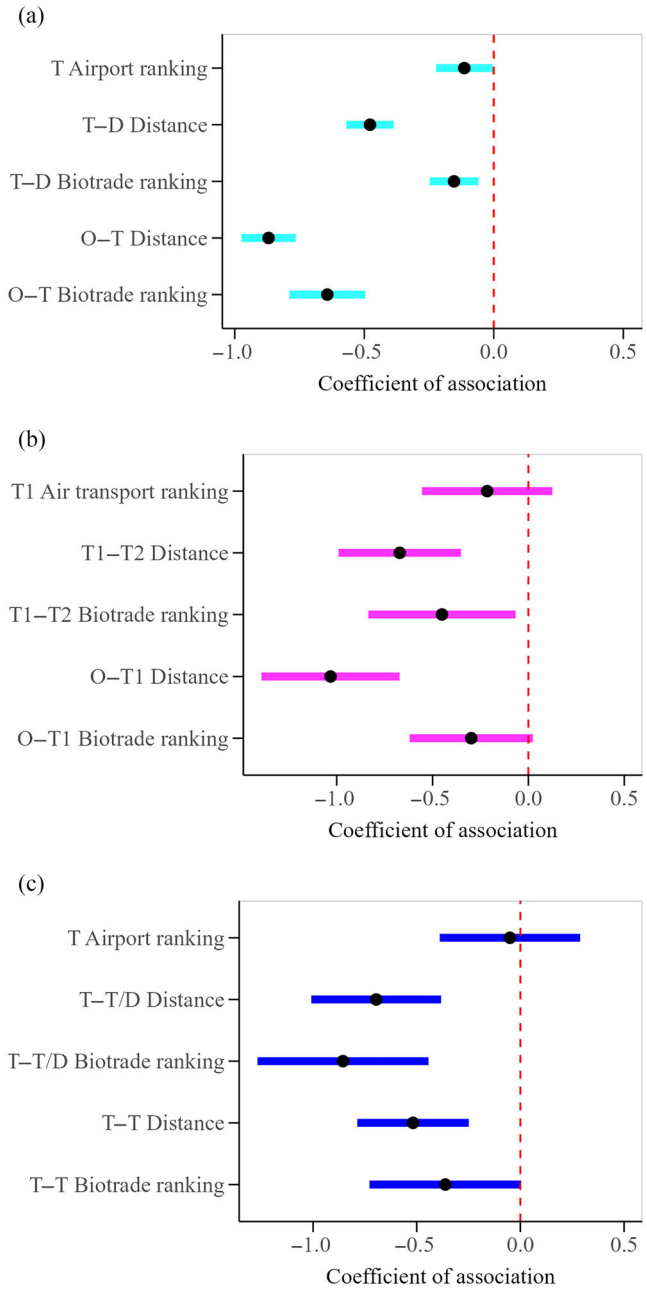

FIGURE 2 Drivers of the use of specific transit countries on illegal wildlife trade routes between product origin countries (O) and destination countries (D): (a) the only transit country on trade routes, (b) the first transit country on trade routes with multiple transit countries, and (c) transit country other than the first transit country on trade routes with multiple transit countries (T, transit country; T1, first transit country; T2, second transit country; T–D, link between the transit and destination countries; O–T, link between the origin and transit countries; T1–T2, link between the first and the second transit country; O–T1, link between the origin and the first transit country; T–T, link between the transit country and its subsequent transit country; coefficient of association, associations with the dependent variable; bars, 95% confidence intervals that do not overlap zero indicate a significant association between the driver and the dependent variable).

sit countries in longer supply chains (i.e., with multiple transit countries) exhibited a functional division of labor: the first transit country primarily functioned as a rapid transit hub, and the subsequent transit countries primarily served as covert transport routes.

Trafficking networks differed in structure and complexity across different species. High-value products (i.e., ivory, rhinoceros horn, and pangolins) primarily originated in Africa, were transported through Africa, Western Europe, West Asia, or Southeast Asia, and ultimately reached East and Southeast Asian markets, forming dense and multicontinental networks. Key transit countries included Belgium, Kenya, the United Arab Emirates, Ethiopia, Qatar, South Africa, Germany, Turkey, Singapore, France, the Netherlands, and Thailand. Driven by high profits and intense international enforcement pressure (Stiles, 2014; Gwynn Guilford, 2013; Mandima, 2016), traffickers of these products frequently rely on multiple transit countries to conceal shipments. By contrast, trafficking routes for marine species, reptiles, and birds were generally simpler, with Europe and Latin America playing a more prominent role. Marine species mainly originated from coastal countries in Africa and Latin America and were transported through Belgium, France, Poland, and the Netherlands before reaching East Asia, Southeast Asia, and European markets. Reptiles had more diverse origins (Africa, East Asia, South Asia, and Latin America) and were commonly routed through Western Europe, Africa, and Southeast Asia (e.g., Belgium, Kenya, France, Malaysia, Thailand) before reaching markets in East Asia, South Asia, and Europe. Birds, mainly originating from Latin America, Southeast Asia, and Africa, were transported through Spain, the Netherlands, France, or the United Kingdom in a few instances before entering European or Asian markets. Overall, these products relied far less on transit countries than high-value mammals (dependency roughly follows: reptiles > marine species > birds). These species are often easily disguised or mixed into legal shipments and are difficult for enforcement officers to identify accurately by appearance or taxonomy due to a wide variety of taxa (Keskin et al., 2023).

Transit countries greatly facilitated the volume of ivory, pangolins, rhinoceros horn, and other species. Without transit countries, cross-border trade typically requires direct contact between origin sellers and destination buyers, which concentrates risk and limits the scale of transactions. Transit countries enable sellers to quickly recoup funds by passing goods to local intermediaries, who then redistribute them to the highest-paying markets to maximize profits. Many of these countries are global trade hubs that have advanced logistics for handling millions of legal shipments daily, where traffickers can forge documents, repackage, or alter products (e.g., carving ivory into handicrafts) to launder them (TRAFFIC, 2002).

Transit countries provide opportunities for engaging in illegal wildlife trade, particularly among economically underdeveloped countries with loose trade connections, weak airport infrastructure, and distant geographic locations. For example, origin countries from central and southern Africa and destination countries in Southeast Asia are particularly reliant on the assistance of transit countries. Wildlife markets are often limited

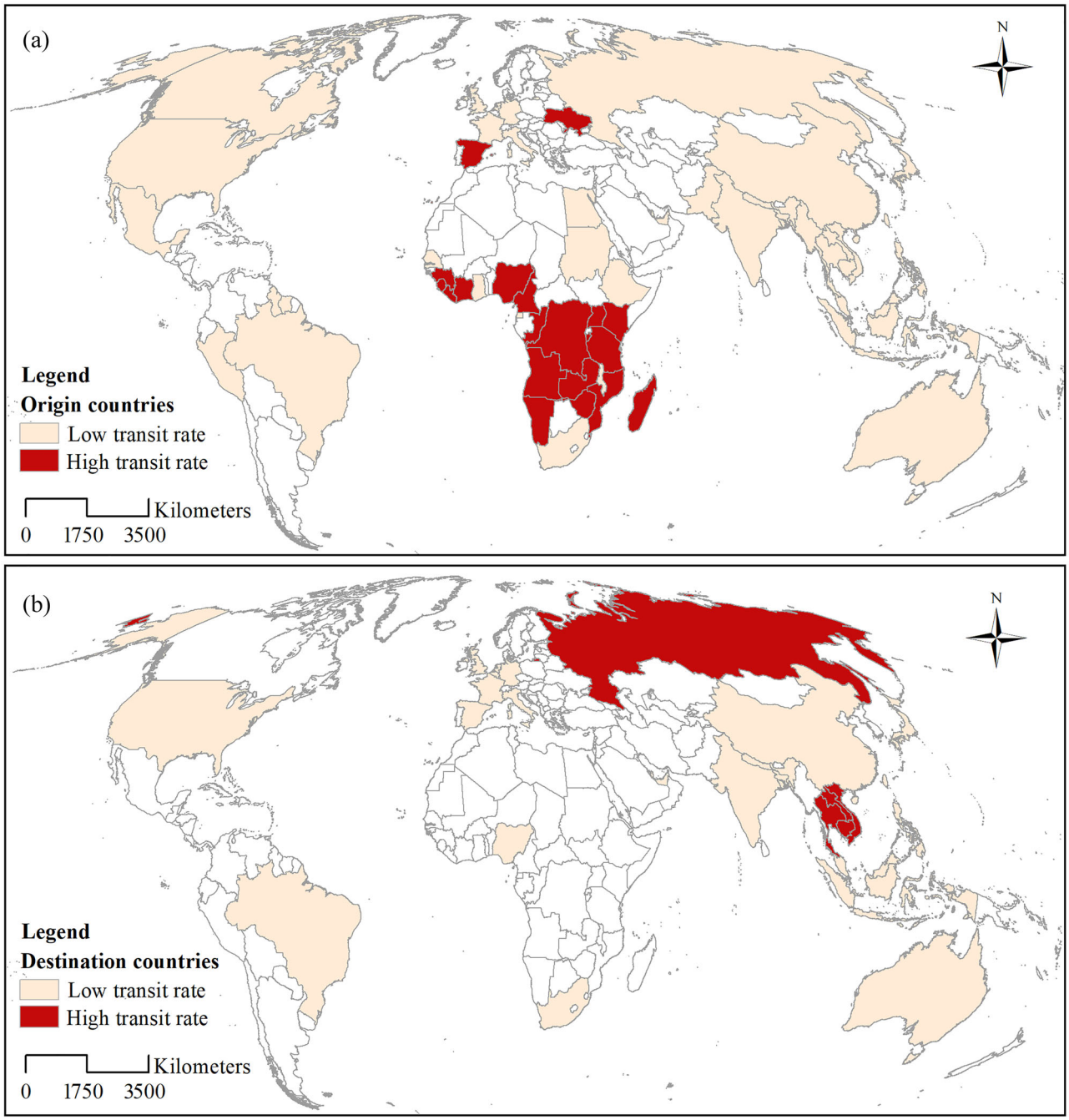

FIGURE 3 Distribution of the primary (i.e., over 10 trade routes) origin and destination countries in illegal wildlife trade: (a) origin countries and (b) destination countries (low transit rate, <50% of trafficking routes for an origin or destination country involve transit countries; high transit rate, 50% or more of trafficking routes involve transit countries).

in scale in economically underdeveloped origin and destination countries. The low volume of legal wildlife trade between them indicates weak trade links and a lack of legitimate trade channels for concealing illegal wildlife products, which increases the difficulty of direct transportation from origin to destination countries. Moreover, long geographical distances increase transportation risks and costs, and poor airport infrastructure further limits the capacity for independent wildlife trafficking. Against this backdrop, transit countries can provide larger markets, more extensive trade networks, and advanced logistical systems, which allow these origin and destination nations to access the illegal wildlife trade.

Despite long-standing international efforts to combat illegal wildlife trade, interventions have largely focused on origin and destination measures, such as strengthening law enforcement, regulating markets, and promoting species conservation. However, transit countries have received little attention, which leaves many transit routes as regulatory blind spots and results

in limited effectiveness of enforcement. Our results support calls for international organizations, such as the CITES Conference of the Parties, to pay special attention to transit countries, particularly high-frequency hubs, such as Belgium, Kenya, Thailand, the United Arab Emirates, Ethiopia, Qatar, France, Singapore, and Germany. These nations often serve as critical bridges between economically underdeveloped origin and destination countries that have weak trade ties, and can facilitate large-scale illegal transactions. International collaborative efforts should be made to identify common smuggling corridors based on high-frequency routes, enhance inspections at key ports, and deploy species identification technologies, particularly on high-risk commodities, such as ivory, pangolins, and rhinoceros horn. Given that the emergence of transit nodes is associated with, for example, geographic proximity, trade connectivity, and transport infrastructure, attention should be paid to the countries that have these characteristics but have not appeared prominently in the seizure records.

We used seizure data from C4ADS and TRAFFIC, which are the best available data for illegal wildlife trade (Keskin et al., 2023). However, some highly covert transactions may be undetected and unrecorded. In response, we used several strategies to mitigate the data limitations. First, we included only cases with fully traceable trade routes, rather than relying on records from single seizure points. This allowed us to identify those countries that were not directly subject to seizures but were actively involved in trade routes based on reports from other nations. This mitigated gaps in the reporting of some countries due to limited enforcement or reporting capacity. Second, we evaluated sample coverage with species accumulation curves, which indicated that we captured 79% of transit countries. The main transit countries we identified largely correspond with those identified by Patel et al. (2015) and Runhovde (2017). Finally, the proportion of air transport cases in the TRAFFIC database increased from 11% to 51% after filtering for cross-border cases. The prominence of air transport in transnational trafficking in our dataset is consistent with the reported seizure and offence data from Europe (Mundy-Taylor, 2013). Our results indicate the importance of global collaboration in monitoring and enforcement at key transit hubs and in gathering detailed and systematic data for a comprehensive understanding of illegal wildlife trade.

AUTHOR CONTRIBUTIONS

Conceptualization: Xiaodong Chen. *Methodology*: Jiamei Niu. *Investigation*: Jiamei Niu and Xiaodong Chen. *Writing*: Jiamei Niu, Xiaodong Chen, Weihua Xu, and Jianguo Liu.

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DATA AVAILABILITY STATEMENT

The data on illegal wildlife trade can be accessed through the following platforms: the ROUTES Dashboard (http://www.routesdashboard.org/) and the Wildlife Trade Portal (https://www.wildlifetradeportal.org/). Administrative boundaries at the national level are available from the GADM database (https://gadm.org/). Socioeconomic indicators, including GDP, GDP per capita, population density, governance index, merchandise exports, airport infrastructure status, and the number of trade partners, are sourced from the World Bank's open data repository (https://data.worldbank.org.cn/). Data on the trade volume of biological products are provided by UNCTAD's Biotrade Initiative (https://unctadstat.unctad.org/EN/Biotrade.html), and information on armed conflicts is available from the Uppsala Conflict Data Program (https://ucdp.uu.se/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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