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The gravity of wildlife trade

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ABSTRACT

Unsustainable trade in wildlife products both legally and illegally is a leading cause of population declines and increased extinction risk in commercially valuable species. However due to the clandestine nature of illegal trade and paucity of overarching studies of legal trade our understanding on international trade networks is patchy. We develop a gravity–underreporting modelling framework to analyse and compare: (i) data on the legal trade in mammalian, avian and reptilian products from recorded by The Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) and (ii) to data on the seizures of illegal products entering the USA between 2004 and 2013. We find substantial differences in the factors driving legal trade for the 3 taxonomic groups considered, indicating different drivers for different product markets. Illegal imports for all groups were associated with increasing exporter GDP. We found higher probabilities of underreporting for avian and reptile products, and in general central Africa, central Asia, Eastern Europe and Pacific Island states showed higher underreporting than other regions, indicating the existence of complex trade networks and the potential for the laundering of illegal products through legal markets. Our results show the important regional and economic trends driving wildlife trade. Our new modelling framework can also help illuminate previously unseen aspects of illegal and legal wildlife trade, which can help with the implementation of interventions to curb the impact of trade on wild populations.

1. Introduction

The legal trade in wildlife products globally is vast with an estimated value in excess of US$300 billion in 2005 (Engler and Parry-Jones, 2007). Unsustainable harvesting of wild populations driven by demand can lead to population reductions or even extirpation of species from some areas (Harris et al., 2017; Harrison, 2011; Sreekar et al., 2015). Furthermore, with unregulated trade, humans, native species and livestock are at risk from disease and pathogens which can lead to significant outbreaks, causing both social and economic harm (Rosen and Smith, 2010; Wyler and Sheikh, 2008). Wildlife trade is now one of the most pressing threats to species survival globally.

To address this, The Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates the trade in species of conservation concern between its 183 signatory countries (CITES, 2016a), through a system of appendices and permits/licenses (CITES, 2016b, 2015). As a result, CITES maintains a publically available database of legal trade in restricted species which contains approximately 15 million records (CITES and UNEP-WCMC, 2016). Unfortunately, despite being an excellent resource, the data collection relies on the submission of annual reports, which can be undermined by weak domestic legislation and governance (Reeve, 2006). Consequently, there are inconsistent reporting standards and submission of annual reports across the signatory countries (UNEP-WCMC, 2013), leading to potential underreporting issues and undermining the reliability of some data. More broadly, a lack of integration with economic, human development and governance issues driving wildlife trade (Hinsley et al., 2016; Phelps and Webb, 2015; Reeve, 2006), the low priority given to CITES, and a dearth of resources for its implementation (Poole and Shepherd, 2016; UNODC, 2010) has undermined the ability of CITES to monitor legal trade (Challender et al., 2015).

Due to the illicit nature of illegal wildlife trade (IWT) and the complexity of the criminal networks involved, it is difficult to characterise, quantify and police (Haas and Ferreira, 2015). While similarities between IWT and other flows of illicit goods (e.g. drugs and weapons) exist (Broad et al., 2003), the degree of expertise needed to successfully import some wildlife products may have led to the development of product specific and idiosyncratic networks (Petrossian et al., 2016; Reuter and O'Regan, 2016; UNODC, 2013). Reliable information on the flow of IWT, is difficult to obtain and while several organisations maintain databases of seizures; for example the United States Fish and Wildlife Services Law Enforcement Management

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Information System (LEMIS), the European Union Trade in Wildlife Information eXchange (EU-TWIX) and the World Customs Organisation Customs Enforcement Network (WCO-CEN); the majority are not publically available.

In addition there is a strong taxonomic bias in the literature to high value trade in products from globally threatened species such as tigers (Nowell, 2000), elephants (Beyers et al., 2011; Stiles, 2004) and rhinoceros (Biggs et al., 2013; Milliken, 2014). Consequently our understanding of IWT is geographically biased towards pathways for those products (Kurland and Pires, 2016). Furthermore, available data on the products, volumes and values of the wildlife product being traded illegally present underreporting problems (Blundell and Mascia, 2005; Broad et al., 2003), making any quantification challenging.

Gravity modelling is a technique commonly used in the study of international trade to characterise the drivers and strength of bilateral trade routes (Anderson, 1979; Gómez-Herrera, 2013). In their simplest forms, these models assume the level of bilateral trade (gravity) is determined by economic masses of the countries and distance between them, in the same way the Newtonian gravity estimates the attraction between two bodies. These models can be easily augmented with other terms such as institutional distance, common language and contiguous border (Anderson and Wincoop, 2001) and thus can be used to explore what national level factors determine the volume of trade between two countries.

Here we develop a gravity modelling–underreporting framework, a technique new to the IWT literature, but well established in the study of international trade, and apply it to a database of trade in mammalian, avian and reptilian products requiring CITES permits between 2004 and 2013. We then apply the same modelling framework to seizures of illegally traded products (from the same groups) entering the USA from the LEMIS database. We use this framework to explore the drivers of both legal trade in species of conservation concern and IWT in the USA. We provide the first global overview of factors driving the legal trade in mammal, bird and reptile products from species of conservation concern and estimates of regional trade flows accounting for underreporting. Further, we use the framework to assess the sources of underreporting in both datasets, allowing us to identify potential flows of illegal wildlife products into the USA that are currently undetected.

2. Materials & methods

2.1. Data collection

We obtained data on imports and exports of products from 3 groups, mammals, birds and reptiles, between 2004 and 2013 from the CITES database (CITES and UNEP-WCMC, 2016). We included all source types except ‘I’ (seizures and confiscations) and ‘U’ (unknown), and all the purpose types. All the data were requested directly from the UNEP-WCMC and were received on the 16th March 2016. To reduce the impact of many small transactions on our model we used a comparative tabulation of the data, where the trade is summed if they have the same information in several fields (taxon, term, importer, exporter, country of origin, purpose of transaction source of specimen and year). We then counted each record as a single transaction, regardless of the quantity of goods seized/traded. We excluded all records for which the export country was not known and for which the import and export country were the same.

We also obtained seizure records from the LEMIS (TRAFFIC and WWF, 2014) database for the same period, these data were taken from the website http://wildlifetradetracker.org/?db=lemis (accessed on the 20th of March 2016) and the records were manually coded into taxonomic groups. We included all country pairs where legal trade in wildlife products had been reported to CITES between 1996 and 2013. Our country pairs were unidirectional, such that if a pair of countries both import and export to each other it was represented by two observations (e.g. USA to China and China to the USA were included separately). We included re-exports in the same manner as direct trade, and data on the original source country was not included. We assumed the original import of re-exported goods was included in the database separately from the re-export record.

In line with the gravity modelling framework (see below), we modelled the volume of trade in wildlife products between the country pairs as a function of importer and exporter gross domestic products (GDPs) (The World Bank, 2015) and several multilateral resistance terms (Anderson and Wincoop, 2001): the distance between the countries (as measured by the great circle distance between the capital cities), whether there was a contiguous border and if they shared a common language. We also included several additional variables hypothesised to influence the volume of trade and/or rates of reporting between the two countries. For the data on illegal trade, since the importing country is always the same (the USA), only terms relating to the exporter could be included. For consistency we used the same terms for the legal and illegal trade models.

2.1.1. Control of corruption

We hypothesised that countries with higher levels of corruption will trade higher volumes of wildlife products as control over the issuing of permits becomes more lax. We also hypothesised that since the harvesting, export and import of illegal wildlife products often requires the collusion of public officials, the degree to which those officials exercise public power for private gains would increase the level of illegal trade and decrease the rate of reporting for both legal and illegal trade. These data were given in standard normal unites ranging from -2.5 to 2.5 with a higher number referring to less corruption (data taken from www.govindicators.org (Kaufmann et al., 2010)).

2.1.2. Global environmental fund benefits index for biodiversity (BIB)

This is a composite measure of the diversity of habitats available in a country and the degree to which they are protected, where countries with a large range of habitats score highly (e.g. Brazil). We hypothesised that countries with a higher biodiversity benefits index score will trade in higher volume than those with lower biodiversity potential (data taken from http://data.worldbank.org/ (Pandey et al., 2006)).

2.1.3. Environmental performance index (EPI)

The EPI is a measure of environmental performance by country, it has multiple factors including pollution, natural resource management and biodiversity protection. We hypothesised both legal and illegal trade is more likely to move from countries with a low EPI score to countries with a higher EPI score, as better environmental regulations could cause international supply displacement for illegal wildlife products. We used the 2014 figures obtained from http://epi.yale.edu/data (Hsu et al., 2014).

2.1.4. Biodiversity protection

This is the total score from the biodiversity and habitat section of the EPI indicators, it accounts for 25% of the overall EPI score. In this indicator, countries are rated based on the proportion of nationally and internationally important biomes and species found inside the country that are under some kind of official protection (Hsu et al., 2014). We hypothesised that countries with a high score will be more likely to report both legal and illegal trade and will trade in lower volumes as the sources of the products will likely be under legal protection. We took this variable from the EPI 2014.

2.1.5. IUCN member organisations per million people

We constructed this variable by dividing the number of IUCN affiliated organisations in a country by the population in millions. This was used as a proxy for the countries' investment in conservation and civil society engagement. We hypothesised the higher the number of IUCN organisations the lower levels of underreporting.

2.1.6. CITES legal status

These variables describe the legal status of the importer and exporter as defined by the CITES national legislation project (CITES, 2016b). The countries are divided into 3 categories: category 1 countries have legislation that is generally believed to meet the requirements for the implementation of CITES, category 2 countries have legislation that is believed generally not to meet all the requirements of CITES and category 3 countries have legislation that is believed generally not to meet the requirements of CITES (CITES, 2016b).

2.2. Data analysis

2.2.1. Gravity model framework

We employed a gravity modelling framework to analyse bilateral trade flows (Anderson and Wincoop, 2001; Anderson, 1979; Burger et al., 2009). The framework is based on Newton's gravity law and expresses the volume of trade between two countries as a function of their economic mass (usually GDP) and the distance between them (Anderson, 1979). This can be expressed as:

$$y_{ij} = K\frac{M_i^{\beta_1} M_j^{\beta_2}}{d_{ij}^{\beta_3}},$$

where y_{ij} is the volume of trade between countries i and j, K is a constant, M_i is the mass of the country of origin, M_j is the mass of the importing country (both usually represented by a country's GDP), d_{ij} is the geographic distance between i and j, β_1 is ability of i to generate trade flows, β_2 the ability of j to attract trade and β_3 is the impedance factor between i and j (Burger et al., 2009). This equation can be converted into a linear form by taking logarithms of both sides, leading to.

$$\ln y_{ij} = \ln K + \beta_1 \ln M_i + \beta_2 \ln M_j - \beta_3 \ln d_{ij} + \varepsilon_{ij},$$

where ε_{ij} is the error term assumed to be independent and identically distributed. This equation can also be easily augmented to include a variety of other terms relevant to the characterisation of bilateral trade (Anderson and Wincoop, 2001; Head et al., 2010) (Supplementary methods).

We can estimate the β terms using a variety of regression techniques. To be able to model trade while taking underreporting into account, we embedded the gravity framework within a zero-inflated negative binomial (ZINB) regression to estimate the parameters of our gravity model. Using a generalised linear model to estimate gravity model parameters is already well established (Egger and Staub, 2015; Gómez-Herrera, 2013) and by using the zero-inflated negative binomial method we were able to account for underreporting through modelling overdispersion and zero inflation (Burger et al., 2009; Zuur et al., 2009). We suspected zero inflation in the illegal trade data due to its clandestine nature and to a lesser extent in the legal trade data as a result of the inconsistent submission of annual reports to CITES (UNEP-WCMC, 2013). For a detailed explanation of the ZINB process please see the Supplementary methods. Finally, using the ZINB method means we can overcome the issues associated with a more traditional log-normal specification of a gravity model; namely biases created by the log transformation, failure of the homoscedasticity assumption and how to treat zero valued trade flows; all of which can lead to biased and inefficient parameter estimates (Burger et al., 2009). We used Vuong's tests and AIC comparisons to test if the zero-inflated negative binomial significantly improved the fit over a standard negative binomial model.

The ZINB model is composed of two sub-models, a binomial logistic sub-model (henceforth the underreporting model) and a negative binomial sub-model (henceforth the trade model). The underreporting model estimates the probability that the observed zeros are false based on the explanatory variables provided, and the second, trade model, estimates the influence of our explanatory variables on the observed counts, adjusted for the probability of zero-inflation from the underreporting model. Thus in our model of legal wildlife trade the probability of underreporting is a composite of all the processes generating underreporting in country pairs where trade is taking place: that trade takes place but no permit was issued, that trade has taken place and a permit issued but the permit was not recorded by the issuing body, and that trade took place but no annual report was submitted to the CITES secretariat. For the illegal trade data, lack of seizures due to customs officials either missing a shipment or officials not being present drives underreporting. We then used the fitted values from the trade model to estimate the gravity of trade between the country pairs in our dataset.

We created a maximal model containing only the first order effects. To allow more straightforward comparison across the different models and, to be consistent with the existing trade literature, we did not simplify the model (Burger et al., 2009). We applied the modelling process to 6 datasets: mammals, birds, or reptiles for both legal and illegal trade. All analyses were performed using R (3.1.1) (R Core Team, 2014), and the ZINB regressions were estimated using the 'zeroinfl' function from the package 'pscl' (Jackman, 2015; Zeileis et al., 2008).

We then used the models based on the LEMIS data of illegal seizures to predict the probability of underreporting of illegal trade into the USA for the countries in our dataset. Our predictions for underreporting were simply a measure of how likely it is that there were illegal products entering the USA from a country that was not reported, or in other words, how likely zero trade from that country was likely to be false (zero inflation).

2.2.2. Uncertainty analysis

We tested the robustness of parameter estimates, predicted probabilities of underreporting and trade counts by performing ordinary non-parametric bootstraps of our final models. We ran 1000 bootstrap replicates for each model. From these replicates we calculated robust confidence intervals for our parameter estimates than were available from the 'zeroinfl' function in R. We also used a parametric bootstrap to estimate the uncertainty in our fitted values for both the zero and trade models in all 6 analyses. We used the 'boot' function from the 'boot' package in R (Canty and Ripley, 2015) and a custom function written for the parametric bootstrap.

3. Results

We removed from our dataset all the countries which did not have data for the variables considered in the models where either the importing or exporting country was missing and where the importing and exporting country were the same. This left 371,300 transactions (193,905 reptiles, 68,280 birds and 109,115 mammals) and a total of 7736 country pairs in our analysis. In our analysis period (2004–2013) the country pairs reported an average of 25.1 reptile, 8.8 bird and 14.1 mammal transactions per pair. Of the 7736 country pairs we analysed, 53.2%, 41.5% and 50.8% traded in reptilian, avian and mammalian products respectively. In our database of illegal trade entering the USA we had 8827 mammal seizures, 3346 avian seizures and 6354 reptilian seizures from 171 different countries. Of the 171 countries 64.9% were the source of mammalian products seized, 56.7% avian and 62.6% reptilian.

Our gravity model for legal wildlife trade in CITES shows markedly different drivers of trade volume between the 3 groups (Fig. 1). The largest positive correlate of trade is different in all three groups highlighting this fact: importer GDP (reptiles, effect size 0.43 standard error (SE) 0.02), common language (birds, 0.81, SE 0.09) and contiguous border (mammals, 1.37 SE 0.13). There are some common drivers between the 3 groups, with GDP of both importer and exporter being positively correlated with trade volumes, as would be expected by the gravity framework. Distance however was only significantly negatively correlated with trade volumes in reptile products, and not in the other two groups. Control of corruption in the exporting countries was significantly positively correlated with trade volumes in all three groups

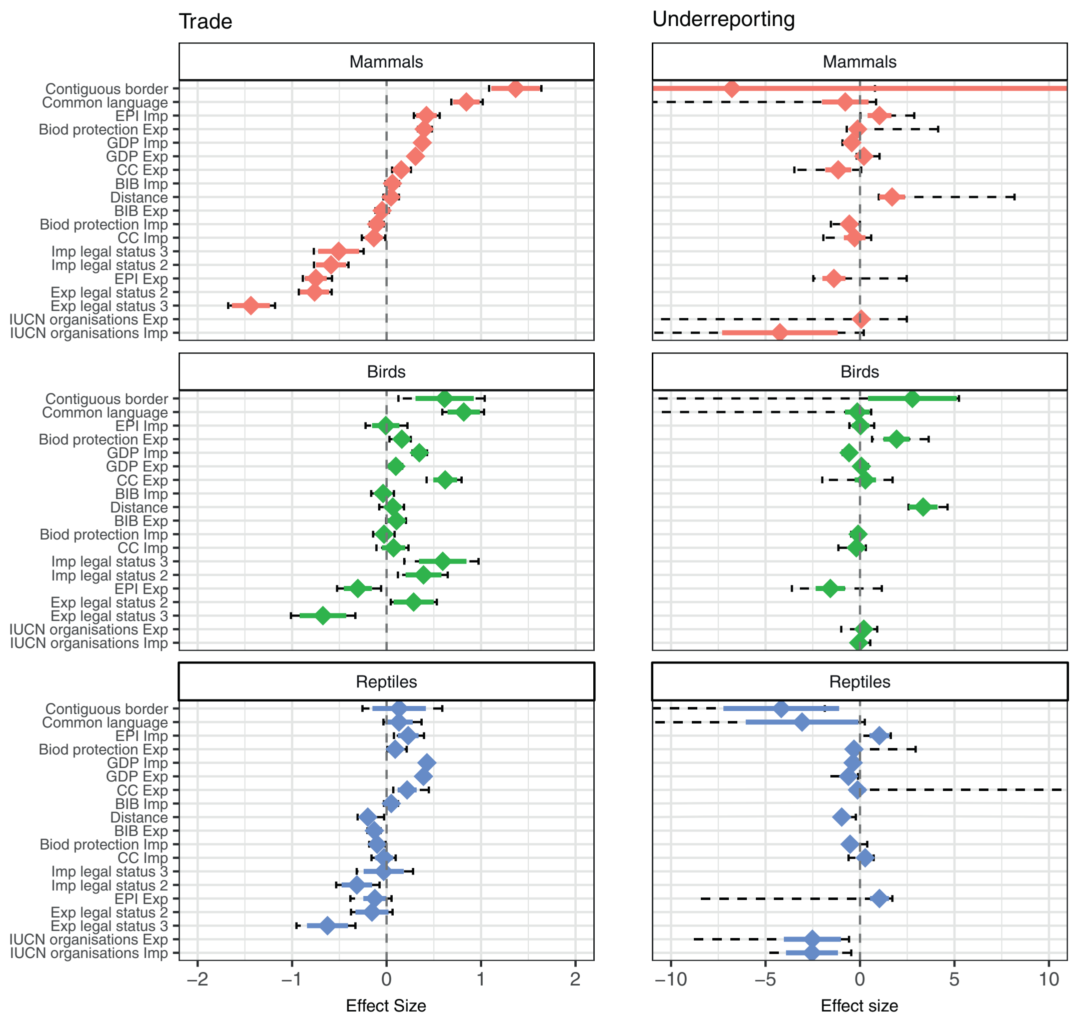

Fig. 1. Zero-inflated gravity model of CITES monitored trade in species of conservation concern separated into three taxonomic groups. The figure shows the effect size of all the variables. The left column shows the results from the negative binomial regression concerning trade volume and right column shows the results of the binomial logistic regression for underreporting. The coloured lines are the model generated confidence intervals and the dotted black lines are the more conservative bootstrap derived confidence intervals, both at 95%. Exp = exporter, Imp = importer, BIB = Benefits from biodiversity index, EPI = Environmental performance index, GDP = Gross Domestic Product, CC = corruption control. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(effect sizes of 0.22, SE 0.05, 0.62, SE 0.06 and 0.16, SE 0.04 for reptiles, birds and mammals respectively), indicating less corrupt countries trade more in CITES listed species. Biodiversity protection in exporter countries was also positively correlated with trade volumes across all three groups (effect sizes, 0.09, SE 0.03, 0.16, SE 0.04 and 0.38, SE 0.03 for reptiles, birds and mammals respectively). In all cases the exporter country CITES legal status was negatively correlated with trade volumes, legal status 2 and 3 countries export less than status 1, but importer country legal status was negatively correlated with trade in reptilian and mammalian products but positively correlated with avian products, indicating countries with a legal status of 2 and 3 import more avian products than legal status 1. Several other variables showed significant correlations in one or two of the groups but not all 3 (see Fig. 1).

Our regional gravity of legal trade for the 3 groups (Fig. 2) show some clear patterns, in all cases Europe is the largest importer regionally, followed by Asia and North America. In all cases the largest volume of trade was also within Europe, and European countries were the largest exporters of goods. Africa was a much larger exporter of avian and mammalian products than reptilian, being responsible for 19%, 21.9% and 9% of global exports in the 3 groups respectively. After Europe, Asia was the largest exporter and importer of products from all three groups. When we consider the countries individually, the USA is by the far the biggest importer in all three groups, with Japan and the UK being second and third for reptiles, UK and Canada for birds and the UK and Germany for mammals (Figs. A8, A9, A10). We experienced some difficulty fitting the underreporting model for legal trade. Our initial variable selection led to instability and very large SEs associated with the estimates for CITES legal status. As a result we removed these two variables from the zero portion of the model, however the fit is still poor, as evidenced by the large bootstrap confidence intervals (Fig. 1).

Our gravity model of illegal trade entering the USA (Fig. 3) shows GDP and common language to be positively correlated with trade volumes in all the taxa considered. For mammals and birds the largest influence on trade was whether there was a contiguous border between the USA and the exporting country with effect sizes of 2.1 (SE 0.95) and 4.8 (SE 0.99) for avian and mammalian products respectively. Notably, distance was positively correlated with illegal trade in mammalian products (1.02, SE 0.26), negatively correlated with trade in avian products (− 0.76, SE 0.27) and not significantly correlated with illegal trade in reptilian products. We also found trade in mammalian and reptilian products to be negatively correlated with countries who have a CITES legal status of 2 (effects sizes of − 0.92, SE 0.33 and − 0.96, SE 0.38 respectively), indicating less illegal trade from these countries than seen from countries with a legal status of 1. We also found GDP to be positively correlated with illegal trade in all groups (effect sizes:

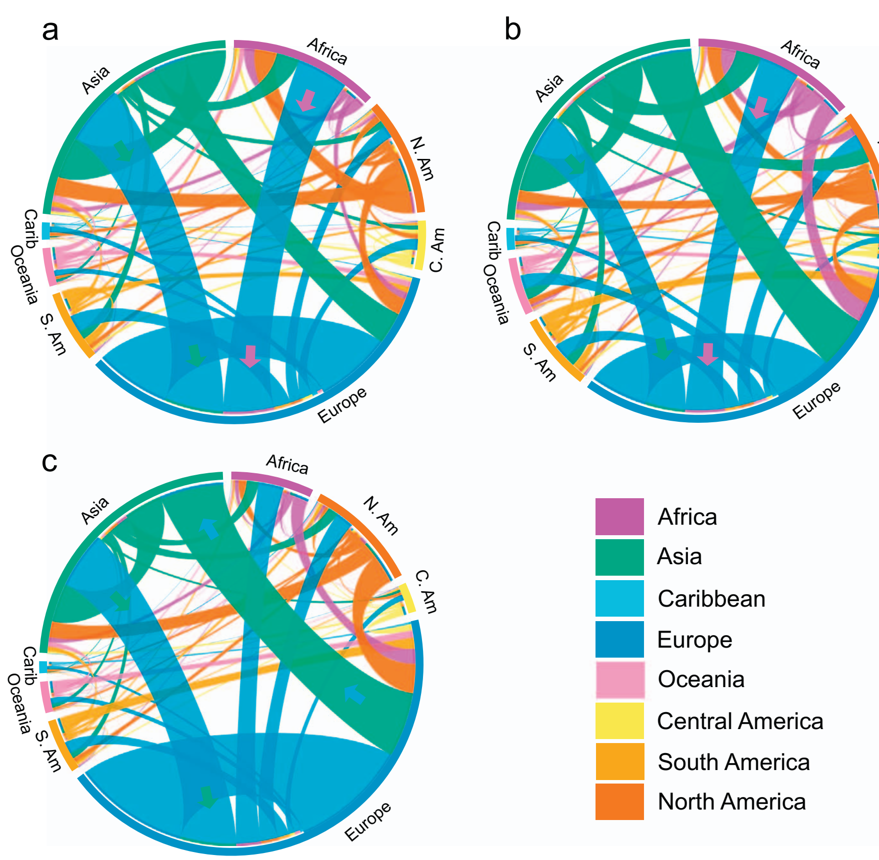

Fig. 2. Regional trade gravity for the 3 taxonomic groups considered. Panels a, b, and c, are mammals, birds and reptiles respectively. Chord diagrams made using (http://mkweb.bcgsc.ca/tableviewer/).

mammals 0.5 SE 0.09, birds 0.43 SE 0.09 and, reptiles 0.39 SE 0.09).

We found that underreporting in illegal trade was negatively correlated with exporter GDP in all groups (effect sizes of − 0.85, SE 0.24, − 1.26, SE 0.35, and, − 1.16, SE 0.45 for mammals, birds and reptiles respectively). Biodiversity protection was negatively correlated in 2 groups; reptiles and mammals (effect sizes of − 1.08 SE 0.5 and − 0.77 SE 0.3); as was common language; mammals and birds (effect sizes of − 1.85 SE 0.82 and − 1.96 SE 0.9).

Finally, we found clear regional trends in the underreporting of illegal trade entering the USA (Fig. 4) with central Africa, central Asia, eastern Europe and some Pacific island states showing a higher probability of underreporting than other regions in all 3 groups. We also found more countries with an underreporting probability of greater than 0.5 for avian (52) and reptilian (43) products that mammalian (34) products (panels b and c on Fig. 3).

4. Discussion

4.1. Legal trade

We show the drivers of international trade in species of conservation concern vary depending on the products considered. The large variations in the influence of the drivers between our broad taxonomic groups are likely the result of different market structures and supply–demand relationships. Our results highlight how nuanced, product specific approaches should be taken to address the impact of wildlife trade and how changing economic conditions could cause unpredictable market responses.

As expected we found exporters of legal status 3 trade less in all categories, since trade from these countries is by definition likely to be outside of the CITES framework (CITES, 2016b), but counterintuitively countries with legal status 2 and 3 imported more avian products. This indicates the ability of CITES to capture information on trade is heterogeneous across taxonomic groups, with different countries likely driving the demand in different groups. The ability of CITES to regulate trade, and therefore prevent unsustainable harvesting, varies depending of the group of products considered. This has profound implications for the role of CITES in conservation with low information groups more at risk of overexploitation from unsustainable trade. This is especially important for groups such as orchids, timber, fish and corals (to name a few examples), which are less well studied, are often hard to identify and/or traded in very high volumes globally.

We find this taxonomic heterogeneity is then exacerbated by a geographic heterogeneity with less corrupt countries exporting higher volumes of trade in our results. Given local governance issues influence the submission of annual reports to CITES (Reeve, 2006), this result likely does not indicate more corrupt countries export less but instead that exports from these countries are less likely to be captured by CITES. Thus large parts of the market likely occur outside the influence of CITES. The failure of high GDP countries such as Brazil, India or China, to feature in the top 10 importing nations for any of the groups (except China which is 9th for reptilian products), despite GDP being a positive driver of trade across all groups, also indicates high volumes of trade may be occurring outside of CITES. While it could be that these countries are simply not trading in CITES controlled wildlife products, ample evidence suggest this is not the case (Antunes et al., 2016; Liu et al., 2016; Sharma et al., 2014; UNODC, 2016). Instead, it seems likely that trade is taking place, but it is not captured by CITES.

This geographic bias in information capture explains some of the taxonomic biases we found, but only if certain low information areas contain a high proportion of the trade in certain products (e.g. birds in South East Asia). Thus, increasing monitoring capacity in areas where we expect to see more trade than currently observed is essential to improve the ability of CITES to prevent unsustainable harvesting. More research to identify the taxonomic biases in reporting, and better support for national CITES authorities to identify problematic products, is

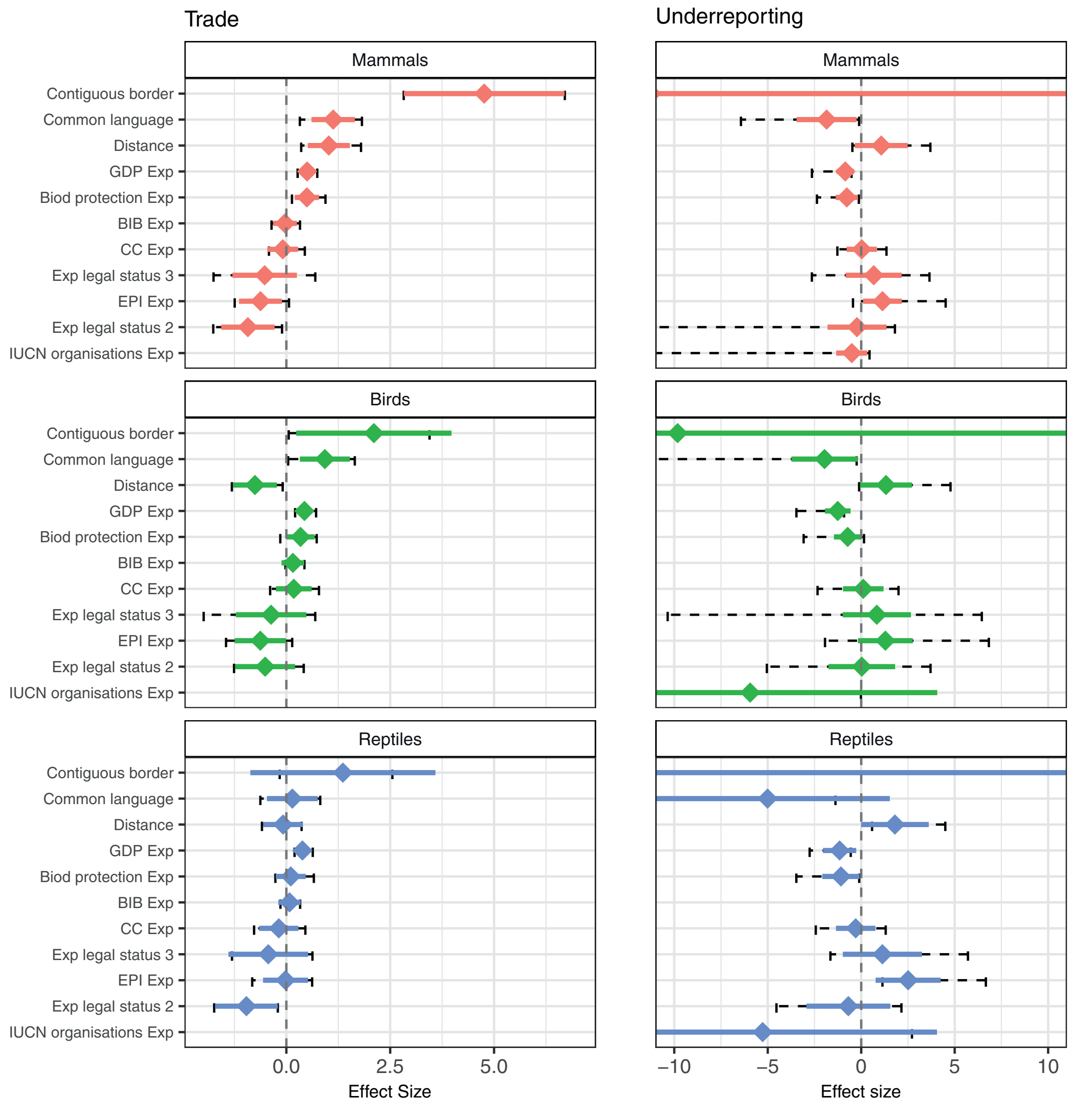

Fig. 3. Zero-inflated gravity model of illegal wildlife trade into the USA based on LEMIS data. The figure shows the effect size of all the variables. The left column shows the results from the negative binomial regression concerning trade volume and right column shows the results of the binomial logistic regression for underreporting. The coloured lines are the model generated confidence intervals and the dotted black lines are the more conservative bootstrap derived confidence intervals, both at 95%. Exp = exporter, Imp = importer, BIB = Benefits from biodiversity index, EPI = Environmental performance index, GDP = Gross Domestic Product, CC = corruption control. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

needed to ensure CITES can regulate trade effectively across all groups.

Generally we found trade within CITES to be in line with the assumptions of a gravity model, with trade volumes increasing with the GDP of the importer and exporter countries and, while only trade in reptilian products decrease with distance, avian and mammalian products have a strong positive correlation with contiguous borders and common language, both of which are proxies for distance. Interestingly we found biodiversity protection in exporter countries has a positive influence on trade volumes for all the groups. In this case, biodiversity protection is a measure of how many highly biodiverse but threatened habitats fall within a country's protected areas, thus countries with higher biodiversity tend to trade more wildlife products.

The complex nature of wildlife trade networks presents a challenge for our analysis. By modelling bilateral trade flows we are, in some cases, likely not capturing the intended destination of the goods or origin in others. This is exacerbated by our broad taxonomic groupings and the product specific differences in market dynamics, and potential errors in the data reported to CITES such as inflated trade record due to unused export permits (e.g. Nijman and Shepherd, 2011). Therefore, we are not able to make inferences about the role of transit countries in these networks with confidence, or suggest pathways by which individual products move across the globe. By flattening the data we are assigning the same weight to different transaction, while this is essential to allow cross product comparison, we are losing some information about trade volumes. Finally, using a flattened comparative tabulation could introduce errors in trade volumes if the trade is reported inconsistently between importers and exports, potentially leading to over estimations. However, applying a gravity model to better resolution data on individual products (such as elephants) could be a valuable method to augment existing network studies in the study of both legal and illegal wildlife trade(e.g. (Patel et al., 2015; Poole and Shepherd, 2016)).

4.2. *Illegal trade*

Like legal trade our results show illegal trade broadly conforms to the gravity model framework with GDP being a positive driver of trade. Again, there were differences between the groups which suggest different pathways exist for the different products. In all three taxa our models predicted the highest trade gravities of illegal products were

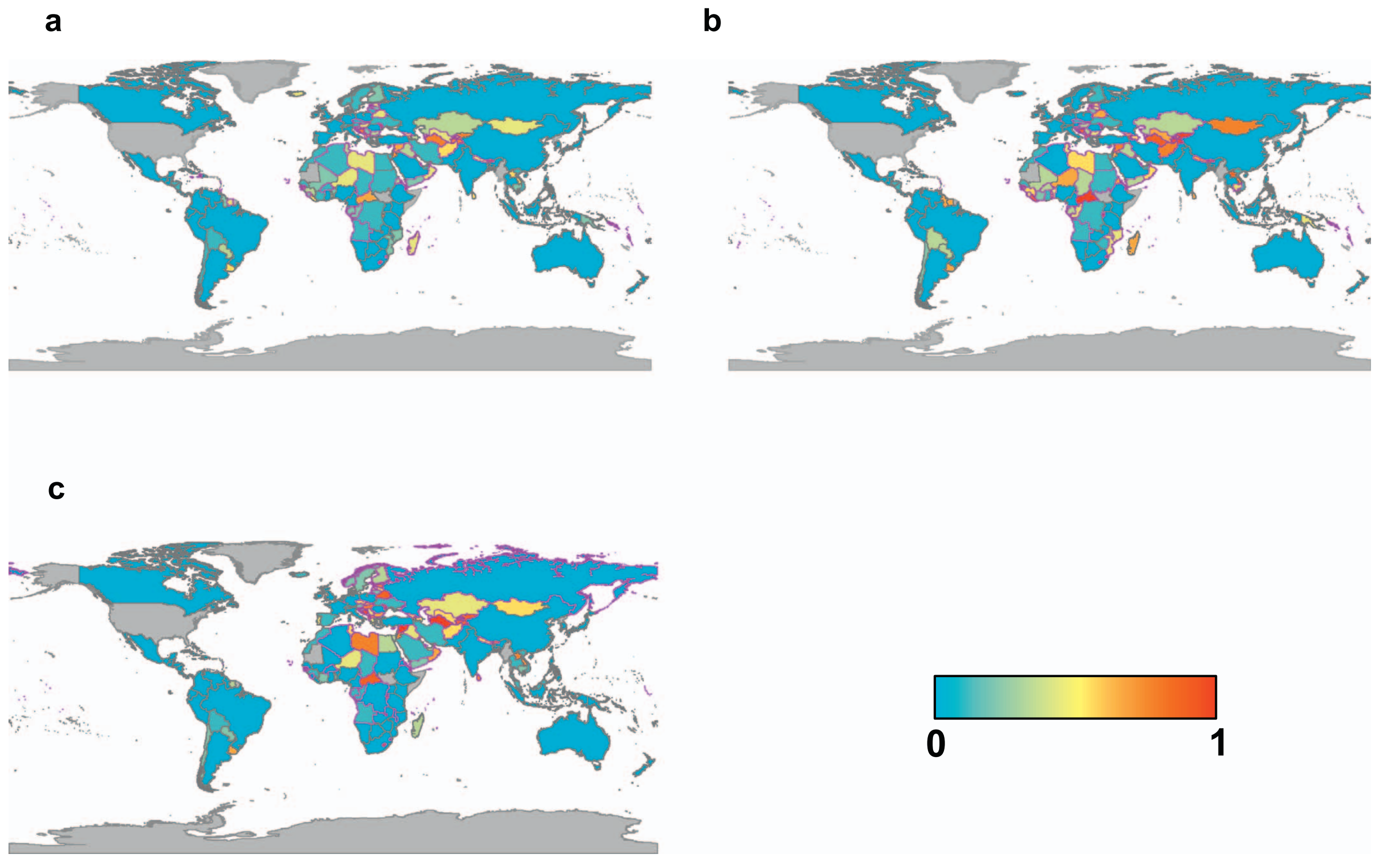

Fig. 4. The average underreporting probability of illegal wildlife imports into the USA as predicted by the underreporting model for illegal trade. Panels a, b and c are for mammalian, avian and reptilian products respectively. Countries which reported no trade in the analysis period are outlined in purple. Countries with no data are in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from Canada, Mexico and China, which is in line with previous studies (Petrossian et al., 2016), and not surprising given all three are major trading partners of the USA and two have long, relatively porous and currently un-walled borders with the USA. Our results are contrary to the traditional narrative of illegal wildlife products flowing from the developing to the developed world (Roe et al., 2002). However, the majority of illegal wildlife products entering the USA are seized at airports (Petrossian et al., 2016), thus the high volumes of illegal wildlife products coming from developed nations likely indicates the complex, multistage journeys that many of these goods take before reaching their intended destination.

This is important when we consider the results for underreporting (Figs. 2 and 3). Our model predicts underreporting of illegal wildlife trade to be concentrated in central Africa, the Middle East, Central Asia, Eastern Europe and parts of South East Asia. Most of the countries with high underreporting probabilities are poor, have high levels of corruption and are currently conflict zones. As a result, they are the countries less likely to have direct trade or air links with the USA. It is likely therefore in many cases the high level of underreporting is caused by both a lack of detection and a lack of direct trade into the USA. Instead products from these places are arriving in the USA via a better connected neighbour, or across several stages leading to the kind of complex networks seen in other studies (Patel et al., 2015). These complex trade networks also increase the probability of an illegal product subsequently being laundered through legal domestic markets at some point in the journey (e.g. ivory in China (Gabriel et al., 2012)).

Interestingly, our results show a very high probability of underreporting from the small number of Pacific Island States we were able to include. Being geographically isolated and economically weak, with low law enforcement capacity and relatively poor governance (McCusker, 2006), Pacific Island nations have been implicated in smuggling of people, drugs, and wildlife previously (Broadhurst et al., 2012; Shepherd et al., 2012; UNODC, 2013), validating our results. Given their small populations and economies Pacific Island nations are thus probably transit ports for illegal wildlife products destined elsewhere (Shepherd et al., 2012). Research into the extent and nature of these networks is a priority, to enable more effective surveillance both in the nations themselves and by international bodies such as INTERPOL.

We also found taxonomic biases in the detection of IWT (mirroring the results from legal trade), with underreporting in avian and reptilian products more likely than mammalian products. There are several explanations for these results; maybe that mammalian products are more likely to be identified and seized by Customs officials, or it could also be the result of greater seizure effort (e.g. training for Customs officials and monitoring effort) being directed towards mammalian products. This is then exacerbated by the existence of different networks for each product (Reuter and O'Regan, 2016), resulting in avian and reptilian products not only being less likely to be identified, but that their most probably points of entry are also less likely to be monitored.

The heterogeneous detection of IWT products is reflecting the biases in our understanding of trade networks towards charismatic mammalian species. Our study, however, concentrates on 3 of the most well studied groups (reptiles, mammals and birds), and the impacts may be more pronounced in less well understood markets, such as orchids, invertebrates, timber and corals. Consequently, these species may be more at risk from unsustainable harvesting and increased extinction risk as their trade is less likely to be detected and intercepted. It is important therefore to increase detection capacity for less well known products, through both training and the implementation of new technologies such as DNA barcoding (Johnson et al., 2014; Mendoza et al., 2016) and stable isotope analysis (Bowen et al., 2005).

Gravity modelling has the ability to illuminate general trends in trade networks and test factors driving the movement of wildlife products globally, but the degree to which it can explain networks is limited by data availability. Ideally therefore future attempts to study illegal wildlife trade should integrate data from a number of sources such as CITES, LEMIS, EU-TWIX, the World Customs Organisation Harmonised System, and other national reporting systems to establish a more complete overview of the network (Chan et al., 2015). Historically, monitoring and enforcement alone has not proved successful at controlling both legal and illegal wildlife trade (Challender and MacMillan, 2014; Challender et al., 2015). Instead our results support a multipronged product specific, approach, utilising market forces, community engagement alongside more traditional enforcement and monitoring approaches (Challender et al., 2015; Cooney et al., 2016).

5. Conclusion

Our analysis has gone beyond previous descriptive studies of legal and illegal wildlife trade globally, identifying some of the drivers of trade and providing a quantitative assessment of trade flows that account for the regional reporting biases inherent in the data. We have shown how the legal trade in species of conservation concern for different products are driven by different market forces, a trend that is mirrored in illegal trade entering the USA, highlighting the need for product specific interventions and monitoring strategies. We have also highlighted regional and taxonomic biases in CITES efficacy and IWT detection, which may result in undetected overexploitation of commercially valuable species, leading to increased extinction risk. Finally, we have demonstrated a relatively simple modelling methodology that can be easily used to monitor changes in trade networks over time. We hope our modelling framework proves a useful tool for researchers and practitioners alike.

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Appendix A. Supplementary data

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