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Unveiling the patterns and trends in 40 years of global trade in CITES-listed wildlife

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ABSTRACT

Wildlife trade can provide commercial incentives to conserve biodiversity but, if unsustainable, can also pose a threat. CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) aims to ensure international trade in CITES-listed species is sustainable, legal and traceable. However, large-scale temporal and spatial patterns in wildlife trade are poorly known. We address this by analysing the CITES Trade Database: > 16 million shipment records for 28,282 species, from 1975 and 2014. Over this period, the volume of reported trade in CITES-listed wildlife quadrupled, from 25 million whole-organism equivalents per year to 100 million, and the ratio of wild- to captive-sourced trade in mammals, birds, reptiles, invertebrates and plants declined by an order of magnitude or more. Our findings start to reveal the scale of the legal wildlife trade, shifting trade routes and sources over time and we describe testable hypotheses for the causes of these changes.

1. Introduction

Awareness that large-scale human impacts such as land use change, pollution and anthropogenic climate change are depleting the diversity of life on Earth is increasing (Tittensor et al., 2014). The harvesting of animals and plants is one of the key threats to biodiversity (Joppa et al., 2016). A major component of biological resource use is the international trade in wildlife, both legal and illegal (Broad et al., 2003; Sutherland et al., 2009), and CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) is the key legal framework regulating trade and mitigating the effects of legal, international trade on wild populations. Despite criticisms over its effectiveness (Schonfeld, 1985; Matthews, 1996), for its emphasis on regulatory measures (Abensperg-Traun, 2009) and suggestions for improvement (Phelps et al., 2011), CITES is the primary mechanism for protecting species from overharvesting for international trade.

CITES entered into force in July 1975 and enables Parties to cooperatively regulate international wildlife trade through the agreed-upon listing of species traded or species potentially threatened by trade in three Appendices with differing levels of protection and trade restrictions imposed, though the majority of listed species can be traded. International trade is regulated through a system of permits; the CITES authorities are required to verify legal acquisition of specimens and assess whether trade is likely to be detrimental to the species prior to granting a permit for trade. The CITES Trade Database is the primary repository for data on the legal wildlife trade and is derived from annual reports compiled by CITES Parties. It contains data on permits issued over the last 40 years for trade in over 28,000 species of the 35,000 species regulated by CITES. This amounts to 16.75 million individual shipment records (as of 2016).

Whilst analyses of legal CITES trade exist, they primarily focus on individual species (e.g. Mcallister et al., 2009; D'Cruze and Macdonald, 2015) and individual taxonomic groups, such as birds (Beissinger, 2001), reptiles (Carpenter et al., 2004; Auliya et al., 2015; Robinson et al., 2015), amphibians (Carpenter et al., 2014), cetaceans (Fisher and Reeves, 2005), or animals traded as pets (Bush et al., 2014). However, the big picture is lacking, with no comprehensive analysis of the entire CITES Trade Database across all taxa to date, and no assessment of how broad spatial and temporal patterns change over time for different taxonomic groups. To explore if trade is detrimental to populations and species, we need to better to understand the temporal and spatial trade patterns and the factors that have influenced them, such as supply,

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Table 1
Details of the categorisation of CITES source codes into wild and captive datasets and the sources of wildlife trade that were excluded from the analysis, based on CITES source codes reported on permits (see Resolution Conf. 12.3 (Rev. CoP17): https://cites.org/sites/default/files/document/E-Res-12-03-R17.pdf).

Source category	Code	Definition
Wild	W	Specimens taken from the wild
	U	Source unknown
	X	Specimens taken in "the marine environment not under the jurisdiction of any state"
	R	'Ranched' specimens are those taken as eggs or juveniles from the wild, where they would otherwise have had a very low survival probability, and reared in a controlled environment, often with the release of some of the offspring back into the wild
	[Blank]	Source unreported
Captive	C	An animal is 'captive-bred' when it is produced in a controlled environment under certain conditions, including that a) reproduction took place in that environment, b) the breeding stock was established in line with the provisions of CITES and national laws without detriment to the survival of the species in the wild, c) that the breeding stock is maintained without the introduction of specimens from the wild, except for the occasional additional of animals to prevent/alleviate deleterious inbreeding or exceptionally for use as breeding stock, (where the CITES Scientific Authority advises this is non-detrimental) and d) the breeding stock has either produced offspring of second-generation (F2) or subsequent generations in a controlled environment, or be managed in a manner that has been demonstrated to be capable of reliably producing F2 offspring. Additional details in CITES Resolutions Conf. 10.16 (Rev.)
	D	Appendix-I animals bred in captivity and Appendix-I plants artificially propagated for commercial purposes. Additional details in CITES Resolutions Conf. 12.10 (Rev. CoP15).
	A	Plants that are artificially propagated, when they are grown under controlled conditions and have been derived from cultivated parental stock
	F	Animals born in captivity (F1 or subsequent generations) that do not fulfil the definition of 'bred in captivity' (Source code 'C').
Excluded from analysis	I	Confiscated or seized specimens
	O	Pre-convention specimens

demand, policy formulation and other interactions, across scales from detailed single species or genera, to broad macroscopic perspectives.

With this in mind, we review and analyse the full CITES Trade Database, focussing on four key aspects of trade in CITES-listed wildlife and wildlife products: (i) how trade levels have changed through time for different taxonomic groups; (ii) how spatial patterns of trade have changed through time; (iii) whether there have been shifts from wild-sourced to captive-sourced (as defined in Table 1) wildlife and wildlife products; and (iv) what initial factors explain the observed patterns.

2. Methods

2.1. Data preparation

The CITES Trade Database (https://trade.cites.org) consists of all reported legal wildlife trade exported from or imported by CITES Parties (currently 183), as compiled in their official annual reports. The database also includes records reported by the EU of trade in taxa listed under the EU wildlife trade regulations but that are not listed in the CITES appendices. Only trade records for CITES-listed taxa for the years for which the annual reporting has been completed at the time of analysis (1975–2014) were extracted (16,729,761 from the total of 16,753,001 records). Each record in the database details a single shipment between two countries for products deriving from a single taxon. Records are unidirectional; i.e. either incoming (as reported by the importing state) or outgoing (exporting state reported). Records specify the states of origin, of export and of import, source (e.g. wild-sourced or captive-bred), product type (e.g. live individuals or skins), purpose (e.g. trophies or commercial), units of measure, and the reporter type (importer or exporter) of the traded product. In some cases the shipment was a re-export of a wildlife product that was originally exported from another country. Such re-exports were removed from the data to prevent double counting. A total of 6,857,947 shipment records were thus removed from the total of 16,729,761. The remaining records were then aggregated by year, taxon, source, product and unit to yield 813,992 time-series. These were then split into four 'reporter-source' datasets according to whether the trade was exporter- or importer-reported and whether it involved products sourced from wild or captive populations (see Table 1 for the source codes interpreted as wild-sourced or captive-sourced).

To summarise and make the data equivalent across the heterogeneous types of products, we transformed products reported in trade to whole organism equivalents (WOEs), where possible. For example, five skulls represent five WOEs, whereas we assume that four ears are sourced from two animals and so represent two WOEs (Table S1). We assumed that different products were sourced from independent animals, so, for the example above, the five skulls and four ears were assumed to be sourced from seven separate animals. This assumption was necessary in the absence of information on the supply of different commodities from the same specimen. However, not all products could be converted to WOEs; for example, meat and timber, as well as items such as skin fragments or feathers. All products that could not be converted to WOEs were therefore excluded from further analysis (excluding 105,744 time-series, or 13% of the total). The taxonomic groups which had the majority of time-series that could not be converted to WOE were mammals (20,157 exporter reported and 16,575 importer reported), plants (20,762 and 7085) and reptiles (10,322 and 11,536; Table S2). For each reporter-source combination, we summarised trade within broad taxonomic groups, for which the nature of trade is qualitatively different: mammals, birds, reptiles, amphibians, fish, invertebrates and plants. Within each group, WOE products can be reported in different units (e.g. numbers of individuals, kg or m^3). We used trade reported in 'numbers of individuals' for which there were orders of magnitude more shipments than for any other unit of trade (e.g. kg, m^3). Our method aims to capture as much trade as possible in a consistent manner across taxonomic groups, although we note that our method excludes certain wildlife products such as meat, often reported in units of mass, and timber, often reported in units of volume. Linking these product types to individual organisms will require information on conversion coefficients, which is the subject of ongoing work.

2.2. Analysis

To determine how global trade in each taxonomic group varied through time, we summed trade in WOEs for each group across all CITES Parties. As a robustness check, for each reporter-source dataset (e.g. importer reported – wild-sourced) we used a correlation analysis to investigate, for each taxonomic group, whether the trade patterns were correlated with changes over time in the product types being traded. Specifically, we calculated the correlation between the sum of trade in WOE products and a time-series representing the proportion of all transactions made up of WOE products. Prior to the correlation analysis, the time series were pre-whitened in order to correct for statistical autocorrelation that is known to artificially inflate the correlation coefficient for time-series (Agiakloglou and Tsimpanos, 2012). Pre-whitening was accomplished for each pairwise time-series correlation

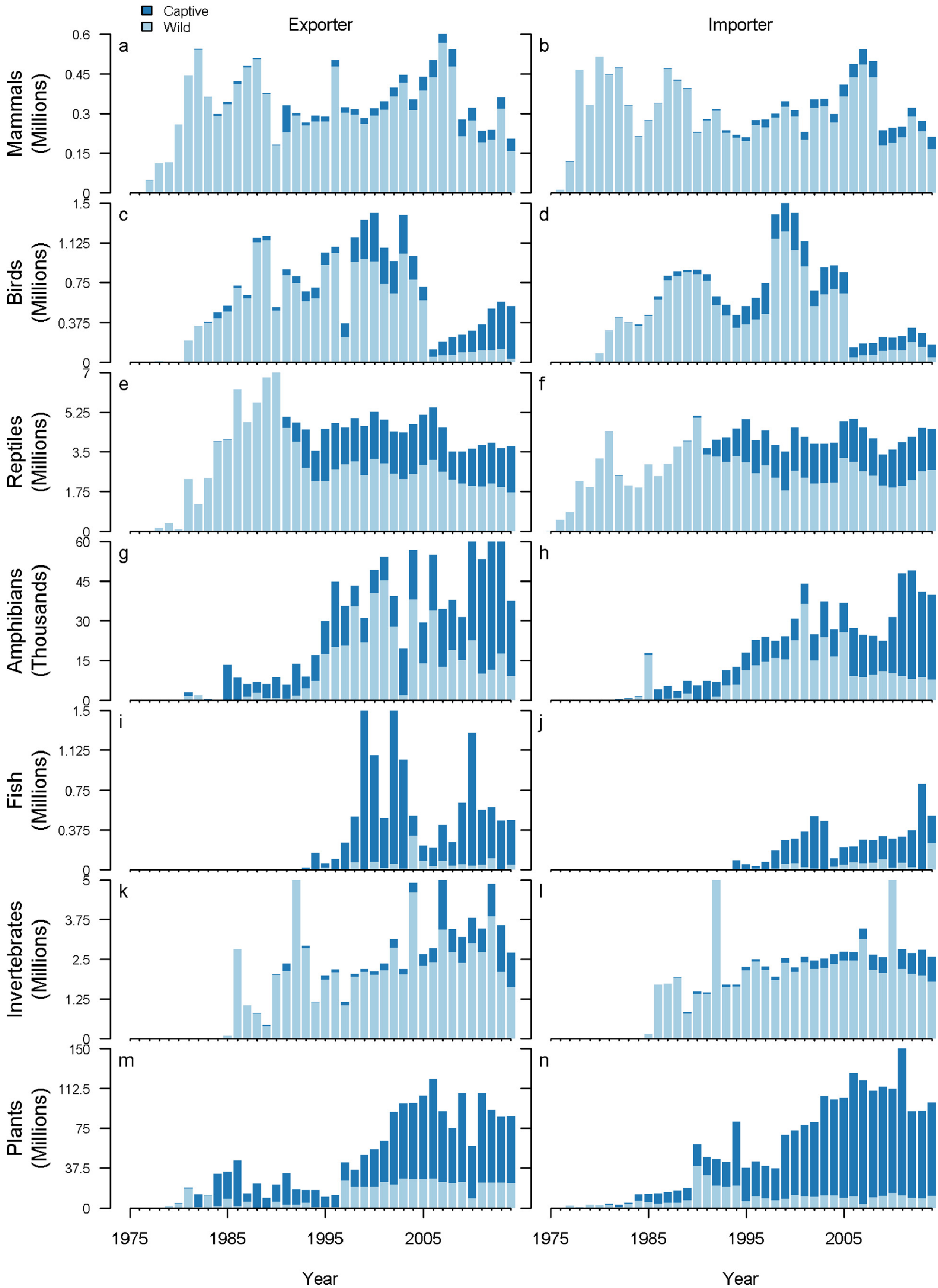

Fig. 1. Volumes of trade in wildlife and derived goods aggregated to whole organism equivalents for 7 taxonomic groups as reported by countries of export (a, c, e, g, i, k, m) and countries of import (b, d, f, h, j, l, n). "Captive" organisms (dark blue) include trade reported as source codes C, D, F, A (see Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by fitting a first-order autoregressive correlation structure — AR(1) — to one of the time series and removing this serial correlation from the other time-series (Francis and Hare, 1994).

To explore potential shifts from wild-sourced to captive-sourced wildlife WOEs, we analysed time-series of the ratio of WOE trade from wild sources to that from captive sources for the broad taxonomic described above as well. We also analysed time-series for taxonomic orders within each broad group to check for variation within the group-level trends. Because the CITES data are thought to contain measurement error as a result of differences in reporting practice (for example reporting as actual trade or the permits issued) and mis-reporting, we applied a state-space time-series modelling technique that filters the data and provides an estimate for the true underlying time-series and its uncertainty (Petris et al., 2009). Specifically, we applied a linear Gaussian state space model with a time-varying trend using the Kalman filter and smoother algorithms to estimate the underlying state, with variance parameters estimated via maximum likelihood (Durbin and Koopman, 2012). The ratio time-series were log-transformed to meet the assumption of Gaussian errors. All state-space model analyses were conducted using the DLM package in R (Petris, 2010). To assess the significance of any trend in the ratio over time, we also fitted Poisson generalized linear models with a log link function with the wild to captive ratio as the dependent variable and time as the independent variable.

We assessed the degree of agreement between the ratio of wild- to captive-sourced trade reported by exporters and its importer reported counterpart by calculating the correlation between the two time-series after pre-whitening and filtering the series as described above. We used the correlation analysis described above to assess agreement between importer and exporter reported time-series (Text S1).

As an independent analysis of the degree of agreement between importer and exporter reported data, we extracted shipment records where we could match the exporter reported value for the shipment with the importer reported value. We filtered the database to identify shipments where both importer and exporter reported shipments had the same export permit number as well as the same recorded taxon, product, purpose, source, unit and exporting state. Of the 9,871,814 direct trade shipments of CITES listed taxa in the database, 1,250,817 shipment records (13%) were matched by importer and exporter and the quantity reported in the shipment was compared.

To evaluate the spatial patterns of wild-sourced trade in wildlife products in each taxonomic group, we aggregated the 9,871,814 direct trade shipments of CITES listed taxa by year, taxonomic group, WOE, unit, exporter and importing state. We then visualised trade flows in number of individuals between states for each taxonomic group for the four five-year periods between 1995 and 2014, using a circular network diagram (Gu et al., 2014).

3. Results

Wildlife products are legally traded internationally in substantial volumes; on average over 100 million WOEs were reported in trade per year between 2005 and 2014, up from 9 million WOEs reported as exported per year between 1975 and 1985 (Table S3).

3.1. Global temporal trends

The temporal patterns were generally qualitatively similar for both exporter and importer reported datasets, but total reported exports were greater than total reported imports for all taxa except plants (Fig. 1, Table S3). In total, between 1975 and 2014, plant WOEs were traded at the highest volume (1.80 billion reported by exporters), followed by reptiles (152 million), invertebrates (79.8 million), birds (24.1 million), mammals (13 million), fish (12.8 million) and amphibians (1.07 million).

There was considerable variability in the volumes of WOE trade through time, with the coefficient of variation higher for exports than imports, most notably for fish (exports 14 times more variable than imports) and amphibians (exports 5 times more variable). Despite this variability, a notable trade downturn was observed for wild-sourced birds in 2006 when total reported exports and imports fell by 86%, likely caused by the EU ban on imports of wild birds (Decision 2005/760/EC and subsequent decisions). A similar downwards shift appears to have occurred in 2009 for wild-sourced mammals, when exports and imports both fell by approximately 50%, but since there was oscillatory behavior prior to 2009, the downturn may reflect a short-term adjustment.

The product composition of WOE trade in each taxonomic group remained broadly consistent over time (Figs. S1–S7). For mammals, wild-sourced trade was predominantly in skins, whilst captive-sourced trade comprised mostly live organisms. Trade in birds, amphibians, fish and plants was dominated by live organisms, whilst the main reptile products were skins and live organisms, and invertebrate trade consisted of live organisms, raw corals and shells. We found no evidence that trade patterns of WOEs were determined by changes in the products being traded, for example more shipments being traded as products that cannot be aggregated to WOEs (Fig. S8). Despite the number of taxa listed by and states party to CITES growing monotonically since the origins of the Convention, we also found no evidence that trends in the numbers of taxa being traded or numbers of states involved in trade are important predictors of the volume of trade in wild-sourced products (Fig. S9, Tables S3–S6).

3.2. Global spatial trends

Underlying the broadly stable pattern of global trade volumes of wild-sourced WOEs described above, we found the spatial configuration of trade to be dynamic (Figs. 2, and S10–S15).

The spatial trade patterns for wild-sourced birds showed the most substantial changes of all taxonomic groups (Fig. 2). From 1995 to 2004, African states (Senegal, Guinea and Mali) were the major exporters, whilst European states (Italy, Portugal, Spain and France) were the main importers and, although trade was taxonomically diverse, the Yellow-fronted Canary (*Serinus mozambicus*, taxonomy as listed under CITES), Cut-throat Finch (*Amadina fasciata*), Red-cheeked Cordon-bleu (*Uraeginthus bengalus*) and Senegal Parrot (*Poicephalus senegalus*) were important taxa for these trade flows. However, trade declined in the mid-1990s and collapsed in the period 2005–2009. The only significant trade route to emerge during that period was between Uruguay and Mexico and comprised almost entirely (96–98%) of Monk Parakeet (*Myiopsitta monachus*).

3.3. Shifts from wild to captive sources

In the decade following the first recorded shipments of both wild- and captive-sourced products, mammals, birds, reptiles, invertebrates and plants were predominantly wild-sourced (Fig. 3, Table S8). For these groups, there is evidence of a substantial and significant shift towards more captive-sourced products over time. Ratios declined by one or more orders of magnitude across the whole time-series for each of these groups, the time varying slopes of ratio of wild- to captive-sourced trade from state space models were predominantly negative and there were more years in which the slope was significantly negative as opposed to being positive, meaning that the modeled ratio was declining through time as more captive-sourced specimens were traded (Fig. 3). Amphibians and fish have been predominantly captive-sourced for most of the analysis time period. For all groups other than amphibians and fish, generalized linear model slope coefficients were significantly negative (Table S9).

There was strong correspondence between the ratio of wild- to captive-sourced trade reported by importers and exporters for mammals, reptiles and invertebrates ($p < 0.05$; *t*-test of correlation

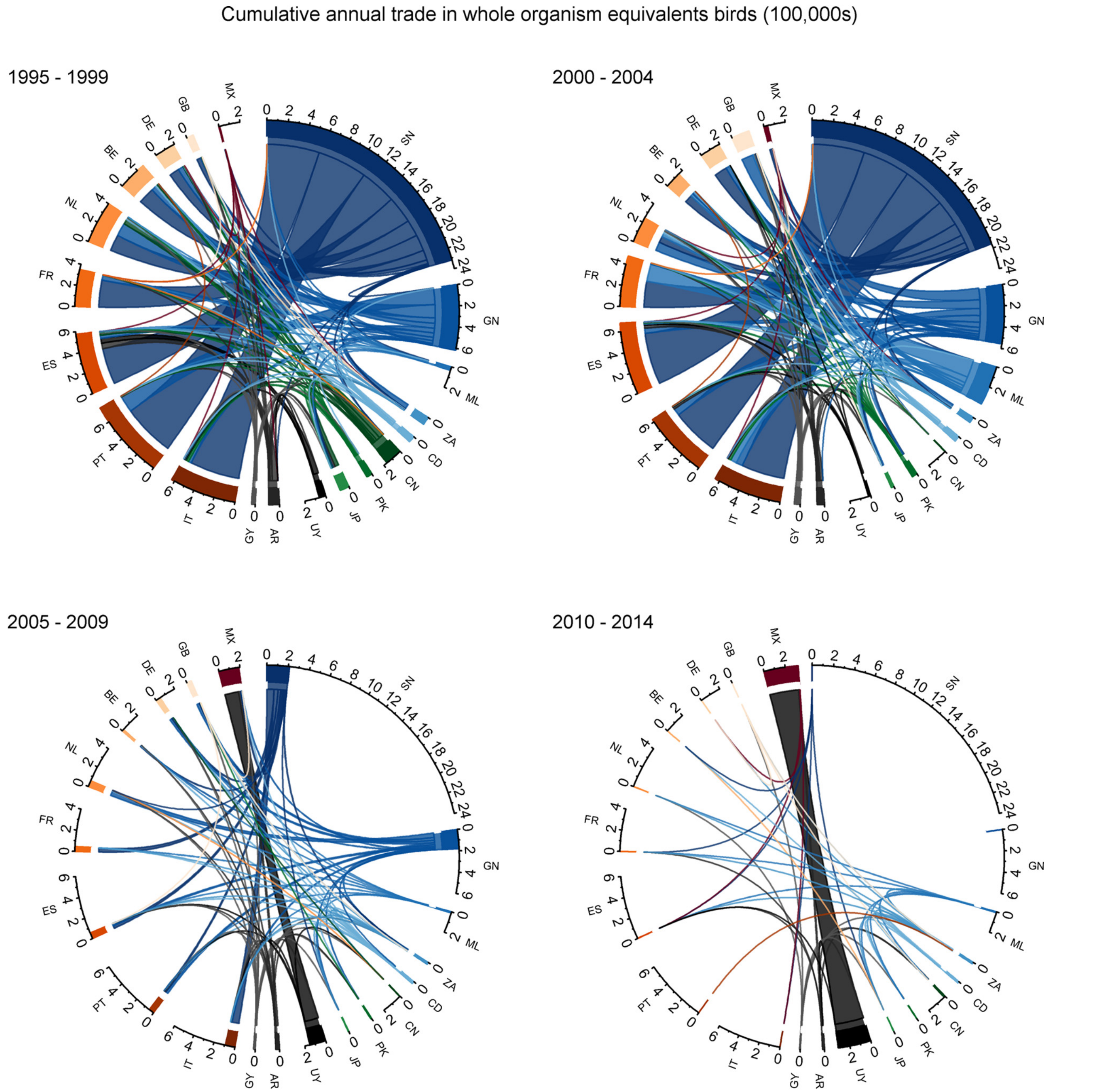

Fig. 2. Spatial patterns in CITES-listed trade in wild-sourced birds within four-year period (100,000 s of whole-organism equivalents) as reported by the state of export. States are grouped by CITES region and arranged as segments around the outside of the plot, labelled by ISO2 code (Table S7) and indicated by colour. Numbers around the perimeter of segments indicate trade volumes. For each state segment, two bars are plotted around the perimeter. The outer bar is the combined imports and exports of WOEs for that state. The paler bar adjacent and inside indicates total exports. These total exports are linked to importing countries by trade flow ribbons, which lead from and match the colour of the export bar of the exporting state. So in the 2010–2014 period, Uruguay's cumulative imports and exports (the outer bar) were approximately 300,000 WOEs, and the export bar indicates that the nearly all of this trade comprised exports to Mexico. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

statistics after pre-whitening). Independent analysis of individual shipments showed that of 1,250,817 shipments matched by export permit number, taxon, product, purpose, source, unit and exporting state, 81.5% were reported with identical quantities by exporters and importers, 13.3% were reported with a greater volume exported than imported and 5.2% with a greater volume imported than exported.

When decomposed to the order level there was evidence of opposing trends to those of the group level shifts identified above for birds, mammals and plants. All orders of birds shifted from wild to captive over time, except for Galliformes (gamefowl or gamebidrds), which saw a shift towards wild-sourced trade after 2001 although volumes of trade were low (100 s of WOEs) (Fig. 4). Three of the five mammalian orders that could be compared also showed a decline in the ratio of wild to captive sourced products. Trade in products sourced from Perissodactyla (odd-toed ungulates) or Proboscidea (elephants and their relatives) shifted to more wild sourced products after 1995 and 2000, respectively (Fig. 5). For plants, only the Gentianales (families Apocynaceae, Gelsemiaceae, Gentianaceae, Loganiaceae and Rubiaceae) and Liliales (15 plant families) showed evidence of opposite trends to those of the group as a whole. Trade shifted towards more wild-sourced

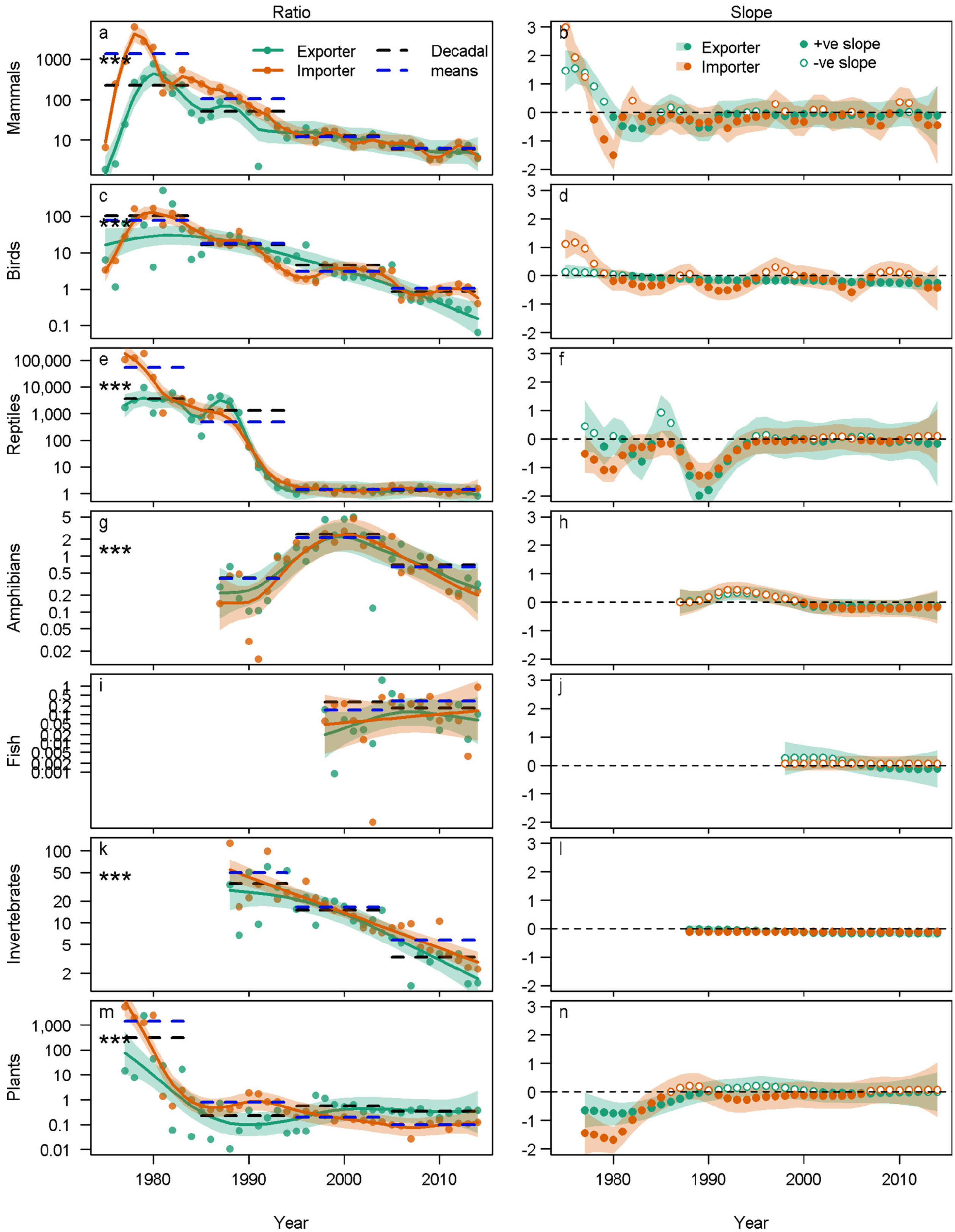

Fig. 3. Ratios of wild-sourced to captive-sourced trade through time 1975–2014 (a, c, e, g, i, k, m), with points indicating trade data and lines representing filtered estimates of the true level of trade according to Gaussian state space models. Shaded polygons show 95% confidence intervals around this estimate. Stars indicate ratios reported by countries of import and countries of export that are significantly correlated ($p \leq 0.05$). Time varying slopes of the trend in these ratios as estimated by the state space models (b, d, f, h, j, l, n). Open symbols in (b, d, f, h, j, l, n) indicate the slope is positive and closed symbols indicate the opposite. Shaded areas indicate the 95% confidence interval of the estimated slope.

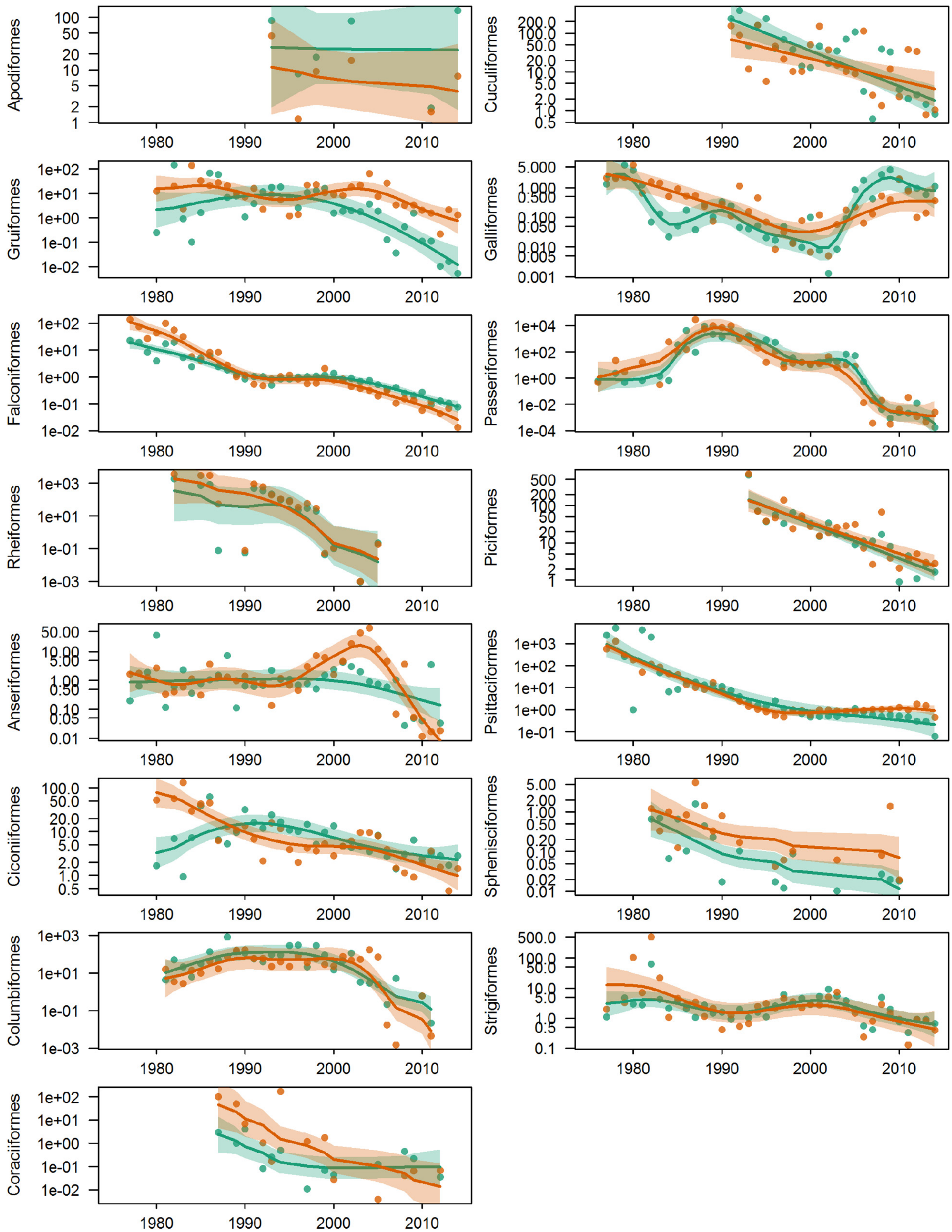

Fig. 4. Ratios of wild-sourced to captive-sourced trade through time (1975–2014) for taxonomic orders of birds, with points indicating trade data and lines representing filtered estimates of the true level of trade according to Gaussian state space models. Shaded polygons show 95% confidence intervals around this estimate.

products after 1995 for Gentianales, whilst for Liliales, there has been a steady increase, especially for exporter reported trade (Fig. S16). For reptiles and invertebrates there were no orders that showed a shift towards more wild-sourced trade (Figs. S17 & S18). However, for amphibians and fish, which as groups showed no strong temporal trend in wild- to captive-source trade ratios, the orders Anura (frogs) and

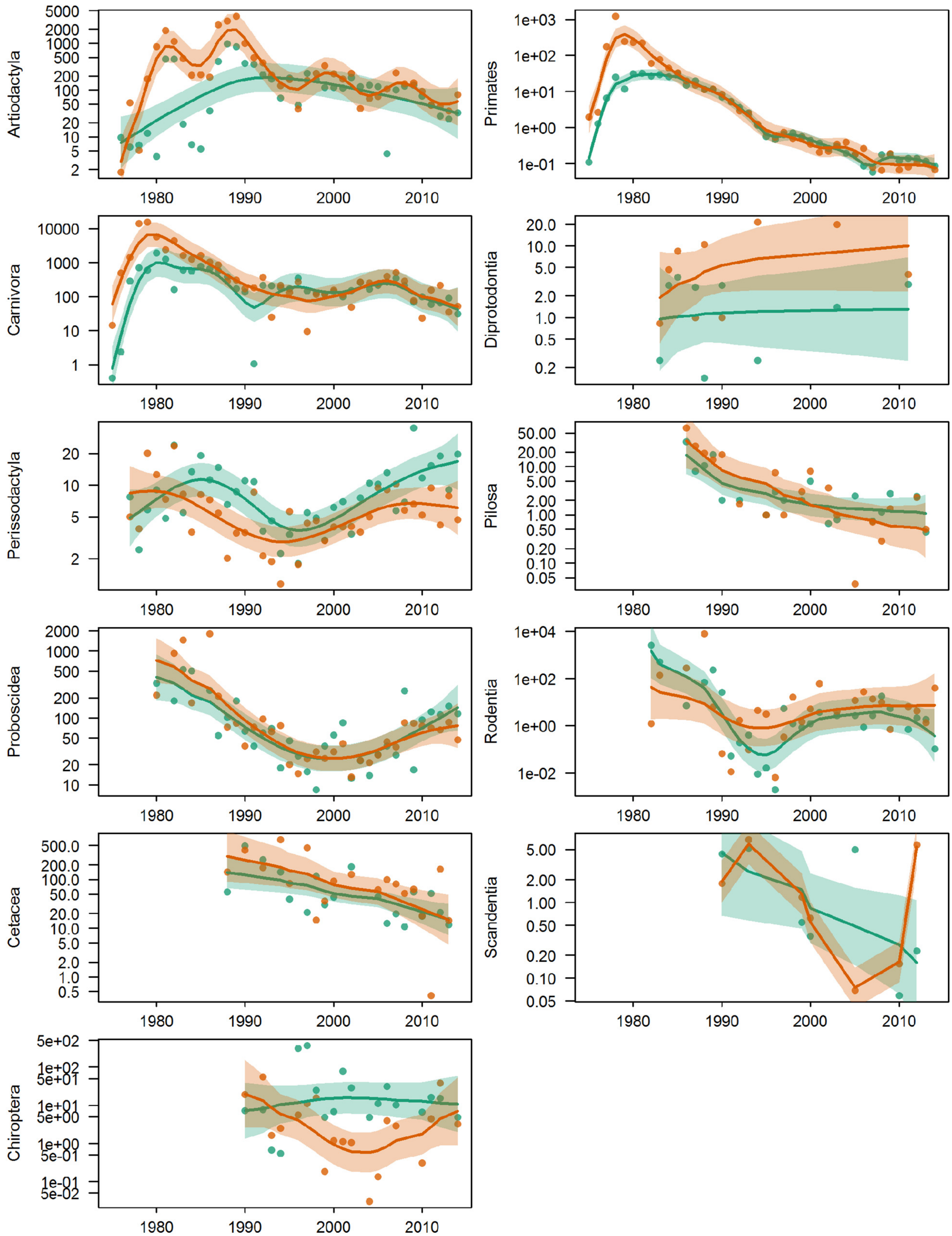

Fig. 5. Ratios of wild-sourced to captive-sourced trade through time (1975–2014) for taxonomic orders of mammals, with points indicating trade data and lines representing filtered estimates of the true level of trade according to Gaussian state space models. Shaded polygons show 95% confidence intervals around this estimate.

Table 2
Hypotheses that might explain the shift in reported volumes of wildlife trade from wild-sourced to captive-sourced products.

Hypothesis	Description
H1. Reliability	For particular taxa, those with a physiology and ecology that is suitable for breeding in captivity, and, for which the demand is relatively stable, captive breeding can provide a reliable supply of products. The breeding biology of the organisms will determine the speed of production as well as the capacity of meet demand surges.
H2. Quality	Captive breeding of organisms can ensure high quality products for example, the quality of skins for leather goods or the health of animals for the pet trade.
H3. Supplying in-demand products	Captive breeding can more easily control for attributes of organisms that are in-demand, for example, albinism. However, surges in demand for particular attributes can be met more feasibly for organisms whose breeding biology is sufficiently rapid to meet such demand growth.
H4. Negative perception of wild-sourced products	Demand for wild-sourced specimens could have declined because of negative perceptions about wild harvesting, collecting or hunting whilst perceptions about captive-bred populations are more positive.
H5. CITES is limiting Wild-sourced trade	CITES Parties are required to conduct 'non-detriment findings' (NDFs), which take into account population data, trade levels and population management (see Smith et al., 2011 for an overview) prior to allowing trade in wild-sourced products to take place. This regulation, could be limiting the amount of wild sourced trade to sustainable levels and excess demand is being met by products sourced from captivity.
H6. Wild populations have declined	Wild populations of species in demand may have declined in size to the extent where supply of wild-sourced products cannot meet demand. Instead, the excess demand is met by products sourced from captive–bred populations.
H7: Misreporting	Products sourced from wild specimens might be misreported as being captive sourced either mistakenly or purposefully.

Syngnathiformes (pipfishes and seahorses) showed a systematic shift towards more captive-sourced products (Figs. S19 & S20).

4. Discussion

The aim of CITES is to regulate the international trade in CITES-listed animals and plants so that trade in wildlife and wildlife products is legal, sustainable and traceable. It does this by enabling international cooperation and regulation between Parties. Our analysis, over a 40-year period of trade in CITES-listed species, has unveiled some noteworthy shifts in trade routes, volumes and source (from wild-sourced to captive-bred) of wildlife products over time.

Beyond an initial, general steep increase in trade volume whilst the taxonomic and geographic coverage of CITES rapidly expanded, there are no consistent patterns in wild-sourced trade across all taxonomic groups, indicating that even at the very broad taxonomic level, trade is determined by a multiplicity of factors, such as: ecological dynamics, regulatory decisions affecting supply, fashions of consumer demand and other socio-economic factors (e.g. Challender et al., 2015). Despite this we find broad support that CITES trade has shifted from wild- to captive-sourced wildlife products. There are several possible hypotheses to explain this finding (Table 2), and none is likely to explain all the patterns in isolation; it is more likely that all apply but their relative importance varies across taxa, products and geography.

For particular taxa whose physiology and ecology is suitable for breeding in captivity, sourcing products from captive-bred populations might have several advantages over those from wild-sourced populations. First, for demand that is relatively stable over time, captive breeding might provide a more reliable supply, since the managed populations can avoid environmental or ecological fluctuations that can affect wild populations (MacGgregor, 2002; Natusch and Lyons, 2014) (H1, Table 2). Second, captive bred populations might ensure a higher quality of product, for example animals bred for skins can be managed to protect the skins from damage that might occur in the wild (H2) (Hutton and Webb, 2003) or animals destined for the pet market have a reduced parasite load (Lyons and Natusch, 2015). Third, captive breeding facilities can more easily control for particular properties that are in-demand, for example albinism (H3). Furthermore, public perceptions of sourcing products from wild populations could affect the balance of demand for wild-sourced versus captive-sourced products. It has been documented previously that consumers perceive wild- and captive-sourced products differently (Bulte and Damania, 2005). A growing perception that exploitation of wild populations is undesirable could cause a shift towards captive-sourced trade (H4).

The Convention may have successfully alleviated increased utilisation of wild populations for some taxonomic groups by regulating supply of wild-sourced products to sustainable levels and supporting trade in captive-sourced products (H5). CITES Parties are required to conduct 'non-detriment findings' (NDFs), which take into account population data, trade levels and population management (see Smith et al., 2011 for an overview) prior to allowing trade in wild-sourced commodities to take place. If implemented effectively, this should prevent unsustainable trade. Trade in wild-sourced products has been relatively stable for most taxonomic groups since the early to mid-1990s (Figs. 1 & S9) whilst trade in captive-sourced products has increased, which supports this hypothesis. CITES also recognises that building livelihoods from sustainable use of wildlife goods will ensure effective conservation and there is evidence that wild populations of utilised species fare better than non-utilised species (Tierney et al., 2014). At the same time, there is also evidence that captive-breeding facilities can both support local livelihoods (Natusch and Lyons, 2014) and reduce pressure on wild-populations (Damania and Bulte, 2007; Nogueira and Nogueira-Filho, 2011). So, combined with the benefits arising from captive-breeding programmes where it is found to be true, this hypothesis (H4) may result in the positive conservation outcomes.

However, some NDFs are based on insufficient national level information regarding, for example, baseline population data and population management information (Smith et al., 2011) so not all legal trade has been sustainable (e.g. Dutton et al., 2013). The shift from wild to captive sourced products could therefore also have arisen because wild populations of species in demand for trade have declined. Consequently, supply of wild-sourced products cannot meet the demand and captive-breeding expands to meet the remaining demand (H6). The taxonomic and geographic diversity of trade in wild-sourced commodities has increased for nearly all taxonomic groups over last two decades, during which there has been little change in trade volumes (Fig. S9). This might result from depletion of historically important populations, followed by supply shifting to other geographic populations or taxa that are subsequently utilised to meet the market demand.

Misreporting of wild-sourced products as captive, either mistakenly or purposefully (H7), could contribute to a shift in the reported balance of wild- to captive-sourced trade, if the practice increased in prevalence over time. It is difficult though to find a mechanism to explain why rates of misreporting would increase through mistakes alone, it would require that periodically or systematically through time, substantially more mistakes were made in reporting the sources of products and that this rate of misreporting has since remained at high levels. The hypothesis appears more likely for purposeful misreporting, especially if NDFs have limited the supply of wild-sourced products at levels below the demand. This hypothesis would be favoured for species whose wild populations remain abundant or that are unsuitable or expensive to breed in captivity.

There are notable order-level exceptions to the shift from wild- to captive-sourced products. The increasing trade in wild-sourced elephants (Proboscidae) and rhinos, zebras and tapirs (Perissodactyla) is likely to result from demand for trophies, combined with the unsuitability of these species for captive breeding. One inference from these exceptions is that in other mammalian orders more suited captive breeding, the beneficial characteristics of captive breeding—reliability, quality and desirable attributes—might be driving the shift towards more captive sourced trade.

For Galliformes, where increases in wild-sourced trade was mainly due to trade in Ocellated Turkey (*Meleagris ocellata*), the volume of trade is very small relative to the overall trade volumes of birds, and is probably a result of trade in trophies. Trade in Liliales is concentrated mainly in snowdrops (*Galanthus* species). There is discussion under CITES about the correct source code for trade in these bulbs, because the production system can be heavily managed, prompting some to argue that although the bulbs are in the wild they should be classed as artificially propagated (McGough et al., 2014).

For birds, both the 1992 U.S. Wild Bird Conservation Act prohibiting import of wild birds, and the EU's 2005 decision to ban imports of wild birds (Decision 2005/760/EC and subsequent decisions), were followed by a notable decline in the number of wild-sourced birds traded internationally, and declining taxonomic and geographic diversity of the bird trade. These regulatory changes were not implemented to manage trade to sustainable levels, rather they aimed to reduce the spread of avian diseases. However, they have had the effect of forcing supply of bird products in Europe and the US to shift towards captive sources. In addition, the trade bans altered the spatial patterns of invasion risk through the opening of new trade routes (Reino et al., 2017). The international market for wild birds shifted to Mexico, where substantial imports of Monk Parakeet (*Myiopsitta monachus*) from Uruguay resulted because of regulatory changes in 2008 that made it illegal to purchase native Mexican parrots as pets. These imports coincided with a growth in feral populations of Monk parakeets (Hobson et al., 2017).

Ecological controls are another potentially important factor determining trade patterns. The recovery and sustainable management of the wild American alligator (*Alligator mississippiensis*) population (Hutton and Webb, 2003) is associated with the notable transition of the U.S. from major importer to major exporter of wild-sourced reptiles. Further exploration of how country-level socio-economic changes (e.g. changes in disposable income or cultural trends) and environmental disturbances (e.g. forest fires or coral bleaching) can explain global spatial patterns of reported trade through time may help to elucidate the potential consequences of such impacts in the future. This is particularly important given forecasts of more frequent and intense extreme events (Bindoff et al., 2013).

Whilst the overarching trade patterns were broadly similar, reported trade levels differ substantially between importers and exporters, partly because of known reporting issues: trade can be reported based on the number of permits issued or based on the actual volume of products traded, source or purpose codes on permits can differ, or reporting rates may be lower for trade imports. Substantial discrepancies have also been documented between CITES and customs data records (Blundell and Rodan, 2003; Blundell and Mascia, 2005; Foster et al., 2014), reinforcing reporting uncertainties. However, much like comparable analyses on data-poor fisheries (Costello et al., 2012), the threat posed by unsustainable trade necessitates an analysis of the available data, even if incomplete. There is a strong case for producing a best estimate of the actual trade in CITES listed species accounting, where possible, for the sources of discrepancy described above.

In summary – we have shown that wildlife products are legally traded internationally at volumes of on average 100 million WOEs per year over the last 10 years (up from 9 million WOEs per year between 1985 and 1995). CITES was enacted to provide protection to wildlife populations at risk from international trade. As well as the increase in trade volume, our analysis has unveiled major shifts in the dynamics of this trade over time, including volumes of individual taxa, sources and routes, which we hypothesise change rapidly in response to ecological, socio-economic, and political drivers. New trade routes continue to emerge, and new taxa are being traded. Perhaps most strikingly, we have documented a clear increase in the proportion of trade that is captive-sourced for almost all taxonomic groups. We describe and discuss seven hypotheses for why these shifts might arise, but the shift may have implications both for wild populations and for the communities that may be dependent upon them for income. Our analysis represents a first step at documenting global-scale trends in the legal, international wildlife trade across all taxa. For a more complete understanding, and to be able to predict the consequences of decisions for trade and wildlife populations, a holistic analysis incorporating the CITES trade data, information on population dynamics of traded organisms, and an understanding of the scale and patterns of illegal trade will ultimately be required.

Supporting tables are available online providing values used for conversion to whole organism equivalents for different taxonomic groups, statistics of wildlife trade volume, taxonomic and geographic diversity, states party to CITES. Supporting figures are also available online showing the term composition of trade in each taxonomic class and plants, proportion of transactions that can be aggregated to whole organism equivalents and spatial patterns of CITES-listed trade for each functional group. Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.04.017.

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Author contributions

The project was designed by MH, SG and KM; MH, DT, SG and GB performed the analysis. MH and DT led the writing of the article with contributions from all authors.

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