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The ecological drivers and consequences of wildlife trade

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ABSTRACT

Wildlife trade is a key driver of extinction risk, affecting at least 24% of terrestrial vertebrates. The persistent removal of species can have profound impacts on species extinction risk and selection within populations. We draw together the first review of characteristics known to drive species use – identifying species with larger body sizes, greater abundance, increased rarity or certain morphological traits valued by consumers as being particularly prevalent in trade. We then review the ecological implications of this trade-driven selection, revealing direct effects of trade on natural selection and populations for traded species, which includes selection against desirable traits. Additionally, there exists a positive feedback loop between rarity and trade and depleted populations tend to have easy human access points, which can result in species being harvested to extinction and has the potential to alter source–sink dynamics. Wider cascading ecosystem repercussions from trade-induced declines include altered seed dispersal networks, trophic cascades, long-term compositional changes in plant communities, altered forest carbon stocks, and the introduction of harmful invasive species. Because it occurs across multiple scales with diverse drivers, wildlife trade requires multi-faceted conservation actions to maintain biodiversity and ecological function, including regulatory and enforcement approaches, bottom-up and community-based interventions, captive breeding or wildlife farming, and conservation translocations and trophic rewilding. We highlight three emergent research themes at the intersection of trade and community ecology: (1) functional impacts of trade; (2) altered provisioning of ecosystem services; and (3) prevalence of trade-dispersed diseases. Outside of the primary objective that exploitation is sustainable for traded species, we must urgently incorporate consideration of the broader consequences for other species and ecosystem processes when quantifying sustainability.

Key words: biodiversity conservation, ecosystem function, ecosystem services, trafficking, trophic cascades, wildlife trade.

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I. INTRODUCTION

Globally, over 100 million plants and animals are traded every year (Harfoot *et al.*, 2018). Trade coverage is expansive, with at least 24% of the world's terrestrial vertebrates being traded (Scheffers *et al.*, 2019; Hughes, Marshall & Strine, 2021; Marshall *et al.*, 2022), along with thousands of plant and invertebrate species that receive far less research and policy attention (Fukushima, Mammola & Cardoso, 2020; Marshall *et al.*, 2022). The exploitation of species to support this trade is a known driver of extinction risk (Maxwell *et al.*, 2016; Scheffers *et al.*, 2019). Driven by a demand for wildlife as food, products and pets, trade is a major global industry, with the illegal wildlife trade (IWT) alone worth US \$7–23 billion annually (Nelleman *et al.*, 2014). Along with implications for biodiversity, the industry also impacts human society, with approximately 800 million people in the rural tropics dependent on wildlife for long-term food and livelihood security (Nielsen *et al.*, 2018). The scale of the industry attracts organised criminal groups, posing governance risks (Lawson *et al.*, 2014), while contact between humans and wildlife along the supply chain has resulted in zoonotic disease outbreaks (Karesh *et al.*, 2005), including the ongoing Covid-19 pandemic (Yuan *et al.*, 2020).

High levels of trade persist across a range of spatial scales, underpinned by varied socio-cultural and economic drivers. In some regions, the highest volumes of wildlife are traded locally (Corlett, 2007), as economically marginalised rural communities in the tropics are often dependent upon wildlife products for food or medicines (Bowen-Jones, Brown & Robinson, 2003), with the greatest trade volumes consisting of larger or more abundant species (Petrozzi *et al.*, 2016). The proliferation of road networks into remote forests increases access to markets, and combined with economic growth in regions such as South-East Asia, has fuelled a rapid rise in demand for wildlife as luxury food, traditional medicine, or pets from urban and international markets (Wilkie *et al.*, 2011). Here, demand for wildlife is often driven by wealthy consumers willing to pay a premium for desirable species (Bowen-Jones *et al.*, 2003; Shairp *et al.*, 2016), making

rhino horn worth its weight in gold. Cultural factors can also influence the demand for species. For instance, buddhist traditions of merit release also involve huge numbers of bird species (Gilbert *et al.*, 2012; Su *et al.*, 2015), including 680,000 individuals annually worth US \$235,000 in net profit to sellers at two temples in Phnom Penh, Cambodia (Gilbert *et al.*, 2012).

Exploitation of wildlife to supply this demand has driven widespread population declines and local extinctions of traded species, with a recent meta-analysis finding an average of 62% declines in abundance of traded species where trade occurs (Morton *et al.*, 2021). In turn, trade is frequently cited as a driver of elevated extinction risk, with a greater proportion of threatened *versus* non-threatened birds, mammals, and reptiles traded (Scheffers *et al.*, 2019). Hunting for trade is harder to detect than other anthropogenic disturbances (Peres, Barlow & Laurance, 2006), but it has left vast areas of 'empty' or 'half-empty' ecosystems, whereby seemingly intact habitat is denuded of much of its faunal communities (Wilkie *et al.*, 2011; Lindsey *et al.*, 2013). Nearly half of the pantropical forest area is thought to have lost a significant proportion of its mammal communities due to hunting, often to supply trade (Benítez-López *et al.*, 2019).

Beyond reductions in species' populations, extraction for trade also has implications for many ecological processes, such as seed dispersal, herbivory, and predation. Widespread population declines diminish the strength of ecological interactions, with implications for ecosystem function and second-order cascading effects for other plant and animal communities (Gardner *et al.*, 2019). In this review, we (i) identify species characteristics that influence wildlife trade demand, then (ii) consider how demand for these characteristics impacts selection and population viability, (iii) investigate the cascading impacts of wildlife trade for ecological communities and networks, and finally, (iv) outline some conservation interventions undertaken to mitigate the impacts of trade. In light of these findings, we provide a brief discussion as to how the trade of wildlife impacts ecosystem services and rural communities living alongside wildlife.

II. SPECIES CHARACTERISTICS THAT INFLUENCE TRADE VALUE AND DEMAND

In any supply chain, traded products are targeted to maximise yields while minimising investment and effort. In general, wildlife trade, whether it be for pets or products, often targets traits aligned with both forms of r/K selection theory, or more recently life-history theory. Thus, animals may be targeted based on a suite of desirable traits conducive for a specific trade demand, such as when they are above average in size or abundance. Taking lessons from the commercial trade of fishes, Atlantic cod (*Gadus morhua*) was targeted for both of these characteristics – they were large in size and historically a highly abundant fishery in the northern Atlantic (Hutchings & Myers, 1994). In eastern Canada, targeting of large individuals created a positive feedback whereby the unsustainable offtake of large-bodied fishes, and consequently those with the largest reproductive output, caused the fishery to collapse in the late 1980s (Hutchings & Myers, 1994).

Similar evidence can be found in the trade of terrestrial wildlife. r -selected species may be targeted for the pet trade or the commercial trade of meat because of characteristics such as high fecundity, small body size, or early maturity (Mohanty & Measey, 2019). Conversely, K -selected species can be characterised by large body sizes, long life expectancy, low reproductive output, longer generation times, and greater parental investment. These species may be targeted for their relatively large body size, but owing to their population dynamics and reproductive biology, tend to be more susceptible to population declines due to unsustainable offtake (Wright, 2003). We summarise below evidence for the suite of life-history traits that are targeted in the wildlife trade such as size, abundance, morphology, and rarity.

(1) Size

Large-bodied species are often in high demand in wildlife trade value chains (Johnson *et al.*, 2010; Ripple *et al.*, 2015; Toomes *et al.*, 2022). Scheffers *et al.* (2019)'s analysis of 7638 globally traded terrestrial vertebrates found a significant positive relationship between body mass and a species' presence in trade (Fig. 1A). These findings may be biased given the increased detectability and scientific attention towards larger species, but there are several reasons why larger species may be in higher demand. Species traded for food or products are often sold by weight, and thus deliver higher value per unit effort for hunters (Wilkie *et al.*, 2011). Larger animals are also generally easier to detect and roam across larger areas, therefore encountering human settlements and roads more frequently (Wilkie *et al.*, 2011). In the parrot (Psitticidae) pet trade, size is also a factor determining attractiveness (Tella & Hiraldo, 2014; Romero-Vidal *et al.*, 2020). Populations of larger animal species have thus been depleted across much of the world with major consequences for ecosystem function (Benítez-López *et al.*, 2019) (see Section IV).

(2) Abundance

Akin to large-bodied animal species generating high value per unit effort, this premise extends to highly abundant species or species with high reproductive output. For example, in the Philippines, flying foxes (both *Pteropus* and *Acerodon* species) are hunted for the local bushmeat trade, largely because they are one of the last remaining, abundant, large mammals found in the forest of central Luzon (Scheffers *et al.*, 2012). Similarly, species with high reproductive output, such as several species of python (e.g. Burmese python *Python bivittatus* and reticulated python *Malyopython reticulatus*) and frogs (e.g. for the trade in frogs' legs; Warkentin *et al.*, 2009), are targeted in the pet and product trade.

Trade of highly abundant species has a higher likelihood of sustainability than the trade in species with small population sizes. However, where constant, insatiable market demand persists, it has the potential to cause rapid population declines and drive once-common species to crisis. Less than 40 years ago, black-winged myna (*Acridotheres melanopterus*) was considered common, but the Indonesian songbird trade has driven a precipitous decline with an estimated wild population of less than 250 individuals now remaining (BirdLife International, 2022a). Similarly, trade in white-rumped shama (*Copsychus malabaricus*), a formerly abundant passerine bird, has caused substantial declines across much of its range (Eaton *et al.*, 2015; Leupen *et al.*, 2018), despite suitable habitat remaining and an ability to survive in transformed habitats (Edwards *et al.*, 2014).

(3) Distinctive morphology

Aside from the aforementioned importance of body size in hunting and trade for consumption, distinctive species-specific morphological characters also influence demand for other purposes. Demand for certain morphological traits has resulted in the large-scale exploitation of various species, such as elephants for their ivory (Wittemyer *et al.*, 2014) or pangolins for their scales (Ingram *et al.*, 2019). Generalising which traits are highly valued is challenging, given that demand for specific traits is often species specific, varying by types of trade and socio-cultural factors (Gilbert *et al.*, 2012). Scheffers *et al.* (2019) found that evolutionarily distinct terrestrial vertebrate species are more likely to be traded (except for amphibians), indicating that trade is often driven by demand for distinctive features and uniqueness (Fig. 1B).

Evidence for the relationship between trait distinctiveness and trade are highlighted in smaller-scale consumer choice and market studies of particular groups. For example, orchid species with multiple white flowers are in greater demand (Hinsley, Verissimo & Roberts, 2015), while horn size among bovid species is the best predictor of price in African trophy hunting reserves (Johnson *et al.*, 2010). Within the avian pet trade, characteristics associated with beauty – often colour, pattern, and song quality – are important determinants of demand (Burivalova *et al.*, 2017; Ribeiro *et al.*, 2019;

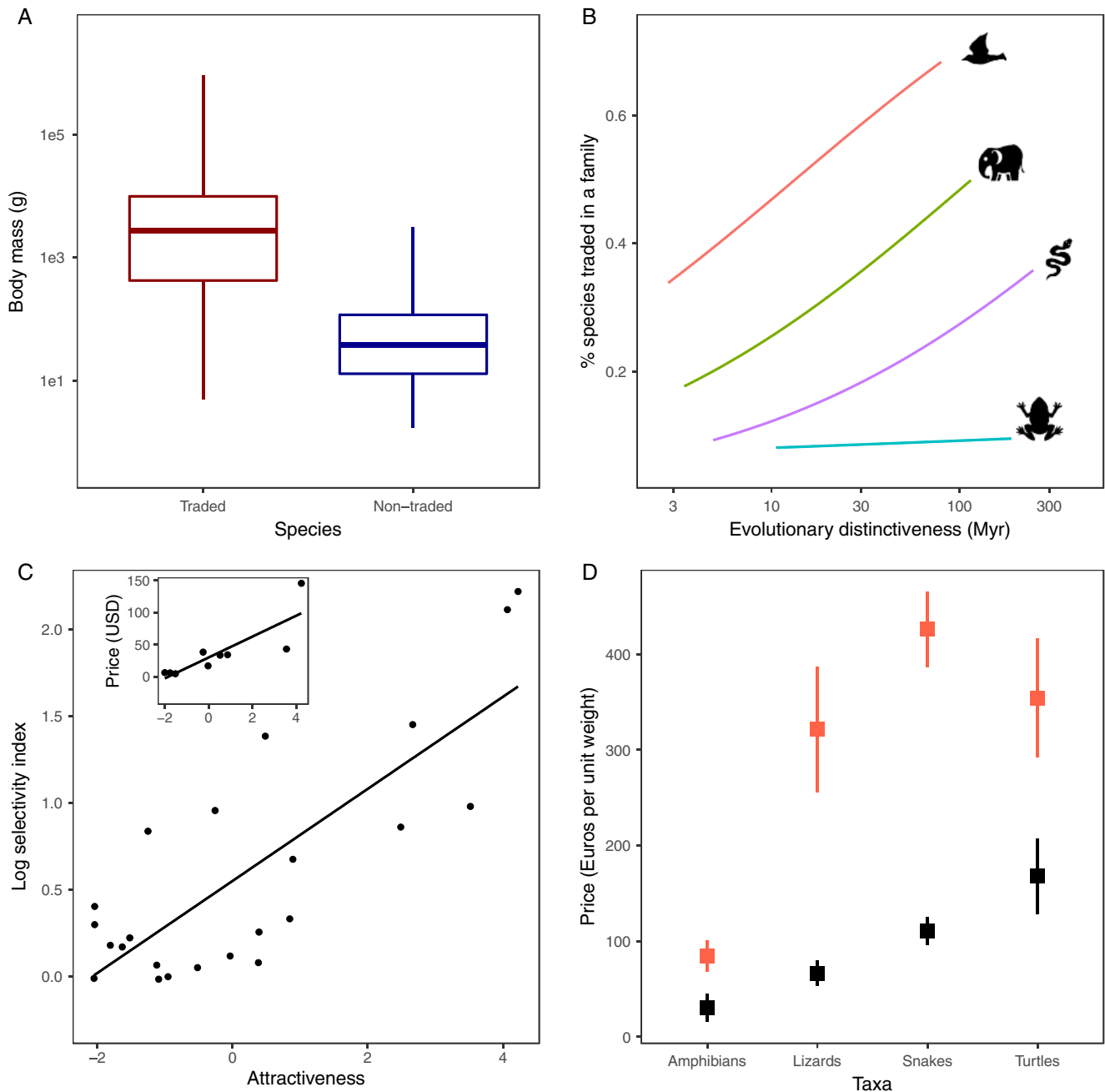


Fig. 1. (A) Body mass of traded and non-traded mammal species. Boxplots show the first quartile, median and third quartile, while whiskers denote maximum and minimum values excluding outliers, which are shown as data points. (B) The relationship between the proportion of traded species within a family and the mean family-wide evolutionary distinctiveness of all four vertebrate classes. Shaded regions denote 95% confidence intervals of a logistic generalised linear model fitted in the original study. (C) The most attractive parrots in Colombia are preferred as pets and are more expensive (inset). Selectivity index refers to the Savage selectivity index and is calculated as the proportion of a species recorded in the pet trade (resource use) divided by the proportion of that species recorded in the wild (resource availability); species with a higher index value are perceived as more attractive. Values range from 0 (full negative selection) to infinity (full positive selection) with 1 representing parrots reported in the pet trade in proportion to their abundance in the wild. Parrot attractiveness is an index based on body size, proportion of the body with bright plumage and ability to imitate human speech. Shaded areas show 95% confidence intervals of a linear model fitted in the original study. (D) Selling prices (per unit adult body mass) of exotic pet species in France according to CITES listing. Species that have a CITES status (red) are more expensive than species with no CITES listing (black). Bars show standard errors. Figures are reproduced from existing publications. A and B are from Scheffers *et al.* (2019) reproduced using the raw data. C is from Romero-Vidal *et al.* (2020) and D is from Courchamp *et al.* (2006) using data extracted from published figures using the MetaDigitise package in R (Pick *et al.*, 2019).

Romero-Vidal *et al.*, 2020). For example, globally, birds with greater colour uniqueness are generally more likely to be traded as pets (Senior *et al.*, 2022). A recent study in Colombia and Mexico highlighted the greatest predictors of both price and exploitation in parrot species as size, proportion of the body with bright plumage, and ability to talk (Fig. 1C; Tella & Hiraldo, 2014; Romero-Vidal *et al.*, 2020). Bright coloration and distinctive pattern is also a strong driver in the trade of freshwater crayfish (Chucholl & Wendler, 2017).

(4) Rarity and threat

Rarity or threat status often determines species' value and demand across different taxa (Palazy *et al.*, 2012; Regueira & Bernard, 2012; Sung & Fong, 2018). Rare species can command extremely high prices. For example, the five most expensive turtle species traded in Hong Kong are all Critically Endangered, the most expensive of which sold for over US \$38,000 per individual (Sung & Fong, 2018). In Vietnam, individuals from the higher echelons of society pay premium prices for rare, wild-caught species, considered to convey wealth and status (Shairp *et al.*, 2016).

There is growing evidence across taxa and regions for a positive feedback between rarity and price – the Anthropogenic Allee Effect (AAE) – whereby a species' value increases with rarity, thus incentivising further exploitation (Courchamp *et al.*, 2006). For instance, having corrected for adult body mass, CITES-listed amphibian, lizard, snake, and turtle species sold in 2006 by the largest herpetologist retailer in France commanded ~2 to 4-fold higher prices than those not listed by CITES (Fig. 1D; Courchamp *et al.*, 2006), while in Brazilian bird markets, consumers of higher socio-economic status from urban areas are more likely to engage in the trade of CITES-listed species (Ribeiro *et al.*, 2019). Similarly, rarity is an important factor influencing the demand for stag beetle species by collectors in Japan, where the rarest species can sell for over US \$5,000 (Tournant *et al.*, 2012).

III. IMPACTS OF TARGETED DEMAND ON SELECTION AND POPULATION VIABILITY

(1) Selection against desirable traits

Demand for unique traits within species may promote artificial selection and/or loss of trait variation in some species via human-induced evolution. For instance, the reduction in the frequency of the silver morph in red fox (*Vulpes vulpes*) in Canada resulted from selective harvesting for the fur trade (Haldane, 1942). Elephants have long been exploited for ivory (Wittemyer *et al.*, 2014) and as poachers usually target large-tusked individuals, average tusk sizes have declined by roughly 24% since the 1970s in certain heavily exploited populations, owing to artificial selection (Chiyo, Obanda & Korir, 2015). The evolutionary consequences of exploitation

has also been shown in ungulate horn sizes (Pigeon *et al.*, 2016), although this remains a topic of debate (Coulson *et al.*, 2018). In sexually dimorphic species, a male bias in individuals traded can occur where desired features are found only in males (Regueira & Bernard, 2012). Trade may also dilute unique phylogeographic populations through the release of pets or repatriation of confiscated animals from illegal trade (Le *et al.*, 2020; Oklander *et al.*, 2020).

Within species populations, the preferential targeting of distinct sizes or age classes has the potential to imperil the viability of the wider population. Streams in Hong Kong, where the Endangered big-headed turtle (*Platysternon megacephalum*) is harvested, are characterised by the absence of large, mature adults (Sung, Karraker & Hau, 2013). Conversely, in Madagascar, the ploughshare tortoise (*Astrochelys yniphora*) is on the verge of demographic collapse, owing to the sustained collection of small juveniles to fuel the international pet trade (Mandimbahasina *et al.*, 2020). In this case, juveniles are preferentially targeted as they are easier to conceal and can be transported in larger numbers. These examples show that even within taxonomic groups, exploitation for trade can select for vastly different traits, highlighting the challenges in predicting and managing its impact without an understanding of the local economic and cultural factors influencing the use of species.

(2) Overharvesting of rare species

In severe instances, high price–rarity relationships can drive an AAE. This has significant conservation implications, as highly threatened species can potentially be exploited to extinction. For instance, the last Javan rhino (*Rhinoceros sondaicus*) of the subspecies *annamiticus* was shot for its horn in Vietnam in 2010 (Brook *et al.*, 2014). As the perceived rarity of a species increases (such as through moving a species from CITES Appendix II to Appendix I), trade volumes can peak during the transition period (Rivalan *et al.*, 2007), emphasising how the perception of rarity can itself be a threat to rare species.

Even where there is no AAE, demand for already rare species is a cause for conservation concern. For instance, demand for the Critically Endangered rufous-fronted laughingthrush (*Garrulax rufifrons*) is pushing the species to extinction, with an estimated wild population of fewer than 250 individuals (BirdLife International, 2022b) and 61 individuals were identified across 174 visits to 11 Javan bird markets between 2016 and 2020 (Nijman *et al.*, 2020). The authors, however, found no evidence of the species value increasing over time, and prices were comparable to other more abundant songbirds present within markets (Nijman *et al.*, 2020).

The rarity of newly described reptiles has resulted in some species being targeted for commercial trade within a year of their formal description (Altherr & Lameter, 2020). Over 5% of reptile species described after 1999 have already been recorded in trade, with a mean lag time of eight years between description and trade (Marshall, Strine & Hughes, 2020). The scientific discovery, description, and

publication of new species can further be abused by traffickers who then actively target these species (Esmail *et al.*, 2020). For example, the newly described monitor lizard of the Philippines *Varanus bitatawa* (Sy, 2012) and the Takou marbled gecko (*Gekko takouensis*) entered trade the same year as their description (Marshall *et al.*, 2020).

(3) Population viability as human accessibility increases

Distance to the nearest human settlement or road is often associated with exploitation levels of traded species across the tropics (Koerner *et al.*, 2017; Benítez-López *et al.*, 2019; Morton *et al.*, 2021). In Africa, for instance, mammal populations near human settlements are often the first to become depleted to supply the bushmeat trade, with hunters then travelling longer distances to maintain levels of catch (Coad *et al.*, 2013). Similarly, across Northern Sumatra, offtake for the cage bird trade has extirpated target species within 5 km of roads (Harris *et al.*, 2017). In Thailand, distance to the nearest market was by far the strongest predictor of the occupancy and population density of traded seahorses, masking the effect of environmental variables such as habitat quality (Loh *et al.*, 2016).

Given that over 80% of tropical forests are already within 20 km of roads, and that tropical road networks are projected to increase dramatically (Laurance *et al.*, 2014), connectivity between remote wildlife populations and lucrative urban markets will undoubtedly increase (Clements *et al.*, 2014; Benítez-López *et al.*, 2019). How the shrinking area and density of wildlife within ‘source’ areas, from which individuals repopulate harvested ‘sinks’, impacts the long-term viability of trade is a key question of current and future concern (e.g. Levi *et al.*, 2009).

IV. CASCADING ECOLOGICAL AND COMMUNITY EFFECTS OF TRADE

Exploitation disturbs the myriad ecological interactions occurring within communities. These impacts cascade to non-target species, impacting ecosystem function (Tagg *et al.*, 2020). Research on the cascading community impacts of exploitation has focused on the loss of large-bodied vertebrates, often prevalent in trade (Scheffers *et al.*, 2019) and subsistence use (Peres, 2000). Large-bodied species are also often sensitive to population declines following exploitation (see Section III) and thus their populations are depleted or extirpated across much of the tropics (Wilkie *et al.*, 2011; Lindsey *et al.*, 2013; Benítez-López *et al.*, 2019).

The focus on larger vertebrates reflects the research bias towards this group in the wildlife trade literature (Morton *et al.*, 2021). Trade-induced declines of small vertebrate, invertebrate, and plant species may also have ecological consequences. For instance, Mongolian marmots (*Marmota sibirica*) are a keystone species on the Mongolian steppes, with

their communal burrowing systems associated with increased abundance of several other species (Suuri *et al.*, 2021). However, exploitation for Mongolian marmot meat and skins has contributed to substantial population declines with unquantified repercussions for other species (Kolesnikov *et al.*, 2009). Without directly measuring the community impacts of exploitation-driven declines, ascertaining the functional consequences of trade in these groups remains a research frontier (see Section VI).

In some instances, studies on the impacts of subsistence hunting are used to provide evidence of the likely ecological impacts if hunting was for commerce. Ultimately, however, the cascading ecological impacts of extirpation will remain the same whether hunting is for market or household use.

(1) Trophic cascades in animal communities

While some large carnivore species are directly persecuted for trade (Dinerstein *et al.*, 2007), their higher energetic requirements also make them particularly susceptible to the depletion of prey *via* exploitation for trade. A study of 199 populations across 11 carnivore species revealed that cyclical decreases in prey abundance caused a five- to sixfold greater decline in the largest *versus* the smallest carnivore species (Carbone, Pettoelli & Stephens, 2011). Thus, where wildlife trade causes severe reductions in the prey base, predators are also likely to decline. For instance, in areas of Gabon hunted heavily to supply the bushmeat trade, leopards (*Panthera pardus*) occurred at reduced densities and shifted their diets towards smaller prey species, with their populations extirpated completely in the most heavily exploited sites, despite not being directly hunted (Henschel *et al.*, 2011).

Trade-induced declines of large-bodied species can also increase the abundance of medium- and small-bodied species through reduced predation or competitive release (Wright, 2003; Prugh *et al.*, 2009). For example, at moderate levels of hunting, medium-sized primate populations in the Amazon increased due to the absence of larger primate species with similar diets (Peres & Dolman, 2000). Similarly, populations of meso-predators often increase substantially following the extirpation of large predators, driving elevated rates of bird nest predation (Prugh *et al.*, 2009). In both African savannas and tropical forests, rodents increase in abundance where large herbivores are depleted (Galetti, Bovendorp & Guevara, 2015; Young *et al.*, 2015; Koerner *et al.*, 2017). For example, in heavily hunted sites in the Brazilian Atlantic forests, rodent abundance doubled (Galetti *et al.*, 2015). The competitive release of rodents can further alter communities, including through increasing predatory snake and bird populations in savannas where large-bodied mammals are extirpated (McCauley *et al.*, 2006).

Some large-bodied vertebrates provide resources directly for smaller consumers. For instance, mineral salt licks created and maintained by the trampling of large mammals are frequently used by frugivorous bat populations during their reproductive season (Ghanem & Voigt, 2014). However, in the Western Amazon, forests exploited to supply bushmeat

to local markets have reduced large mammal abundances and subsequently have a higher proportion of degraded mineral licks, resulting in declines of these bat populations (Ghanem & Voigt, 2014). Dung beetles rely on mammalian faeces for food and nesting substrate (Halffter & Favila, 1993). In the Neotropics, overhunting of mammals has driven co-declines of many dung beetle species and an overall loss of dung beetle diversity (Feer & Boissier, 2015; Bogoni, da Silva & Peres, 2019), with implications for ecosystem processes (Feer & Boissier, 2015). For instance, in the Brazilian Atlantic Rainforest, exploitation levels were associated with increases in small dung beetles, shifting the community towards smaller-bodied, generalist dung beetle species that feed on the pelleted dung of the remaining smaller-bodied mammals (Culot *et al.*, 2013).

(2) Population declines from invasive traded species

Sometimes pets become pests. For example, Krysko *et al.* (2011) showed that 85% of 140 non-native reptiles and amphibians introduced to Florida, USA, arrived *via* the pet trade. As mentioned above, perceived charisma and attractiveness is a major driver in the pet trade and charismatic traits have links to biological invasion (Jarić *et al.*, 2020). In fact, invasiveness is often selected for in the global pet trade, because traits associated with commercial success are often the same traits linked to invasion success (Gippet & Bertelsmeier, 2021). For example, in ants, only 1.66% of the total 15,377 species are considered invasive, yet this jumps to 10.96% when considering traded species (Gippet & Bertelsmeier, 2021).

The worldwide market for pets has already led to the establishment of several hundred invasive species with detrimental economic (Diagne *et al.*, 2020) and ecological impacts, which scale from individual species to entire ecosystems. A notable example of invasive species impacts are Burmese pythons, introduced and established in the everglades of South Florida, USA, where they have caused widespread declines in small- to medium-sized mammals and represent a novel predator for nesting bird colonies (Fig. 2A; Orzechowski, Romagosa & Frederick, 2019; Soto-Shoender *et al.*, 2020). Similar ecological consequences from predation are being observed for black-and-white tegus (*Salvator merianae*) and Nile monitors (*Varanus niloticus*) introduced to South Florida (Mazzotti *et al.*, 2020; Offner, Campbell & Johnson, 2021). Novel interactions from invasive species can also trigger shifts in habitat preferences and trait evolution in native congeners (Stuart *et al.*, 2014).

Invasive species from the pet and product trade further threaten native biosecurity, including the introduction of novel pathogens or shifts in host–vector relationships. For example, the trade in amphibians is linked to the introduction of the lethal chytrid fungus, which is driving a global decline across amphibian species (Fisher & Garner, 2020). Following the decline of medium-sized mammals in response to the introduction of Burmese pythons, mosquitoes shifted blood meals towards small-bodied rodents that serve as the

reservoir host, triggering an increased prevalence of the Everglades virus (Hoyer *et al.*, 2017).

(3) Altered seed dispersal networks

Approximately 75% of woody plant species in tropical forests are animal dispersed (Howe & Smallwood, 1982). Overexploitation for bushmeat trade has reduced populations of many large-bodied frugivores, which are obligatory seed dispersers for many large-seeded tree species and important long-distance seed dispersers (Vidal, Pires & Guimarães, 2013). For example, over 70% of individuals hunted by an average Central African village have a seed dispersal role (Abernethy *et al.*, 2013), while African forest elephants (*Loxodonta cyclotis*) – which in some forests disperse the seeds of over 96 tree species (Blake *et al.*, 2009) – are now restricted to 6–7% of their 1984 range, primarily due to hunting for their ivory (Poulsen *et al.*, 2018).

In tropical forests, seed dispersal determines the recruitment of plant species by allowing seedlings to escape density-dependent mortality (Janzen, 1970; Terborgh, 2020). Multiple studies in exploited forests have reported increased clustering of seedlings, reduced seed dispersal distances, and lower removal rates of seeds of large-seeded animal-dispersed tree species, indicating dispersal limitation (Brodie *et al.*, 2009; Abernethy *et al.*, 2013; Harrison *et al.*, 2013; Poulsen, Clark & Palmer, 2013). For example, hornbill species have declined across much of their range owing in part to the pet and casque trade (Trail, 2007). In Central Africa, sites with the highest hunting pressure had the lowest abundance of white-thighed hornbill (*Bycanistes albotibialis*) and subsequently the highest seed dispersal failure rates of the hornbill-dispersed *Sauidia kamerunensis* (Trolliet *et al.*, 2017).

Many small- to medium-sized species are also seed dispersers and, where large-bodied seed dispersers are overexploited, their competitive release may partially compensate for their loss (Wright, 2003; Culot *et al.*, 2017; Bagchi *et al.*, 2018). For instance, Sethi & Howe (2009) showed that despite the populations of three hornbill species being significantly lower in hunted and logged forests, only one of three hornbill-dispersed tree species was dispersal limited, likely due to seed dispersal from the non-hunted mountain imperial pigeons (*Ducula badii*). However, increased dispersal by smaller-bodied species does not have a compensatory effect for all tree species, and is likely to be skewed towards species with smaller seeds (Blake *et al.*, 2009) and across smaller distances (Culot *et al.*, 2017). In heavily exploited sites, or when large-bodied species have become depleted, medium-sized seed dispersers may also become overexploited (Wright, 2003).

Many avian frugivores and fruit bat species are also key seed dispersers. Despite this, the ecological impacts of the overexploitation of these groups has seldom been directly explored and remains largely unknown. Overexploitation of frugivorous birds and fruit bats may particularly impact the connectivity of forest patches across fragmented landscapes, given their greater ability to traverse human-dominated landscapes than many large terrestrial mammals (Sekercioglu, 2006; Abedi-Lartey *et al.*, 2016). For instance,

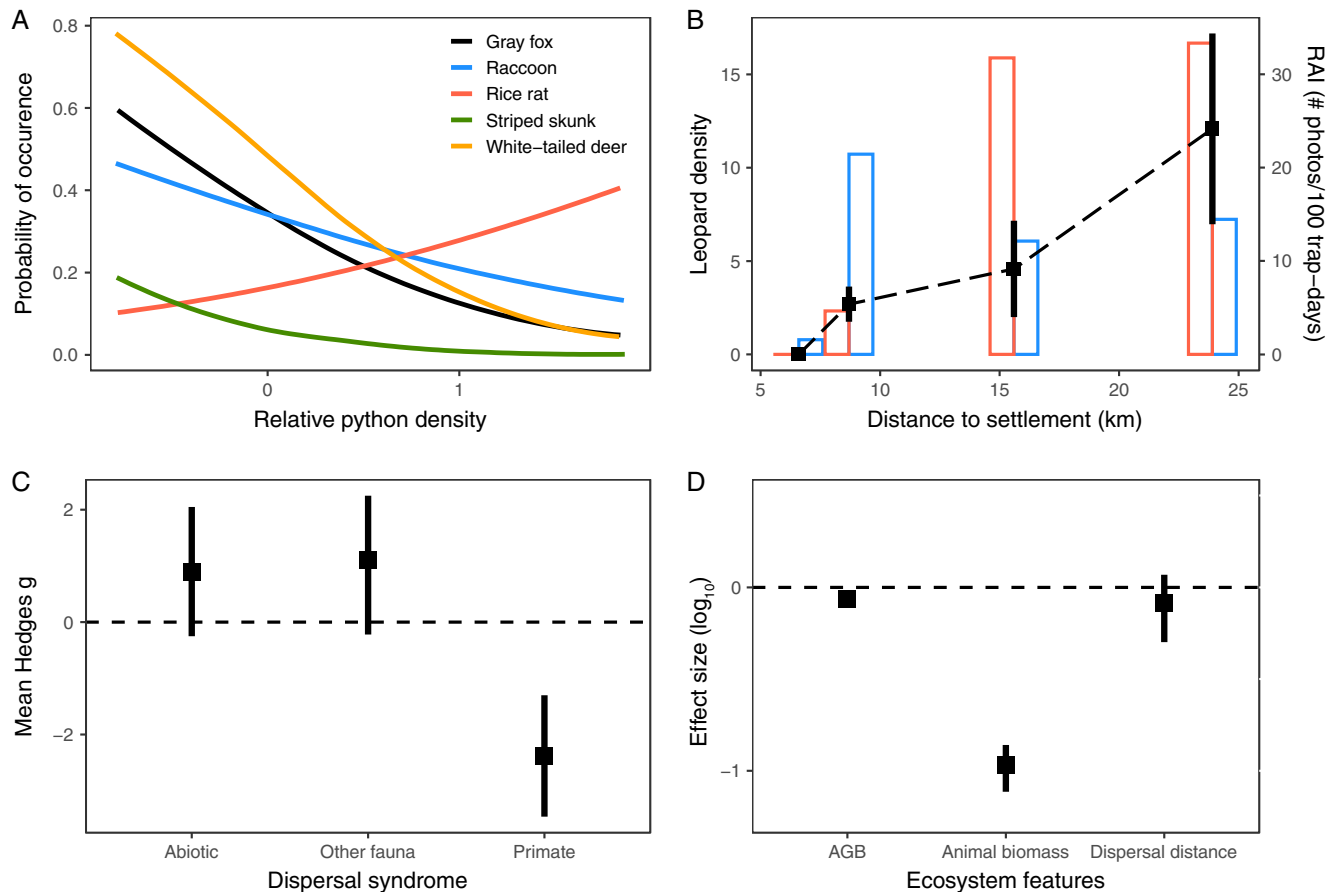


Fig. 2. (A) Species-specific occupancy probability of grey fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), rice rat (*Oryzomys* sp.), striped skunk (*Mephitis mephitis*) and white-tailed deer (*Odocoileus virginianus*) as a function of the density of invasive Burmese python (*Python molurus bivittatus*). (B) Camera trap estimates of the relative abundance index (RAI) of medium (blue bars) and large (red bars) prey, and leopard population density per 100 km² (black line with standard errors) at four study sites in central Gabon. (C) Effect sizes of defaunation on regeneration of woody plant species with different dispersal methods with 95% confidence intervals. Negative effect sizes indicate defaunation reducing regeneration. (D) Effects of hunting on aboveground biomass (AGB), biomass of medium- and large-bodied animals and mean seed dispersal distance with 95% confidence intervals. The effects of disturbance were estimated as log response ratios by dividing the value of the disturbed sites by the value of the sites where that disturbance was not present. Figures from: A, Soto-Shoender *et al.* (2020); B, Henschel *et al.* (2011); C, Gardner *et al.* (2019); D, Poulsen *et al.* (2013). Data extracted using the MetaDigitise package (Pick *et al.*, 2019).

straw-coloured fruit bats (*Eidolon helvum*) are considered one of sub-Saharan Africa's longest-distance seed dispersers, dispersing seeds up to 75 km away from their parent trees across highly fragmented landscapes (Abedi-Lartey *et al.*, 2016). Exploitation for the bushmeat trade has, however, resulted in widespread population declines of this species (Kaminski *et al.*, 2011).

(4) Altered seed predation and herbivory rates

Alterations to post-seed dispersal processes can also impact plant recruitment. The overexploitation of larger seed predators, and subsequent release of smaller-bodied seed predators (particularly rodents) that favour smaller seeds, was thought to buffer the impacts of reduced dispersal of large-

seeded tree species (Dirzo, Mendoza & Ortiz, 2007; Wright *et al.*, 2007). However, small-bodied seed predators may compensate, or even increase, seed predation rates of large-seeded tree species in overexploited forests (Galetti *et al.*, 2015; Rosin & Poulsen, 2016; Culot *et al.*, 2017). For example, in Brazil, demographic simulations calibrated with empirical data suggest that the competitive release of rodents where larger seed predators were extirpated by hunting increased seed mortality rates of a large-seeded tree species by 7–30% (Culot *et al.*, 2017). Thus, the hunting of large-bodied seed dispersers and seed predators may synergistically reduce the recruitment of large-seeded tree species (Culot *et al.*, 2017).

The exploitation of large herbivores for trade may also alter plant communities. In tropical forests, the loss of

herbivores for bushmeat is likely to reduce further the recruitment of large-seeded, old-growth tree species that often invest more into anti-herbivore defences (Terborgh, 2013). Reduced herbivory rates in exploited forests therefore competitively favour fast-growing, pioneer species (Poulsen *et al.*, 2013). Similarly, in herbivore-mediated savannas, experimental enclosures that mimic overhunting for bushmeat revealed that exclusion of herbivores increased flower diversity, in turn fostering larger, more functionally redundant and resilient plant–pollinator networks (Guy *et al.*, 2021).

(5) Shifted plant composition and carbon stocks

A global/pan-tropical meta-analysis of 43 defaunation studies (including hunting-induced defaunation), revealed a reduction in the regeneration of large-seeded primate-dispersed plants, but no change in abiotically dispersed and smaller-seeded species (Fig. 2C; Gardner *et al.*, 2019). Thus, overexploitation of large-bodied vertebrates for trade may result in long-term shifts of tropical plant community assemblages, reducing plant diversity (Abernethy *et al.*, 2013; Harrison *et al.*, 2013) and degrading tropical carbon stocks (Bello *et al.*, 2015; Peres *et al.*, 2016).

Large-seeded, animal-dispersed tree species are particularly important for carbon storage, being taller and having higher wood density (Bello *et al.*, 2015), and thus exploitation of their seed dispersers has implications for this ecosystem service. In Central Africa, for instance, a forest hunted for bushmeat contained 15.7% lower aboveground biomass (AGB) *versus* equivalent non-hunted sites (Fig. 2D; Poulsen, Clark & Palmer, 2013). Similarly, in Carlos Botelho State Park, Brazil, the seed dispersal services for carbon sequestration of three threatened, traded species has been valued at up to US \$538,518.38 per year on carbon markets, although values vary depending on the composition of the seed predator community (Bello *et al.*, 2021).

Modelled simulations projecting the impacts of defaunation on forests suggest that shifts towards smaller-seeded and abiotically dispersed species, including liana species which impede tree growth and increase mortality (Jansen, Muller-Landau & Joseph Wright, 2010), will significantly reduce AGB (Bello *et al.*, 2015; Peres *et al.*, 2016; Chanthorn *et al.*, 2019). This could cause a loss of 5.8% AGB across the Amazon, with heavily exploited areas losing up to 37% of AGB (Peres *et al.*, 2016), although biomass effects may take centuries to be detected given the time lags between faunal depletion and tree lifespans (Brodie *et al.*, 2009). Osuri *et al.* (2016) suggest less impact on carbon storage is likely in Australasian and Asian forests, where a higher proportion of hardwood tree species are wind dispersed (but see Chanthorn *et al.*, 2019).

The impact of exploitation, and in particular wildlife trade, on long-term forest composition and carbon storage is still highly uncertain. As hunting does not always reduce recruitment of animal-dispersed tree species (e.g. Hazelwood *et al.*, 2020), some suggest that current models overestimate

carbon loss by failing to account for species-specific ecological interactions and traits, functional redundancy between target and non-target species (Bagchi *et al.*, 2018; Hazelwood *et al.*, 2020), and the functional impacts of other drivers of defaunation (e.g. fragmentation). Exploitation for trade often occurs simultaneously with alternative forest disturbance types, which can synergistically interact to deplete traded populations (Symes *et al.*, 2018). Osuri *et al.* (2020)'s meta-analysis showed that different drivers of defaunation have distinct impacts on avian and mammalian abundances: hunting causes stronger declines of mammals (particularly frugivore, herbivore, carnivore, and large-bodied species) than habitat conversion and degradation, whereas the effect of hunting *versus* alternative disturbances across avian guilds and body sizes was less clear. Nevertheless, an overrepresentation of target mammal species in hunting studies compared to community-wide metrics in habitat conversion and degradation studies may bias the results (Osuri *et al.*, 2020). Future work directly exploring the ecological effects of different drivers of defaunation and the interactions between them will improve modelled predictions of the impact of exploitation for trade on tropical carbon stocks.

V. CONSERVATION INTERVENTIONS

Because trade occurs across multiple scales, encompassing a diverse set of drivers, wildlife trade requires a multi-faceted conservation approach. The impact of conservation interventions on species and livelihood outcomes vary dramatically across interventions and context (see Sas-Rolfes *et al.*, 2019; Cooney *et al.*, 2021; Fukushima *et al.*, 2021). Here, we consider the utility of some of the main interventions – regulation and enforcement, community-based approaches, captive breeding and wildlife farming, and translocations and rewilding – for maintaining biodiversity and ecological function.

(1) Regulatory and enforcement approaches

The principal approach to addressing wildlife trade has been through regulatory and enforcement-based interventions (Sas-Rolfes *et al.*, 2019). CITES is the primary framework for regulating international wildlife trade, although individual Parties remain responsible for legislating and enforcing these regulations. CITES Parties list species in one of three Appendices, each with a corresponding set of trade controls and restrictions that range from stringent controls under Appendix I to greater flexibility for sustainable utilisation under Appendices II and III. CITES Parties can export listed species after a positive non-detriment finding (NDF). NDFs are scientific assessments that establish the volumes in which species can be traded without trade being ‘detrimental to their survival’ whilst maintaining populations ‘throughout their range at levels consistent with their roles in ecosystems’ (CITES, 1973, p. 2). Despite being central to the

sustainability of legal international trade in listed species, the scientific rigour of NDFs has been questioned (Castello & Stewart, 2010; Nijman, 2015; Morton *et al.*, 2022) and most assessments are not publicly available, rendering scrutiny of their methods and findings unfeasible (Morton *et al.*, 2022).

These issues are particularly pertinent to the ecological impacts of trade, with a 2020 CITES report finding that only one of 36 publicly available NDFs adequately considered the impact of trade on species' functional roles within ecosystems (CITES, 2020). For certain species, basic population data are unavailable and difficult to assess (Natusch *et al.*, 2019), yet many CITES parties also fail to monitor populations and off-take levels effectively, often due to financial and technical constraints (Phelps *et al.*, 2010). Increased collaboration and transparency of NDFs between CITES Parties and external partners could improve the scientific robustness of assessments (Phelps *et al.*, 2010; Morton *et al.*, 2022). Smith *et al.* (2011) also propose using CITES-listed species as focal species in studies exploring species' functional roles. This would improve our understanding of the ecological roles of species within ecosystems, whilst providing a robust evidence base to ensure trade quotas are set at levels that do not jeopardise species' functional roles.

The effectiveness of CITES in its current form is frequently debated (Cooney *et al.*, 2021; Challender & MacMillan, 2019). Mammal species have been associated with improved conservation status after being listed on CITES Appendix I, whereas Appendix I listings had a detrimental effect for reptiles (Mialon, Klumpp & Williams, 2022). In addition to problems with NDFs, criticisms of CITES include compliance issues of member Parties (Phelps *et al.*, 2010), regulations causing a spike in trade volume between their announcement and implementation (Rivalan *et al.*, 2007; Mialon *et al.*, 2022) and taxonomic biases towards charismatic species (Marshall *et al.*, 2020). CITES has also been criticised for failing to incorporate socio-economic factors and the local context of listing decisions, which can divert conservation resources towards species not threatened by international trade and restricts communities from benefitting economically from sustainably managed trade (Cooney *et al.*, 2021).

While predominantly implemented to protect target species or mitigate zoonotic disease spread, trade bans can indirectly benefit ecosystems through reducing the establishment of invasive species (Cardador *et al.*, 2019). For instance, following the EU's 2005 trade ban on wild-caught birds, avian invasion risk within the region declined substantially (Reino *et al.*, 2017). However, in response to the EU ban trade flows were redirected, resulting in increased invasion risk in other regions such as the Afro- and Indomalayan tropics (Reino *et al.*, 2017).

At the national and local scale, enforcement efforts are undertaken through a variety of measures, including anti-poaching patrols within protected areas (PAs), improved detection of illegal wildlife use through trade chains, and increasing penalties for engaging in trade (Sas-Rolfes *et al.*, 2019). Over 46% of the global budget on tackling illegal wildlife trade between 2013 and 2016 was spent on PA management (World Bank Group, 2016). Enforcement within PAs is critical

to protecting traded populations and has been associated with greater abundances of exploited species (Hilborn *et al.*, 2006). Despite this, populations of traded species are declining across many PAs, albeit often at reduced levels relative to unprotected areas (Morton *et al.*, 2021). This likely reflects both high demand and that PAs across the tropics often lack the requisite technical, human, and financial capacity required for effective management (Bennett, 2011). Emerging tools such as SMART (spatial monitoring and reporting tool) offer the potential to increase the efficiency of enforcement efforts, allowing enforcement officers to collect and utilise spatially explicit data on illicit trade events (Critchlow *et al.*, 2016).

The economic rationale for enforcement-based approaches is to increase the opportunity costs of engaging in unsustainable trade (Chen, 2016). However, failing to account for market forces where wildlife trade is one of few livelihood opportunities can drive illegal markets that are difficult to regulate and monitor (Cooney *et al.*, 2021). Increased prices as supply is restricted also creates the potential for higher profits, reducing the effectiveness of existing enforcement measures (Challender & MacMillan, 2014).

(2) Bottom-up community-based approaches

Wildlife trade supports the food and livelihood security of many economically marginalised communities. As such, community engagement is an essential component of conservation efforts aiming to ensure the sustainability of trade (Challender & MacMillan, 2014). At the international scale, CITES has begun formally recognising the importance of incorporating community outcomes into the implementation of trade regulations – so long as community engagement does not undermine principles of sustainability. In 2013, the treaty adopted a resolution acknowledging the adverse impact that trade restrictions can have on community livelihoods and urging parties to address these in their implementation (Cooney & Abensperg-Traun, 2013). Despite this, the resolution only applies to the implementation of CITES listings rather than their adoption, and several authors have suggested that local and indigenous communities be given a formal voice at CITES conferences, enabling direct contributions to decision-making (Cooney & Abensperg-Traun, 2013; Challender, Harrop & MacMillan, 2015).

At the local scale, a variety of community-based conservation (CBC) measures have been used to increase the net benefits of living alongside wildlife and/or to help communities develop non-wildlife-based livelihoods (Roe & Booker, 2019). Interventions vary depending on local property rights and have often used an incentive-based approach, including direct payments for biodiversity outcomes (Clements *et al.*, 2013), revenue-sharing schemes (Martin, Martin & Vigne, 2013), employment opportunities, and allowing communities to benefit from legal wildlife land uses – including the sustainable use of natural resources (Abensperg-Traun, 2009). Key to the success of many CBC interventions is the level of community engagement in project design and decision-making (Roe & Booker, 2019). High engagement builds trust between communities and

conservation groups, helps ensure that projects are tailored to local cultural values (Roe & Booker, 2019) and that benefits accrue equitably at the community level (Cooney *et al.*, 2017). For success, CBC measures need to address the root causes of trade (Roe & Booker, 2019), and are often most effective when conditional upon specific conservation outcomes and when communities are aware of the link between benefit accrual and conservation (Cooney *et al.*, 2017).

Securing improved land tenure can also help empower communities to manage and generate benefits from wildlife-based land uses (Naidoo *et al.*, 2016). For example, Namibia has conditionally devolved communal land to communities, allowing them to manage and benefit directly from the sustainable use of their wildlife resources, including 75% of revenues from ecotourism and trophy hunting (Naidoo *et al.*, 2016). Similarly, allowing landowners rights to benefit from wildlife resources can incentivise the private sector to protect habitat outside of state-run PAs. For instance, in South Africa, private landowners can benefit from the management and commercial utilisation of wildlife, resulting in large areas of marginal land being converted to wildlife-based land uses, ranging from gazetted private reserves (Clements *et al.*, 2019) to commercial wildlife ranches (Taylor *et al.*, 2021). As these properties need to be financially viable, there are concerns about the ecological impacts of certain management practises (Pitman *et al.*, 2016). Nevertheless, private reserves can complement the PA network in protecting priority species for conservation (Clements *et al.*, 2019), including heavily traded species, such as rhinos (Clements *et al.*, 2020). While direct assessments of the effectiveness of community- or privately run reserves in maintaining ecosystem function is a research frontier, incentivising the protection of habitat outside of PAs offers the potential to maintain ecological processes across wider landscapes (Kiffner *et al.*, 2020).

Community-based measures are not a panacea to wildlife trade issues and enforcement is often still necessary. Where communities are supportive of conservation objectives, however, they can contribute to enforcement efforts. This can be through conducting patrols, such as in the buffer zones of Nepal's two largest PAs, where 50% of park revenue from ecotourism is used to support social projects in surrounding villages, leading to high uptake in voluntary community anti-poaching patrols (Martin *et al.*, 2013). Community members can also act as informants, providing important intelligence to enforcement agencies (Anagnostou *et al.*, 2020). In Sumatra, for instance, patrols using information from local informants were 40% more effective at detecting snares set to capture tigers (Linkie *et al.*, 2015). As those aiding enforcement face a substantial risk of retaliation, building strong partnerships between community informants and law enforcement is essential (Anagnostou *et al.*, 2020).

(3) Captive breeding/wildlife farming

Regulated trade of farmed and/or captive bred species is often proposed as an option for reducing the overexploitation

of wild populations (Biggs *et al.*, 2013; Burivalova *et al.*, 2017), and the last 40 years has seen a global shift of CITES-reported trade volume towards captive bred species (Harfoot *et al.*, 2018). The underlying rationale is that satisfying demand from cheaper, captive sourced individuals reduces prices and incentives for illegal harvesting of wild populations (Bulte & Damania, 2005). However, limited empirical assessments of the effectiveness of wildlife farming make it challenging to draw conclusions on its efficacy (Sas-Rolfes *et al.*, 2019). For species that can be farmed cheaply, and where consumer preferences allow, this does appear to be a viable conservation mechanism (Tensen, 2016). For example, farming and ranching has contributed to displacing illegal wild harvesting of crocodile species in Africa and South America (Abensperg-Traun, 2009; Sas-Rolfes *et al.*, 2019). As crocodylians are a long-lived, highly fecund group, high numbers of eggs and hatchlings can be harvested and reared captive without affecting wild populations, provided the harvesting of large adult individuals remains low (Revol, 1995; Fukuda *et al.*, 2020).

A major co-occurring risk of wildlife trade is that it seeds biological invasions (Gippet & Bertelsmeier, 2021). For species traded live, a shift towards trade in captive sourced species may also reduce the establishment of invasive species due to their lower fitness in the wild (Carrete & Tella, 2015). For instance, following the EU's trade ban on wild-caught birds, a shift towards trade in captive bred individuals coincided with a 33.5% decline in the annual growth rate of newly reported non-native avian species in Spain and Portugal, despite the abundance and diversity of birds in pet markets remaining stable (Cardador *et al.*, 2019).

To reduce pressure on wild populations and their associated delivery of ecosystem functions, farmed products need to provide an effective and cheaper substitute (Biggs *et al.*, 2013; Tensen, 2016). Rearing some species is not cost-competitive *versus* exploiting wild populations (Brooks, Robertson & Bell, 2010) and farming of slow-reproducing species may be unable to satisfy demand (Lyons & Natusch, 2011). In such cases, captive-breeding schemes can enable laundering of wild-caught wildlife (Nijman & Shepherd, 2009; Lyons & Natusch, 2011). For example, it has been estimated that at least 80% of green pythons exported legally from Indonesia are actually wild caught (Lyons & Natusch, 2011). Various methods of certification to avoid laundering have been proposed and vary greatly by product and species. In snakes, proposed methods include chemically branding skins, genotyping, isotope analysis, physiological indicators, microchips, and retaining captive-bred individuals' eggshells as proof of provenance (Lyons & Natusch, 2015). However, in some cases, consumers are also prepared to pay premium prices for wild-caught individuals (Shairp *et al.*, 2016). For example, in Northern Vietnam, despite widespread commercial farming of porcupines, restaurants still secure most supply from illegal, wild populations due to consumer preference for wild meat and the higher cost of farmed porcupines (Brooks *et al.*, 2010).

(4) Conservation translocations and trophic rewilding

In certain instances, conservation translocations may be needed to re-establish depleted or locally extinct populations. Although traditionally focused on species recovery, conservation translocations can also promote ecosystem recovery through restoring degraded ecological processes (Polak & Saltz, 2011). These ecological benefits are recognised in the related field of trophic rewilding, defined as species reintroductions or ecological replacements specifically to restore ecological functions (Seddon *et al.*, 2014). Documented cases of trophic rewilding following trade depletion are rare, and a review of the effectiveness of restoration efforts in reinstating plant–animal interactions found limited examples in important trade hotspots such as South-East Asia and Central Africa (Genes & Dirzo, 2022).

As exploitation continues to deplete target populations, alongside interrupted dispersal and recolonisation from increased habitat fragmentation, translocations and rewilding may become increasingly important conservation tools (Galetti *et al.*, 2017). One example is Gorongosa National Park, which was at the centre of Mozambique's civil war, during which high levels of bushmeat trade and the sale of wildlife trophies to fund militia groups contributed to a > 90% decline in the abundance of large herbivores and the extirpation of all top predators except lions (*Panthera leo*) (Hatton *et al.*, 2001; Stalmans *et al.*, 2019). In 2007, a public–private restoration project was established to recover the parks megafaunal populations through a variety of measures, including the translocation of six large herbivore species (Pringle, 2017). By 2018, herbivore biomass had recovered to approximately 95% of the pre-war baseline (Stalmans *et al.*, 2019) and important ecological functions had been restored, including the suppression of the invasive woody shrub *Mimosa pigra* (Guyton *et al.*, 2020). Additionally, a 62 km² fenced sanctuary in the park, installed to accelerate the recovery of translocated species, contained a larger and more complex seed dispersal network, suggesting this may occur more widely as populations recover (Correia *et al.*, 2017). While the community currently comprises a greater proportion of medium-sized ungulates than pre-war (Stalmans *et al.*, 2019), the greater prey biomass has enabled the successful translocation of African wild dogs (*Lycan pictus*), with future translocations of leopards planned (Bouley *et al.*, 2021). The top-down pressure from a functionally intact carnivore guild may shift the ecosystem closer to the pre-war baseline.

Given the socioeconomic and cultural drivers of trade, social factors should be incorporated into habitat feasibility assessments, and translocations should occur only after the original source of exploitation pressure has been addressed (Gama *et al.*, 2015). For instance, in Mozambique, exploitation pressure reduced substantially following the war, and while some illegal extraction remains, its impacts have largely been mitigated through the bolstering of park law enforcement and close collaboration with buffer zone communities to implement a

range of CBC projects (Pringle, 2017). Post-release monitoring is also important to evaluate translocation success, although the ecological effects of reintroductions are rarely directly assessed (Seddon & Armstrong, 2019). Monitoring the functional roles of translocated species is technically challenging and resource demanding (Taylor *et al.*, 2017), and given ecological restoration is often one of multiple objectives, proxies such as population recovery are frequently used (Ewen, Soorae & Canessa, 2014). This risks oversimplifying the complexities of species interactions within communities and the reestablishment of translocated populations does not always restore species functions (Andrews *et al.*, 2022) or guarantee populations' continued genetic diversity (Tensen *et al.*, 2019).

VI. FUTURE DIRECTIONS

For many of the potential impacts of trade, both on species populations and the cascading ecological and community effects, there is relatively sparse evidence. This makes further research critical as we move towards a more holistic understanding of the ecological and evolutionary impacts of trade. This dearth of research in part reflects the difficulty in quantifying the degree of offtake, or even in finding suitable control areas that have not been exploited for trade (Harrison *et al.*, 2013). Consequently, three major broad research questions remain.

(1) Functional impacts of trade in smaller vertebrates and invertebrates

While the cascading community effects of population declines of large-bodied vertebrates has received considerable research attention, particularly for subsistence-use and bushmeat trade, those resulting from trade-induced declines of small-bodied taxa are less understood. In particular, invertebrate trade has received little attention (Marshall *et al.*, 2022). Such groups also play important functional roles, including as obligate pollinators and insectivores, within complex networks of interactions (e.g. Potts *et al.*, 2010). Addressing this knowledge gap will provide a better understanding of the potential impacts of trade on ecosystem functioning.

(2) Trade and ecosystem services

The extent to which trade erodes the long-term food and livelihood security for local people dependent on wildlife consumption for protein remains a core question in many regions (Nielsen *et al.*, 2018). So too is understanding the intersection between trade – including when sustainably harvested populations occur at far lower densities – and the viability of ecotourism (Naidoo *et al.*, 2016) and availability of non-timber forest products (Forget & Jansen, 2007; de Angeli *et al.*, 2021). For example, fruit bats provide valuable pollination services to humans (e.g. flying fox *Pteropus hypomelanus* pollination of the cultivated durian fruit *Durio zibethinus*) yet

many populations are over-hunted (Aziz *et al.*, 2017). Within island systems that are depauperate in species and lack functional redundancy, the impacts of trade on services may be particularly acute (McConkey & Drake, 2015). Economically evaluating the services provided by traded species can potentially incentivise and fund conservation initiatives.

(3) Trade and disease

We need greater scrutiny of the potential links between trade and disease. For instance, in Brazil, overhunted forests have a greater proportion of rodent species hosting hantavirus, which is potentially fatal in humans (Muylaert *et al.*, 2019). This intersection between overexploitation and land-use change points to greater contact between people and diseased wildlife, with a recent study revealing degraded landscapes harbour up to 144% higher abundances of disease-carrying wildlife (bats, rats, etc.) than primary systems, and mammal species harbouring greater numbers of pathogens are more likely to occur in human-modified landscapes (Gibb *et al.*, 2020). The trade in live animals in wet markets is known to be linked to transmission of diseases in wildlife (e.g. chytrid; Schloegel *et al.*, 2009), as well as humans (e.g. Covid-19, SARS; Yuan *et al.*, 2020), pointing to the need for improved animal husbandry and cleanliness at slaughter.

VII. CONCLUSIONS

- (1) Wildlife trade selectively targets groups of species bearing particularly desirable characteristics and can drive major population declines. In doing so, large proportions of functional groups can be lost, with evidence of substantial cascading ecological effects in some ecosystems.
- (2) The selective loss of large-bodied vertebrates in particular has detrimental effects on ecosystem functioning, yet trade of large-bodied species rarely occurs in isolation. We thus need to move towards a systems-wide understanding of trade impacts that will support more accurate projections of long-term shifts of population and community dynamics, and functional provisioning.
- (3) Given the sheer scale of trade, a precautionary principle to offtake should be implemented outside of data-rich systems. This approach suggests taking preventative actions against trade when uncertainty exists for select species and shifts the burden of proof that offtake is sustainable to proponents of a trade activity.
- (4) Tackling unsustainable wildlife trade must be a central priority for conservationists and environmental policy makers, as well as those working in development. It requires large-scale international investment to transition to sustainable trade that protects exploited species and associated ecological interactions, and ultimately prevents ecosystems from moving towards tipping points and long-term state shifts.

VIII. AUTHOR CONTRIBUTIONS

L. J. H and D. P. E conceived the ideas and developed the review-framing concept. L. J. H wrote the first draft. All co-authors contributed to subsequent drafts with substantial academic input and approved the final version.

IX. CONFLICT OF INTEREST

All authors declare that there are no conflicts of interest.

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