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A theory of change to improve conservation outcomes through CITES

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Understanding the effectiveness of Multilateral Environmental Agreements (MEAs) is critical to addressing international environmental issues. Here we articulate the implied theory of change (ToC) underpinning the design and operation of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), based on an analysis of the Convention's documented evolution. We use this as a framework to critically evaluate the effectiveness of the Convention, with respect to its stated aims, using a range of theoretical and empirical insights. Although achieving success in various ways, CITES is proving ineffective at deterring illegal and/or unsustainable exploitation of many listed species for international trade, which we attribute to implementation and compliance issues and the Convention's design, including a principal focus on deterrence through state-led law enforcement. Informed by this analysis we develop a modified ToC which could support more effective implementation of CITES. This ToC is intended for application at the species level and incorporates an in-depth examination of the social-ecological systems (SESs) within which species are harvested, used, and traded. This species-system ToC explicitly considers formal and informal institutions, and the use of institutional diagnostics to inform potential revisions to institutional arrangements along supply chains. We argue that taking this approach when considering whether and how to implement trade measures under CITES could enhance the effectiveness of these measures in reducing overexploitation and support legal, traceable, and more ecologically and socially sustainable international trade in wild species. Finally, we highlight the role that CITES could play in the broader global biodiversity governance regime; better alignment with other relevant MEAs could lead to more effective biodiversity conservation overall.

KEYWORDS

CITES, effectiveness, governance, institutional diagnostics, policy, social-ecological system, theory of change, wildlife trade

1 Introduction

Understanding the conditions under which Multilateral Environmental Agreements (MEAs) are effective is critical to addressing international environmental issues (Young, 2018; Petersson and Stoett, 2022). However, elucidating the impact of MEAs on conservation outcomes, against an appropriate counterfactual, is complicated (Young, 2017). The nature of issues may vary between contexts and scales (Ostrom, 2007) and the effectiveness of actions agreed in MEAs depends on many factors, including political will and the capacity and resourcing of key actors (e.g., public agencies), which can affect the degree of compliance by states (Kalfagianni and Young, 2022). There may be time lags between policies and their impacts on the ground (Underhal, 2010) and the activities of different actors, including non-state actors (e.g., NGOs and businesses), in both the regulatory and non-regulatory spheres, may influence outcomes in unanticipated ways. Such factors, among others (in particular, MEA design), have been suggested as causes of failure (Kalfagianni and Young, 2022). Therefore, to inform future design and implementation, there is a need to better understand the conditions under which MEAs are, and are not, effective (Young, 2018).

There has been much debate about the effectiveness of CITES, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, which entered into force in 1975 (e.g., Burns, 1990; ERM, 1996; Abensperg-Traun, 2009; Vincent et al., 2022). The Convention text does not include a specific goal or statement of purpose, but the preamble makes it clear that the treaty is concerned with international cooperation for the protection of wild species from overexploitation for international trade (Dickson, 2003). The CITES Strategic Vision (2021–2030) clarifies that the focus is on ensuring that international trade in wild species is legal and sustainable (CITES, 2019a). CITES operates by listing species (currently ~41,000) in one of three Appendices, which correspond to different levels of restriction on international trade (CITES, 2023a). It is implemented through national legislation and a system of permits (Wijnstekers, 2018). Commercial, international trade in wild-sourced specimens of the 1,099 species listed in Appendix I is prohibited. Most species (39,230) are included in Appendix II, with international trade closely regulated (CITES, 2023a).

The Convention has been deemed successful in promoting international cooperation (Bowman, 1998; IUCN, 2001) and indirectly for conservation (e.g., by raising the profile of species; Supplementary Material 1) but in problem-solving terms, i.e., whether CITES is solving the problem for which it was designed (Young, 1999; Underhal, 2002), there are few clearly verifiable successes. Attributing conservation outcomes to the implementation of CITES is difficult due to various confounding factors (IUCN, 2001) and there have been few attempts to evaluate the impact of the treaty on species populations against appropriate counterfactuals (see, for example, Hiller and 't Sas-Rolfes, 2024). Heid and Márquez-Ramos (2023) conclude that CITES has been effective for vertebrates and that populations of listed species have increased over time, but they inherently assume that this is

attributable to CITES alone rather than in combination with other conservation measures, including non-regulatory interventions, and supporting social legitimacy factors. Booth et al. (2020) used process tracing to aid causal inference in examining the role of regulation, including CITES, on manta rays (*Mobula* sp.) in Indonesia and reported some positive conservation outcomes. Otherwise, there are seemingly few cases in which the evidence suggests that implementation of the treaty has ensured the protection of species from overexploitation for international trade over sustained periods (IUCN, 2001; Challender et al., 2015, 2022a).

Reviews of the history of CITES (Mitchell, 1977; Boardman, 1981) indicate that there is no evidence that its design explicitly considered how the provisions of the treaty would contribute to a clear overall goal beyond what is stated in the preamble. One way of examining the Convention's design is using a theory of change (ToC). Theories of change are decision support tools to describe and illustrate how and why a desired change is expected to happen (Centre for Theory of Change, 2021; Biggs et al., 2017). They explicitly consider the causal links between activities or interventions that are implemented, how they lead to outputs, and how outputs, in turn, lead to desired outcomes and/or impact (Mayne, 2017; Rice et al., 2020). Critically, ToCs articulate the underlying assumptions that need to hold at each stage along impact pathways for the ToC logic to work (Mayne, 2017). Having been used frequently in international development, ToCs are now being used increasingly in conservation (e.g., Biggs et al., 2017; Durant et al., 2022).

As CITES approaches 50 years old, limited evidence of measurable success in meeting its aims raises fundamental questions about the effectiveness and impact of the Convention (CITES, 2022a; Wyatt, 2021a). Here, we briefly review measures that Parties are required to take when implementing CITES, to elucidate the activities that are expected to lead to impact. We then present an implied ToC for CITES that summarizes our understanding of the logic underpinning the expected conservation outcomes of the Convention, based on document analyses. Specifically, we consider key measures that the Parties are required to take as laid out in the Convention text and Resolutions on the role of national-level Management Authorities (CITES, 2019b) and Scientific Authorities (CITES, 2000) and other Resolutions in effect in April 2024. Using the ToC as a framework, we then use theoretical and empirical insights to critically evaluate the design and effectiveness of the Convention in problem-solving terms. Based on this analysis, we subsequently present an extended ToC which highlights the conditions under which CITES could be more effective. This ToC is intended for application at the species level and incorporates an in-depth understanding of the social-ecological systems (SESS) within which species are harvested, used, and traded. We then discuss the associated implications for the Convention. Finally, we highlight the role that CITES could play in shaping the broader global biodiversity governance regime, which could lead to more effective MEAs that make a greater contribution to biodiversity conservation. This article should be of interest to the CITES Parties and observers as well as conservation practitioners and academics internationally.

2 Implementing CITES

Parties to CITES (currently 184 States and the European Union) are required to take measures to implement the Convention. Key measures outlined in the Convention text comprise prohibiting international trade (the export, re-export, import and introduction from the sea) in specimens in violation of the treaty, penalizing trade in, and possession of, such specimens, and providing for the confiscation of such specimens (CITES, 1973). Parties are also required to designate Management and Scientific Authorities. The Parties have discretion over the type of measures used to enforce the Convention but are obliged to enact implementing legislation, which should be binding on both public agencies and private persons (de Klemm, 1993). This legislation is the cornerstone of the Convention because compliance requires effective enforcement and appropriate penalties (Vasquez, 2003; Paternoster, 2010). The Convention text (CITES, 1973) specifies additional measures that Parties are required to take. Parties may also adopt stricter domestic measures regarding the harvest, possession, and/or trade of listed species, including prohibiting such activities (CITES, 1973). Guidance on legislation to implement the Convention makes it clear that for effective implementation the taking and possession of and the domestic trade in indigenous species listed in the Appendices be restricted or prohibited (de Klemm, 1993; CITES, 2007).

Management and Scientific Authorities have different roles. Management Authorities are responsible for granting permits and certificates for international trade in listed species where they are satisfied that specimens are acquired legally and sustainably (CITES, 1973). They are also responsible for reporting to the CITES Secretariat on permits and certificates issued, facilitating effective implementation of the Convention, and inter alia, raising awareness of the treaty among relevant actors (CITES, 2019b). Scientific Authorities are mainly responsible for conducting non-detriment findings (NDFs) that assess whether international trade in species included in Appendix I or II would be detrimental to the survival of the wild species concerned. Conducting NDFs is therefore a key tenet of the Convention, and these assessments inform Management Authority decisions on whether or not to grant relevant permits or certificates for trade (CITES, 1973).

CITES has evolved flexibly to support implementation and compliance by Parties. This includes adopting Resolutions, which provide guidance on implementation (e.g., on law enforcement and making NDFs) and on cooperative action (e.g., addressing emerging trade challenges). It also includes Decisions, which typically provide instructions to CITES bodies (e.g., the Standing Committee) to undertake certain tasks. The National Legislation Project (NLP) was developed to evaluate Parties' legislation and assist them in ensuring that it meets the minimum standards necessary to implement the treaty. The Review of Significant Trade process was developed to formulate remedial measures for Parties in cases of non-compliance regarding Appendix-II listed species (Jenkins, 2000). The threat and application of trade sanctions is also used to support compliance by Parties (Sand, 2013). The Parties to the Convention have recognized the importance of socio-economic and livelihood aspects of wildlife

trade in implementing the treaty (Cooney and Abensperg-Traun, 2013) but these aspects are not, by default, considered in decisions to amend the Appendices (Cooney et al., 2021). The CITES listing criteria have also evolved over time (Wijnstekers, 2018) and include provisions for "lookalike" species (as referred to in the Convention text), recognizing species identification challenges for law enforcement. Due to concerns about illegal trade, CITES has since 2017 recorded seizures of listed species centrally and some Parties have explicitly designated Enforcement Authorities to help prevent trafficking of these species (Wyatt, 2021a).

The Convention has also evolved in terms of trade measures. Aligned with the Appendices, this includes the use of national export quotas (used for ~200 species; CITES, 2022b), ranching of crocodylians, annotations to the Appendices (which denote further trade provisions for species), and *ad hoc* interventions for particular species (e.g., elephants; Wijnstekers, 2018). Resolutions have been adopted for many taxa and for certain thematic issues (e.g., wild meat), which typically recommend further measures to be taken by Parties to ensure that international trade is not detrimental to wild species (e.g., consumer behavior change interventions). However, provisions in Resolutions are not legally binding (Sand, 1997), and implementation varies considerably among Parties.

3 Critically evaluating CITES using a theory of change

Here we develop an implied ToC for CITES, based on document analyses, which reflects the logic that the Convention appears to be based on. We use this ToC to evaluate the effectiveness of the Convention in problem-solving terms, and to identify where any shortfalls may be arising in the logical steps between activities and expected impact.

Evaluating a ToC first requires the articulation of activities, outputs, outcomes, and the expected impact, together with the causal links between them, including the underlying assumptions that need to be met, and consideration of enabling conditions and external factors. Enabling conditions are important because they can enable (or if absent, inhibit) implementation of the activities and the achievement of outputs and outcomes. The next step is critiquing the ToC to ensure that it is robust, i.e., logical, coherent, and plausible, and whether the assumptions will realistically be met, or not (Mayne, 2017). Mayne (2017) presents a typology of assumptions, differentiating between: rationale assumptions, which identify the underlying hypotheses on which interventions are founded; causal-link assumptions, which are key conditions necessary for a particular causal link in a ToC to be realized (if these assumptions do not hold then results along the chain will not be achieved); and at-risk assumptions, which represent potential gaps in intervention design that may present a serious risk to the intervention working and may mean that corrective action is needed.

Recognizing that the forming of a MEA is an exercise in negotiation and scientific diplomacy, the implied CITES ToC (Figure 1) presupposes that the drafters intended it to incorporate all measures necessary to achieve impact, i.e., to solve the problem

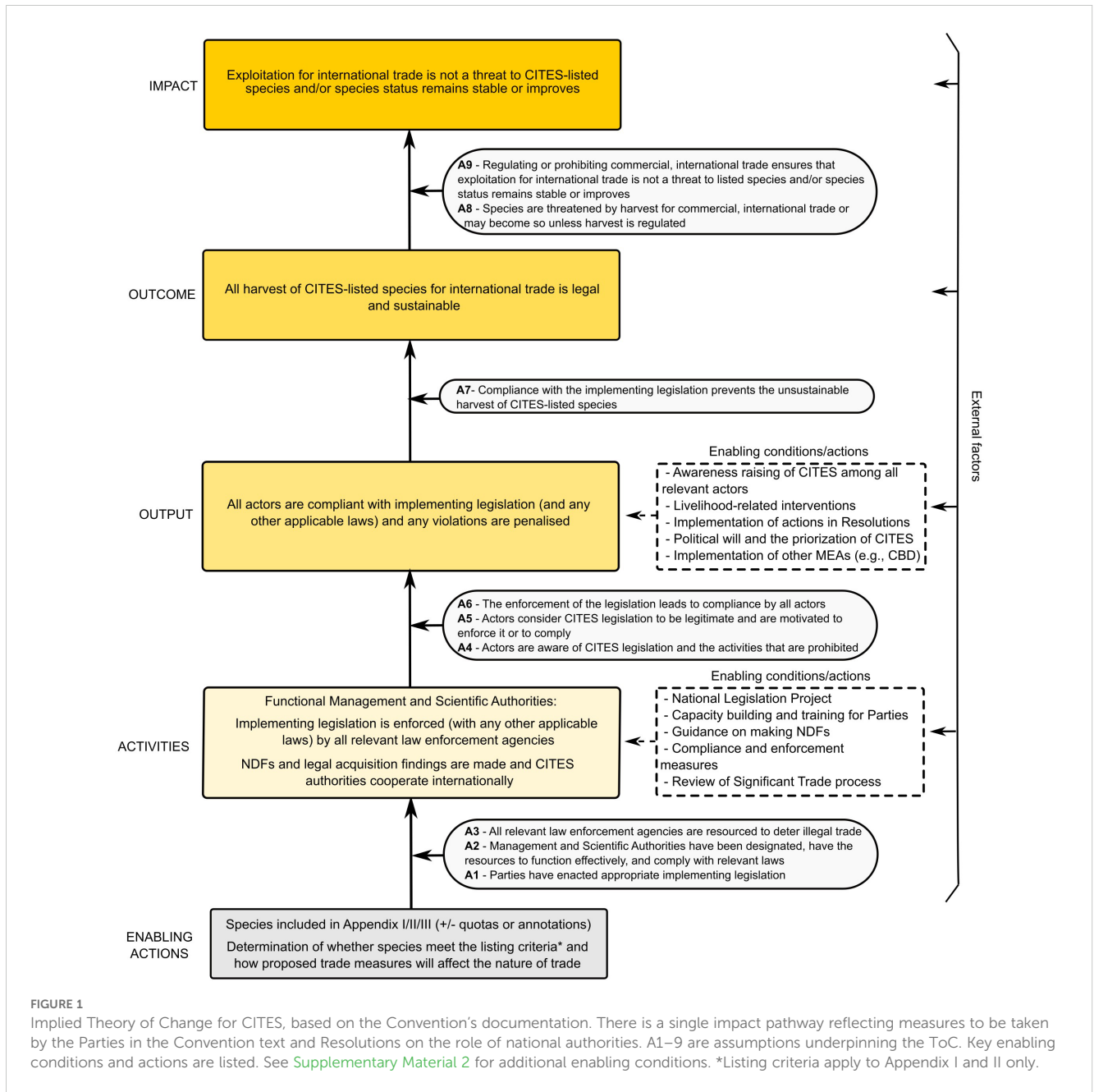


FIGURE 1

Implied Theory of Change for CITES, based on the Convention's documentation. There is a single impact pathway reflecting measures to be taken by the Parties in the Convention text and Resolutions on the role of national authorities. A1–9 are assumptions underpinning the ToC. Key enabling conditions and actions are listed. See [Supplementary Material 2](#) for additional enabling conditions. *Listing criteria apply to Appendix I and II only.

for which it was designed. This seemingly reflects the thinking at the time (Layne, 1973; King, 1974; Boardman, 1981). The ToC also reflects the thinking behind the Convention as it has evolved and guidance for Parties has been developed (e.g., de Klemm, 1993). The intended **Impact** is that exploitation for international trade is not a threat to CITES-listed species and/or that the status of these species remains stable or improves because exploitation is ecologically sustainable, i.e., offtake does not result in the degradation of biodiversity at the species or ecosystem level (Freese, 1997).

The desired **Outcome** is that any harvest of CITES-listed species for international trade is legal (based on a legal acquisition finding) and sustainable (based on an NDF).

We recognize one **Output**, which is that all existing or would-be actors (e.g., individuals, companies, and corporations) within the

jurisdiction of a Party are compliant with the implementing legislation and actors who do violate such laws are penalized.

The ToC has a single pathway by which **Activities** lead to the Output, and in turn, to the Outcome. These Activities comprise Parties establishing and maintaining functional Management and Scientific Authorities, enacting the implementing legislation, enforcement of this legislation (and any other applicable laws) by all relevant law enforcement agencies, and international cooperation with other Parties in implementing the Convention (Activities in Figure 1).

These Activities are supported by various **enabling conditions and actions** (e.g., capacity building for national authorities, Figure 1; [Supplementary Material 2](#)). The Output is also supported by various enabling conditions and actions, which may

relate to particular taxa and be implemented by one or more different actors along international supply chains (Figure 1; Supplementary Material 2). Some taxa may be subject to few (if any) additional measures, whereas others may be the focus of interventions at the sub-national (e.g., livelihood-based interventions), national (e.g., certification systems and field management) and/or international levels (e.g., collaborative international law enforcement operations). External factors are unrelated to Activities but may affect achievement of the Outcome or Impact, for example the wider social, political, and economic context (Koleros and Mayne, 2019).

The ToC relies on critical assumptions (A1–9 in Figure 1) related to measures to be taken by the Parties that need to hold at each stage along the impact pathway for the ToC logic to work. In the remainder of this section, we critically evaluate the extent to which the assumptions have been met, or not, score their achievement on an ordinal scale from 1–5, and characterize them using Mayne's typology. This includes consideration of whether any failure to meet the assumptions relates to implementation and compliance issues and/or the Convention's design. Compliance may refer to Parties' implementation of the treaty (e.g., enactment of legislation) or actors (e.g., individuals and corporations) complying with applicable laws (Vasquez, 2003) and for each assumption we clarify which is pertinent.

3.1 Parties have enacted appropriate implementing legislation (A1)

Parties are obliged to provide for the implementation of CITES through national law, but many have been slow, or have failed, to enact legislation adequate to implement the treaty, likely undermining any deterrent effect of such laws (ERM, 1996; Wyatt, 2021a). The NLP evaluates Parties' legislation in terms of meeting the minimum standards necessary to implement the treaty; these include provisions for designating Management and Scientific Authorities, prohibiting trade in specimens in violation of the Convention, penalizing prohibited trade, and confiscating specimens possessed or traded unlawfully (Vasquez, 2003). Parties are classified depending on whether their legislation meets (Category 1), partially meets (Category 2), or generally does not meet these requirements (Category 3). In 2023, 60% of Parties (111 countries) had legislation in Category 1, 25% (45 countries) had legislation in Category 2 and 14% (25 countries) had legislation in Category 3, excluding recent accessions (CITES, 2023b). This represents an increase of ~9% of Parties' legislation being in Category 1 in the last 20 years (Reeve, 2002). However, in late 2023, 40% of Parties (73 countries), mainly in Africa (33 countries) and Asia (19 countries), did not have legislation which meets the requirements to implement CITES, despite having been Parties for decades in some cases and having been subject to trade suspensions for this reason (e.g., Djibouti and Liberia; CITES, 2023b).

Wyatt (2021a) conducted a detailed analysis of legislation implementing CITES and reported that only a subset of Parties had laws that contain the measures necessary to implement the treaty. Based on this analysis, 77 of the 183 (plus EU) Parties studied

(42%) had legislation which does not prohibit violations of the Convention and 45 Parties (25%) had laws which only partially prohibit such violations. In both cases, these Parties were mainly in Europe, Africa, and Asia. A minimum of 119 Parties (65%) had legislation with provisions to confiscate wildlife. At least 118 Parties (64%) had legislation with provisions to penalize violations, typically using fines and/or prison terms, but these may not act as a deterrent (Section 3.6; Wyatt, 2021a). Where legislation has been enacted, issues within national legal frameworks may also undermine its deterrent effect. For example, Ghana's Act 43 and Wildlife Conservation Regulations (1971, 1983) prohibit the hunting of certain species but not trade or export (Wyatt, 2021a) and in various countries domestic trade in some Appendix-I listed species is legal despite it being predominantly illegal to trade them internationally (CITES, 2022c).

3.2 Management and Scientific Authorities have been designated, have the resources to function effectively, and comply with relevant laws (A2)

Practically all Parties have designated both Management and Scientific Authorities (only four Parties have not designated the latter; CITES, 2022d) but there has been historically, and remains, considerable variation in the capacity and competence of designated agencies, impeding effective implementation of the treaty. Reviews of the first two decades of CITES implementation indicate that the Convention was not a priority for several Parties, resulting in a lack of available resources and capacity for national authorities in both developed and developing countries (Heppes and McFadden, 1987; Burns, 1990; ERM, 1996). There remains variation between Parties: authorities in some countries are comparatively well-resourced (e.g., the US), but most Parties are developing countries and face high opportunity costs (Baker, 1999; Challender and MacMillan, 2016), may lack the political will to prioritize CITES (Reeve, 2006), and may be affected by corruption and/or political interference (U.S. Department of State, 2023). Despite substantial support provided to Parties in recent decades (Reeve, 2002; CITES, 2022e), a lack of capacity and of human, financial, and technical resources persist as the main challenges to implementing the treaty effectively (Wellsmith, 2011; Dongol and Heinen, 2012; Ariffin, 2018; CITES, 2019c; Wyatt, 2021a; Kilonzo et al., 2024). Based on recent implementation reports (CITES Biennial reports and Implementation Reports), of 66 Parties, 67% have one or more Management, Scientific and/or Enforcement Authority that has insufficient financial resources to function effectively. 67% of these 66 Parties reported that they had insufficient staff, and 56% that they had insufficient skills to function effectively. Of 123 Parties that provided information, 88% stated that more staff, and 92% that tools or equipment, are needed to enhance effectiveness (CITES n.d.). This is not limited to developing countries; research highlights human (e.g., insufficient trained personnel) and technical (e.g., lack of equipment) resource constraints among Parties in most regions of the world including Europe, North America, Africa and Asia (John, 2019; Sollund, 2021; CITES, 2022f, g). Critically, there

remains limited capacity among Parties to conduct robust NDFs (Dumenu, 2019; Cohen et al., 2020; Morton et al., 2022).

3.3 All relevant law enforcement agencies are resourced to deter illegal trade (A3)

Implementing CITES requires that Parties deter all actual and potential actors from illegally exporting specimens of listed species for international trade, through effective enforcement and appropriate penalties (de Klemm, 1993; CITES, 2007). This also applies to illegal extraction and domestic trade where Parties have implemented legislation to control these activities. Guidance on legislation to implement the Convention makes it clear that for effective implementation the taking and possession of and the domestic trade in indigenous species listed in the Appendices be restricted or prohibited (de Klemm, 1993; CITES, 2007). Enforcement of applicable law(s) involves one or more law enforcement agencies (e.g., police forces, customs authorities, and protected area agencies) as well as CITES authorities. Actors may violate laws for various reasons (Section 3.6) and deterrence theory suggests that to be effective, sanctions must be sufficiently certain, severe, and swift (Beccaria, 1764/2009, Paternoster, 2010). Regulatory theory indicates that perfect compliance is hard to achieve mainly because as compliance increases, the cost of enforcement increases disproportionately (Baldwin et al., 2012). Where resources are limited, aiming for the socially optimal level of enforcement - the point at which the extra costs of enforcement exceed the resulting benefits to society (Becker, 1968) - may be an attractive public policy option, but knowing where the optimal point lies relies on an understanding of the benefits to society of enforcing CITES, which is indeterminate in most cases. It has been theorized that where resources are limited, deterrence can be achieved by reducing enforcement effort and increasing penalties (Becker, 1968; Polinsky and Shavell, 2000), but empirical evidence across different crime types indicates that the certainty of being punished, and more specifically the probability of apprehension, has a much greater impact on reducing illegal activity than penalty severity (Section 3.6; Nagin, 2013; Wilson and Boratto, 2020).

Increasing the probability of apprehension can be prohibitively expensive (Clements et al., 2020) and evidence indicates that this is not happening in many places. Resources devoted to law enforcement for all types of crime may be limited in less resourced countries, and in line with this, insufficient resources are being provided by, or directed to, Parties to deter illegal harvest of CITES-listed species at the scale needed over sustained periods. The global protected area network, where many listed species occur, continues to be under-resourced (Lindsey et al., 2018). McCarthy et al. (2012) reported a funding gap of US\$76.1 billion annually needed to support an effectively managed protected area network. Coad et al. (2019) reported that of 2,167 terrestrial protected areas (representing 23% of the global terrestrial protected area network) less than a quarter of the sites have adequate numbers of staff and financial resources and there are similar results for marine protected areas (Gill et al., 2017). Where species are maintained on private land, the costs can be

prohibitive; in South Africa one-third of private rhinoceros (hereafter “rhino”; Rhinocerotidae spp.) owners have dis-invested in rhino conservation because, at least in part, they cannot afford to pay the anti-poaching costs (Clements et al., 2020).

Where law enforcement personnel are present either within or outside protected areas, they are frequently chronically under-resourced. Recognizing spatiotemporal variation within and between countries and sites (i.e., some sites, including private reserves, may be well-resourced despite overall under-resourcing in a country [Clements et al., 2020]), research indicates that frontline law enforcement staff in many cases, especially in the Global South, lack adequate training, shelter, and key equipment (e.g., communication devices and vehicles), may operate without adequate staff numbers, and may not receive fair remuneration (Belecky et al., 2019; Afriyie et al., 2021; Singh et al., 2021; Appleton, 2022; CITES, 2022f). In these circumstances, the probability of apprehension of would-be offenders, and therefore deterrence, is likely to be low (if not zero), particularly in remote or hard to reach places and logistically challenging habitats (e.g., dense forest), especially if would-be offenders are trying to avoid detection (Section 3.6; Pires and Moreto, 2011; Travers et al., 2019; Gore et al., 2021). These circumstances can also make law enforcement agents more prone to corruption, especially where legislation (or part thereof) is considered socially illegitimate (Belecky et al., 2021). These issues occur along supply chains, including in end user markets (both physical and online), where detecting illegal trade is not a priority in many instances, and the trade and consumption of Appendix I listed species may be socially legitimate (Section 3.5), undermining deterrence (Ingram et al., 2021; Sung et al., 2021; Vigne and Nijman, 2022).

3.4 Actors are aware of CITES legislation and the activities that are prohibited (A4)

Ensuring that all relevant actors in countries that are Parties to CITES, including would-be offenders and law enforcement agents, are aware of CITES, or at least of the activities that are and are not permitted under implementing legislation, is essential to achieving compliance (Baldwin et al., 2012). A review of the Convention in the mid-1990s concluded that CITES would probably be more effective if there were greater public awareness of the treaty in countries that are Parties to the Convention (ERM, 1996). Despite limited research since, empirical evidence indicates that awareness is low in some countries. John (2019) assessed awareness of CITES among key stakeholders, including law enforcement agents, hunters, and protected area staff in Nigeria. He reported that of 197 respondents, 82 (42%) were unaware that Nigeria is a Party to CITES and 80 respondents (41%) did not know the function of the treaty. Koomson (2019) reported analogous results for Ghana. The awareness of wildlife laws more broadly is mixed and varies with geography, species, and actors along supply chains (e.g., Patankar, 2019; Paudel et al., 2020; Arias et al., 2021; Dery et al., 2022). Unless relevant actors are aware of applicable legislation and comply with or enforce it (Section 3.5–3.6), the treaty will not be implemented effectively.

3.5 Actors consider CITES legislation to be legitimate and are motivated to enforce it or to comply (A5)

Laws implementing CITES, as in other areas of law, need to be perceived as legitimate by actors subject to, and enforcing, them if compliance is to be achieved. Legitimacy refers to the degree to which people recognize the right of an authority to govern their behavior and the tolerance, acceptance or moral rejection associated with products and services that are traded illegally (Beckert and Dewey, 2017; Drahos, 2017). Regulatory theory suggests that actors (individuals and groups), each with their own values, norms, and beliefs, will be more willing to comply with laws and regulations if they consider them to be fair, can benefit from them, and feel an obligation to comply (Drahos, 2017; Moreto and Gau, 2017). If legislation is inconsistent with what actors consider to be right and just, or it violates culturally valued norms, actors may be resistant to or reject it, and feel justified breaking the law (Tyler, 2006; Moreto and Gau, 2017). Legislation (new or existing) on the harvest, use and/or trade of species may not be respected by relevant actors (e.g., rural communities) if it prohibits activities that they consider legitimate. In these circumstances, actors may adopt motivational postures (i.e., beliefs and attitudes relating to authorities) that are dismissive and consequently refuse to defer to the authority's rules (Drahos, 2017). These may be postures of disengagement, where actors disregard authorities and continue business as usual, or game playing where actors identify ways around, and undermine, regulatory authorities (Drahos, 2017). This also applies to law enforcement activities. Law enforcement agents need to consider laws to be legitimate because if not they may exercise undue discretion when enforcing them and be more prone to corruption (Belecky et al., 2021). Authorities that govern with procedural justice, including respecting actors and being trustworthy and unaffected by corruption, will be able to foster greater levels of voluntary compliance and rely less on deterrence (Tyler, 2006; Drahos, 2017).

There are cases in which CITES-related laws are perceived as legitimate (Section 3.9), but the high levels of illegal harvest and international trafficking in listed species over time (UNODC, 2020) suggest a pervasive lack of perceived legitimacy of CITES-implementing legislation. This lack of perceived legitimacy includes within countries that have implemented comprehensive legislation and have functioning and well-resourced implementing agencies (e.g., the US [Olsen et al., 2021] and some EU countries [Halbwax, 2020]). Rhinos and orchids (Orchidaceae spp.) are good examples of the perceived illegitimacy of laws among key actors, but there are numerous others (see Kahler and Gore, 2012; Witter, 2021). Hübschle (2017) reports that the decision by the South African government to declare a moratorium on domestic trade in rhino horn in 2009 lacked social and cultural legitimacy among key actors. Rhino owners, professional hunters, and conservation officials were subsequently involved in the poaching of rhinos from public and private reserves and used elaborate processes to bypass legislation and legal channels to export rhino horns obtained illegally. Rhino owners also took legal action against the South

African government because they felt insufficiently consulted on the moratorium. Research suggests that non-compliance by orchid traders can be linked to negative opinions about CITES, suggesting that some of these actors are disengaged with laws and the authorities and are continuing business as usual (Hinsley et al., 2017, 2018).

3.6 The enforcement of the legislation leads to compliance by all actors (A6)

Legislation implementing CITES may comprise administrative or criminal law (Wyatt, 2021a) and when the treaty was drafted it was apparently assumed by those drafting the treaty that the enforcement of laws would lead to compliance by actors (King, 1974; Boardman, 1981). However, this assumption has not been met for many Parties over the last 50 years, largely because a focus on penalty severity has proven ineffective and law enforcement has lacked a strategic approach. This has resulted in pervasive non-compliance by actors and illegal harvest and trade in many species at local to international levels. Law enforcement efforts have also led to a range of perverse impacts on listed species and different actors. These points are discussed below.

Guidance on implementing CITES (de Klemm, 1993; CITES, 2007) suggests that penalties should be high enough to constitute an effective deterrent for actors and be severe in some cases (e.g., for illegal international trade in large numbers of specimens of Appendix-II listed species), an approach that finds some support in the economics literature (Becker, 1968; Polinsky and Shavell, 2000). There is also contemporary support for the use of high penalties to deter illegal harvest and trade of listed species (see Moreto and Gau, 2017; Leupen et al., 2018). However, there is consistent evidence across a wide range of offence types, including poaching, theft, drug trafficking, and violent crimes, over decades (mainly in the Global North), that penalty severity has little effect on crime levels and that the certainty of punishment - more specifically the probability of apprehension - has greater influence on preventing illegal activities (Leader-Williams and Milner-Gulland, 1993; Doob and Webster, 2003; Dölling et al., 2009; Nagin, 2013; Chalfin and McCrary, 2017; Wilson and Boratto, 2020). Thus, high penalties may be appropriate for organized criminals caught orchestrating the trafficking of large quantities of specimens, and can attract more law enforcement resources, but prevailing evidence suggests that increasing the perceived probability of initial apprehension will be more effective at preventing the illegal extraction of species. Research on the impact of law enforcement, however, has produced mixed results (Gore et al., 2021); studies indicate that greater patrol frequency can reduce the occurrence of snares (Linkie et al., 2015) and overall poaching levels (Hilborn et al., 2006), and lead to greater compliance by actors in terrestrial and marine habitats (Samiolys et al., 2007; Moore et al., 2018) but such effects are not certain (Samiolys et al., 2007; Barichievsky et al., 2017; Atim Nchor et al., 2021) and can vary with the actors involved (e.g., poor local poachers vs. organized poaching gangs; Leader-Williams and Milner-Gulland, 1993).

Despite the implementation of CITES relying on law enforcement, as is common to crime domains in many countries, preventing the illegal extraction and international trade of listed species historically has been impeded by a lack of law enforcement strategies in the developed and developing world (Burns, 1990; Heppes and McFadden, 1987; Reeve, 2002). This includes the enforcement of applicable laws being a low priority for enforcement agencies, a lack of resources for these agencies (Section 3.2-3.3), and a lack of coordination between agencies both domestically and internationally (Oldfield, 2003; Vasquez, 2003; Dongol and Heinen, 2012). Consequently, law enforcement in many countries has largely consisted of basic disruption techniques, including opportunistic and intelligence-led seizures of wildlife but without attempts to address the drivers of illegal extraction and trade (Vasquez, 2003; Duffy et al., 2016). Exceptions exist (e.g., Canada; Wyatt, 2021b), and well-organized (quasi-)militarized approaches have been used (e.g., in parts of sub-Saharan Africa; see Duffy et al., 2019 for a critique) but the lack of a strategic approach remains an impediment to effective enforcement in many parts of the world (Runhovde, 2015; Ariffin, 2018; Jiao et al., 2021; Wyatt, 2021a; Appleton, 2022).

Recognizing this predicament, new approaches are being implemented to improve law enforcement. These include the use of tools such as the Spatial Monitoring and Reporting Tool (SMART), which has demonstrated success in increasing detection of illegal activities (Critchlow et al., 2017), and Situational Crime Prevention (SCP) approaches, which focus on changing the environment in which crime might occur (Gluszek et al., 2022). There are also efforts to improve coordination and cooperation at different levels through national and regional strategies to address illegal wildlife trade, regional Wildlife Enforcement Networks (WENs), and inter-agency collaboration (e.g., the International Consortium on Combatting Wildlife Crime [ICWC]). Yet, illegal extraction and trade in many CITES-listed species continues at local to international levels (UNODC, 2020).

Whether law enforcement results in compliance depends intrinsically on actor risk perceptions and motivations, which are related to cognitive ability, personal experiences, and situational factors, and which may be influenced by formal (e.g., engagement with enforcement officers) and informal (e.g., information on laws in the media) sanctions systems (Paternoster, 2010; Barnum et al., 2020). Many theories have been proposed to explain (non) compliance with regulations (see Oyanedel et al., 2020) but prominent are the deterrence model and normative theories. The deterrence model assumes that rational individuals will evaluate the potential costs and benefits of non-compliant behaviors and engage in them when and where the benefits outweigh the costs (Becker, 1968; Ehrlich, 1973). Normative theories posit that perceptions of legitimacy and fairness of regulations underpin decision-making (Tyler, 2006) and include personal (based on an individual's values), injunctive (perceived moral values of a group) and descriptive norms (perception of what other people do; Oyanedel et al., 2020). Beckett and Dewey (2017) suggest that if individuals know that a behavior is illegal, they must be willing both to break the law and to overcome moral scruples associated with illegality based on the setting and their personal characteristics. Corporations may

respond to deterrence in numerous ways, including accepting penalties as business costs or being creatively compliant, i.e., they avoid breaking, but breach the spirit of, applicable laws (Grabosky, 1995; Baldwin et al., 2012).

Acknowledging limitations to national laws and enforcement (Sections 3.1, 3.3) and that actors do comply in many cases (Harfoot et al., 2018, Section 3.9), the evidence still indicates that in a substantial number of cases actors are not compliant with applicable laws. This results in consistent illegal and/or unsustainable harvest of CITES-listed species for trade and/or trafficking. Although not limited to CITES-listed species, UNODC (2020) report that in the period 1999–2018 there were ~180,000 seizures of trafficked wildlife globally, involving 149 countries and territories and ~6,000 species. This includes cases where extensive enabling conditions and actions have been put in place to support compliance by individuals (and by Parties). For example, the African elephant (*Loxodonta africana*) is split-listed between Appendix I and II and poaching and ivory trafficking continued at concerning levels (Hauenstein et al., 2019) despite the creation of CITES-hosted monitoring systems designed to support decision-making by Parties (i.e. the Monitoring the Illegal Killing of Elephants program (MIKE) and Elephant Trade Information System (ETIS)), and the development of National Ivory Action Plans (NIAPs) to support the application of trade controls on elephant ivory, and efforts to change consumer behavior for elephant products (Di Minin et al., 2022).

In many cases illegal harvest of species occurs on public land, in close to open access conditions, and in circumstances where one or more prior assumptions (A1–5) have not been met. As examples, in the Russian Far East, rural people harvest tigers (*Panthers tigris*) to sell into international trade despite this being illegal, due to economic deprivation, the high financial reward, and the low risk of apprehension (Skidmore, 2022). Paudel et al. (2020) report that most of the incarcerated people they interviewed in Nepal harvested and traded protected species (e.g., greater one-horned rhino *Rhinoceros unicornis*) to supplement their income despite knowing the activities were illegal. In Ghana, logging companies have abused salvage permits to harvest rosewood (*Pterocarpus erinaceus*) illegally and export it legally, facilitated by corruption (Dumenu, 2019). Studies also demonstrate non-compliance by retailers in end markets who sell listed species with little apparent risk of apprehension (Nijman et al., 2016; Foster et al., 2019). Organized crime groups are key actors motivated by profit (Beckett and Dewey, 2017) with the means of coordinating the illegal extraction of species, including high value parts (e.g., elephant ivory), and trafficking them along international supply chains to end consumers (Wyatt et al., 2020; Di Minin et al., 2022). They are known to displace activities spatiotemporally (Moeller et al., 2016) and go to extreme lengths to avoid detection (Wyatt et al., 2020), ultimately undermining regulatory authorities (Drahos, 2017).

While critically important, the enforcement of laws implementing CITES can result in perverse impacts. Regulating or prohibiting international trade and the enforcement of these measures is known to drive trade underground, i.e., it simply continues but illegally (Dickson, 2003; UNODC, 2020, 2024). CITES trade measures may also signal opportunity to actors

including speculative collectors, stockpilers, and organized crime groups, which could, in theory, lead to scarcity-driven price increases that lead to accelerated wild harvest (e.g., rhinos in the 1970-80s; Bergstrom, 1990; 't Sas-Rolfes, 2000; Courchamp et al., 2006). Where commercial international trade is prohibited, the long-term withholding or destruction of stockpiles can further exacerbate this situation by creating additional scarcity (e.g., elephants, 't Sas-Rolfes et al., 2014). Trade restrictions can also remove incentives for local actors to conserve species and their habitats (e.g., leopard *Panthera pardus* in Southern Africa [Jenkins, 2000]) and can increase the risk of actors coming in from outside and harvesting species at higher rates (Abensperg-Traun, 2009; Cooney et al., 2017). Establishing and enforcing trade measures can also direct harvest pressure to other species and locations; as one example, as turtle species (Testudines spp.) have been added to CITES incrementally, illegal harvest has shifted repeatedly to turtle species not subject to trade measures under CITES (CITES, 2016a).

3.7 Compliance with the implementing legislation prevents the unsustainable harvest of CITES-listed species (A7)

Compliance with applicable laws by actors in countries that are Parties to CITES should prevent the unsustainable harvest of CITES-listed species because Parties are encouraged to regulate the extraction and domestic trade in indigenous species listed in the Appendices as well as international trade (Section 3.3). There is limited definitive research on the provisions of Parties' legislation regarding domestic and international trade, but analyses suggest that many listed species are subject to laws designed to prevent overexploitation for domestic and international trade (CITES, 2018, 2022d). However, implementing laws may have different provisions for harvest and trade in wildlife at domestic and international levels; this can result in CITES-listed species still being overexploited even if actors are compliant with the relevant laws. This may happen if harvest for domestic trade is less regulated than harvest for international trade, or unregulated. Examples include the white-lipped peccary (*Tayassu pecari*), included in Appendix II and threatened by harvest for local and domestic trade in parts of South America (Keuroghlian et al., 2013). Marine turtles (Cheloniidae spp.), included in Appendix I, and the South American giant river turtle (*Podocnemis expansa*), included in Appendix II, are used legally for subsistence and commercial purposes in parts of the Caribbean and the Americas respectively, but this threatens these species, at least in some places (Ingram, 2022). In such circumstances, this assumption is not met.

3.8 Species are threatened by harvest for commercial, international trade or may become so unless harvest is regulated (A8)

CITES was established on the assumption that commercial, international trade is a dominant threat to species (Hutton and Dickson, 2000). The IUCN Red List of Threatened Species

(hereafter "Red List") indicates that ~16,000 species are threatened by overexploitation, but this includes a range of types of exploitation at different scales from local to international and subsistence to commercial (Challender et al., 2023). Within this group, 2,211 species (but potentially up to 8,796) are likely threatened by international trade either solely or in addition to domestic use or trade, whether legal or illegal. Examples include pangolins (*Manidae* spp. [Challender et al., 2020]) and sawfishes (*Pristidae* spp. [Dulvy et al., 2014]) (Challender et al., 2023). Yet many CITES-listed species face other more acute threats (e.g., agriculture; Harfoot et al., 2021) that CITES is not designed to address.

3.9 Regulating or prohibiting commercial, international trade ensures that exploitation for international trade is not a threat to listed species and/or species status remains stable or improves (A9)

The Convention's design assumes that, if species are (actually or potentially) threatened by overexploitation for commercial international trade, regulating or prohibiting this trade by including species in the Appendices is an appropriate solution and will improve the conservation status of the species (Dickson, 2003; Moyle, 2003). However, this approach prioritizes international regulation while largely overlooking how actors may respond to trade measures in complex social-ecological systems (SESs; Challender et al., 2022a; Cooney et al., 2021). There is little robust research causally linking the implementation of CITES to species status over time, but prevailing evidence suggests that there are few cases in which implementation of the treaty has ensured the protection of species from overexploitation for international trade over sustained periods (IUCN, 2001; Challender et al., 2015, 2022a). In many cases, trade measures, even when accompanied by multifaceted enabling conditions and actions, have failed to result in the stabilization of, or improvement in, species status. Examples include the listing of Agarwood (*Aquilaria malaccensis*) (Newton and Soehartono, 2001) and the European eel (*Anguilla anguilla*) in Appendix II (Pike et al., 2020) and the inclusion of pangolins (Challender et al., 2020) and various freshwater turtles (e.g., Asian narrow-headed softshell turtle *Chitra chitra*) in Appendix II and later Appendix I (Cota et al., 2019). The Red List indicates that some CITES-listed species have improved in status over time (e.g., greater one-horned rhino [Ellis and Talukdar, 2019]). Conversely, 40% of listed species - and 78% of Appendix-I listed species - are globally threatened on the Red List, despite in many cases having been subject to Appendix I trade measures under CITES for decades (CITES, 2022h). Populations of nearly half (46%, 4,248 taxa) of the CITES-listed species that have been assessed on the IUCN Red List are declining, 20% (1,871 taxa) are stable, and only 2% (188) are increasing (CITES, 2022h). This lack of apparent impact may be because species status is not being assessed against an appropriate counterfactual of even greater population decline (Grace, 2021). For long-lived species or those that are slow to reproduce, evidence of positive impacts may take a long time to materialise. This lack of

apparent impact may also be because all or some of the preceding assumptions (A1–7) have not been met. However, even if these assumptions were met, listing species under CITES would not necessarily reduce the threat from commercial international trade because of potential perverse impacts (Section 3.6).

Where CITES-listed species have improved in status (or more commonly, not been adversely affected by illegal harvest and trade), institutional factors have typically been very important. Key insights from institutional analyses indicate that property rights regimes (e.g., land tenure and use rights) are vital for incentivizing sustainable wildlife harvesting (‘t Sas-Rolfes, 2017; Child, 2019). Wildlife that occurs under open access (or near-open access) conditions is far more likely to be harvested at unsustainable levels than those owned and controlled by interested and affected actors (Murphree, 2003; Ojanen et al., 2017), consistent with the principal-agent model in economic theory (Laffont and Martimort, 2009). This suggests that establishing clear, appropriately assigned, and enforceable property rights over populations of particular species and their habitats is crucial to preventing overexploitation (Alchian and Demsetz, 1973). This approach has facilitated population increases and improvements in the conservation status

of CITES-listed species at local and national levels and ensured compliance by key actors in a range of cases, in large part because the legitimacy of laws among local actors and the institutional settings have been considered explicitly. Examples are rhinos in southern Africa (‘t Sas-Rolfes et al., 2022; ‘t Sas-Rolfes and Emslie, 2024), markhor (*Capra falconeri*) in Pakistan (Frisina and Tareen, 2009), vicuña (*Vicugna vicugna*) in South America (Lichtenstein and Ros, 2021), several crocodylians (Hutton and Webb, 2003), and various species managed on communal conservancies in Namibia (NACSO, 2015).

3.10 Overall assessment

Sections 3.1–3.9 highlight that the current CITES approach is proving somewhat ineffective because of both implementation and compliance issues (A1–7), including non-compliance by Parties and actors within countries, and the Convention’s design (A3, A6, A8 and A9; Table 1). Assumptions A1–7 are causal link assumptions, but they do not hold, to varying degrees, for many Parties, actors, and circumstances. This implies that the Activities are not being

TABLE 1 Assumptions in the implied CITES ToC in Figure 1, assumption type based on Mayne (2017), assumption score, and justification.

Assumption	Assumption type	Score	Justification
A1. Parties have enacted appropriate implementing legislation	Causal link	2	Appropriate implementing legislation has been enacted by 60% of the Parties
A2. Management and Scientific Authorities have been designated, have the resources to function effectively, and comply with relevant laws	Causal link	4	Management and Scientific Authorities have been designated by virtually all Parties, but most are developing countries and there is a pervasive lack of capacity and human, technical and financial resources among Parties
A3. All relevant law enforcement agencies are resourced to deter illegal trade	Causal link, at-risk	4	Chronic and pervasive under-resourcing of law enforcement agencies, especially in the Global South, indicates that the probability of apprehension for would-be offenders is likely to be low in many cases; there are exceptions (e.g., some private reserves)
A4. Actors are aware of CITES legislation and the activities that are prohibited	Causal link	3*	There is a general lack of research, but evidence indicates low levels of awareness of CITES among key actors in some countries; awareness of wildlife laws more broadly varies with geography, species, and actor
A5. Actors consider CITES legislation to be legitimate and are motivated to enforce it or to comply	Causal link	3	Evidence indicates a lack of perceived legitimacy of laws relating to the harvest and trade of certain species and suggests this is the case in many instances Laws are legitimate in some cases, especially where local actors and institutions have been explicitly considered in governance decisions
A6. The enforcement of the legislation leads to compliance by all actors	Causal link, at-risk	3	Law enforcement can result in greater compliance, but this is not certain Actors are compliant in lots of cases but not in many others, resulting in illegal harvest and international trafficking in many CITES-listed species
A7. Compliance with the implementing legislation prevents the unsustainable harvest of CITES-listed species	Causal link	3*	Analyses suggest that compliance with implementing laws should prevent the unsustainable harvest of many CITES-listed species, but there are exceptions
A8. Species are threatened by harvest for commercial, international trade or may become so unless harvest is regulated	Rationale	4	Many species are threatened by overexploitation, but research suggests that only a subset of 2,211 species likely threatened by international trade are threatened by harvest for commercial, international trade
A9. Regulating or prohibiting commercial, international trade ensures that exploitation for international trade is not a threat to listed species and/or species status remains stable or improves	Causal link, rationale, at risk	4	Interventions under CITES have had limited impact on species’ conservation status and can result in perverse impacts on species, wider biodiversity and people Where listed species have improved in status, institutional factors and the legitimacy of laws among local actors have been critically important

Assumption score based on 1=assumption met in all cases, 2=assumption met in more cases than not, 3=assumption met/unmet to a similar extent (uncertainty denoted by *), 4=assumption unmet in more cases than met, 5=assumption unmet in all cases.

carried out by some Parties; appropriate laws are not being enacted and relevant national agencies are being insufficiently resourced, while relevant actors may be unaware of CITES or the implementing legislation - but even where they are, they may consider such laws to be illegitimate and feel justified breaking them. This leads to the Output, and subsequently, the Outcome, not being fully achieved. A8 is a rationale assumption and reflects one of the hypotheses underpinning the treaty, but it does not hold for many taxa. A small proportion (3%) of CITES-listed species have been deemed threatened with extinction and are (potentially or actually) affected by (international) trade, i.e., are included in Appendix I, but most species, including the 28,000 orchids (Hinsley et al., 2018), were included in the Appendices because they resemble other taxa (i.e., are “lookalikes”), and evidence suggests that <2,211 species are threatened by commercial international trade. A9 is a rationale and causal link assumption, which has been met for a few taxa but not for many others; numerous listed species are not improving in status or even remaining stable, meaning that the Impact is not being achieved.

A3, A6, and A9 are also at-risk assumptions and present serious risk to CITES’ effectiveness. There is uncertainty regarding the extent to which A6 is met, but our assessment is that A3 and A9 are unmet in more cases than they are met (Table 1). This reflects the principal focus on state-led law enforcement to achieve compliance by individuals and corporations within countries, recognizing that law enforcement has been, and remains, inadequately resourced in many, if not most, countries. This results in a low probability of apprehension for would-be offenders intent on extracting and trading CITES-listed species, which is inherently related to conservation not being a priority in many countries, high opportunity costs of prioritizing and implementing the Convention, and weak governance, especially in developing countries. This is demonstrated by high levels of illegal extraction and international trafficking of many listed species. Perverse effects may also result from trade restrictions, including the accelerated wild harvest of species that these measures were designed to protect (Courchamp et al., 2006). In these circumstances, CITES is not, by definition, solving the problem for which it was designed.

4 Actionable recommendations – improving conservation outcomes through CITES

What can be done to improve the effectiveness of CITES in a world where Parties may or may not have enacted appropriate implementing legislation, where national authorities and law enforcement agencies are persistently under-resourced, where relevant actors may not be aware of applicable laws (or may consider them illegitimate), resulting in a pervasive lack of compliance by actors and many listed species being negatively affected by unsustainable and/or illegal extraction for illicit international trade? The CITES Standing Committee discussed the merits of a review of the effectiveness of the Convention at its 74th meeting in March 2022 and decided that such a study was not

needed. Various Parties and observers emphasized that the focus should be on capacity building among Parties (see also Orenstein et al., 2022). Capacity building is important, but our findings suggest that this approach alone will fail to prevent the overexploitation of listed species for international (and local and domestic) trade and trafficking at scale in the foreseeable future. This is because several at-risk and causal link assumptions for CITES have not been met (Table 1). Regarding at-risk assumptions, there is a chronic lack of resources to enforce applicable laws and most Parties are developing countries that face high opportunity costs related to implementing the treaty; available budgets are limited, and external funding is uncertain (Maxwell et al., 2020). It is implausible that the annual funding deficit of tens of billions of dollars needed to adequately manage terrestrial and marine protected areas respectively (McCarthy et al., 2012; Gill et al., 2017) will be resolved imminently and on a sustainable basis. The result is that there will be an inadequate probability of apprehension for would-be offenders intent on illegally extracting listed species within such sites (but likely also beyond them), even if Parties have enacted appropriate implementing legislation. In addition, law enforcement effort does not necessarily result in compliance by actors, and regulating or prohibiting international commercial trade does not necessarily solve the problem and can lead to perverse impacts.

4.1 A proposed species-system ToC to improve conservation outcomes through CITES

Empirical insights demonstrate that where species, including some CITES-listed taxa, have improved in status, an understanding of the relevant social-ecological systems (SESs), including institutional arrangements, has been critical to informing effective context-specific interventions (Section 3.9, Fromentin et al., 2022). A systems approach to preventing the overexploitation of species for international trade is important, recognizing the increasingly globalized nature of the world (e.g., telecoupling – interactions between distant SESs; Hull and Liu, 2018), increasing global trade (UNCTAD, 2022), and the potential for unintended feedbacks (Section 3.9, Larrosa et al., 2016). To reduce the uncertainty of conservation outcomes linked to CITES trade measures, we therefore propose an approach based on developing an in-depth understanding of the SESs in which species are harvested, used, and traded along international supply chains, which explicitly considers relevant institutions, both formal and informal. This understanding can then support the devising of robust interventions that are specific to these systems. We define institutions as “systems of established and prevalent social rules that structure social interaction” (Hodgson, 2006), which comprise informal (e.g., sanctions, customs, traditions, and codes of conduct) and formal rules (constitutions, laws, and property rights; North, 1991). Given their impact on human behavior, institutions are crucial to achieving sustainable wildlife trade, but have received little attention in conservation science (t Sas-Rolfes, 2017). Where

institutions have been considered, they have informed interventions to support sustainability in a range of contexts (Lichtenstein and Ros, 2021; Partelow et al., 2022; 't Sas-Rolfes et al., 2022).

Our proposed approach explicitly includes the use of institutional diagnostics, a method for identifying the critical features of specific problems in complex systems and then crafting institutional arrangements to address them through guiding the future behavior of key actors (Young et al., 2008, 2017). This involves considering the characteristics of the problem, including the extent to which it is well understood, or not; the key actors involved, including individuals and corporations; their incentives and current practices relating to resource use; and the role of other stakeholders including government and law enforcement agencies (Young et al., 2008). (Re)forming institutions is ideally undertaken with all relevant actors and stakeholders at appropriate scales - for example, through participatory or representative processes (Mavah et al., 2022) - to ensure that new or amended systems of rights and rules around resource use are legitimate to actors along supply chains.

Institutional arrangements should be resilient but adaptable, formal and informal institutions should align to avoid non-compliance by actors, and the arrangements should “fit”, i.e., they should be well-matched to the problem in terms of scale and socio-economic setting (Young et al., 2008, 2017).

Here, we outline a new extended species-system ToC, which we propose would improve the effectiveness of CITES (Figure 2). We discuss application of the approach and include a case study on pangolins in Supplementary Material 3 to further demonstrate its potential application. This ToC focuses on the problem-solving mission of CITES but, critically, situates CITES trade measures among broader institutional arrangements along supply chains. It includes investigation of, and potential reforms to, institutional arrangements to ensure alignment between formal and informal institutions along supply chains, and relies on Parties and other actors implementing interventions that are specific to the system and their role(s) in it. These interventions may or may not be legislative in nature but if so, they may comprise tighter or more relaxed laws to align with the SESs and informal institutions. The ToC has separate

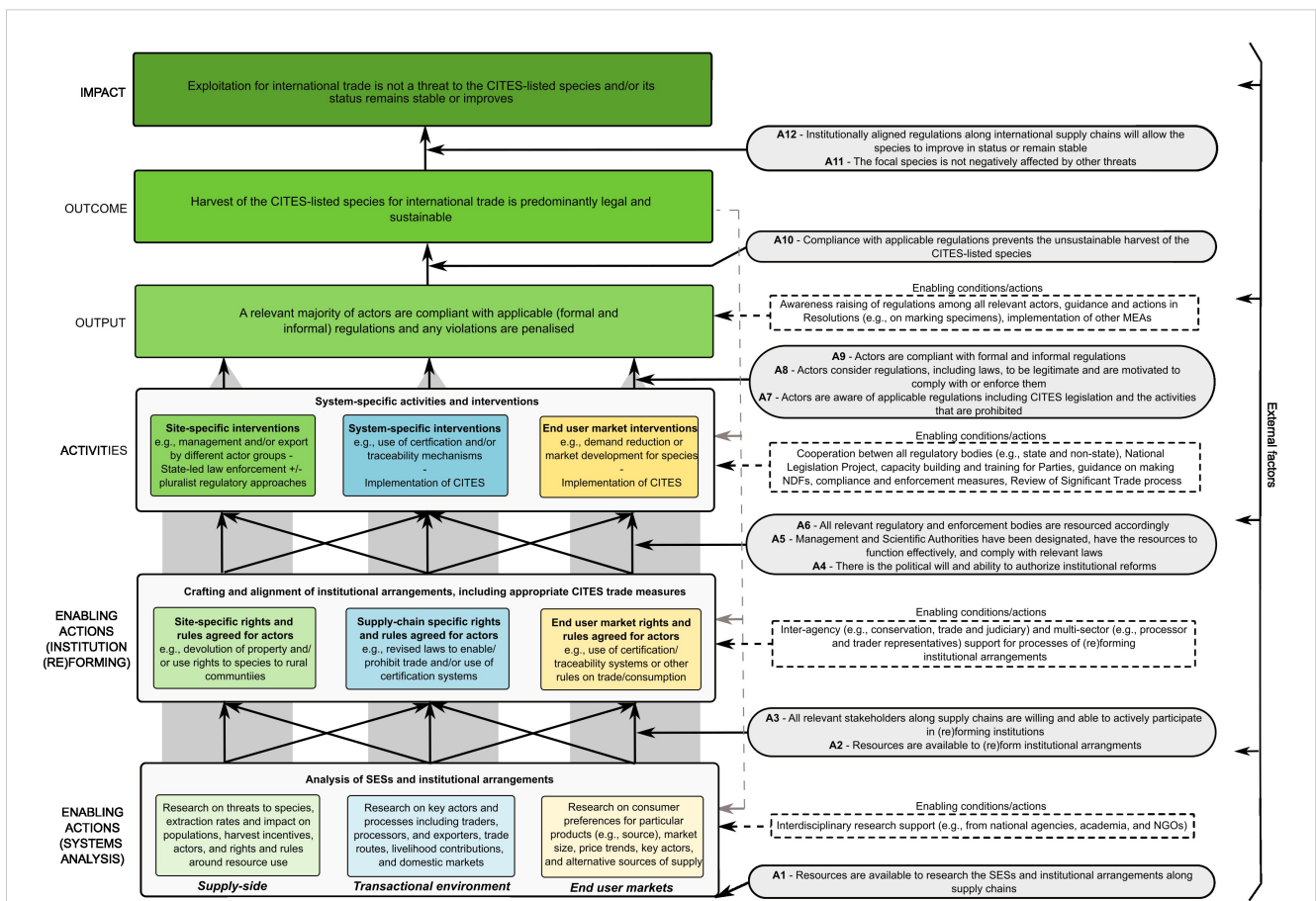


FIGURE 2

Proposed species-system Theory of Change highlighting the conditions under which CITES could be more effective. CITES trade measures are situated among broader institutional arrangements along supply chains. Multiple impact pathways reflect the different stages of international supply chains with Parties and other actors implementing Activities as appropriate based on their role(s) in the system. Activities on the supply side may be at the site, sub-national or national level as appropriate, in one or more countries. A1–12 are assumptions underpinning the ToC (see Table 2). Diagonal arrows indicate knowledge exchange related to systems analysis and institution (re)forming to inform the Activities. Grey dashed arrows indicate an adaptive management approach. Dashed line boxes include enabling conditions and actions (see also Supplementary Material 2). Note that once institutional arrangements have been (re)formed, Parties would propose amendments to the CITES Appendices to establish or revise trade measures for particular species as needed to align with new or revised institutional arrangements.

impact pathways for three conceptual stages of supply chains, following Challender et al. (2022a). These are the supply-side, which comprises the resource system(s) (i.e., sites) at which species occur; the transactional environment, encompassing those parts of the system beyond the resource system(s) up to the point of export to international end user markets (including the country of harvest and intermediary countries); and end user markets. Although this approach has principally been designed for application at the international level it could be used to align formal and informal institutions for species and defined systems within a given country.

The **Impact** and the **Outcome** are similar to those in Figure 1, but the modified approach does not, by default, rely principally on state-led law enforcement or assume that this is the optimal solution to prevent the overexploitation of CITES-listed species for international trade. The **Outcome**, like the **Output**, does not refer to all actors because there will always be some actors willing to violate regulations even if the result of their rule-breaking is ecologically insignificant. The **Output** is therefore that a relevant majority of existing or would-be actors in countries that are Parties to CITES are compliant with applicable regulations, including existing and/or new formal laws and informal rules.

Enabling Actions (Systems Analysis) entails research and analysis by Parties, industry, and/or other researchers to understand the relevant SESs and institutional arrangements along supply chains for species. This research should seek to understand factors including:

- *Supply side*: Threats to the species, including but not limited to exploitation, harvest incentives, extraction rates for use and trade at different scales (local to international), and property rights;
- *Transactional environment*: Actors (including traders and processors), social performance measures (e.g., livelihood contributions and dependency on income from trade in the species), and domestic markets; and
- *End user markets*: Consumers (including preferences related to particular products), intertemporal price trends, alternative sources of supply, and market size.

The next step is the use of institutional diagnostics to identify the critical factors impeding the achievement of ecological sustainability regarding the harvest and trade of the taxa (e.g., the perceived illegitimacy of current laws), which may exist at one or more stages of the supply chain. Challender et al. (2022a) present a SES framework of international wildlife trade that could be used to support such research.

Enabling Actions (Institution (re)forming) refers to the process of Parties and other actors using the research and analysis to craft and align institutional arrangements along supply chains, including compliance mechanisms, while ensuring that any future harvest of the species for international (and where appropriate local and domestic) trade is ecologically sustainable. CITES trade measures would therefore fit within a wider institutional and governance landscape which involves all relevant sectors, actors, and stakeholders within and among Parties (e.g., rural communities, processors, exporters, retailers, industry bodies, product consumers,

and conservation agencies). Trade institutions should explicitly consider key economic and social trends (e.g., economic development and human demographic trends) and potential risks and challenges associated with new or revised arrangements (e.g., implementation in areas with weak governance). There are various methods for achieving input from diverse actors (e.g., public consultations, community-based governance processes, and national and international workshops; Grabosky, 1995; Mavah et al., 2022) and these processes would not need to be convened by CITES. Institutional reforms may involve, for example, the devolution of land tenure and/or use rights over species to rural communities, the use of hunting quotas or time-based limits on offtake for particular actors, the use of certification systems, or other context-specific measures. Institutional arrangements on the supply side should be prioritized because they are typically most critical to ensuring that any harvest of species is ecologically sustainable. A range of methods exist to evaluate the likely effect of revised arrangements on outcomes, meaning that they could be evaluated before being implemented. These methods include Bayesian Belief Networks, theories of change, and strategy games (Colyvan et al., 2011; Biggs et al., 2017; Travers et al., 2019; Bennett et al., 2021). Once institutional arrangements have been (re)formed, Parties would propose amendments to the CITES Appendices to establish or revise trade measures as needed to align with these broader institutional arrangements.

The **Activities** are interventions necessarily specific to the SES in question, which may be implemented at one or more stages of the supply chain by different actors under new or revised institutional arrangements (Figure 2). On the supply side, this may comprise management and the harvest and export of specimens of species by rural communities and/or other private actors, who may or may not own populations of the species. These activities could be implemented at the most appropriate scale (e.g., site, sub-national or national) within one or more range states for the species, and pluralist regulatory approaches could be used to support compliance with any formal and/or informal regulations where applicable (e.g., the use of Smart regulation; Gunningham and Sinclair, 2017). In end user markets, activities may be programs to influence consumer demand or develop markets for wildlife products under circumstances where these activities will be likely to benefit species. State-led law enforcement will be needed at some level along supply chains, but if property rights have been appropriately assigned to interested and affected actors at the supply-side stage, are clear, and can be enforced, there would be less reliance on such law enforcement. Where compliance mechanisms have been designed to fit a SES well, this could also mean less reliance on state-led law enforcement. Among the activities to be implemented, CITES trade measures would need to be implemented (Figure 2). The **Activities** along the supply chain jointly lead to the **Output**, which in turn, leads to the **Outcome** (Figure 2). The Enabling Actions, Activities and Output are supported by **enabling conditions** and in circumstances where the Outcome is not being achieved, adaptive management could be used to amend institutional arrangements accordingly.

The proposed approach does not deliver a guaranteed outcome. However, it does have the potential to enhance the effectiveness of

interventions to ensure that international (and local and domestic) trade in CITES-listed species is legal and ecologically sustainable by tailoring such measures to species and SESs. To be effective, various assumptions must be met (Figure 2, Table 2), some of which also appear in Figure 1. This is because the approach won't address all the implementation, compliance, and design issues with CITES. For instance, it will not ensure that Parties enact implementing legislation, but it can inform new or revised laws to ensure that they are appropriate to the species and SESs. The approach won't ensure that sufficient resources are made available to CITES authorities and law enforcement agencies (see Section 4.2). But in cases where property rights are appropriately assigned and enforced it can help ensure less reliance on state-led law enforcement. Inclusive approaches to (re-)forming institutions can also ensure that relevant actors are aware of new or revised institutional arrangements. As such, actors that have been consulted on, and/or involved in, the co-design of institutional arrangements, should be more likely to consider these arrangements legitimate and

comply with them (Young et al., 2008; Gunningham and Sinclair, 2017).

The approach also has challenges. Aligning formal and informal institutions along supply chains is complex because the issues are multi-sector, multi-scale and involve diverse actors. This may require revising national and/or sub-national laws and informal rules and sanctions systems, which may involve protracted processes, and there will likely be a need for trade-offs between different actors, sectors, and agencies. There will need to be the political will to authorize revised institutional arrangements, which may be challenging, especially where the devolution of land tenure and/or use rights is concerned. Another challenge will be the application of this approach to the many species included in CITES (current and future). Therefore considering broader groups of species together may be most appropriate (e.g., taxonomic groups or species with similar harvest and trade dynamics). This may be needed to avoid perverse impacts (e.g., shifting harvest pressure to other species). The process presented in

TABLE 2 Justification for the assumptions in the proposed species-system ToC in Figure 2.

Assumption	Assumption type	Justification
A1. Resources are available to research SESs and institutional arrangements along supply chains	Causal link	Resources are needed to conduct research into the SESs along international supply chains for species (or taxonomic groups)
A2. Resources are available to (re)form institutional arrangements	Causal link	Resources are needed to convene/consult with all relevant stakeholders to (re)form institutional arrangements
A3. All relevant stakeholders along supply chains are willing and able to actively participate in (re) forming institutions	Rationale, causal link	The engagement of all relevant stakeholders along supply chains is essential to ensure that stakeholder voices are heard and considered in decision-making, which is important to ensuring the social legitimacy of existing or revised institutional arrangements
A4. There is the political will and ability to authorize institutional reforms	Causal link	There will need to be political will to authorize institutional reforms, especially regarding formal institutions such as laws and property rights
A5. Management and Scientific Authorities have been designated, have the resources to function effectively, and comply with relevant laws	Causal link	Designation and adequate resourcing of CITES authorities will be needed so that CITES trade measures can be implemented as needed along international supply chains subject to revised institutional arrangements
A6. All relevant regulatory and enforcement bodies are resourced accordingly	Causal link	Regulatory and enforcement bodies, both state-designated and informal (e.g., sanctions systems within local communities), need to have the resources necessary to perform their duties according to the revised institutional arrangements
A7. Actors are aware of applicable regulations including CITES legislation and the activities that are prohibited	Causal link	Actors need to be aware of the institutional arrangements to comply with applicable laws and rules
A8. Actors consider regulations, including laws, to be legitimate and are motivated to comply with or enforce them	Rationale, causal link	Actors need to consider the new/revised institutional arrangements, including formal and informal rights and rules, to be legitimate if they are to be motivated to, and comply with them
A9. Actors are compliant with formal and informal regulations	Rationale, causal link, at-risk	Actors need to be compliant with the applicable rights and rules under revised institutional arrangements for the Output to be achieved
A10. Compliance with applicable regulations prevents the unsustainable harvest of the CITES-listed species	Causal link	Compliance by actors with applicable regulations is necessary for the Outcome to be achieved
A11. The focal species is not negatively affected by other threats	Causal link	For the status of the species to remain stable or improve, the species should not be negatively affected by other threats
A12. Institutionally aligned regulations along international supply chains will allow the species to improve in status or remain stable	Rationale	Institutionally aligned regulations along international supply chains for species, informed by evidence of the impact of exploitation and any other threats, is necessary for the Impact to be achieved

Note that unlike the implied CITES ToC in Figure 1 these assumptions need to be met for SESs along international supply chains for particular species rather than for CITES overall.

Figure 2 will also require resourcing (see Section 4.2). Despite these challenges, there are precedents. Examples include supply chains for pythons (*Pythonidae* spp.) (Lyons and Natusch, 2016), crocodylians (Aust et al., 2022), and vicuña (Lichtenstein and Ros, 2021), and many non-CITES listed commodities (e.g., cotton *Gossypium* sp.; Fayet and Vermeulen, 2014).

4.2 Implications for CITES

The proposed approach would need to be led by interested and affected Parties, with input from the private sector, researchers, civil society and NGOs. Aligning formal and informal institutions regarding the harvest and international trade in species along supply chains would mean SES-specific, and therefore diverse, approaches to species management among Parties. Most extreme would be commercial international trade in particular species from some range states and the concurrent use of commercial trade (or stricter) bans in others. Given adequate political will and allocation of resources, the Parties and other actors could apply this approach to most listed species, i.e., most of the 39,230 species included in Appendix II (including “lookalikes”), under existing provisions. Exporting Parties could subsequently implement the relevant provisions of the Convention and use tools such as national export quotas as appropriate. Parties further along supply chains, including end user markets, could revise institutional arrangements, including laws, to prohibit or enable the possession, processing, sale and/or consumption of the species and their derivatives as appropriate.

For species in Appendix I, species that have been transferred from Appendix I to II and have export quotas set by the CoP (e.g., African elephant), and species that have export quotas set by Resolution (e.g., leopard), revised institutional arrangements require further consideration because decision-making on CITES trade measures is not unilateral. Under a scenario where systems analysis and institution (re)forming processes indicate that the most appropriate institutional arrangements for a particular species differ markedly between range states (e.g., commercial international trade vs. a commercial trade ban), split-listing could be used, i.e., different populations of a species could be included in Appendix I and II respectively. This would provide range states for a given species the flexibility to pursue the conservation of the species in a manner best suited to the national and sub-national context, while coordinating with Parties and other actors along international supply chains.

Split-listing is currently used for only a few species and the Parties have agreed that it should be avoided because of the enforcement problems it can create (CITES, 2016b). However, the approach has proven effective for managing international trade in various taxa. These include the southern white rhino (*Ceratotherium simum simum*, 't Sas-Rolfes and Emslie, 2024), various crocodylians, and the vicuña (Lewis, 2009; Morton et al., 2022), and there is recognition that split-listing can support appropriate management of species at the sub-national, national, and international level (Brook and Webb,

2000; Bauer et al., 2018), especially where populations in trade can be distinguished (Doukakis et al., 2009).

A major challenge to split-listing species would be achieving agreement at Conferences of the Parties (CoPs), particularly where this involves relaxing trade controls for charismatic species. Parties and observers regularly have polarized opinions on proposed trade measures, especially where they relate to charismatic species (Webb, 2013; Bauer et al., 2018; 't Sas-Rolfes et al., 2024). Arguments for and against these measures are frequently expressed in terms of the precautionary principle but often under the assumption that tighter regulation of trade is the most precautionary option ('t Sas-Rolfes et al., 2024). In some circumstances this may be the case, but the precautionary principle is not unidirectional (Challender et al., 2022b) and in other cases well-regulated international (and/or domestic) trade may be the most precautionary option, or the most precautionary policy option may be uncertain ('t Sas-Rolfes et al., 2014). If split-listing were to be used, the CoP could incentivize successful outcomes by establishing goals with range states (e.g., population targets for species) against which to measure progress.

Critically, application of this approach would go beyond current decision-making in CITES, which does not involve consultation with relevant actors (e.g., resource users) by default, may lack an underpinning evidence base (Cooney and Abensperg-Traun, 2013), may result in incoherent interventions along supply chains (Section 3.1; CITES, 2022c), and is characterized by high levels of uncertainty as to conservation outcomes. The proposed approach would entail systems analysis to generate knowledge of particular species and SESs and collective decision-making by relevant Parties, informed by input and evidence from relevant actors and stakeholders, to ensure that new or revised rights and rules on harvest and trade are socially legitimate to key actors and are situated within, and align with, formal and informal institutions along supply chains. It would then require subsequent engagement with CITES to align these arrangements with formal trade measures under the Convention.

The Parties could reduce the inherent uncertainty of listing decisions by broadening Annex 6 (*Format for proposals to amend the Appendices*) of Res. Conf. 9.24 (Rev. CoP17) to include additional factors that are critical to understanding the SESs in which the harvest, use, and trade of species takes place, including social and economic considerations (Cooney et al., 2021). CITES listing proposals largely overlook factors critical to evaluating the potential impact of trade measures, including the role of, and incentives for, different actors (including end market consumers), market size, and price trends for wildlife products (Cooney and Abensperg-Traun, 2013; Challender et al., 2019, 2022a). Guidance would be needed to support Parties in including such information in listing proposals but requiring proposing Parties to provide a detailed justification for proposed trade measures, including any new and/or revised institutional arrangements along supply chains, an evaluation of any potential risks identified (e.g., perverse impacts and/or feedbacks), and any critical mitigation measures - informed by social and/or economic

insights - would enable a more realistic assessment of likely conservation outcomes (Cooney et al., 2021). This will not prevent the political nature of decision-making (Webb, 2013) on amendments to the Appendices, but it could ensure that the Parties have the most robust scientific evidence to inform decision-making in the best interests of the conservation of species.

The suggested approach will require Parties to be bold. They will need to decide whether to adopt trade measures for species that are tailored to specific SESs and integrated into broader institutional settings, and therefore more likely to contribute to legal, traceable, and ecologically and socially sustainable international trade, or rely principally on state-led law enforcement as currently. The current approach may give the illusion that CITES is effective (Moyle, 2003; Challender et al., 2024), even in cases when it may not be, and in many cases cannot be.

4.3 CITES and the broader biodiversity governance regime

The challenge of preventing the overexploitation of wildlife is not limited to CITES. The Convention is one of several MEAs aiming to achieve this; others include the Convention on Biological Diversity (CBD) and Convention on Migratory Species (CMS). There are also intergovernmental agencies involved in wildlife trade regulation, including the United Nations Office on Drugs and Crime (UNODC), among others, and increasingly, public health agencies, representing a polycentric governance ecosystem (Lanchberry, 2006). The role and effectiveness of CITES therefore needs to be considered in the context of the broader global biodiversity governance regimes with which it interacts. Treaties may shape regulatory ecosystems, but in themselves do not necessarily constitute full regulatory regimes (Levy et al., 1995). With a specific and narrow remit, CITES cannot constitute the entire global biodiversity governance regime for exploited wildlife but it can play an appropriately coordinated and constructive role in this regime (Velázquez-Gomar et al., 2014).

CITES is well-placed to play a central role in ensuring that the harvest of species for international (and local and domestic) trade is ecologically sustainable. In contrast to some other relevant MEAs, CITES obligates Parties to the Convention to enact implementing legislation and has sanctions systems in cases of non-compliance. This is a recognized strength of CITES, even if the treaty is currently not as effective as it could be (Sand, 2013). Successful application of the approach proposed in this article has the potential to enable policies enacted through CITES to contribute concurrently to achievement of the aims and targets of other MEAs. For example, it could contribute to Target 5 of the post-2020 Global Biodiversity Framework on ensuring that the harvest, trade, and use of wild species is legal and sustainable, and Target 9 on ensuring benefits and livelihoods for people through sustainable management of wild species and the protection of customary sustainable use by indigenous peoples and local communities. Importantly, joint implementation presents the potential for collaborative funding to ensure that appropriate institutional arrangements are implemented to the benefit of CITES-listed species and people

along supply chains. For example, the Memorandum of Understanding on the conservation of the saiga antelope (*Saiga tatarica* and *S. borealis*) between CMS and CITES and is widely acknowledged as highly successful at supporting the conservation and sustainable use of the species (Yukasheva, 2017). This would address, in part, a key challenge to the approach that we propose: resourcing. A focus on joint implementation (CITES, 2022i), could open up funding from sources including the Global Environment Facility (GEF), but for the approach to be used widely would require substantial funding from sources likely including the private sector, biodiversity-related economic instruments, and impact investors (Xu et al., 2021).

5 Discussion

Multilateral environmental agreements (MEAs) are increasing in number (Young, 2018) but evidence of their effectiveness is mixed at best and there are few agreements that have been successful in problem-solving terms, i.e., demonstrably improved the state of the environment (Young, 1999; Petersson and Stoett, 2022). Major impediments include resource constraints, governance conditions, and a lack of political will (Perino et al., 2022; Petersson and Stoett, 2022). A recent meta-review suggested that international treaties would be more effective if they included enforcement mechanisms (Hoffman et al., 2022). CITES has such mechanisms, which have been described as effective (Sand, 2013), but the Convention demonstrates limited verifiable success in problem-solving terms.

Regulatory mechanisms are typically oversimplistic in design (Baldwin et al., 2012) and it is increasingly recognised that if MEAs are to be effective they need to go beyond simple solutions (Ostrom, 2007; Kalfagianni and Young, 2022). CITES has recognised the complexity of achieving ecological sustainability in international wildlife trade (Wijnstekers, 2018) but implementation continues to rely principally on state-led law enforcement. Additional measures have been adopted for numerous species to support implementation, but the treaty is proving ineffective for many of these species. This is primarily because law enforcement is insufficiently resourced, but even in circumstances where it is, compliance by actors is not guaranteed, and regulating or prohibiting international trade in species does not necessarily alleviate the threat of overexploitation. While it is important not to conflate implementation issues with ineffectiveness (Petersson and Stoett, 2022) it is equally important to recognise design flaws where they are identified, to inform corrective action.

It is nearly 50 years since CITES entered into force. The Convention can continue to operate along the lines that it has in recent decades, characterised by a high degree of uncertainty as to likely conservation outcomes for species included in the Appendices and pervasive non-compliance by actors in many countries that are Parties to the Convention. The Parties could heed calls from some (see Wyatt, 2021a) for more stringent approaches to managing wildlife trade, including the imposition of higher penalties for CITES-related violations. However, this risks over-criminalizing wildlife trade and is unlikely to be successful unless there is an

adequate probability of apprehension for would-be offenders; as our analyses suggest, this is unrealistic in many contexts. Alternatively, the Parties could recognise that the predominant focus on state-led law enforcement is a design flaw that poses a serious risk to the Convention's effectiveness in many circumstances.

One way forward would be for Parties to apply the species-system approach proposed here; managing international trade based on an in-depth understanding of the relevant SESs, aligning formal and informal institutions along supply chains, and integrating CITES trade measures into broader institutional arrangements. The approach presents resourcing challenges but where institutional arrangements are robust and appropriate, there will be a higher probability of achieving long-term conservation gains. Using an adaptive management approach would mean that such arrangements could be amended periodically as needed, recognising the dynamic nature of wildlife trade. Where interventions to address other complex issues (e.g., alcohol prohibition and drug use) have previously overemphasized law enforcement to influence human behaviour at scale, more realistic approaches are now being implemented, in part because of recognition that relying primarily on law enforcement is unfeasible and counter-productive (Schrad, 2010; Santos, 2020; Sánchez-Avilés, 2020). The time has come for a more realistic approach to implementing CITES.

Our proposed approach has several implications for policymaking. It would mean greater involvement of researchers from a broader range of disciplines, including the social sciences, in evidence-gathering to inform policy options along supply chains. It would also require the input of diverse actors and stakeholders at each stage of, and along, these supply chains. Crucially, it would require collective political will and leadership from the Parties (Cheung et al., 2023), bold decision-making in CITES, and effective implementation of the Convention and specific interventions by all relevant actors. Crafting the most appropriate institutional arrangements for supply chains containing diverse actors and agencies will not be easy and will require trade-offs, explicit recognition of uncertainties - including potential perverse impacts of policies and interventions - and a willingness from Parties and other actors to engage in adaptive management, to achieve agreed outcomes.

This approach will also mean recognising that the precautionary principle is not unidirectional and that acting in the best interests of CITES-listed species will require understanding the biological, economic, social, and governance components of SESs to devise the most appropriate policies. This may involve tightening or relaxing CITES trade measures and associated rights and rules for actors, which may differ between range states for a given species. If this can be achieved, and the most appropriate evidence-informed policies and management interventions adopted, humanity will have the best chance of avoiding the overexploitation of species for international (and local and domestic) trade. This would place CITES on track to play its full role in nature recovery over the next 50 years.

Author contributions

DC: Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. M'tS-R: Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. SB: Writing – review & editing. EM-G: Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1425267/full#supplementary-material>

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