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Abstract

Conservation is predominantly an exercise in trying to change human behaviour – whether that of consumers whose choices drive unsustainable resource use, of land managers clearing natural habitats, or of policymakers failing to deliver on environmental commitments. Yet conservation research and practice have made only limited use of recent advances in behavioural science, including more novel behaviour change interventions. Instead conservationists mostly still rely on traditional behaviour change interventions – education, regulation and material incentivisation – largely without applying recent insights from behavioural science about how to improve such approaches. This paper explores how behavioural science could be more widely and powerfully applied in biodiversity conservation. We consider the diverse cast of actors involved in conservation problems and the resulting breadth of behaviour change that conservationists might want to achieve. Drawing on health research, we present a catalogue of types of interventions for changing behaviour, considering both novel, standalone interventions and the enhancement of more traditional conservation interventions. We outline a framework for setting priorities amongst interventions based on their likely impact, using ideas developed for climate change mitigation. We caution that, despite its promise, behavioural science is not a silver bullet for conservation. The effects of interventions aimed at changing behaviour can be modest, temporary, and context-dependent in ways that are as-yet poorly understood. We therefore close with a call for interventions to be tested and the findings widely disseminated to enable researchers and practitioners to build a much-needed evidence base on the effectiveness and limitations of these tools.

1. Introduction

Although conservationists have achieved some notable and heartening victories in recent years (Bolam et al., 2021; Knowlton, 2021), the fight to avert the sixth mass extinction is still being lost. In most places, wild species, the habitats they depend upon, and the diverse benefits they generate for people remain in grave decline (IPBES, 2019). This stems, in large part, from unrelenting growth in the underlying drivers of humanity's impacts on the environment (Tittensor et al., 2014) – our population size, and even more importantly (especially in wealthier countries) our per capita demand for resources; these trends have proven difficult to reverse. But many conservation actions are also less effective than they might be because conservation scientists and practitioners often pay insufficient attention to the complexities of human behaviour (Clayton and Brook, 2005; Cowling, 2014; Saunders et al., 2006; Schultz, 2011; Selinske et al., 2018). This review explores how this challenge might be addressed by examining progress and limitations in applying new advances in behavioural science.

2. The fundamental importance of changing behaviour

Almost all conservation problems originate in the actions and choices of people (Balmford and Cowling, 2006; Saunders et al., 2006; Schultz, 2011). For example, the post-apartheid clearance of Cederberg fynbos remnants and the resulting red-listing of over 100 endemic plant species in 12 years originated in the demand for rooibos tea among health-conscious consumers overseas (Raimondo and Von Staden, 2009). The overharvesting of many African coastal fisheries has been driven in considerable measure by political decisions to sign damaging distant-water fishing agreements (Alder and Sumaila, 2004). And the spread of aquatic invasive species in North America is in part enabled by recreational boat-users failing to adequately clean their boats before moving them between water bodies (Clarke Murray et al., 2011). Thus to be effective, the majority of conservation interventions require changes in human behaviour (Cinner, 2018; Cowling, 2014; Saunders et al., 2006; Schultz, 2011). Consider the IUCN's catalogue of intervention types (Table 1; IUCN 2012). Three of the six categories – Education and awareness, Law and policy, and Livelihood, economic and other incentives – are intended to alter the choices made by consumers, producers, and those who influence their decisions (e.g. policymakers, communicators and investors). The remaining intervention categories focus more directly on the protection and management of populations and habitats, but their effectiveness also depends on human behaviour changes: the actions of conservation agents in implementing the interventions, and the reactions of stakeholders who are impacted by those actions (e.g. protected area neighbours, or those harvesting a managed population).

Shifting people's behaviours in ways that benefit nature is complex (Clayton and Brook, 2005; Reddy et al., 2017; Selinske et al., 2018; Vlek and Steg, 2007). The target audience may respond to an intervention in unexpected ways, potentially exacerbating a problem, or creating new problems (Blanken et al., 2015; Rode et al., 2015). Interventions that are effective for one group of stakeholders may have little impact on others (Burgess et al., 2018). More broadly, people do not necessarily use all available information, follow formal rules or behave in an economically rational fashion (Kahneman, 2011; Marteau et al., 2012; Thaler, 2018). In part because conservation programmes are largely run by biologists, interventions are commonly designed in ways that fail to consider how people will implement and respond to them, and that often do not address underlying drivers of environmental degradation (Williams et al., 2020). We contend that the sector is failing to show sufficient awareness of the power (and indeed limitations) of new developments in behavioural science that are increasingly deployed in other sectors (Burgess, 2016; Cinner, 2018; Rare and The

Behavioural Insights Team, 2019; Reddy et al., 2017; Thomas-Walters et al., 2020a; Travers et al., 2021).

3. Relevance of behavioural science

In recent decades, theories and evidence from behavioural science – which we define as the scientific study of behaviour informed by a wide range of disciplines including psychology, sociology, economics, anthropology, political science – have shed considerable light on the social, motivational, cognitive, cultural, and contextual processes underlying behaviour. These have in turn informed interventions which have helped encourage societally valued behaviour change, from reductions in smoking, obesity and addiction, to improvements in development assistance, tax compliance, and climate change mitigation (Bollinger et al., 2020; Datta and Mullainathan, 2014; Duflo et al., 2011; Hallsworth et al., 2017). This progress in understanding human behaviour and how to change it is relevant for conservation interventions in two ways. First, integrating evidence from behavioural science into the design of existing conservation interventions – currently based largely on education, regulation, and material incentivisation – may enhance their effectiveness. Second, behavioural science has identified other, novel interventions for effectively changing behaviour, some of which may be unfamiliar to most conservationists. We explore both these routes throughout this review.

To illustrate how behavioural science evidence can enhance the effectiveness of traditional interventions, consider the approach – frequently deployed in conservation campaigns – of trying to persuade consumers, farmers, or politicians to change their behaviour by informing them about its environmental impact. It has long been established that broad-brush attempts to increase knowledge are often insufficient to shift behaviour (Kollmuss & Agyeman 2002). Behavioural science shows instead that information campaigns can be more effective when they target discrete audience segments and account for their values, motives, norms, and social and physical realities (Cheng et al., 2011; Kahan et al., 2012; Kusmanoff et al., 2020). For example, in the United States, switching from pro-social to self-interest messaging can increase adoption of solar panels (Bollinger et al. 2020; but see van der Linden 2018; Kraft-Todd et al. 2018); and emphasizing how junk-food marketing undermines autonomy and social justice can be more effective than traditional health-based messaging in reducing unhealthy food choices by adolescent males (Bryan et al., 2019).

Behavioural science also suggests interventions not commonly used by conservationists (Michie et al., 2013, 2011). For instance, simple alterations to the physical micro-environments in which choices are made (so-called choice architecture) can have striking effects on behaviour (Hollands et al., 2017; Thaler and Sunstein, 2009). One such intervention involves changing default settings on sign-up documentation, so that participants must opt out of (rather than into) individually or societally more desirable choices. This strategy has increased commitments to organ donation (Johnson and Goldstein, 2003), uptake of higher-benefit retirement plans (Benartzi and Thaler, 2013; Thaler and Sunstein, 2009), and household subscriptions to renewable energy programmes (Ebeling and Lotz, 2015; Liebe et al., 2021). Other related interventions that have proven effective include reducing the size of wine glasses in bars, which may lower alcohol consumption (Pechey et al., 2016; Pilling et al., 2020), and painting brightly coloured footprints between toilet blocks and wash stations, which has increased handwashing among Bangladeshi schoolchildren (Dreibelbis et al., 2016).

Yet despite the promise and breadth of behaviour change interventions, researchers and practitioners have been slow to explore and apply the potential of behavioural science for biodiversity conservation. Work has been done to inform behaviour change interventions for related environmental issues, particularly energy use, water use, recycling, and transport

(Byerly et al., 2018; Nisa et al., 2019; Osbaldiston and Schott, 2012). But there has been far less behavioural science work addressing, for example, demand for threatened species, wildlife harvesting, or land management, all of which are central to conservation outcomes (Mackay et al., 2018; Marselle et al., 2021). We do, however, acknowledge the noteworthy contributions of the research traditions around human dimensions of wildlife (Fulton et al., 1996; Manfredo et al., 2020), conservation psychology (Clayton and Myers, 2015; Saunders, 2003; Selinske et al., 2018), and social marketing (Green et al., 2019; McDonald et al., 2020; Veríssimo, 2019) in introducing and integrating behavioural and social science evidence and theories into conservation science and practice. The evidence base on interventions for shifting behaviours in these domains is nevertheless limited and rarely linked to theory (Byerly et al., 2018; MacFarlane et al., 2020; Olmedo et al., 2018; Veríssimo, 2019). Moreover, effects on target behaviours are typically assessed only through self-reporting, if at all (Kidd et al., 2019; Nilsson et al., 2020).

The rest of this review aims to encourage wider integration of behavioural science in biodiversity conservation, extending recent calls by developing a framework for identifying and prioritising potentially effective behaviour changes and interventions for achieving them (Fig. 1; see also Selinske et al., 2020). Starting with the familiar territory (for conservation biologists) of threatening processes and the wide range of actors and behaviours shaping them, we then unpack the interventions that might achieve behaviour change. We explore attributes to consider in identifying which behaviour changes and interventions to prioritise. Throughout, we use examples from conservation and other fields to illustrate the promise of behaviour change interventions, their likely limitations, and the complexities involved in realising their potential. We close with a call for experimental testing, evaluation, and reporting of both novel interventions and modifications of more traditional behaviour change approaches.

4. Identifying key actors and behaviours

To investigate the effective use of behavioural science in conservation, we convened a three-day workshop bringing together an international group of behavioural scientists from health research, psychology, economics, and marketing, and conservation scientists from academia and NGOs (see online Appendix for further workshop details). To catalyse consideration of a wide range of behaviours, we began by compiling a series of threat chains: simplified models describing our understanding of the reasons for the undesirable state of a conservation target, from changes in ecological dynamics to the socioeconomic mechanisms and underlying drivers likely to be responsible. We derived threat chains using the grey and peer-reviewed literature and participants' working knowledge. For tractability, the workshop typically considered only one of potentially several threats to each population or habitat. Participants then identified key actors along the threat chain and suggested changes in behaviour which could potentially reduce the focal threat.

For example, a major threat to the Hudsonian godwit population overwintering on Chiloé Island in Chile is their ingestion of litter on beaches (Fig. 2; DE, pers. obs.). Tracing the causes of this backwards (reading the red boxes in the figure from left to right), the litter is left by residents and visitors who lack access to waste bins, have limited concerns for the ecological consequences of poor waste management, and use many products sold in non-recyclable or non-degradable packaging. Additionally, there is no collection of plastic waste washing ashore from aquaculture operations, which dispose of plastic directly into the sea. Behaviour changes by specific actors that might reduce the threat to godwits (blue boxes) include increased litter collection by citizens or local agencies, reduced littering by residents and visitors, and the cessation of at-sea disposal of plastics by those working in the aquaculture industry.

We repeated this threat-chain exercise for examples that collectively spanned habitat loss and degradation, overexploitation, invasion and disease, pollution and climate change, as well as terrestrial, freshwater and marine ecosystems and higher- and lower-income countries (Table A1 in online Appendix). For each threat chain, we identified relevant actors and suggested multiple behaviour changes that could potentially reduce the focal threat. Looking across all threat chains, we classified actors into groups defined by the ways they impact conservation targets and identified a broad array of important behaviour changes conservationists might seek to mitigate those impacts (Table 2).

These behaviourally defined groups of actors range from primary producers and extractors (e.g. farmers, fishers and mining operators) and conservation and environmental managers – whose activities directly impact conservation targets – through to consumers of goods derived from or linked to the conservation targets, and those involved in manufacturing, shipping or selling those goods. Other actor groups impact conservation targets in less direct but nonetheless potentially significant ways – through providing financial support, making or delivering policy, or influencing other actors through voting, communicating, or campaigning for particular outcomes. These groupings are approximate, and inevitably incomplete.

The different ways in which actors influence threats in turn suggest diverse opportunities for behaviour change interventions. Changes in the behaviour of more proximal, downstream actors (*sensu* Thomas-Walters et al. 2020a) are likely to impact a conservation target directly – for example fishers changing how or where they harvest their catch. Changes in the behaviour of actors further upstream in contrast tend to impact a conservation target indirectly, by influencing the behaviour of downstream actors – for instance voters increasing pressure on policymakers to remove subsidies for unsustainable fishing practices, which then shifts fisher behaviour. Upstream interventions aimed at delivering such chains of behaviour change could influence large numbers of downstream actors but can be correspondingly complex and politically challenging (Thomas-Walters et al., 2020b).

5. A catalogue of behaviour change interventions

So what types of interventions are capable of influencing such a wide-ranging mix of actors and behaviours? Building on similar efforts in the health sector (Hollands et al., 2017; Michie et al., 2011; Swinburn et al., 1999), we produced a simple catalogue of behaviour change interventions that distinguishes between level of delivery (individual versus population) and the broad mechanisms through which the behaviour is influenced (see Table 3, with generic and conservation-specific examples for each intervention class). The relevance and potential effectiveness of the different intervention types is likely to vary depending on context and characteristics of the behaviour change and actor. For example, sometimes a small number of individuals or organisations – very active hunters, highly-regarded farmers, or large transnational corporations, perhaps – may play disproportionate, keystone roles (Folke et al., 2019; Osterblom et al., 2015). In such situations narrowly targeted interventions may be most effective. In other instances, interventions might be more effectively directed at large numbers of people. Addressing complex behaviours may often necessitate interventions at both individual and population level.

5.1. Individual-level interventions

Behaviour change interventions targeting specific individuals or groups of individuals fall into two classes: interventions that target an individual’s capability, and those targeting their motivation (Michie et al., 2013, 2011). Capability-focused interventions aim to improve a person’s physical, psychological, or management resources to perform, modulate, or resist an activity. A new behaviour may not be successfully adopted because the individual does not possess the requisite skills or knowledge. Capability-building interventions are a traditional part of the conservationists' toolbox but are sometimes overlooked. For example, offering Amazonian households coupons for chicken to reduce consumption of wild meat was only successful when advice about how to cook chicken was provided (Chaves et al., 2018). Behavioural science can also shed light on how to improve existing efforts to enhance capability. For example, increasing numbers of female instructors in a farmer outreach scheme in Mozambique significantly increased uptake of sustainable land management techniques (Kondylis et al., 2016). Such effects of messengers on capability-building efforts are rarely evaluated in the conservation literature (Byerly et al., 2018).

Motivation has been the subject of intense research in behavioural science, spawning many kinds of interventions. All of them target the processes that energize, direct, and sustain behaviour (Michie et al., 2011; Ryan and Deci, 2000). These can be an individual's reflective thought processes, often predictive of important and infrequent behaviour, or the automatic processes characteristic of habitual and frequently performed behaviour (Kahneman, 2011; Marteau et al., 2012; Strack and Deutsch, 2004). Note that motivation is irrelevant in the absence of capability. Many individuals may want to protect nature in general or a particular place or species but lack the understanding or ability that allows them to do so. Unfortunately, these complexities are often overlooked in persuasive communications. In conservation, the repertoire of motivation-focused interventions has largely been limited to education and individual material incentivisation. Behavioural science can enhance the effectiveness of these traditional interventions. For example, working with Islamic leaders to incorporate conservation messages into sermons increased community awareness of turtle conservation in Malaysia (Clements et al., 2009). Likewise, tailoring motivational messages to the values of wealthy Vietnamese professionals through appeals to their strength of character is likely to prove more successful in reducing the use of rhino horn than messages emphasizing the animals' rarity and suffering (Offord-Woolley, 2017). Behavioural science also suggests many other ways to motivate actors (e.g. Michie et al. 2013; Teixeira et al. 2020). Inducing pride in charismatic local species, fostering pro-environmental changes in norms through peer-to-peer conversations, and providing dynamic feedback on individuals' environmental impacts have all motivated positive behaviour change (DeWan et al., 2013; Green et al., 2019; Karlin et al., 2015).

However, while capability and motivation can be important for behaviour change, no change will happen without the physical or social opportunity to realize the change (Michie et al., 2011). For example, wild meat hunters may not change their behaviour without alternative ways to ensure their livelihoods, and city dwellers may decide not to cycle to work if they jeopardise their safety by doing so (Fowler et al., 2017; Van Gils et al., 2019). While opportunity may be enhanced through individual-level interventions, it is typically shaped by population-level circumstances (e.g. infrastructure or economic environment). Moreover individual- and population-level interventions may interact – so a motivation-focused intervention may convince policymakers to invest in cycling infrastructure, for example, creating opportunity which may in turn increase city dwellers' motivation to travel by bike (Kraus and Koch, 2021).

5.2. Population-level interventions

Despite the potential efficacy of individual-level interventions, tackling many of the underlying causes of conservation problems, such as society-wide unsustainable consumption of resources, typically requires intervention at the population level. We identify four types of behaviour change interventions that operate at this level. The first encompasses physical microenvironment interventions that change the characteristics of products and services or the environments within which they are available (e.g. shops, restaurants, workplaces or websites; Hollands et al., 2017; Marteau et al., 2020). These interventions embrace the concept of choice architecture, also known as nudging; they usually operate through non-conscious routes to action, and have gained considerable popularity since the publication of the book *Nudge* (Thaler and Sunstein, 2009). Notable examples with conservation relevance include changing the relative availability of plant- and meat-based meals in cafeterias (Garnett et al., 2019; Gravert and Kurz, 2019); altering the positioning of high- and lower-footprint options on menus and in buffets (Garnett et al., 2020; Kurz, 2018); and providing accessible litterbins in outdoor spaces (Schultz et al., 2013). Extensive research in other sectors suggests that physical microenvironment interventions can have significant effects on behaviour (Marteau et al., 2015, 2012; Nisa et al., 2019), sometimes disproportionately impacting higher-footprint segments of the population (such as those eating more meat) whose behaviour might be harder to shift by other means (Ebeling and Lotz, 2015; Garnett et al., 2019; Liebe et al., 2021).

The second type of population-level interventions relates to the physical macroenvironment. It involves changing the basic physical and organizational structures and facilities needed for the operation of a society or organization (Swinburn et al., 1999). These systems, which include the educational system, built infrastructure, industries, and the media, exert direct effects on behaviour by influencing what actions can feasibly be performed (Creutzig et al., 2015). As described above, they can also act as constraints on other intervention types, such as capability-building or motivation, thereby limiting the extent to which behaviours can be readily changed (Creutzig et al., 2015; Seto et al., 2016): individuals cannot switch from wild meat to chicken, for instance, if limited production means chicken is not available at a competitive price. Conservation-relevant interventions targeting the physical macroenvironment include increasing the availability of public transportation in urban and suburban areas, scaling-up renewable energy supplies, and incorporating greater environmental literacy into school curricula.

A third population-level class of interventions involves altering the economic environment of actors by introducing, modifying, or removing taxes, subsidies, and other material incentives, which can act as powerful drivers of individual and organizational behaviour (Andreyeva et al., 2010; Marteau et al., 2019). This type of intervention has commonly been advocated as central to confronting biodiversity decline, in large part due to its effectiveness in changing behaviour across actors and affecting both the supply and demand of goods and services (James et al., 2001; Myers, 1998). Examples include public or market-based payments to farmers and other land managers to protect or restore the biodiversity or ecosystem service values of natural habitats (Jayachandran et al., 2017; Pattanayak et al., 2010), and the removal of subsidies or introduction of taxes on environmentally harmful products (Springmann et al., 2017). Despite commonly being recommended in conservation, such interventions face numerous challenges (Pattanayak et al., 2010; Wunder, 2007): payments are often only weakly linked to environmental performance or to individual actors' costs (so schemes may be inefficient); implementation is commonly constrained by poor governance; and imposition of taxes is often politically unpopular (Marteau, 2017; Wunder et al., 2018). Although not yet widely utilised, it seems plausible that behavioural science could enhance the effectiveness of economic interventions. For example, altering the default cost-share in negotiated on-farm conservation actions significantly increased farmer contributions and lowered the cost of resulting agreements to the taxpayer (Wallander et al., 2017). Other routes for enhancing the performance of economic interventions might include framing payments in terms of what individuals stand to lose from non-participation (drawing on ideas about loss aversion); increasing scheme uptake through the use of trusted messengers; and emphasizing social norms that align with scheme compliance (Cinner, 2018).

The fourth set of population-level interventions target the institutional environment by changing the voluntary and regulatory codes of practice to which organizations must conform. These interventions – such as introducing, modifying, or removing fines; establishing or altering institutional standards; or banning certain behaviours outright – may be implemented by governments or private organizations (Vandenbergh and Gilligan, 2017). Institutional interventions are again a conventional part of the conservationist's arsenal and include rules about harvesting potentially vulnerable populations, restrictions on access to particular areas, and regulations of farming or forestry practices. More recent ideas include instituting sustainability standards for public procurement of farmed or harvested goods, strategically realigning business practices with the Sustainable Development Goals (Österblom et al., 2017; Waddock, 2020), and shortening the working week to reduce greenhouse gas emissions and improve worker wellbeing (King and Bergh, 2017). Evidence from behavioural science may be used to design and enhance the effectiveness of such interventions. In one example, an experiment manipulating signs aimed at discouraging theft of petrified wood in an Arizonan national park found that a descriptive norm (describing the theft behaviour of others) actually increased theft by showing it was widespread, whereas an injunctive norm (asking visitors not to steal) reduced theft (Cialdini et al., 2006). As with interventions based on education and material incentives, behavioural science could potentially yield many opportunities for enhancing the effectiveness of interventions targeting institutional environments.

Finally, in this section it is worth noting that, as with climate change, fully addressing the underlying drivers of the biodiversity crisis requires even broader, system-level interventions which re-organise the political and economic system (Otero et al., 2020). In the environmental space, the most prominent example of such macro-economic reorganisation is perhaps the proposed Green New Deal (Mastini et al., 2021); others include a fundamental shift from indefinite economic growth towards zero growth or even de-growth (D'Alessandro et al., 2020; Jackson, 2009; Kallis et al., 2018). Such interventions clearly have greater transformative potential than individual- and population-level interventions. While at present it remains challenging to see how they could be implemented, behavioural science may have an important role to play in understanding what motivates transformative social change.

6. Exploring the diversity of potential interventions

How might this array of traditional and novel behaviour change interventions increase impact across the breadth of problems which conservationists are trying to tackle? We sought to explore this question using our panel of heuristic threat chains (Table A1 in online Appendix). Considering first the Hudsonian godwit example, potentially promising interventions for achieving relevant behaviour changes (blue boxes in Fig. 2) could include installing and emptying bins to reduce littering (a physical microenvironment intervention aimed at consumers); introducing a tax on non-degradable packaging (an economic intervention targeting consumers); and regulating against the at-sea disposal of plastics (an institutional intervention aimed at producers – in this case the aquaculture sector). To be enacted, each intervention may also require lobbying politicians (i.e. motivational interventions targeting policymakers) to introduce supporting policies and regulations.

The diversity of desirable behaviour changes and possible interventions for delivering them was underscored when, as a heuristic exercise, we considered ways of addressing each of our example threats in turn (see online Appendix). Across the 12 threat chains we examined in detail, workshop participants suggested 130 interventions which might deliver beneficial behaviour changes (see Table 4, which sorts them into intervention and actor groupings). These suggestions were quite diverse. Proposed interventions for tackling examples of habitat loss or degradation, for example, included incentivising forest retention by providing Amazonian ranchers who do not deforest with better training in animal husbandry, and enhancing water quality for threatened vendace populations by simplifying the administrative burden of farmers participating in catchment management schemes. Ideas for tackling other threats included reducing local overexploitation of Caribbean fisheries by providing refrigeration to traders to reduce supply chain wastage; slowing the expansion of alien lionfish in Mexican waters by training chefs in how to handle and cook them; and reducing the impact of climate change on alpine plant communities in Snowdonia by encouraging climbers to make social media commitments to avoid using sensitive routes during warmer weather.

Some of the listed interventions have been implemented and found to be at least partially successful. An awareness-raising campaign describing recommended hygiene measures to reduce the spread of aquatic invasive species has been linked to an increase in self-reported adoption of those behaviours by recreational boat-users and anglers around Lake Michigan (Seekamp et al., 2016). Likewise, efforts to recover South Asian vulture populations following inadvertent but devastating die-offs from feeding on carcasses contaminated with the veterinary drug diclofenac have been boosted by removing from patent a safer alternative with which smallholder farmers can treat cattle (Galligan et al., 2020). This latter example involved several linked interventions including motivating a multinational corporation to cede its patent, thereby altering the economic incentives for local pharmaceutical manufacturers, who in turn provided a more sustainable option for cattle-owners. Other sequences of interventions are even more complex (asterisks in Table 4) and, as with efforts to reduce litter on Chiloé’s beaches, many will hinge on first motivating upstream policymakers.

While we considered only a few example threats and our exploration of promising interventions was not systematic or comprehensive, the distribution of suggestions across actors and intervention types (shown by shading in Table 4) does hint at some interesting patterns. Most of the identified interventions were aimed at producers and extractors, and consumers, with fewer directed towards conservation managers, supply-chain manufacturers or sellers, and fewer still at actors further upstream. Interventions aimed at producers and consumers were spread across several intervention classes, though quite heavily focused on economic incentives (for producers) and motivational interventions (for consumers). Suggested interventions changing the behaviour of upstream actors (so that they provide financial support, institute policy, or otherwise influence the behaviour of downstream actors) were focused almost entirely on motivation. These patterns might in part reflect genuine constraints on what interventions are possible, but we suggest more expansive thinking may identify rewarding interventions of kinds we failed to imagine (white cells in Table 4).

7. Selecting behaviours and interventions to focus on

Clearly in tackling any threat to a population or habitat of conservation concern, several human behaviours could be targeted, each through multiple interventions. So how can conservationists practically narrow their focus? Work on prioritising climate change interventions can help. This proposes that the impact of a behaviour change intervention is a function of the degree to which the target behaviour change would, if achieved in full, influence the outcome of interest (its technical potential); and the degree to which the target behaviour can be changed (its behavioural plasticity) by the intervention over the period of interest (Dietz et al., 2009; Nielsen et al., 2021a). Both depend on the scale and nature of the behaviour change sought, while the latter also depends on the specific intervention. These two attributes may often co-vary negatively. For example, while timing devices can successfully shorten how long people spend showering, and plastic bag taxes can persuade people to use canvas bags (i.e. they have high behavioural plasticity), both behaviour changes have low technical potential to reduce greenhouse gas emissions. Conversely, switching from petrol to electric vehicles or avoiding air travel has high technical potential, but interventions to achieve these changes speedily and at scale remain elusive. One other consideration is that while some interventions may appear promising, they might not be feasible to implement or deliver at scale (the concept of initiative feasibility; Nielsen et al., 2020; Vandenbergh and Gilligan, 2017). This may be because of cost, political inertia, vested interests of policymakers or corporations, or indeed political feedback: if they are effective in changing behaviour, beneficiaries of the current behaviour may pressure policymakers to limit or even reverse their implementation (Carattini et al., 2019; Klenert et al., 2018; Oreskes and Conway, 2011).

Assessing the relative technical potential, behavioural plasticity, feasibility and cost of alternative intervention options is core to effective and efficient efforts to develop and deliver interventions that change behaviour (Nielsen et al., 2021a; Nisa et al., 2019). In the context of biodiversity conservation, existing evidence can provide some guidance, but the views of those with behavioural expertise and with familiarity with the focal threat will also be key. Such assessment was beyond the scope of our workshop but thinking briefly about the godwit interventions suggested above indicates that trade-offs between technical potential and behavioural plasticity may not be uncommon (see also Selinske et al. 2020; Thomas-Walters et al. 2020b). Taxing non-degradable packaging, for instance, may have high behavioural plasticity but low technical potential: people may change what they buy, but without other interventions will still leave litter on beaches. Conversely, stopping at-sea waste disposal could substantially impact how much washes ashore, but a ban may be difficult to enforce and hence have little effect on behaviour. Both taxation and introducing bans may also be politically costly. The third option of installing and emptying litterbins might be the most promising and affordable intervention, as littering strongly impacts litter build-up, and may be reduced by bin provisioning (Schultz et al. 2013).

Two further issues are important when prioritising interventions. Obviously, many conservation targets face multiple threats, so if mitigation efforts are to be efficient the likely ability of candidate interventions to enhance the state of the focal population or habitat must be compared across all main threats. Finally, some behaviour changes might benefit multiple conservation targets: delivery of co-benefits should also be considered when assessing the relative merits of alternative candidate interventions.

8. Cautions and caveats

Although behavioural science has considerable untapped potential to contribute to biodiversity conservation, it is of course not a panacea. Several important cautions are in order. Behaviour change may require multiple, linked interventions (Table 4), with the success of one contingent on the successful deployment of others. Leakage effects may arise whereby an intervention simply displaces a behaviour: in a conservation example, reducing Japanese consumers' use of rhino horn has been linked to increased demand for the horns of now critically endangered saiga antelope (Kitade and Toko, 2016; Thomas-Walters et al., 2020b).

Rebound effects are also possible: where an intervention reduces personal expenditure (through cutting household energy bills, for instance) people may plausibly respond by spending more on other, higher footprint activities (e.g. overseas air travel) (Hertwich 2005; Sorrell et al. 2020). Moral licensing, where individuals undertaking one pro-social action feel justified in not taking others (Hofmann et al., 2014; Merritt et al., 2010); and crowding-out, where providing extrinsic motivation for a behaviour reduces intrinsic motivation (Cinner et al., 2020; Promberger and Marteau, 2013), also require consideration. Evidence suggests, however, that such negative spillover effects may be quite limited (Künemund and Rein, 1999; Maki et al., 2019; Promberger and Marteau, 2013), but relevant studies are scarce.

Behaviour change interventions also raise important ethical concerns. For example, population-level interventions using choice architecture (or nudging) have been criticized for undermining personal autonomy and for being undemocratic and non-transparent in defining what is considered societally good or bad behaviour (Schmidt and Engelen, 2020; but see Bruns et al., 2018; Paunov et al., 2019). Considering this carefully is especially important given the context of power imbalances between different actors involved in, and affected by, conservation, both now and in the past (Sandbrook, 2017). Other population-level interventions may also reinforce socioeconomic inequalities unless designed to protect vulnerable and/or poorly represented groups (Dietz and Whitley, 2018). For example, physical macroenvironment interventions to improve low-carbon infrastructure and to reduce air pollution may favour wealthier over poorer neighbourhoods, and economic environment interventions, such as offering tax benefits to incentivize energy-efficiency investments in housing, may benefit homeowners and wealthier households who can afford such investments (Owen et al., 2020). We note, however, that such ethical concerns are not unique to the sorts of interventions reviewed here but rather apply to much policymaking. Citizen engagement through deliberative and other processes comprise an important set of interventions to engage citizens, communities, and different stakeholder groups in the design of behaviour change interventions to ensure their impacts are equitable (Bowie et al., 2020; OECD, 2020; Stern et al., 2021).

Most significantly, evidence across sectors shows that the effects of behaviour change interventions are (like many other interventions) typically modest (Nisa et al., 2019; Thomas-Walters et al., 2020b). When properly evaluated, behaviour change interventions sometimes fail to produce behaviour change (Veríssimo et al., 2018a), even when they draw on theoretically plausible mechanisms. Conveying educational conservation messages through a Tanzanian radio show, for instance, failed to reduce demand for wild meat (Veríssimo et al., 2018b); and in a recent UK study an array of interventions using tailored information provision, peer-based descriptive norms, loss aversion, and material incentives failed to increase car-sharing (Kristal and Whillans, 2020). In other instances, studies are too underpowered to detect true effects (Byerly et al., 2018; Palm-Forster et al., 2019), or effect sizes are small (Nisa et al. 2019, but see van der Linden & Goldberg 2020). Some evidence suggests that the latter is particularly true of habitual behaviours reinforced by the social or physical environment, or when the benefits of behaviour change to the actor are limited or delayed (Marteau et al., 2012; Verplanken et al., 2008). Effects may also wane over time (Bernedo et al., 2014; Ferraro and Price, 2013), particularly if a treatment is withdrawn or if it requires maintenance to remain functional (Hanna et al., 2016; van der Linden, 2015).

Importantly, the effects of behaviour change interventions are typically context- and actor-dependent. For example, the remarkable impact of subtle linguistic cues on voter turnout in the United States revealed by one study (Bryan et al., 2011) could not be replicated in a second (Gerber et al., 2016); and placing vegetarian meals before meat dishes in buffets increased vegetarian sales in one cafeteria but not another at the same university (Garnett et al., 2020). Individual studies may thus have low external validity, and the power of interventions tested in other contexts needs to be explicitly evaluated, not assumed (Camerer et al., 2018; Henrich et al., 2010). Taken together, these considerations suggest that conservationists interested in shifting human behaviours may be well advised to implement multiple (though separately tested) interventions, each with a potentially small but additive effect (Ferraro and Price, 2013; Thomas-Walters et al., 2020b).

9. Growing the field

This review has illustrated the potential of behaviour change interventions in conservation, their diversity, and crucially, some of their limitations. We also hope that it provides some guidance on how to select promising interventions by characterizing the dynamics of the focal threats, identifying actors and behaviours, considering a wide range of candidate interventions, and prioritising among them based on their likely impact, feasibility, and cost. Given its potential societal benefits, and the methodological and conceptual insights that might emerge from working in a diverse array of field settings, we hope that devising and testing interventions to avert the extinction crisis can also motivate behavioural scientists to become more engaged in biodiversity conservation (Nielsen et al., 2021b).

We close by stressing the clear need for learning by doing – testing and reporting on interventions applied within real-world conservation programmes. Like other fields, behavioural science faces significant challenges of generalisability and reproducibility (Henrich et al., 2010; Nelson et al., 2018; Simmons et al., 2011). Given that evidence is especially limited in conservation (Byerly et al., 2018; Palm-Forster et al., 2019), we urgently need to build an evidence base (Ferraro and Pattanayak, 2006; Veríssimo et al., 2018a). Where possible, behaviour change interventions should be tested singly (rather than in bundles), in adequately powered experiments or quasi-experiments, delivered in field settings, and involving real-world actors (Baylis et al., 2016; Reddy et al., 2017). Particular attention should be paid to selection bias, whereby interested participants self-assign to a treatment group, thereby confounding estimation of its impact (Veríssimo et al., 2018a). Effects should be assessed over the long run (and ideally after an intervention has ceased), and measured in terms of actual behaviour rather than knowledge, attitudes, or intentions (Kollmuss and Agyeman, 2002; Nilsson et al., 2020; Sheeran, 2002). Researchers should, where possible, avoid self-reported behaviour, which can be vulnerable to social desirability bias (people's wish to be viewed favourably; Kormos & Gifford 2014; Kidd et al. 2019).

Last, given that effect sizes may be small and potentially context-dependent it is critically important to report non-significant findings (Kristal and Whillans, 2020; Kvarven et al., 2020; Osman et al., 2020; Veríssimo et al., 2018a). A recent comparison of nudge studies in academic articles and the grey literature indicates that a failure to publish lower-effect studies may be systematically distorting our understanding of intervention effectiveness (DellaVigna and Linos, 2020). Preregistration and registered reports (where journals agree to publish a study based on the introduction and methods, before results are available; e.g. Wiik et al. 2020) can substantially improve transparency and reduce publication bias (Nosek et al., 2018; Parker et al., 2019). Ideally, resulting data could then be shared in a transparent and open source manner (as in the Human Behaviour Change Project; www.humanbehaviourchange.org), and in due course synthesised through initiatives such as Conservation Evidence (www.conservationevidence.com/). Sharing and synthesising information in this way should help make experimental tests of interventions as informative for others as possible, and thereby move the significance of behavioural science for conservation from being either overlooked (in many instances) or overstated (in some others), to being better understood and cautiously but widely used.

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Fig. 1. Conceptual framework depicting the proposed six phases of selecting, implementing, and evaluating behaviour change interventions for biodiversity conservation. Image credit: Flaticons.com and Fasil on freeicons.io.

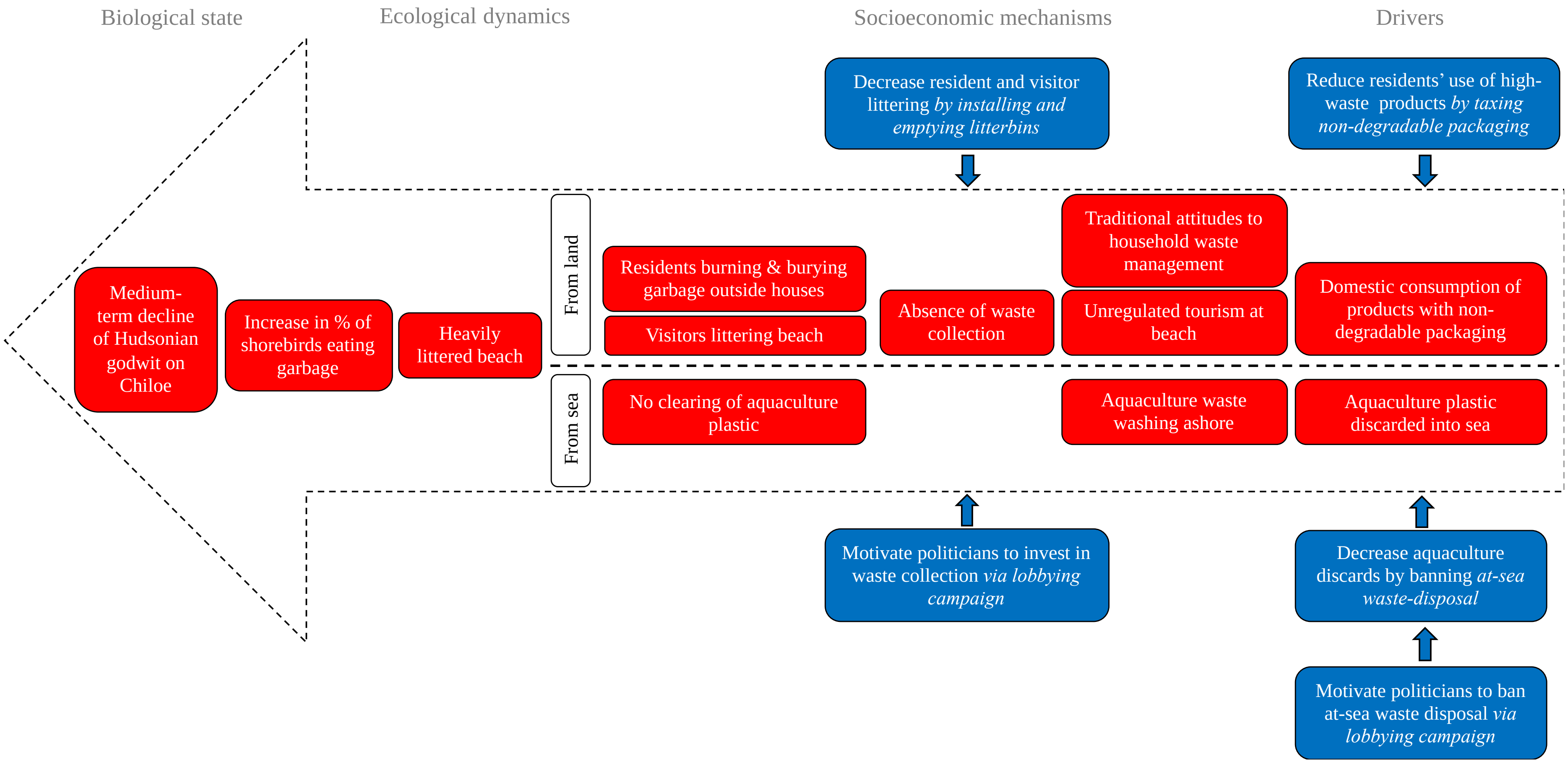

Fig. 2. An illustration of the threat chains we used to explore the breadth of behaviour changes potentially capable of reducing threats to biodiversity. This example characterises (in red boxes) the threat to Hudsonian godwits overwintering on Chiloé Island from ingesting beach litter originating from householders and visitors (above dashed line) and aquaculture operations (below; DE pers. obs.). Potentially beneficial changes in the behaviours of particular actors are in blue boxes, with possible interventions for achieving them in italics. This threat chain addresses only one of several interacting threats impacting the conservation target. The threat chain model is adapted from Balmford et al. (2009).

Table 1. IUCN's level 1 classification of conservation actions (IUCN 2012), and our broad assessment of the general importance (categorised for simplicity as very important/important/likely to be important) of behavioural factors in determining the outcomes of actions in each category.

Category of conservation action		Importance of behavioural factors
1	Land/water protection	Behavioural factors **important** in determining people's responses to formal protected area designation, and **very important** to determining whether stakeholders treat as protected those areas that are not formally designated
2	Land/water management	Behavioural factors **likely to be important** in determining extent or quality of delivery of management actions by all, especially in sites not receiving formal protection, and by stakeholders in non-conservation sectors
3	Species management	Behavioural factors **likely to be important** in determining extent or quality of delivery of actions by conservationists and to be **very important** in determining actions of those harvesting and trading wild species
4	Education and awareness	Behavioural factors clearly **very important** in determining uptake of ideas and interventions
5	Law and policy	Behavioural factors **important** in determining uptake and effectiveness of legislation, policies, regulations, standards, etc.
6	Livelihood, economic and other incentives	Behavioural factors **very important** in determining responses of target actors to interventions

Table 2. Key groups of actors identified through our heuristic threat chains, and examples of changes in their behaviour that might have beneficial conservation outcomes. Actor groups are defined by how their behaviour impacts a conservation target, rather than by occupation or affiliation (see Nielsen et al., 2021b).

Actor group – *and how they impact conservation target*	**Example behaviour changes**
Producers and extractors - *harvest or extract conservation target, or produce goods whose generation impacts target*	Stop or reduce harvest of conservation target; produce food or fibre using less damaging method; switch to growing less harmful product
Conservation and environmental managers - *manage all or part of an area of land or sea for conservation*	Adopt or increase management practices which are beneficial for target; stop harmful management practices
Consumers - *use conservation target directly, something whose production impacts target, or interact with target through recreational activities*	Stop or reduce harmful consumption; start or increase beneficial consumption
Manufacturers, transporters and sellers – *supply chain actors who sell goods produced from or otherwise linked to conservation target*	Reduce sales of unsustainably harvested product; promote less damaging harvesting technology
Investors - *provide financial capital for producers and other actors who impact conservation target*	Withdraw or reduce finance for damaging producers; invest in sustainable producers
Policymakers and deliverers – *design or implement policies or rules which influence how other actors impact conservation target*	Introduce beneficial policy; withdraw harmful subsidy; tax harmful behaviour; enforce conservation legislation
Voters - *influence government to change design or execution of environmental and other policies*	Take environment into account when voting; let politicians know
Communicators - *provide information to others about the impacts of their behaviours and how to change them*	Provide information that enhances capability or motivation of any actor to act more sustainably
Campaigners and lobbyists - *petition policymakers and other actors to change their choices and decisions*	Promote more desirable consumption; lobby for change to government policy

Table 3. Classes of behaviour change intervention, with some general sample interventions, and specific examples of conservation and other environmental interventions. Note that real-world interventions often comprise multiple bundled elements which may span several intervention classes.

	Intervention class	Sample of intervention types	Conservation examples
Individual level	**Capability** The physical, psychological, or management resource to perform, modulate, or resist an activity	Training physical, psychological, or management skills; providing behavioural support	Training fishers in using less damaging fishing gear; making new insights in habitat management available to conservation managers
	Motivation Any process that energizes, directs, and sustains behaviour	Communicating social norms; promoting public commitment; providing social comparison; offering behavioural feedback	Inducing a sense of pride in local habitats and species; lobbying policymakers or corporations to promote ambitious conservation action
Population level	**Physical microenvironment** The settings that people use for specific purposes and where they interact directly with objects and stimuli in those environments	Altering availability, position, presentation, or size of products or objects	Increasing vegetarian meal availability in cafeterias; changing the presentation of products to increase salience; altering defaults to lower-footprint settings
	Physical macroenvironment The basic physical and organizational structures and facilities needed for the operation of a society or organization	Increasing availability of public transport; altering functionality of roads	Increasing public transport options to national parks and nature reserves; increasing the energy efficiency of public buildings
	Economic environment The prices of goods and services	Introducing, modifying, or removing taxes, subsidies, and other material incentives	Introducing taxation on ruminant meat; paying farmers to restore natural habitat on their land; removing subsidies for fossil fuels; governments divesting from environmentally damaging industries
	Institutional environment The voluntary and regulatory codes of practice to which public and private organizations must conform if they are to receive support and legitimacy	Introducing, modifying, or removing fines or other material incentives; establishing or altering institutional standards	Creating a protected area; increasing environmental standards for contractors; introducing or increasing fines for undesirable behaviour

Table 4. Matrix showing a representative array of behaviour change interventions proposed for our 12 example threats (Table A1 in online Appendix), classified by intervention class (rows, Table 3) and actor group (columns, Table 2). Shading denotes the overall distribution of 130 proposed interventions across cells: white=0; light green= 1-4; mid-green=5-9; dark green=>9. Note that many ideas for reducing a harmful behaviour in practice require a series of linked interventions. * Asterisks highlight one example: regulating against overnight office lighting to mitigate climate change might first require persuading voters to send a strong motivational message to politicians. For simplicity other linked interventions are not shown.

	Producers and extractors	Conservation and environmental managers	Consumers	Manufacturers, transporters and sellers	Investors	Policymakers and deliverers	Voters	Communicators	Campaigners and lobbyists
Individual level									
Capability	Reducing deforestation by providing husbandry training to Amazonian ranchers who do not deforest	Stemming spread of Florida invasive plants by improving training in weed recognition	Limiting spread of invasive aquatic species by providing clear hygiene instructions to recreational water users	Reducing Caribbean overfishing by providing refrigeration to cut supply-chain waste Controlling invasive lionfish by providing equipment and training for chefs to cook them					
Motivation	Increasing milkweed availability for monarchs through campaign persuading farmers to tolerate "untidy" fields	Enhancing water quality for vendace by motivating water treatment managers via a performance league table	Reducing mangrove conversion by working with an influencer to reduce demand for shrimp Reducing trampling of alpine plants by encouraging climbers to commit publicly to avoiding sensitive routes	Reducing mangrove conversion for hotels via social media campaign persuading travel companies to market more sustainable accommodation options	Reducing mangrove clearance for tourist infrastructure by making scientific case to insurers to increase premiums to hotels in cleared areas	Reducing vulture exposure to diclofenac by persuading politicians to ban its use *Mitigating climate change by motivating policy makers to restrict overnight office lighting	*Mitigating climate change by encouraging voters to lobby politicians to restrict overnight office lighting	Limiting spread of invasive horticultural plants by persuading radio host to run a feature on the damage done by exotic species	Reducing grazing damage to alpine plants by persuading animal-rights groups not to oppose cull of feral goats
Population level									

Physical microenvironment	Reducing vulture exposure to diclofenac by providing farmers an affordable, vulture-safe alternative drug Enhancing water quality for vendace by simplifying the paperwork for farmers participating in catchment management		Reducing litter ingestion by godwits by installing and emptying bins on beaches Limiting spread of invasive mussels by providing boat users with high-temperature cleaning equipment						
Physical macroenvironment			Reducing kittiwake deaths in offshore windfarms by cutting electricity usage through investment in energy-efficient housing						
Economic environment	Increasing milkweed availability for monarchs through business innovation competition for milkweed products		Reducing litter ingestion by godwits by taxing non-degradable packaging	Reducing vulture ingestion of diclofenac by removing patent on alternative, so local companies are incentivised to manufacture it					
Institutional environment	Reducing litter ingestion by godwits by regulating against at-sea disposal of plastics Increasing kittiwake chick survival by reducing quotas for sand-eel fishing		*Mitigating climate change through restrictions on office lighting	Reducing international spread of invasive bivalves by mandating at-sea ballast water exchange by cargo vessels	Reducing Amazon deforestation through regulation restricting the provision of credit to low-deforestation municipalities	Mitigating climate change by reducing incentives to policymakers to oppose action by banning large campaign donations			