POLICY PERSPECTIVE

The past and future role of conservation science in saving biodiversity

David R Williams[1,2] (iD) | Andrew Balmford[3] | David S Wilcove[4]

[1]Sustainability Research Institute, School of Earth and Environment, University of Leeds, Leeds, UK

[2]Bren School of Environmental Science and Management, University of California Santa Barbara, California

[3]Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

[4]Woodrow Wilson School of Public and International Affairs and Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey

Correspondence
David R Williams, Sustainability Research Institute, School of Earth and Environment, University of Leeds, Leeds, LS2 9JT. UK.
Email: d.r.williams@leeds.ac.uk

Abstract

Global biodiversity losses continue despite tremendous growth in the volume of conservation science and many local successes. Research that can achieve conservation science's aims—arresting declines in biodiversity and preventing extinctions—is therefore of ever greater importance. Here, we ask whether conservation science, as currently performed, is progressing in such a way as to maximize its impact. We present a simple framework for how effective conservation research could progress, from identifying problems to diagnosing their proximate and ultimate causes, and from proposing, to designing, implementing, and testing responses. We then demonstrate that for three well-known examples—South Asian vultures, whooping cranes, and bycatch of procellariform seabirds—published studies appear to follow this sequence, with considerable benefits. However, for a representative sample of the wider conservation literature, we find no evidence of such a progression. Instead, the vast majority of papers remain focused on describing the state of nature or on mechanisms directly causing changes, with very little research on designing or implementing conservation responses. This lack of research on the sorts of questions that might most help conservation science deliver its stated mission strongly suggests we will struggle to translate the huge increase in research activity into real-world benefits.

KEYWORDS

albatross, bycatch, conservation action, conservation responses, effectiveness, literature review, research policy, research priorities, threats, vultures, whooping crane

1 | INTRODUCTION

As human populations and per capita consumption continue to grow (Tilman et al., 2017; United Nations, Department of Economic and Social Affairs, Population Division 2019), the loss of wild nature and the benefits we derive from it are accelerating (Brondizio, Settele, J., Díaz, & Ngo, 2019; Ripple et al., 2017; Tittensor et al., 2014). Conserving biodiversity in the face of these increasing human pressures is one of the great challenges of the 21st century and at the heart of the Convention on Biological Diversity's (CBD) Aichi targets (UNEP CBD 2010) and of Sustainable Development Goal 15 (General Assembly of the United Nations 2015).

Since its inception, conservation biology (now more explicitly interdisciplinary and increasingly labeled "conservation science") has been characterized as a mission-oriented discipline aiming to provide the scientific underpinnings to address this challenge (Soulé & Wilcox 1980). In the landmark 1986

book *Conservation Biology: The Science of Scarcity and Diversity*, Michael Soulé (Soulé, 1986) warned that if conservation biology "becomes isolated in the mental world of academia, it will be of little use. Its prescriptions will not be informed by the real-world problems of … the people who are most involved and affected." Three decades on, the enterprise of conservation science (measured by publication rates—Figure S1 in the Supporting Information) is an order of magnitude larger, and we are approaching the reassessment of the CBD's targets. It therefore seems reasonable to ask, as action becomes ever more urgent, how well conservation science research is contributing to the development of "prescriptions" that can address the "real-world problems" facing biodiversity.

We examine this question by mapping the field's development against a simple framework, whereby solution-oriented conservation science emerges from a progressively deeper understanding of the dynamics of threatening processes and towards the design and testing of interventions to address them (Figure 1). Research might start by describing the changing state of nature (say, a change in a species' population size) and then move on (upwards sloping arrow in Figure 1) to identify the proximate mechanism (sensu Balmford et al., 2009) underpinning that change. But problem diagnosis alone is insufficient: to be useful, conservation science needs to support action (Caughley, 1994; Gibbons, Wilson, & Green, 2011). Research should therefore—in collaboration with conservation practitioners and other stakeholders—propose and design responses to undesirable changes, report on their implementation, and test their effectiveness (lower sloping arrow), while continuing to refine our understanding of the threatening mechanism (lower horizontal arrow). However, if targeting the mechanism of change is unlikely to be effective or efficient, research should progress to identifying and understanding the source and ultimate driver of the threat (upper horizontal arrows), and then proposing and designing driver-focused interventions which can be undertaken, monitored, and refined (dashed arrows).

To see if this framework reflects reality, we reviewed the peer-reviewed literature (i.e., excluding non peer-reviewed reports and management documents) pertaining to three well-known examples where targeted research unequivocally helped address real-world problems. In the case of the massive decline of South Asian vulture populations, we found that successful mission-oriented conservation science did indeed follow this pattern. Early papers concentrated on quantifying dramatic population declines in vulture populations (Figure 2a). Establishing the threatening mechanism (incidental poisoning by diclofenac, an anti-inflammatory veterinary drug) took several years, and research has since refined our understanding of how and where this drug enters the vulture food chain. Response-focused work, meanwhile, started once sources of poisoning were identified, and involved (in

sequence) proposing, designing, implementing, and testing a range of interventions, including captive breeding, the provision of uncontaminated carcasses in "vulture restaurants," the identification of a safe alternative to diclofenac, and the establishment of diclofenac-free vulture safe zones. Continued monitoring suggests declines have now slowed, and some populations are beginning to recover (Prakash et al., 2019).

These broad trends—with studies becoming progressively more focused on the sources and underlying drivers of threats; and shifting towards designing, implementing, and testing potential responses—are also characteristic of publications that underpinned the successful conservation of whooping cranes (*Grus americana*) and of procellariform seabirds (Figure 2b, c). The global whooping crane population fell to 15 individuals in a single population by 1938 due to hunting and habitat loss (French, John, Converse, & Austin, 2019). Intensive conservation interventions were implemented, includingthe creation of protected areas, protection from hunting and human disturbance, captive propagation, and the establishment of new populations (French et al., 2019). In each case, conservation actions were supported by intensive monitoring and the testing of new interventions (Figure 2b; Data S1 in the Supporting Information). By the winter of 2016–2017, the wild population had grown to 483 individuals across three populations, although one reintroduction program has been halted due to low levels of success (BirdLife International 2019). Although some procellariform seabirds have long been imperiled by persecution, invasive predators, or intrinsically small ranges, major declines throughout the family were noted in the 1990s (Brothers, 1991). These declines were traced to extensive mortality caused by birds following commercial longlining boats and either grabbing the baited hooks, or being "foul hooked"—with hooks catching the birds' wings or bodies (Brothers, 1991). Intensive research identified the interventions most likely to prevent this bycatch, including using bird-scaring lines behind boats, setting lines underwater, setting lines at night, and using redesigned hooks, and concerted efforts were then made to engage fishers and their management organizations to encourage the use of the most effective interventions, with the most effective measures reducing bycatch by up to 80–100% (Figure 2c; Cox et al., 2007).

In striking contrast to these case studies, we found little evidence that conservation science as a whole is developing a deeper understanding of high-level threats and of conservation responses, or altering its research priorities over time. When we classified a representative sample of 959 articles published over the past 20 years in 20 conservation journals (details in the Supporting Information), we found that nearly half (43%) of the studies merely described the state of nature without linking changes to a threatening mechanism at all, and only 10% linked a mechanism to the source or driver of changes (Figure 3). Moreover, 70% of studies
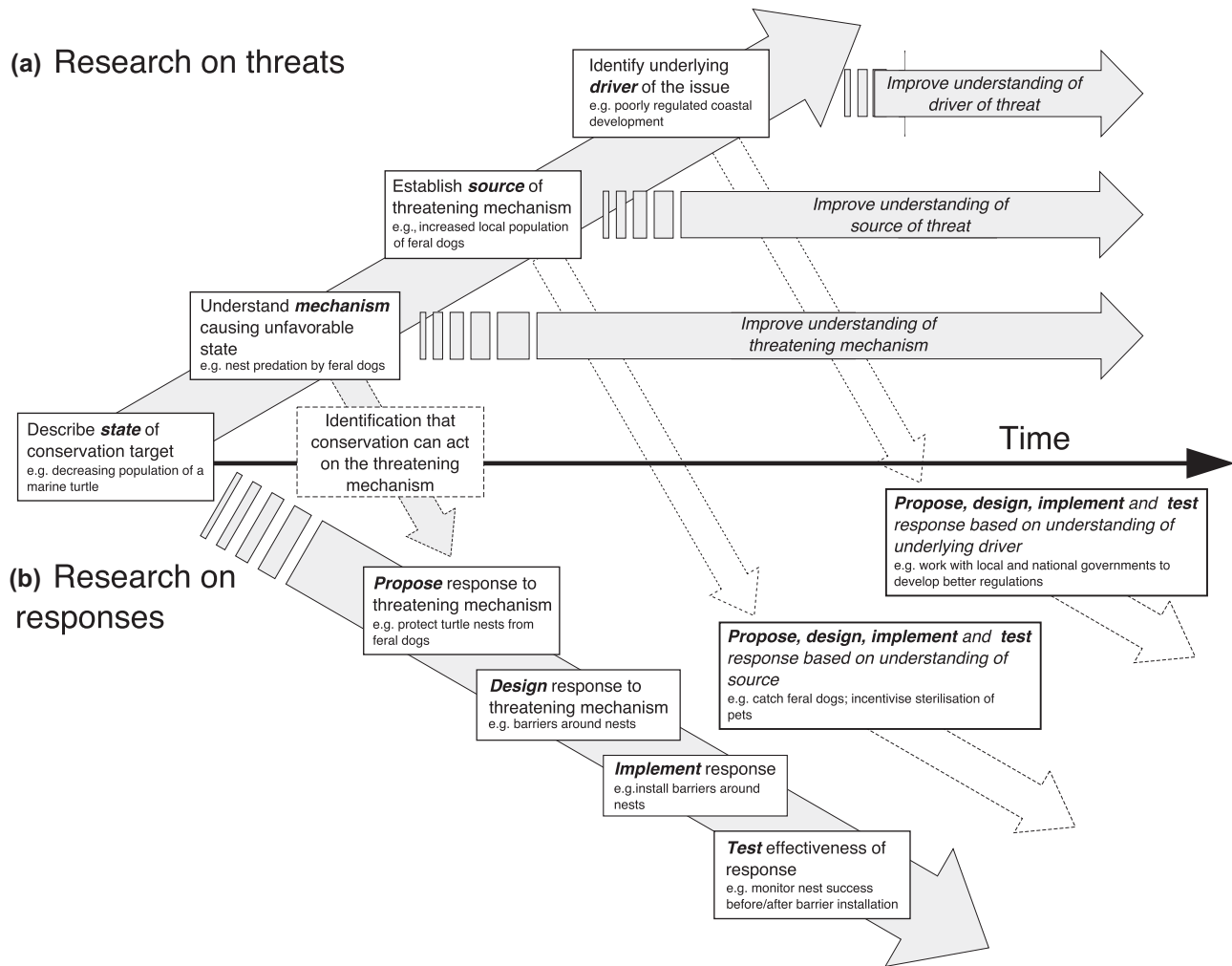
(a) Research on threats

Identify underlying **driver** of the issue
e.g. poorly regulated coastal development

Improve understanding of driver of threat

Establish **source** of threatening mechanism
e.g., increased local population of feral dogs

Improve understanding of source of threat

Understand **mechanism** causing unfavorable state
e.g. nest predation by feral dogs

Improve understanding of threatening mechanism

Describe **state** of conservation target
e.g. decreasing population of a marine turtle

Identification that conservation can act on the threatening mechanism

Time

Propose, design, implement and **test** response based on understanding of underlying driver
e.g. work with local and national governments to develop better regulations

(b) Research on responses

Propose response to threatening mechanism
e.g. protect turtle nests from feral dogs

Propose, design, implement and **test** response based on understanding of source
e.g. catch feral dogs; incentivise sterilisation of pets

Design response to threatening mechanism
e.g. barriers around nests

Implement response
e.g.install barriers around nests

Test effectiveness of response
e.g. monitor nest success before/after barrier installation

FIGURE 1 A research framework for conservation science. A simple framework suggesting how conservation research might progress if it is to deliver prescriptions for addressing real-world problems. Initial characterization of the changed state of a population, community, or ecosystem needs to be followed by diagnosing the mechanism responsible (upwards sloping arrow). This then enables research proposing, designing, implementing, and testing responses to this threat mechanism (lower sloping arrow) and improving our understanding of it (lower horizontal arrow). However, depending on the nature and urgency of the threat, it is often desirable to establish the source of the threat and quickly develop and test responses to it, or to identify, and in due course respond to, the underlying driver(s) (dashed arrows)

did not even propose a response to observed changes. We also found very little evidence that this pattern was changing over time. There were no significant trends in the proportion of studies investigating different levels of threat across years (see the Supporting Information for details). The proportion of studies that failed to describe a response did decrease (from 0.83 to 0.67, chi-squared test for trend in proportions: χ^2 (1, $N = 959$) $= 13.62$, $p = 0.002$) and there were slight, although nonsignificant, increases in the proportion of studies designing and testing responses (from 0.01 to 0.05, and 0.09 to 0.17, respectively; see the Supporting Information for details). The overall proportion of studies examining different levels of threats or responses did not vary across years (chi-squared test of threat category vs. year: χ^2 (12, $N = 959$) $= 15.84$, $p = 0.20$; response category vs. year: χ^2 (16, $N = 959$) $= 23.11$, $p = 0.11$).

2 | IS CONSERVATION SCIENCE ADDRESSING ITS AIMS?

Unlike the literature on South Asian vultures, whooping cranes or bycatch of procellariform seabirds, our wider sample is not a longitudinal assessment of research on a specific issue. We would therefore expect new work on the early stages of threat identification, characterization, and mitigation, to be initiated over time, as new threats are discovered and explored. Nevertheless, if the overall field of conservation science was progressing as proposed in Figure 1, we would still expect to see a growing proportion of research investigating underlying drivers and implementing and testing solutions. The rarity of studies examining the sources and drivers of change implies conservation scientists are not developing an incrementally deeper understanding of the threats affecting wild
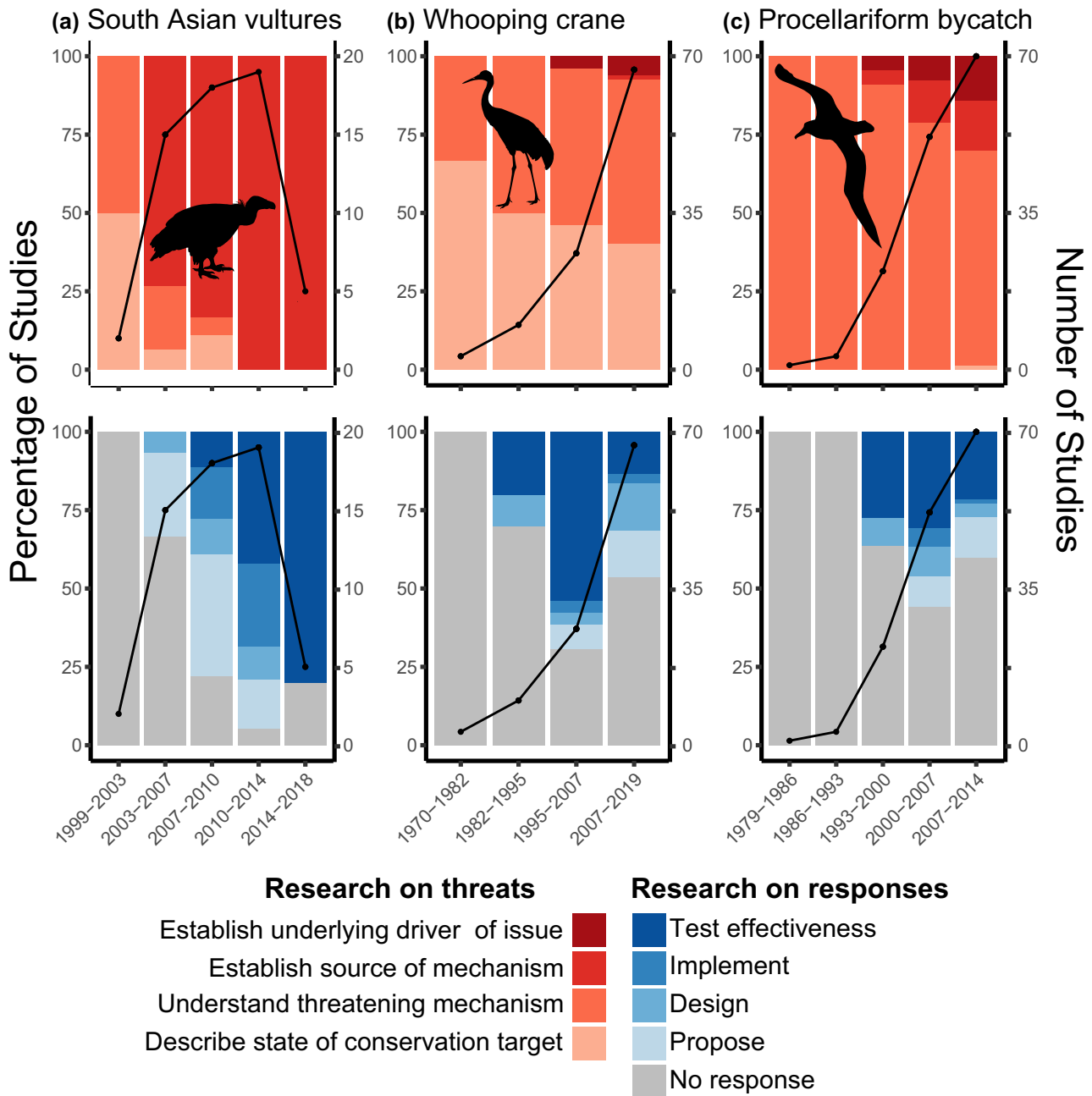
FIGURE 2 Research topics in selected case studies. The number of papers investigating (a) the South Asian vulture crisis, (b) whooping crane conservation, and (**c**) the bycatch of procellariform seabirds over time (black lines) and the percentage investigating different levels of threat and response (shaded bars). Image credits: Birgit Lang, Lauren Anderson and Ferran Sayol.

nature. Moreover, very few studies reached the second step in our response hierarchy of designing workable, socioeconomically realistic interventions—the minimum requirement if conservation science is going to effect change in the real world. Even fewer actually reported on the implementation of conservation actions—the point at which actual conservation can begin.

So why is conservation science seemingly failing to perform the research most likely to safeguard nature? Perhaps the simplest explanation is that these issues are extremely

complex and difficult to research. The state of nature and the mechanisms threatening it can be investigated through ecology—often the field most familiar to conservation researchers (Fisher, Balmford, Green, & Trevelyan, 2009). In contrast, exploring the sources and drivers of those threats, and designing responses to them, requires interdisciplinary research, potentially including economics, political science, human geography, psychology, and many other disciplines. Much has been written on the need for such interdisciplinary research and training (Fisher et al., 2009), and its challenges
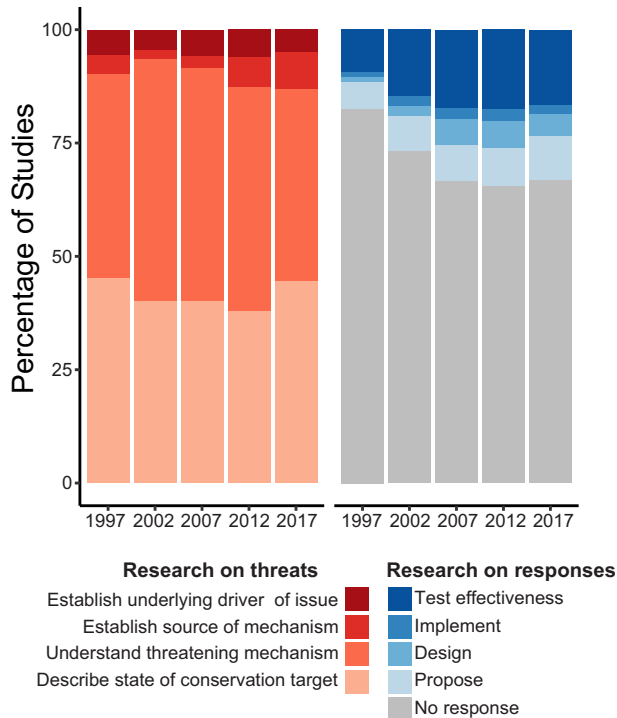
FIGURE 3 Research topics in the wider conservation literature. The percentage of 959 conservation papers sampled from 20 conservation journals that examined different levels of threat and conservation responses, over a 20-year period

(e.g., Pooley, Mendelsohn, & Milner-Gulland, 2014), but our data suggest that conservation science still has considerable progress to make.

Another, non-exclusive, possibility is that the research with the greatest potential benefits for biodiversity may not be well rewarded in academia. There is evidence that the interdisciplinary work this research demands is less likely to be funded (Bromham, Dinnage, & Hua, 2016) and in competitive, single-discipline departments, it may be perceived as less likely to secure promotion and accolades compared to purely ecological studies (Roy et al., 2013). Moreover, interdisciplinary teams are often formed at the behest of government agencies that are focused on solving particular problems, but not necessarily on the peer-reviewed publication of such interventions. The design and implementation of on-the-ground conservation responses are also likely to be locally focused, and hence hard to generalize from, as solutions are dependent on specific socioeconomic and environmental conditions (Waylen, Fischer, McGowan, Thirgood, & Milner-Gulland, 2010). This may reduce the number of citations such research receives, reducing its "impact" in the scientific literature. However, when we tested this idea using our sample of the wider conservation science literature, we found no clear support for the hypothesis that articles investigating higher level threats, or proposing and implementing responses had lower "impact" than other studies—measured either by the

impact factor of publishing journals, or the number of citations received (see the Supporting Information, Figures S2–S4 for details).

These results tentatively suggest fears over the publication payoffs of tackling the drivers of threats or developing effective solutions are misplaced. Nonetheless, the small number of studies that investigated these topics means our findings are preliminary, and there remains the possibility that the most effective conservation studies are inadequately rewarded. We also have no information on papers that are rejected from journals, and it is possible that editorial boards and reviewers are less likely to accept interdisciplinary papers, or those designing and implementing interventions at local scales. However, some journals are actively encouraging studies of this kind (e.g., *Conservation Biology*, Teel et al., 2018), and indeed entire journals are now dedicated to testing the effectiveness of conservation interventions (e.g., *Conservation Evidence*, *Conservation Science and Practice*; Hopkins, Ockendon, & Sutherland, 2015; Schwartz et al., 2019; Sutherland, Mitchell, & Prior, 2012). We also note that our sampling may have failed to capture studies that examine higher level threats and solutions if they are predominantly published in interdisciplinary journals we did not sample (e.g., in environmental economics or industrial ecology). However, we found no evidence of this from reviewing literature on the three conservation case studies we reviewed: studies investigating the sources of threatening mechanisms, and those designing, implementing, and testing responses, were no less likely to be included in the journals we sampled in our wider review than were other studies (chi-squared test of threat category vs. inclusion or not in wider sample: χ^2 (2, $N = 57$) = 0.037, $p = 0.98$; response category vs. inclusion: χ^2 (3, $N = 57$) = 0.20, $p = 0.98$).

3 | ACHIEVING THE AIMS OF CONSERVATION SCIENCE

Not every study can, or should, investigate every step in the framework we describe. Monitoring the state of nature is, on its own, an essential activity for revealing changes (Lindenmayer & Gibbons 2012; Woinarski, Garnett, Legge, & Lindenmayer, 2017), and system-specific studies can reveal very different mechanisms or sources for superficially similar changes. For example, the catastrophic declines in East African vulture populations are, as in South Asia, caused by contaminated carcasses, but linked to retaliatory killing of predators and to ivory poaching (Ogada, Botha, & Shaw, 2016), rather than to veterinary care of livestock. Moreover, conservation intervention may be needed before the full causal chain of threats is understood: swift action established a captive breeding program for California condors (*Gymnogyps californianus*) in the 1980s and likely saved the species

(Walters et al., 2010), while the failure to quickly initiate captive breeding may well have contributed to recent Australian extinctions of a bat, a rodent, and a reptile (Woinarski et al., 2017).

That said, we nevertheless encourage conservation scientists to critically examine their research priorities. Studies have noted that much conservation science is not focused on the most threatened species (Murray, Green, Williams, Burfield, & de L. Brooke, 2015) or serious threats (Di Marco et al., 2017), but we highlight the additional need to think carefully about engaging in research at the right point of the threat and response framework, at the right time. A recent study (Garnett et al., 2019) provides metrics to help researchers understand the state of knowledge of threats and responses. Combining these metrics with our framework could allow conservation researchers to quickly pinpoint where additional research effort could make the most difference.

Ultimately, biodiversity declines are the result of increasing anthropogenic pressures on the environment (Ripple et al., 2017; Tilman et al., 2017; Tittensor et al., 2014), frequently coupled with a lack of decisive governmental action, even when the path forward is clear (Woinarski et al., 2017). The urgency and severity of such pressures accentuate the need for conservation researchers to be as effective and efficient as possible: for many species, there simply is not the luxury of time to edge incrementally towards solutions. Conservation science's response to the South Asian vulture crisis in particular illustrates how a rapid progression of research from identifying changes, to understanding their causes, to designing, implementing, and testing solutions can result in real benefits to biodiversity. We suggest such targeted progressions seem lacking across much of the conservation science enterprise.

We therefore close by offering a challenge to conservation funders and journals: be more supportive of the interdisciplinary and location- and system-specific research required to produce breakthroughs in our understanding of higher level threats, and in our ability to design and execute effective responses. This could involve institutionally supported sabbaticals and leaves-of-absence at institutions actively involved in conservation responses (e.g., NGOs and government departments), to bridge the gap between research and practice, with researchers supporting practitioners to publish details of interventions, as well as monitoring and evaluating progress. Such efforts and their outputs should also be recognized in applications for tenure, promotion, and funding, in a similar way to programs in some U.S. universities that allow tenured faculty to take leaves-of-absence to serve in government posts for 2–4 years without loss of seniority.

To conservation researchers, we offer another challenge: focus on the ultimate goals of conservation science— improving the prospects of wild creatures, the benefits they bestow on people, and the natural habitats they depend on. Conservation science has done much to preserve the natural world in the face of unprecedented pressures and frequent governmental indifference (e.g., Hoffmann et al., 2010), but we believe it can and must do much more if we are to safeguard biodiversity for future generations.

ORCID

David R Williams https://orcid.org/0000-0002-0379-1800

REFERENCES

Balmford, A., Carey, P., Kapos, V., Manica, A., Rodrigues, A. S. L., Scharlemann, J. P. W., & Green, R. E. (2009). Capturing the many dimensions of threat: Comment on Salafsky et al. *Conservation Biology*, *23*, 482–487.

BirdLife International. (2019). *Grubs americana* (amended version of 2017 assessment). In: *The IUCN Red List of Threatened Species 2019. E.T22692156A155547970*.

Bromham, L., Dinnage, R., & Hua, X. (2016). Interdisciplinary research has consistently lower funding success. *Nature*, *534*, 684–687.

Brondizio, E. S., Settele, J., Díaz, S., & Ngo, H. T. (Eds.). (2019). *Global assessment report on biodiversity and ecosystem services of the intergovernmental science—Policy platform on biodiversity and ecosystem services*. Bonn, Germany: IPBES Secretariat.

Brothers, N. (1991). Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation*, *55*, 255–268.

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology*, *63*, 215–244.

Cox, T. M., Lewison, R. L., Žydelis, R., Crowder, L. B., Safina, C., & Read, A. J. (2007). Comparing effectiveness of experimental and implemented bycatch reduction measures: The ideal and the real. *Conservation Biology*, *21*, 1155–1164.

Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besançon, C., Butt, N., … Watson, J. E. M. (2017). Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation*, *10*, 32–42.

Fisher, B., Balmford, A., Green, R. E., & Trevelyan, R. (2009). Conservation science training: The need for an extra dimension. *Oryx*, *43*, 361–363.

French, John, B., Jr., Converse, S. J., & Austin, J. E. (2019). Whooping cranes past and present. In P. J. Nyhus, J. B. French, S. J. Converse, J. E. Austin, & J. h. Delap (Eds.), *Whooping cranes: Biology and conservation* (Chapt. 1, pp. 3–16). New York, NY: Academic Press.

Garnett, S. T., Butchart, S. H. M., Baker, G. B., Bayraktarov, E., Buchanan, K. L., Burbidge, A. A., … Geyle, H. M. (2019). Metrics of progress in the understanding and management of threats to Australian birds. *Conservation Biology*, *33*, 456–468.

General Assembly of the United Nations. (2015). *Transforming our world: The 2030 Agenda for Sustainable Development*. New York, NY: United Nations.

Gibbons, D. W., Wilson, J. D., & Green, R. E. (2011). Using conservation science to solve conservation problems. *Journal of Applied Ecology*, *48*, 505–508.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., … Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, *330*, 1503–1509.

Hopkins, J., Ockendon, N., & Sutherland, W. J. (2015). Our mission to transform conservation practice. *Conservation Evidence*, *12*, 1.

Lindenmayer, D., & Gibbons, P. (2012). *Biodiversity monitoring in Australia*. Canberra, Australia: CSIRO Publishing.

Murray, H. J., Green, E. J., Williams, D. R., Burfield, I. J., & de L.bib31 Brooke, M. (2015). Is research effort associated with the conservation status of European bird species? *Endangered Species Research*, *27*, 193–206.

Ogada, D., Botha, A., & Shaw, P. (2016). Ivory poachers and poison: Drivers of Africa's declining vulture populations. *Oryx*, *50*, 593–596.

Pooley, S. P., Mendelsohn, J. A., & Milner-Gulland, E. J. (2014). Hunting down the chimera of multiple disciplinarity in conservation science. *Conservation Biology*, *28*, 22–32.

Prakash, V., Galligan, T. H., Chakraborty, S. S., Dave, R., Kulkarni, M. D., Prakash, N., … Green, R. E. (2019). Recent changes in populations of critically endangered Gyps vultures in India. *Bird Conservation International*, *29*, 55–70.

Ripple, W. J., Wolf, C., Newsome, T. M., Galetti, M., Alamgir, M., Crist, E., … Laurance, W. F. (2017). World scientists' warning to humanity: A second notice. *BioScience*, *67*, 1026–1028.

Roy, E. D., Morzillo, A. T., Seijo, F., Reddy, S. M. W., Rhemtulla, J. M., Milder, J. C., … Martin, S. L. (2013). The elusive pursuit of interdisciplinarity at the human—Environment interface. *BioScience*, *63*, 745–753.

Schwartz, M. W., Belhabib, D., Biggs, D., Cook, C., Fitzsimons, J., Giordano, A. J., … Runge, M. C. (2019). A vision for documenting and sharing knowledge in conservation. *Conservation Science and Practice*, *1*, e1.

Soulé, M. E. (1986). Conservation biology and the "real world." In M. E. Soulé (Ed.), *Conservation biology: The science of scarcity and diversity* (pp. 1–12). Sunderland, MA: Sinauer Associates.

Soulé, M. E., & Wilcox, B. A. (1980). Conservation biology: Its scope and its challenge. In M. E. Soulé & B. A. Wilcox (Eds.), *Conservation biology: An evolutionary-ecological perspective*. (pp. 1–8). Sunderland, MA: Sinauer Associates.

Sutherland, W. J., Mitchell, R., & Prior, S. V. (2012). The role of "conservation evidence" in improving conservation management, 3.

Teel, T. L., Anderson, C. B., Burgman, M. A., Cinner, J., Clark, D., Estévez, R. A., … John, F. A. V. S. (2018). Publishing social science research in conservation biology to move beyond biology. *Conservation Biology*, *32*, 6–8.

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*, 73–81.

Tittensor, D. P., Walpole, M., Hill, S. L. L., Boyce, D. G., Britten, G. L., Burgess, N. D., … Ye, Y. (2014). A mid-term analysis of progress toward international biodiversity targets. *Science*, *346*, 241–244.

UNEP CBD. (2010). Decision adopted by the conference of the parties to the Convention on Biological Diversity at its tenth meeting.

United Nations, Department of Economic and Social Affairs, Population Division. (2019). *World Population Prospects 2019*.

Walters, J. R., Derrickson, S. R., Michael Fry, D., Haig, S. M., Marzluff, J. M., & Wunderle, J. M. (2010). Status of the California condor (*Gymnogyps californianus*) and efforts to achieve its recovery. *Auk*, *127*, 969–1001.

Waylen, K. A., Fischer, A., Mcgowan, P. J. K., Thirgood, S. J., & Milner-Gulland, E. J. (2010). Effect of local cultural context on the success of community-based conservation interventions. *Conservation Biology*, *24*, 1119–1129.

Woinarski, J. C. Z., Garnett, S. T., Legge, S. M., & Lindenmayer, D. B. (2017). The contribution of policy, law, management, research, and advocacy failings to the recent extinctions of three Australian vertebrate species. *Conservation Biology*, *31*, 13–23.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.