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REVIEW AND SYNTHESIS

Examining Human-Nature Relationships Through the Lens of Reciprocity: Insights from Indigenous and Local Knowledge

Cultural keystone species as a tool for biocultural stewardship. A global review

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Abstract

1. The cultural keystone species (CKS) concept (i.e. 'species that shape in a major way the cultural identity of a people' as defined by Garibaldi and Turner in 2004) has been proposed as part of a common framing for the multiple entangled relationships between species and the socioecological systems in which they exist. However, the blurred and prolific definitions of CKS hamper its univocal application. This work examines the current use of the term CKS to reconcile a definition and explore its practical applications for biocultural stewardship.
2. We ran a search for the words 'cultural' AND 'keystone' AND 'species'. Our search was limited to peer-reviewed articles published in English between 1994 and 2022 (inclusive) and was conducted using Google Scholar, PubMed, Scopus and Web of Science. We extracted and analysed bibliometric information as well as information on (i) the CKS components, (ii) humans' support for CKS and (iii) the definitions of CKS.
3. From the 313 selected documents, the CKS concept appears to be increasingly accepted, as evidenced by a growing corpus of literature. However, the absence of a systematic and precise way of documenting CKS precludes global cross-cultural comparisons.
4. The geographical distribution of authors using the concept is biased. We found that 47% of all the CKS reported and 38% of the works identified in our review were located in North America.
5. Beyond 'supporting identity', several other of nature's contributions to people are associated with the CKS definitions. However, the contributions of the

For affiliations refer to page 9.

sociocultural group to the survival and conservation of the CKS (i.e. stewardship) are made explicit only in one-third of the documents reviewed.

6. To advance biocultural stewardship as a conservation paradigm, we suggest (a) defining CKS as an indissoluble combination of a non-human species and one or more sociocultural groups; (b) acknowledging that species and sociocultural group relations should be classified in a continuum, according to gradients of relationship intensity; and (c) explicitly acknowledging the reciprocal relationships between sociocultural groups and species.

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KEYWORDS
biodiversity, conservation, Indigenous People and Local Communities, local ecological knowledge, nature's contributions to people, reciprocity, socioecological systems

1 | INTRODUCTION

Efforts to address biodiversity decline are often approached through initiatives that overlook the indirect drivers and socio-economic-political consequences of conservation (e.g. Brockington, 2002; Musavengane & Leonard, 2019; Sanborn & Jung, 2021), resulting in ineffective conservation initiatives, particularly when considering their long-term outcomes and implications (Catalano et al., 2019; Díaz et al., 2019). This is the case, for example, of conservation initiatives that restrict access to nature or ignore the ecological relationships and knowledge held by Indigenous Peoples (IP) and Local Communities (LC)[1] who have often long histories of interaction with many landscapes (Armstrong et al. in this special issue; Hu et al., 2020; Kor et al., 2023; Sze et al., 2022; Zafra-Calvo & Geldmann, 2020). These initiatives (sometimes referred to as 'fortress conservation') consider IP and LC as a threat to conserving biodiversity, despite the growing evidence that many areas managed by people for millennia have resulted in biodiversity-rich areas (e.g. Rai et al., 2021). Global conservation agreements prioritize biocentric approaches, such as the protection of biologically threatened and endangered species, but largely ignore ethnotaxa (biological entities recognized by a sociocultural group which 'not necessarily correspond to a biological species from a taxonomic point of view'; Berlin et al., 1966; de Albuquerque et al., 2011, p. 869) and the reciprocal relationships that IP and LC have with them (e.g. Lamb et al., 2023). While strict biodiversity protection continues to be popular, an increasing corpus of research shows that most biodiversity is hosted in areas owned or managed by IP and LC under customary systems of governance and use (Gadgil et al., 1993; Garnett et al., 2018; Gorenflo et al., 2012; M'sit et al., 2021; Pironon et al., 2024). For instance, through their dynamic and locally adapted knowledge systems, IP manage 37% of all terrestrial protected areas and ecologically well-conserved landscapes where observed biodiversity declines were less rapid than lands managed under other systems (Díaz et al., 2019; Garnett et al., 2018; O'Bryan et al., 2021; Reyes-García et al., 2022).

An alternative approach to tackling biodiversity loss is biocultural[2] stewardship. The concept of biocultural stewardship emphasizes two important ideas: (1) biological and cultural diversity are interdependent, tied together via their coexistence, coevolution and common threats (Brechin et al., 1993; Gavin et al., 2015; Rozzi, 2013); and (2) biodiversity stewardship can be achieved through multiple pathways, not only through strict biodiversity protection (Lukawiecki et al., 2022; Wall et al., 2023). While biocultural stewardship has existed within many customary institutions for a long time, it is currently gaining momentum among academics and policymakers.

Recently, it has been proposed that the concept of 'cultural keystone species' (CKS) could be globally operationalized as one potential pathway towards biocultural stewardship (Reyes-García et al., 2023). The CKS concept was inspired by Paine's (1969) use of the term 'ecological keystone' and it was first defined by Garibaldi and Turner (2004) as 'culturally salient species that shape in a major way the cultural identity of a people, as reflected in the fundamental roles these species have in their diet, materials, medicine, and/or spiritual practices'. Under this definition, the term CKS captures the relationships between specific societies or groups of people and their environment, through species that play outstanding roles in their culture.

Clark et al. (2021) proposed that the CKS concept can contribute to biocultural stewardship thinking and action by linking cultural and environmental perspectives (e.g. offering a common framing for the multiple, entangled, reciprocal relationships

[1]"Individuals and communities who are, on the one hand, self-identified as indigenous and, on the other hand, are members of local communities that maintain intergenerational connection to place and nature through livelihood, cultural identity and worldviews, institutions and ecological knowledge."(IPBES https://www.ipbes.net/glossary-tag/indigenous-peoples-and-local-communities).

[2]We acknowledge that the term 'biocultural' bears disparate definitions across academic traditions and thus could be misunderstood (Franco, 2022). Here, we define 'biocultural stewardship' as 'conservation actions made in the service of sustaining the biophysical and sociocultural components of dynamic, interacting and interdependent socioecological systems' (Gavin et al., 2015).

between species and the socioecological systems in which they exist). While the species' contributions to people are intrinsically embedded into the CKS definition, how people care about and support these species has so far largely been overlooked by scholars and policymakers. Nevertheless, integrating IP and LC perspectives in conservation and more generally in the current global ecological crisis is part of the needed transformative changes which imply rebalancing power dynamics to avoid inequalities (Fernández-Llamazares et al., 2021; Arias-Arévalo et al., 2023; Scheidel et al., 2023; Shackleton et al., 2023). Yet these aspects could be crucial in maintaining biocultural diversity. Indeed, when a species not only provides biophysical contributions, but also provides symbolic, linguistic and/or other cultural values (as summarized in the term 'nature's contributions to people'[3]), such species is often carefully managed by a combination of institutional, social and political actions that draw on Indigenous and local knowledge (Rozzi, 2013). Therefore, identifying and recognizing these management actions as a form of reciprocity between people and other species could facilitate bottom-up approaches to empower environmental stewardship by IP and LC and lead to more effective biodiversity conservation (Dawson et al., 2021; Petelka et al., 2022; Rozzi, 2013; Ulate et al., 2018).

Further developing the CKS concept in biocultural stewardship has been hampered by at least three challenges: (1) the varying use of the concept by researchers, IP and LC, (2) geographical, cultural and/or disciplinary biases in CKS studies and (3) ineffective bridging of the divide between academic research and on-the-ground implementation. The original definition by Garibaldi and Turner (2004) has received several criticisms (e.g. Davic, 2004; Nuñez & Simberloff, 2005; Platten & Henfrey, 2009). For instance, Petelka et al. (2022) wondered how CKS can be distinguished from species that are merely culturally or economically important. In that sense, several authors have called for a clearer and quantifiable definition of CKS to avoid misinterpretation errors (e.g. Coe & Gaoue, 2020; Qingwen et al., 2022). Other authors have called for the use of 'culturally important species' (Freitas et al., 2020) as a less restrictive term which has been increasingly adopted in recent literature (Qingwen et al., 2022; Reyes-García et al., 2023; Uprety & Asselin, 2023), although it could downplay a species' role in determining a culture's vitality. New terms with partially overlapping concepts (e.g. 'biocultural keystone species' [Jacques-Coper et al., 2019] and 'ethnobiological keystone species' [Ellen, 2006]) have also emerged. The lack of an operationalizable definition of CKS leads to conflicting interpretations of the concept and limits the comparability of studies within this field. Elucidating the definition of CKS will facilitate the use and application of the concept in conservation policies and actions.

In this context, the overarching goal of this research is to examine the current use of the term CKS to cohere its definition and explore its practical applications for biocultural stewardship. We do so through three specific aims:

- To illustrate the use of the CKS concept in the English-language literature through a bibliometric analysis.
- To analyse the occurrence in the literature of species considered culturally keystone and of sociocultural groups holding CKS.
- To document any evidence of reciprocal relationships between species and the sociocultural groups for which they are culturally keystone, the defining characteristics of CKS according to the published literature and potential shortcomings and challenges for its application in biocultural stewardship.

On the basis of the above, in the last section of this paper, we propose an operationalizable definition of CKS that can be used to foster biocultural stewardship.

2 | METHODS

2.1 | Data collection and analyses

In January 2023, we performed a systematic mapping study with the words 'cultural' AND 'keystone' AND 'species' as keywords. Our search was limited to peer-reviewed articles published in English between 1994, when it was first mentioned (Nabhan & Carr, 1994), and 2022 (inclusive) and it was conducted using Google Scholar, PubMed, Scopus and Web of Science. It resulted in 1251 documents across the four databases.

We removed duplicate documents, documents in languages other than English, websites and book reviews. We screened the resulting 983 documents and further excluded those that did not report the term 'cultural keystone species'. For example, some publications assessed ecological keystone species and discussed their cultural implications but did not directly address their interconnection. From this screening, we obtained 313 documents which we subjected to further analysis. Of these, 203 documents reported examples of CKS (Figure 1) and 110 documents addressed the CKS concept without referring to species or sociocultural groups.

To document the use of the CKS concept in the literature we clustered publications into three groups:

- Group 1 included publications mentioning one or more species considered CKS for a specific sociocultural group;
- Group 2 included publications that used the term 'cultural keystone species', but the publication did not reference any specific species;
- Group* included documents with incomplete information (e.g. missing scientific names of species or a specific reference to the sociocultural group for which the species is keystone) or which cited CKS already documented in the database without further additions.

[3]"Nature's contributions to people (NCP) are all the contributions, both positive and negative, of living nature (i.e. all organisms, ecosystem, and their associated ecological and evolutionary processes) to people's quality of life'. IPBES Glossary (n.d.).

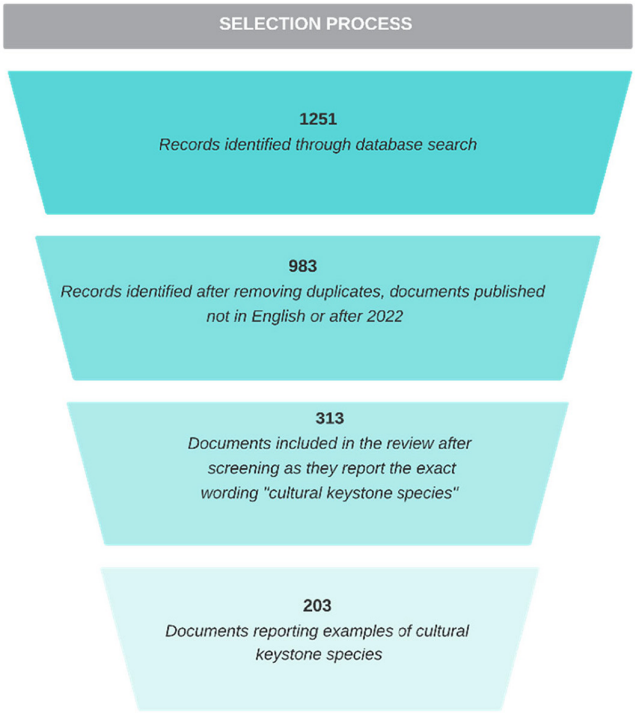

FIGURE 1 Documents selection process of the articles mentioning the wording 'cultural keystone species' included in this literature review.

From the reviewed documents, we extracted, coded and analysed: (i) bibliometric information (i.e. year of publication, first author institutional affiliation, co-authors' first institutional affiliation); (ii) information on the CKS components (i.e. species name, sociocultural group name, location of the CKS); (iii) evidence of people's support for or management of the CKS; and (iv) information of the characteristics defining a CKS (i.e. excerpts including any definition of CKS, presence of the reference to Garibaldi and Turner (2004)). See Appendices 1 and 2 for further details about methods. We also calculated the annual growth rate in the number of publications about CKS since 2003 using log-linear regression (exponential growth rate, % per year) with R. We considered species and sociocultural groups as indissoluble components of a CKS. Missing data on the constituents of a CKS (e.g. scientific names when popular names were reported) were complemented with further literature research. We identified most CKS (95%) by their scientific names, at least at the family level. Six documents did not provide enough information to identify the species, so we contacted the corresponding authors, who provided the scientific names of 20 CKS ambiguously identified in the publications. We excluded the two documents for which we could not identify the scientific names of the species and we did not obtain a response.

We used language, a common proxy for culture, to categorize different sociocultural groups (Kirby et al., 2016) relying on the Ethnologue 2022. Missing data on sociocultural groups (e.g. missing codes of the group's main language) were complemented with secondary information by looking for referenced documents within the documents or additional literature. We excluded 20 documents because the sociocultural group that considers the species as CKS could not be identified.

3 | RESULTS

Of the 313 documents reviewed and published since 1994 that mention the term CKS, 110 (35%) used the concept in the narrative but did not provide any example of a CKS. Several documents mentioned that CKS were an important (or central) tool for conservation but did not include specific information from a case study. For instance, Lyver et al. (2017, p. 99) argue that 'loss of these opportunities and practices, especially around cultural keystone species (Garibaldi & Turner, 2004), has the potential to damage the cultural integrity of the community irreparably'.

A total of 174 articles (56%) included the name of the species and the sociocultural group(s) who consider it culturally keystone. For instance, Pearson et al. (2023, p. 357) claimed that 'For Wabanaki peoples, black ash (*Fraxinus nigra*) is considered to be a cultural keystone species due to its historical role in basketry tradition and associated origin stories. The loss of ash would result in substantial economic, cultural, and spiritual impacts on tribal communities (Voggesser et al., 2013)'.

3.1 | Bibliometric analysis

The year-wise analysis suggests that there is a growing number of published documents using the term CKS (Figure 2). The analysis revealed that since 2003, the rate of publication increased by about 1.54 documents per year ($p < 0.001$). The annual growth rate of publication, modelled as an exponential growth rate, was about 13.6% annually ($p < 0.001$).

The 203 documents with complete information on species and groups were written by 753 authors. Most authors (321) were based in North America (189 in the USA and 132 in Canada), 134 in Europe (53 in the UK, 17 in France and 11 in Germany), and 106 in Oceania (58 in New Zealand, 42 in Australia and 6 in Fiji; Figure 3; see also Appendix 1 for related methodology). Fewer authors are based in Asia ($n = 68$), Central and South America ($n = 62$) and Africa ($n = 40$).

The analysis of the author's institutional affiliations suggests that authors working on the topic are mostly researchers in the natural sciences ($n = 502$), followed by researchers working in the humanities ($n = 87$; see Appendix 2 for methods used to classify them). There is a limited number of community members and members of civil society organizations ($n = 59$), who represent about 8% of all the authors in documents analysed in this study (see Appendix 1 for details on classification).

Similarly, 70% of the first authors were mainly affiliated with life sciences departments ($n = 136$). Of the remaining, 13% were affiliated with humanities ($n = 27$), 2% with economy and policy ($n = 5$) and only 1% with community members/organizations ($n = 3$). The affiliation of the remaining 14% was not specified. Authors affiliated with

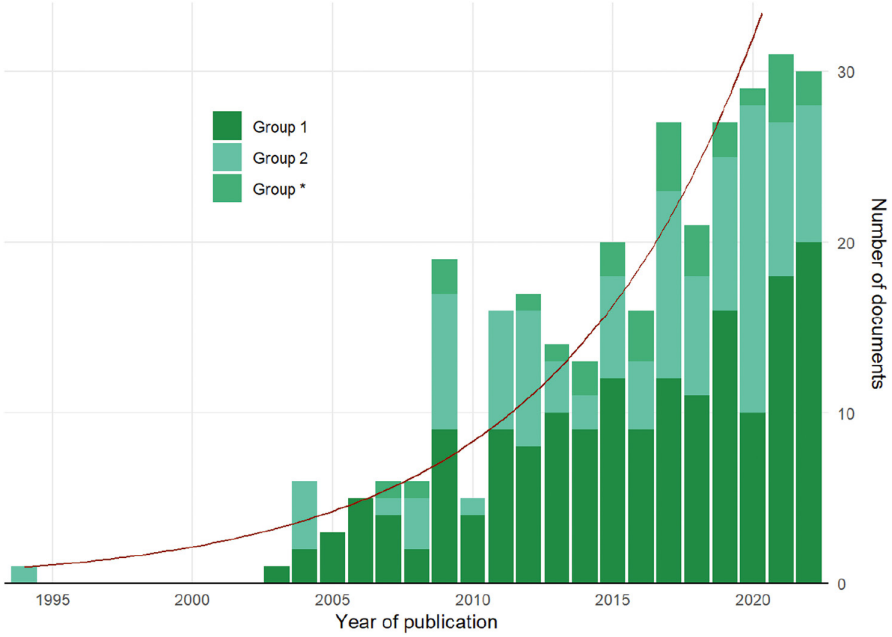

FIGURE 2 Temporal trends in the number of publications per group ($n = 313$). Group 1 provides examples of CKS ($n = 174$); Group 2 only mentions the CKS concept ($n = 110$); Studies in Group * were excluded from CKS analysis due to incomplete data or repetitions ($n = 29$). In the smaller box the line obtained with the regression analysis.

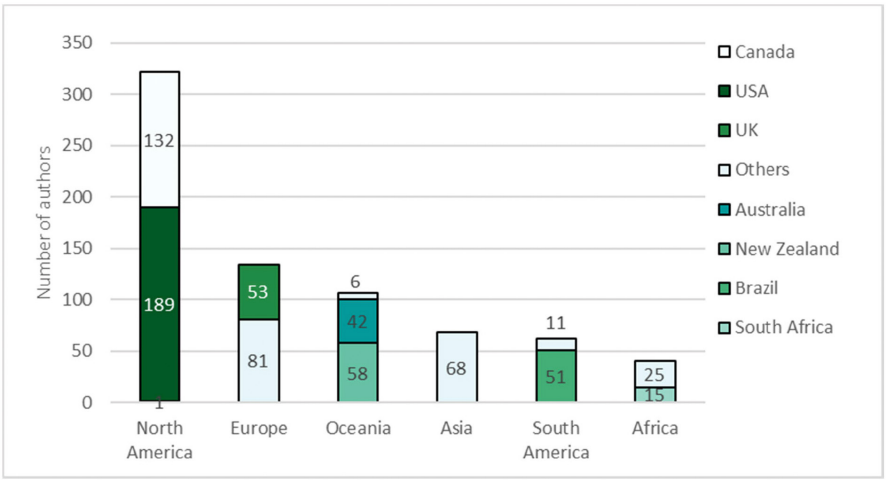

FIGURE 3 Number of authors of publications included in the literature, per continent of their primary affiliations ($n = 203$ articles and 753 authors; see Appendix 1 for methods used).

community organizations included a member of the Swinomish Tribal Community (USA), a member of the Ekuri Community (Nigeria), and a member of the Australian organization 'Northern Land Council', which assists Aboriginal peoples in the Top End of the Northern Territory to acquire and manage their traditional lands and seas.

3.2 | Components of CKS and gaps

In the reviewed documents, we identified 655 CKS, of which 56% were plants ($n = 364$), 44% were animals ($n = 286$), and <1% ($n = 4$) were fungi. A total of 308 distinct species were reported, as some species were culturally keystone to multiple sociocultural groups. Information on CKS referred to 245 distinct groups belonging to 55 linguistic families.

CKS were mainly reported in North America (47%), followed by Asia (20%) and Oceania (15%). We found 25% of all the identified CKS in the USA ($n = 162$ and 15 shared with Canada), followed by Canada 20% ($n = 131$ and 15 shared with the USA) and Australia 9% ($n = 61$). One hundred ninety-nine CKS were reported in the Greater Pacific Northwest including Western USA and Canada. Seventy articles (34%) did not fully report on the components of CKS considered in this review. In particular, 39 articles (19%) did not include scientific names, which are crucial for the correct identification of species, and 42 articles (21%) mentioning 166 CKS did not specify to which specific sociocultural group the species was culturally keystone. For instance, Harding et al. (2022) indicated that salmon is a CKS in North America, for which it was impossible to identify any specific sociocultural group.

3.3 | CKS contributions to people

Out of the 203 articles which reported a CKS, 92 (45% included a definition of CKS and 111 (55%) did not). Seventy-eight per cent of the 203 articles ($n = 159$) cited the work of Garibaldi and Turner (2004).

TABLE 1 Definition of CKS including nature's contributions to people, according to reviewed literature ($n = 203$).

Definitions of CKS reported in the documents included in our literature review	Main nature's contributions to people	# of documents
Species that are culturally salient, outstanding, disproportionately large, fundamental species to a sociocultural group/culture	Food and feed; Materials, companionship and labour; Medicinal, biochemical and genetic resources; Learning and inspiration; Physical and psychological experiences; Supporting identities	64
Species that shape in a major way the cultural identity of a people	Supporting identities	39
Species that are irreplaceable and essential to a sociocultural group and if removed would result in a detrimental impact on their cultural identity	Food and feed; Materials, companionship and labour; Medicinal, biochemical and genetic resources; Learning and inspiration; Physical and psychological experiences; Supporting identities	16
Multi-purpose species	Maintenance of options	4
Species on which people depend for their livelihood	Food and feed; Materials, companionship and labour; Energy; Medicinal, biochemical and genetic resources	2
Species with a high symbolic value for people	Learning and inspiration; Physical and psychological experiences; Supporting identities	2
Species that form a complex incorporating several tangible and intangible system elements	Maintenance of options	2

Of the 91 documents that provide a definition, 70% refer to CKS as species that are culturally salient, outstanding or fundamental to a sociocultural group or culture. Another common defining argument, often added to the previous one, is that CKS shape in a major way the cultural identity of a people. Table 1 summarizes the different and often overlapping characteristics that define CKS in relation to nature's contributions to people. The documents reviewed included four additional definitions of CKS. Ianni et al. 2014 defined CKS as 'species that are used intensively'; Saylor et al. 2017 defined them as species that 'form the contextual base of environmental management decisions'; Barnhill-Dilling and Delborne 2019 defined CSK as species that 'feature centrally in subsistence and spiritual practices of a culture'; and Djoudi et al. 2022 defined them as species 'known to be essential to maintaining cohesive social relationships within a social-ecological system'.

In addition to the definitions, 18 documents stated that the concept of CKS can contribute to developing strategies for species conservation, management and restoration. Four documents mentioned that CKS play an important role in the transmission of traditional ecological knowledge. Finally, two publications pointed out that CKS frequently interact with each other, forming a cultural grouping like a keystone guild (Garibaldi & Turner, 2004; Wilsey & Nelson, 2008).

3.4 | People's stewardship of CKS

Of the 203 documents (consisting of groups 1 and *), 70 provided information about people's practices to favour the presence, abundance and/or persistence of the species which are culturally keystone to their culture. Forty-eight documents referred to the biophysical dimension, including selective harvesting, habitat improvement and other management practices. For example, as mentioned in the case of the Quinault People of Washington State, NW, USA: 'When digging bulbs [of camas (*Camassia quamash*)] from the fire-cleared ground, harvesters intentionally aerated the soil, harvested selectively, and returned young bulbs to the ground to mature at a later date' (Deur & James, 2020, p. 224). Another example is provided by Fawzi et al. (2016, p. 6) among the Marsh Arabs and their relationship to reeds (*Phragmites australis* within their ecosystem in Southern Iraq: 'Traditional resource management included selective harvesting and burning of reeds on a seasonal and phenological basis, multiple-species management (reeds, fish, waterfowl, bird eggs, and rice), burning senescent vegetation to stimulate new growth, spatial and temporal restriction of fish harvest during spawning, and landscape patch management. These management practices were beneficial for reed growth and biomass production, maintained diverse patch dynamics, and increased microhabitat diversity'.

Twenty-eight documents mentioned how people's stewardship of the species is encoded in the language and symbolism of a culture. An example is provided by IP of the Murray-Darling Basin, where an interviewee reportedly claimed 'I can't speak in great detail about our spiritual connection to it other than to say that it is very deep. Murray cray [*Euastacus armatus*] are part of closed ceremonies, part of our secret business. It was also a very well-loved food source, but there were restrictions on who could eat it, and who could not eat Murray crays. It was a big part of our culture' (Noble et al., 2018, p. 1427).

Finally, 26 documents reported institutional, social or political contributions to protecting and managing CKS. These contributions include norms to maintain and support a CKS, sometimes for centuries and millennia, as in the case of salmon and Tsimshian peoples of British Columbia, Canada, as suggested by archaeological evidence (Efford et al., 2023). Thompson et al. (2020, p. 1095) discussed the examples of salmon (*Oncorhynchus* spp.) and Gitga'at peoples 'where traditional harvesting practices and governance has built in checks and balances to guide sustainable resource use, including harvest

protocols and management rights and responsibilities of clan and house leaders (Gitga'at First Nation, 2011)'.

4 | DISCUSSION

Our analysis brings three main insights. First, the concept of CKS appears to be increasingly used, as evidenced by a growing corpus of literature drawing around the idea of CKS (Figure 2). However, the geographical distribution of researchers using the concept and of species identified as CKS are biased. Thirty-eight per cent of the studies using the concept and 47% of all the CKS documented are geographically concentrated in North America, where the concept originated. Second, no systematic and precise way of documenting CKS exists that would allow for global cross-cultural comparisons. Moreover, there is a tendency for authors to not include precise information regarding CKS scientific names and/or sociocultural groups. Finally, while several of nature's contributions to people are embedded in the CKS definitions being used, practices of reciprocal care of CKS by people (contemplated in some of the worldviews embraced by the NCP; Díaz et al., 2018) are made explicit only in one-third of the articles.

Before discussing these results, we would like to acknowledge the important limitations of our work. First, the collection of information for this study is limited by language and terminology issues. We intentionally limited our bibliographic search to publications in English as it is the dominant language in scientific publications. We are aware that studies published in other languages have made a significant contribution to scientific knowledge (Amano et al., 2023; Angulo et al., 2021). However, we also place on record the challenges of the literal translation of the term CKS into another language as well as our inability to conduct a review in each of the languages in which CKS literature may have been published. In addition, our work focuses on CKS, but the literature includes several other similar concepts (e.g. 'culturally important species', 'biocultural keystone species') that might capture the same or very similar ideas (e.g. Campbell et al., 2022; Goolmeer et al., 2022). However, we considered only CKS because they were more clearly defined by Garibaldi and Turner (2004). Further research should also address these similar concepts. A second bias is related to the documentation gaps that result in many species and sociocultural groups being excluded in bibliographic reviews which may be mirrored in the results of this review (Cámara-Leret & Dennehy,2019). These first two biases might, to a certain extent, explain the geographical patterns reported in our results. The third bias of this work arises from the classification of sociocultural groups, an important step for operationalizing the CKS concept. We acknowledge that our approach is inherently reductionist and does not consider intracultural variability; however, it widens previous works by systematically acknowledging the indissoluble relation between a species (identified with its scientific name) and a sociocultural group (identified with its language ISO code), and to our understanding, this combination represents a suitable tool for a global analysis. Thus, some of the languages mentioned in the documents reviewed did not have an ISO code, and we used the code for the larger linguistic group. In many cases, people were bilingual, in which case we used the local language predominant in the study area to categorize the group. Moreover, we found cases in which the species was culturally keystone only to some people within the group. This, for example, was the case of *Betula pubescens* var. *litwinowii* and *Betula pendula* considered CKS for Georgian, Turkish and Russian pastoralist speakers of the Georgian-Turkish border, although those species seemed not to carry the same cultural value for people in the area practicing other livelihoods (Kazancı et al., 2021).

The major finding of this work is that there is a growing academic uptake of the concept of CKS. Although there has been a general increase in publications in the past decade, the rate of increase in CKS literature (between 2016 and 2022) has been 3.3% faster than the annual growth recently assessed by Hanson et al. (2023). We also note that as much as one-third of the documents reviewed use the concept as something already established in the literature, with only two-thirds discussing specific examples of CKS. Despite the seemingly growing interest, our analysis reinforces the results of Coe and Gaoue (2020) regarding the uneven spatial distribution of researchers and evidence regarding CKS. The CKS concept appears to be mainly used by authors located in North America and Oceania, with the documented instances of CKS similarly distributed. One plausible explanation of this geographically biased distribution relates to the fact that the original coining and definition of the concept CKS arose in a North American context and that our search was in English. For example, as many as 51 documents in our search focused on the Greater Pacific Northwest, particularly British Columbia, Canada, where the original proponents of the concept, Ann Garibaldi and Nancy Turner, are based. In addition to Canada, there are also many CKS studies in Aotearoa-New Zealand, Australia, and the USA, probably because of the e numerous cultural, institutional and academic connections between Indigenous communities and Indigenous Studies research across these countries. Although the term CKS might be effectively applied in other geographical contexts, our focus on publications in English likely limited our ability to detect potential uptake in other geographic regions. Moreover, we acknowledge that some IP and LC might not recognize the relevance of the CKS framework as a tool for biocultural stewardship or restoration in their cultural context, and thus not reference it. For instance, an Anishinaabe *kwe* claimed, 'In my culture all species are valuable, we do not believe that one is more important than another, they are all relatives'. While we encourage wider adoption of the concept of CKS to reconcile conservation with cultural priorities and design biocultural stewardship strategies, this adoption should not be forced in contexts where they may not be culturally relevant or suitable.

The second finding of this work is that we continue to lack a systematic and precise way of defining CKS, as already documented by Petelka et al. (2022). Forty-five per cent of the documents reviewed do not include a definition or an explanation of how the species

were identified. This omission results in a high number of articles which likely interpret the concept of CKS in different ways. Among those who use a definition, Garibaldi and Turner's (2004) definition of CKS is the most frequently cited; however, the use of the term is not consistent with the basic elements of the original CKS concept. For example, while authors widely accept that the concept of CKS directly refers to a biological species, some studies do not associate the CKS with a sociocultural group, as also pointed out by Reyes-García et al. (2023). This inconsistent use of the CKS concept underlines a key gap in its different understandings, including the fact that some authors might understand the concept not as 'relational' but utilitarian, underlying the material aspect more than the contribution of the species to the identity of the associated cultural group. Differences in the way the CKS concept is applied could reflect different perspectives, backgrounds and sensitivities about humans, Nature, and how they relate. Nevertheless, in such an interdisciplinary field, we would advocate for scholars in life sciences to be more sensitive to human dimensions of CKS, and for those in social sciences and humanities to be more precise about scientific names, as this could strengthen our understanding of biocultural diversity (Molnár & Babai, 2021; Peruzzi, 2020).

The third finding of this work refers to the lack of attention being paid to people's stewardship of CKS. Being so critical to a sociocultural group, CKS and their habitat are closely managed or protected from degradation to ensure their continual presence of CKS, thus establishing a reciprocal contribution between the two elements peoples and the associated salient species (Thompson et al., 2020; Whyte et al., 2016). We found that 41% of the documents mentioned the CKS contributions to people, whereas people's stewardship of CKS was often disregarded. Indeed, only 34% of the documents reporting CKS contributions to people explicitly highlight the mutual connections between species and the sociocultural group for which it is culturally keystone. Thus, two-thirds of the documents do not clearly state the reciprocity of the relationship between the sociocultural group and the CKS, an aspect that, while not included in the original definition of a CKS, could be crucial for operationalizing the concept in biocultural conservation initiatives (e.g. Goolmeer et al., forthcoming, regarding culturally important species). This is even though reciprocity between Nature and people has recently increased in recognition in some academic and policy frameworks (e.g. Comberti et al., 2015; Díaz et al., 2015, 2018; Ojeda et al., 2022). Indeed, the concept of reciprocity has been variously described, including stewardship practices (e.g. Garibaldi & Turner, 2004), co-production between anthropogenic assets and nature in the creation of nature's contributions to people (Díaz et al., 2018), services to ecosystems (Comberti et al., 2015), people's care and support of nature (Larson et al., 2023; Matuk et al., 2020), or reciprocal contributions between people and nature (Ojeda et al., 2022), among others. Recognizing the reciprocal relationships between the specific IP and LC and the ethnotaxa is critical to co-designing effective management strategies for biological and cultural diversity stewardship (Comberti et al., 2015; Thompson et al., 2020).

4.1 | A proposal to operationalize the concept of CKS for biocultural stewardship

Drawing on the findings of this work, we propose a way to operationalize CKS for biocultural stewardship. Our proposal revolves around the concepts of gradients and reciprocity. We acknowledge that further research is needed for clearly defining CKS; however, we suggest that a CKS could be conceptualized as an indissoluble combination of a species and a sociocultural group (e.g. including geographical and linguistic boundaries) and the reciprocal relations they establish, and we propose a definition based on the ideas (1) that there are different gradients along which a species can be culturally important and (2) that the concept needs to include reciprocity between the sociocultural group and the keystone species. Therefore, the novelty of the proposal lies in acknowledging gradients of the importance of the species (against the current dichotomy), and in underlying the crucial importance of the intrinsic reciprocal and bidirectional relations between the species and the sociocultural group as well as it.

As a preliminary step to facilitate the operationalization of the concept of CKS, we suggest putting aside the dichotomy of a species being a CKS or not and, rather, propose that ethnotaxa could be classified according to gradients which can inform biocultural stewardship initiatives. For instance, ethnotaxa could be classified in a continuum of cultural salience including a first class (possibly named *Cultural Keystone Species* or *Culturally Important Species*) when ethnotaxa are culturally outstanding to the identity of a sociocultural group and maintain a reciprocal relationship (nature's contributions to people [Díaz et al., 2018] including people's contribution to nature [Ojeda et al., 2022]). A main assumption here is that the disappearance of the CKS would cause the erosion of cultural identity. Then, a second class when the ethnotaxa is salient (but not outstanding nor irreplaceable) from a cultural perspective, and the reciprocal contribution is weaker. Finally, a third class if the ethnotaxa have some other cultural association or utilitarian value, but these functions are redundant across other species.

We suggest that the CKS concept should be operationalized as considering ethnotaxa as well as biological species in global conservation policy to address the sociocultural dimensions of species decline. Currently, global policy agreements, tools and guidance such as the IUCN Red List Index prioritize bio-centric approaches and largely ignore ethnotaxa and the reciprocal relationships that people have with them. However, new conservation paradigms have started to be implemented. For example, Indigenous-led conservation can be a mechanism to recentre people in the stewardship of CKS (Clark et al., 2021). This approach necessitates recognizing and supporting Indigenous knowledge systems, rights and governance in global conservation policy. While many CKS are not at risk of extinction globally (i.e. biologically imperilled; Reyes-García et al., 2023), they are often vulnerable to human impacts at local scales, from overharvesting, deforestation and other threats (Baker, 2021; Moola et al., 2007). Moreover, their importance might decline if cultures that nurture them disappear or fade altogether when human languages go extinct

(Cámara-Leret & Bascompte, 2021; Ladle et al., 2023). Declines in local access, abundance or quality of ethnotaxa can also adversely impact the customary use of CKS by Indigenous Peoples and Local Communities. The concept of CKS (and similar concepts such as culturally important species) should be comprehensively explored and it could be critical in identifying the ethnotaxa for implementing (local) biocultural stewardship strategies.

However, previous uses of the concept have had limited contributions to policy development in conservation due to structural power in the implementation of global conservation policies (Shackleton et al., 2023). The limited uptake of the CKS concept could be due to the dominance of Western conservation ideology in research, policies and practice, neglecting Indigenous knowledge systems, values and worldviews. In addition, incongruencies in the use of the term and challenging applications of the concept in the implementation of conservation actions by international or internationally funded NGOs resulted in possibly limited use and diffusion of the concept.

5 | IMPLICATIONS

The Kunming-Montreal Global Biodiversity Framework (KMGBF), which was adopted during the fifteenth meeting of the Conference of the Parties (COP15) to the Convention on Biological Diversity in late 2022, offers a potential policy opportunity for the integration of biocultural approaches, such as the protection of ethnotaxa, in global conservation policy. While the KMGBF does not explicitly refer to ethnotaxa or biocultural diversity by name, it recognizes 'the important linkages between biological and cultural diversity' (KMGBF, 2022) and advances enabling measures that uphold the rights of IP and LC and their customary use of biodiversity. Seven of the KMGBF's 23 targets for policy action over the decade to 2030 reference IP and LC, their rights, territories and traditional ecological knowledge, which are important to the effective stewardship of biodiversity, including ethnotaxa (especially under 'Other effective area-based conservation measures') In spite of the references to IP and LC in the KMGBF, the agreement's emphasis on area-based conservation could be counterproductive and undermine biocultural conservation if the well-documented evidence that state-run protected areas often sever the critical relationships that Indigenous and Local Communities have with biodiversity, while criminalizing livelihood and customary land use activities (e.g. bans on harvesting or cultural burning; Moola & Roth, 2019; West et al., 2006). To contribute to a more robust understanding of the interactions between people and other living entities within social–ecological systems and to advance biocultural stewardship as a conservation paradigm, it is essential to acknowledge the value of long-term local management. Conservation as an initiative should be centred on local values and understandings (Wyborn & Evans, 2021). Indeed, as our findings confirmed, IP and LC often tend to and care about those species considering the CKS species' vital role. Such active and passive caring/tending management strategies based on local norms, rules and beliefs could be crucial in suggesting conservation initiatives which are respectful and inclusive of the local culture (Baumflek et al., 2021; Lyver et al., 2019).

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CONFLICT OF INTEREST STATEMENT

The co-author Irene Teixidor Toneu is an Associate Editor for *People and Nature* but was not involved in the peer review and decision-making process.

DATA AVAILABILITY STATEMENT

The database created with this review is being further analysed for further publications expected by December 2025, after which data will be disclosed. The data are available on a reasonable request to the first author.

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SUPPORTING INFORMATION

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

Appendix 1. Data collection and coding.

Appendix 2. Classification of the CKS author's affiliations.

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