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Towards evidence-based conservation of subterranean ecosystems

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ABSTRACT

Subterranean ecosystems are among the most widespread environments on Earth, yet we still have poor knowledge of their biodiversity. To raise awareness of subterranean ecosystems, the essential services they provide, and their unique conservation challenges, 2021 and 2022 were designated International Years of Caves and Karst. As these ecosystems have traditionally been overlooked in global conservation agendas and multilateral agreements, a quantitative assessment of solution-based approaches to safeguard subterranean biota and associated habitats is timely. This assessment allows researchers and practitioners to understand the progress made and research needs in subterranean ecology and management. We conducted a systematic review of peer-reviewed and grey literature focused on subterranean ecosystems globally (terrestrial, freshwater, and saltwater systems), to quantify the available evidence-base for the effectiveness of conservation interventions. We selected 708 publications from the years 1964 to 2021 that discussed, recommended, or implemented 1,954 conservation interventions in subterranean ecosystems. We noted a steep increase in the number of studies from the 2000s while, surprisingly, the proportion of studies quantifying the impact of conservation interventions has steadily and significantly decreased in recent years. The effectiveness of 31% of conservation interventions has been tested statistically. We further highlight that 64% of the reported research occurred in the Palearctic and Nearctic biogeographic regions. Assessments of the effectiveness of conservation interventions were heavily biased towards indirect measures (monitoring and risk assessment), a limited sample of organisms (mostly arthropods and bats), and more accessible systems (terrestrial caves). Our results indicate that most conservation science in the field of subterranean biology does not apply a rigorous quantitative approach, resulting in sparse evidence for the effectiveness of interventions. This raises the important question of how to make conservation efforts more feasible to implement, cost-effective, and long-lasting. Although there is no single remedy, we propose a suite of potential solutions to focus our efforts better towards increasing statistical testing and stress the importance of standardising study reporting to facilitate meta-analytical exercises. We also provide a database summarising the available literature, which will help to build quantitative knowledge about interventions likely to yield the greatest impacts depending upon the subterranean species and habitats of interest. We view this as a starting point to shift away from the widespread tendency of recommending conservation interventions based on anecdotal and expert-based information rather than scientific evidence, without quantitatively testing their effectiveness.

Key words: biospeleology, cave, climate change, conservation biology, ecosystem management, extinction risk, groundwater, legislation, pollution, subterranean biology

CONTENTS

I. INTRODUCTION

(1) General overview

Modern conservation science benefits from an increasing use of data to support evidence-based conservation interventions (Sutherland *et al*., 2004, 2019, 2020; Salafsky *et al*., 2019; Downey *et al*., 2021) and recognition of biases in terms of where these efforts are placed (Buxton *et al*., 2021; Fonseca *et al*., 2021). First, we are collectively building upon a quantitative understanding of what constitutes effective conservation interventions to ensure the protection and recovery of biodiversity and ecosystems (Sutherland *et al*., 2019). Second, we now appreciate that, given limited resources available for conservation, we need to maximise their effective allocation – for example by redirecting part of the funding devoted to monitoring and inventories towards direct and cost-effective conservation interventions (Lindenmayer, Piggott & Wintle, 2013; Buxton *et al*., 2020). Third, we have now identified how cognitive biases have permeated conservation investments and efforts in the past – for example more attention given to charismatic organisms (Mammola *et al*., 2020b; Adamo *et al*., 2021; Delso, Fajardo & Muñoz, 2021) and visibly appealing landscapes (Watson *et al*., 2014). By openly discussing these issues, we are setting the stage for a more effective allocation of conservation efforts and funding in the years ahead (Buxton *et al*., 2021).

Following recent trends, it is clear there should be a substantial shift of focus towards the species and ecosystems traditionally overlooked in most global conservation agendas, such as caves and other subterranean ecosystems (Sánchez-Fernández *et al*., 2021; Wynne *et al*., 2021; see definition in Section I.2). Due to the intrinsic inaccessibility of subterranean ecosystems (Ficetola, Canedoli & Stoch, 2019) and many impediments to research (Mammola *et al*., 2021a), we currently know too little about subterranean biota to be able to routinely implement cost-effective conservation interventions. To date, conservation of subterranean ecosystems has been dominated by problem-based studies focused on identifying the main drivers associated with subterranean biodiversity decline (Mammola *et al*., 2019a; Gerovasileiou & Bianchi, 2021). For example, we have elucidated the ecological impacts of polluted surface waters percolating underground (Di Lorenzo *et al*., 2015, 2021; Manenti *et al*., 2021), the long-term consequences of climate change on specialised subterranean organisms adapted to thermally stable conditions (Mammola *et al*., 2019c; Pallarés *et al*., 2020a,b; Colado *et al*., 2022), and some of the negative impacts that pathogens and alien species can cause to subterranean ecosystems (Howarth *et al*., 2007; Wynne *et al*., 2014; Howarth & Stone, 2020; Hoyt, Kilpatrick & Langwig, 2021).

However, problem diagnosis alone is notoriously insufficient for implementing conservation (Williams, Balmford & Wilcove, 2020). It is vital to start exploring solution-based approaches, namely proposing and implementing conservation interventions and then monitoring their efficacy. There are examples of habitat manipulation to increase bat survivability under pathogenic stress (Turner *et al.*, 2021), cave habitat restoration for invertebrate populations (Humphreys, 1991; Manenti *et al.*, 2019), and several studies synthesising quantitative knowledge on conservation interventions for managing bat populations, including species roosting or hibernating in caves (e.g. Tobin & Chambers, 2017; Berthinussen, Richardson & Altringham, 2021; Sutherland *et al.*, 2021). More often, however, conservation interventions are indirect and/or not assessed quantitatively. We are frequently guilty of concluding our research papers with lofty, often abstract recommendations such as "We should monitor the population…", "Management of the [habitat/species/population] is strongly advised…", and "It would be important to protect the site.…" Although the intentions are good, this can contribute to an information overload that may complicate, or even misguide, conservation and management efforts (Landhuis, 2016; Jeschke *et al.*, 2019).

Two questions naturally follow concerning conservation and management of the subterranean biome: (*i*) how often have conservation interventions been quantified and statistically tested in relation to various anthropogenic threats; and (*ii*) how has the frequency of the different conservation interventions, whether proposed or tested, changed over time? To approach these questions, we undertook a systematic literature review across a breadth of publications focused on conservation interventions for subterranean ecosystems (Fig. 1). Our efforts were designed to build a quantitative understanding of the number of interventions that have (or have not) been tested, as well as to target threats, organisms, systems, and types of conservation interventions lacking research. Finally, we build upon positive cases of successful conservation to provide examples of robust study designs that monitor the effectiveness of conservation interventions.

(2) Definition of subterranean habitats used in this review

We used the term 'subterranean habitat/ecosystem' in a broad sense to encompass all lightless subterranean spaces, dry or filled with water, generally representing buffered climatic conditions, and where organisms do not encounter surface habitats in all three dimensions. The latter condition excludes soil habitats. For the purpose of this analysis, we divide subterranean habitats into six artificial categories: (*i*) caves – cavities of different origins [karst, volcanic, tectonic, glacier caves, and other voids formed by solution or erosion] that are directly accessible to humans; (*ii*) show caves – caves made accessible to the general public for tourism, managed by a government or commercial organisation; (*iii*) artificial – all subterranean spaces of man-made origin, such as mines, bunkers, blockhouses, and water conduits; (*iv*) groundwater – aquatic subterranean habitats such as aquifers, springs, cenotes, and subterranean rivers; (*v*) fissural systems – all fissures and pore spaces whose size prevents human entry, with similar habitats occurring close to the surface usually listed under the umbrella term *shallow subterranean habitats* (Culver & Pipan, 2014); these habitats are only accessible *via* indirect means, for example using subterranean sampling devices (Mammola *et al.*, 2016); and (*vi*) marine/anchialine – saline groundwater habitats represented through the ecotone that extends from the coast to fresh groundwater. Marine subterranean ecosystems (e.g. submarine caves) are those subject to direct marine influence, whereas 'anchialine' is generally used for subterranean or semi-subterranean water bodies with a marine origin that has penetrated inland and remains isolated from the ocean (Sket, 1996).

II. MATERIALS AND METHODS

We conducted a systematic literature review to amass an extensive list of publications that discussed and/or tested conservation interventions for subterranean species or habitats – including terrestrial, freshwater, and marine/anchialine subterranean systems (see Section I.2 for definitions). The PRISMA workflow (Moher *et al.*, 2009; Page *et al.*, 2021) and a summary of this review is provided in Fig. 1A. Throughout the text, we use the term 'intervention' in a broad sense, namely any direct or indirect action associated with the conservation of the species/system (see Section II.3 for further details).

(1) Systematic literature search

On 03 February 2021, we performed standardised literature searches in the *Web of Science*. Different search terms were initially trialed by S.M. and M.B.M. in a scoping exercise to refine the procedure, that is running a search and considering the relevance of the first 200 references. Based upon this exploratory trial, we refined search terms to minimise the number of irrelevant references. We found that using overly broad search terms (e.g. 'subterranean habitat', 'groundwater') resulted in an overwhelming number of articles. For example, a search with the term 'groundwater' yielded >37,000 papers, most of which were irrelevant because they referred to (hydro)geological aspects. At the same time, more specific subterranean biology terms such as 'caves' captured several archaeological, palaeontological, and medical papers – for example the term 'cave' is used in Osteology. The final search string that maximised both specificity and sensitivity was (Search #1):

TS = ("cave" OR "subterranean biology") AND TS = ("conserv*" OR "managem*" OR "restorat*" OR "preserv*" OR "policy" OR "policies" OR "politic*" OR "protect*" OR "reintroduc*" OR "regulat*" OR "legislat*" OR "IUCN" OR "CITES" OR "sustainabil*") NOT TS = ("surgery" OR "surgical" OR "medicine" OR "Neanderthal" OR "osteology" OR "bones" OR "anthropology" OR "Homo" OR "therapy" OR "art" OR "cranial" OR "paleontolog*").

This search yielded 3,269 papers. In parallel, we conducted a second search for groundwater and anchialine systems (Search #2) using the search string:

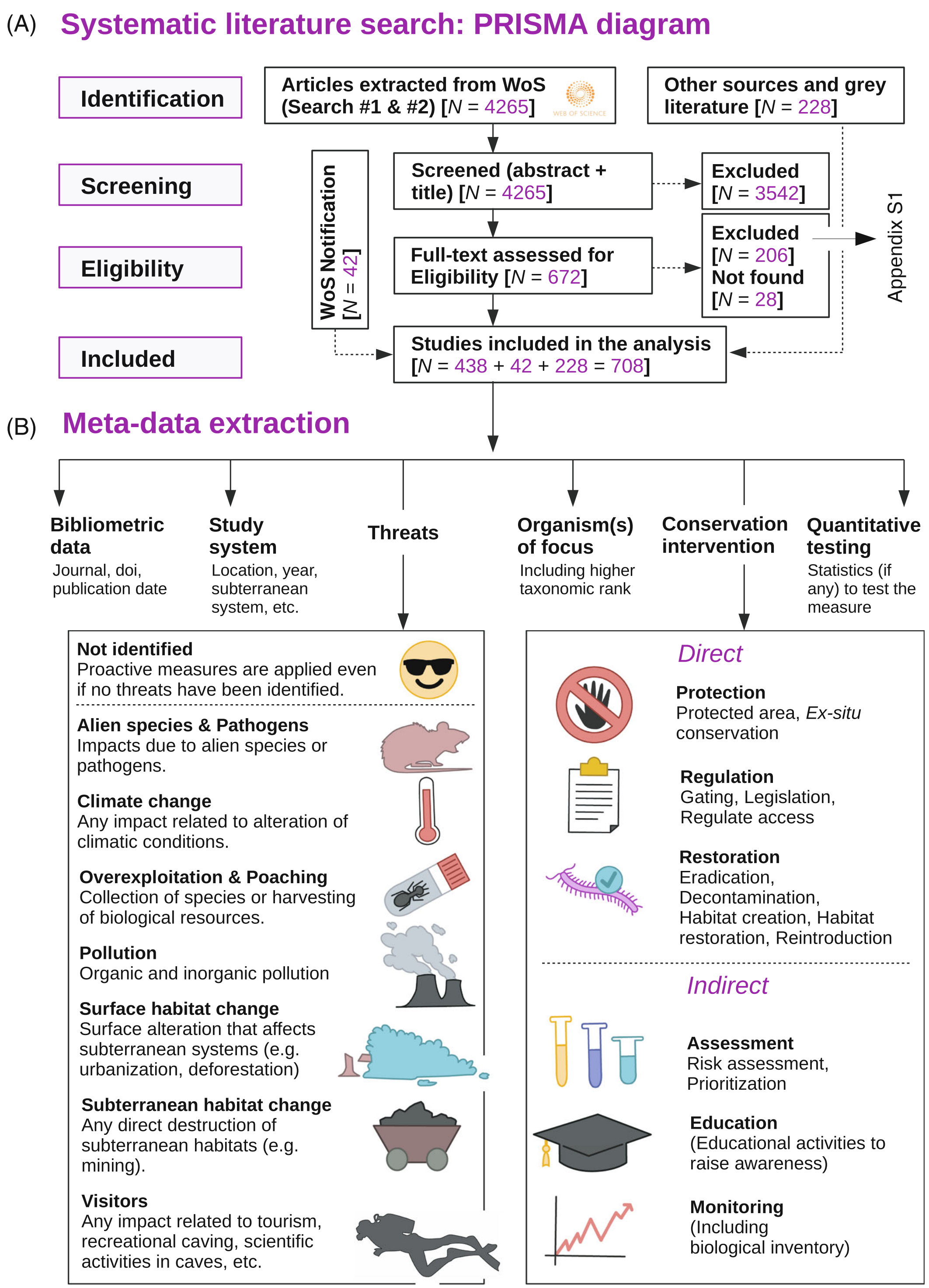

Fig. 1. Summary of the sampled literature and extracted metadata. (A) PRISMA diagram depicting the flow of information through the different phases of the systematic literature review. For the list of studies extracted from the *Web of Science*, including excluded studies with reasons for exclusion, see Appendix S1. (B) Summary of the metadata collected for the database. For the link to the data repository see Section VII. Original silhouettes by Irene Frigo.

TS = ("groundwater" OR "anchialine") AND TS = ("fauna" OR "stygob*" OR "organism*") AND TS = ("conserv*" OR "managem*" OR "restorat*" OR "preserv*" OR "policy" OR "policies" OR "politic*" OR "protect*" OR "reintroduc*" OR "regulat*" OR "legislat*" OR "IUCN" OR "CITES" OR "sustainabil*").

This search yielded an additional 998 papers, with less than 100 papers overlapping with Search #1. All papers originating from these two searches ($N = 4,265$) were screened for inclusion in the review based on an agreed set of criteria (Appendix S1). We included studies that: (*i*) statistically tested the effectiveness of conservation interventions (e.g. gating to prevent access to caves), based on quantitative variables describing the status of species or ecosystems (e.g. population or range trends) (hereafter 'testing'); (*ii*) discussed or recommended conservation interventions without testing their effectiveness; (*iii*) discussed research priorities for conservation of subterranean biodiversity and/or performed risk assessments; and (*iv*) focused on surface management/protection measures that affect subterranean ecosystems. Studies were excluded that either: (*i*) focused on non-subterranean habitats (see Section I.2) or (*ii*) did not focus on the biological component of the target subterranean ecosystem (e.g. studies examining methods to restore cave-wall paintings at archaeological sites).

We carried out the initial screening by making independent selections based on titles and abstracts. To test the consistency of selection criteria, S.M. and M.B.M. independently classified the first 100 papers and calculated inter-rater agreement using Cohen's kappa. The value of kappa was 0.7, well above the standard threshold of acceptable inter-rater agreement of 0.4 (Cohen, 1960). Given this result, we used these criteria to screen the remaining papers based on their titles and abstracts. If it was evident that a given study did not address our key research questions, we discarded it. Subsequently, we examined the full text of the references taken forward from this screening ($N = 708$) to determine if they addressed our research questions (Appendix S1).

For both *Web of Science* searches, we set up an alert for relevant references when they entered the *Web of Science* database from February to October 2021, which generated an additional 42 references.

(2) Additional literature, cross-validation, and caveats

To ensure a better coverage of the current conservation literature (Gusenbauer & Haddaway, 2020; Sutherland *et al.*, 2020), we cross-checked the final database with the list of papers focusing on subterranean ecosystems included within the Conservation Evidence database ($N = 15$, of which 11 were also available in the *Web of Science*; online database accessed on 03 February 2021 using the query "Habitat = Rocky Habitats & Caves" and manually extracting relevant entries; Sutherland *et al.*, 2019). We further cross-checked the final database with the lists of papers analysed in three ongoing systematic literature surveys focusing on the environmental impacts related to the exploitation of caves for tourism (E. Piano, G. Nicolosi, S. Mammola, B. Baroni, E. Cumino, N. Muzzulini, V. Balestra, R. Bellopede & M. Isaia, unpublished), on alien species in subterranean ecosystems (G. Nicolosi, L. Verbrugge, M. Isaia & S. Mammola, unpublished), on conservation of cave-dwelling bats (M.B. Meierhofer, J.S. Johnson, J. Perez-Jimenez, F. Ito, P.W. Webela, S. Wiantoro, E. Bernard, K.C. Tanalgo, A. Hughes, P. Cardoso, T. Lilley, S. Mammola, unpublished), plus a recent synthesis of current knowledge regarding marine caves (Gerovasileiou & Bianchi, 2021). These cross-checks yielded 37 additional papers that were missed from our initial searches, which we also included. Finally, we conducted an unstandardised search for grey literature (Haddaway *et al.*, 2020), including articles not in English (Nuñez & Amano, 2021). All these additional sources ($N = 228$) were labelled as 'Others' within the database.

Given that our analysis is based on a single literature database plus unstandardised grey literature searches, we acknowledge that it is not a fully comprehensive coverage of the literature (Gusenbauer & Haddaway, 2020). For example, through our initial search, we captured 9 out of 11 of the papers in Conservation Evidence focusing on bat conservation available in the *Web of Science*. As a result, our estimation of the volume of the literature should be taken as an approximation of the real number of studies. We operated under the reasonable assumption that the biases were homogeneously distributed across conservation interventions and taxa, allowing us to draw meaningful inferences using proportional data. Nevertheless, any comparison of absolute numbers of studies should be taken with caution.

(3) Metadata extraction

For all relevant references included in the final database, we extracted detailed metadata and information (Fig. 1B). We recorded the geographic and taxonomic scope, type of threat, and conservation intervention applied, as well as a list of all tests used to analyse the conservation intervention, the test statistic, the degrees of freedom, number of observations, whether the measure was significant, and the direction of the effect.

We determined the main threats to subterranean ecosystems based on recent syntheses (Mammola *et al.*, 2019a, 2020a; Wynne *et al.*, 2021) complemented by our expert opinion. We grouped threats into the following eight categories: (*i*) Alien species & Pathogens (impacts due to alien species or pathogens); (*ii*) Climate change (impacts related to the alteration of climatic conditions); (*iii*) Overexploitation & Poaching (indiscriminate collection of species or overexploitation of biological resources); (*iv*) Pollution (organic and inorganic pollution events); (*v*) Surface habitat change (habitat alteration at the surface that affect subterranean systems; e.g. urbanisation); (*vi*) Subterranean habitat change (direct destruction of subterranean habitat; e.g. mining); (*vii*) Visitors (disturbance related to tourism exploitation of caves, recreational caving, etc.); and (*viii*) Not identified (when proactive conservation interventions are applied or suggested even if no threats were identified) (Fig. 1B).

Likewise, we determined the main conservation interventions based on general conservation science literature (Sutherland *et al.*, 2019) and our knowledge and expertise regarding subterranean ecosystems (Mammola *et al.*, 2019a, 2020a; Wynne *et al*., 2021). We classified conservation measures as 'indirect' or 'direct' (Fig. 1B).

Indirect interventions (Fig. 1B) are activities that increase knowledge useful for implementing practical conservation. Such interventions that indirectly enhance the protection of subterranean ecosystems were classified into: (*i*) Education (dissemination or education program to raise awareness of the subterranean biome); (*ii*) Monitoring (biological inventories and short- or long-term monitoring programs of the quality/status of a species, habitat or ecosystem); or (*iii*) Assessment [with two categories: Prioritisation (interventions to prioritise species/habitat/ecosystem for conservation, for example identifying hotspots of biodiversity to be protected, identifying cost-effective interventions, or fundamental questions to be answered to achieve better protection); and Risk assessment (assessments of the status of conservation/extinction risk of a species/habitat/ecosystem)].

Direct interventions (Fig. 1B) have clear relevance for practical conservation of subterranean fauna and habitats, and are classified into: (*i*) Protection [with two categories: Protected area (interventions to establish legal protection for the site); and *Ex-situ* conservation (interventions focused on species outside natural habitats; for example captive breeding programs established to rear and reintroduce an imperiled species)], (*ii*) Regulation [with three categories: Gating (install and maintain gates/fences at the entrance to or inside caves, or any other action to restrict human access); Legislation (legal actions to protect biodiversity); and Regulate access (regulation of access to the site; for example restricting recreational users in winter months and regulating visits to show caves)]; and (*iii*) Restoration [with five categories: Eradication (interventions for controlling the spread of alien species); Decontamination (practices for removal or hindering the spread of pathogens); Habitat creation (interventions to create new, previously non-existing habitat; for example excavating an artificial refuge for bats); Habitat restoration (interventions to restore habitat; for example bioremediation of pollutants, removal of abandoned pitfall traps); and Reintroduction (species reintroductions)].

(4) Data visualisation and statistical analyses

We conducted all analyses in R version 4.1.0 (R Core Team, 2021), using the packages 'ggplot2' version 3.3.4 (Wickham, 2016) and 'circlize' version 0.4.13 (Gu *et al*., 2014) for data visualisation. For all analyses and figures, we record an individual mention of a conservation intervention as the minimum measurement unit; there may be multiple measurements/tests per study (mean ± S.E. recommended interventions per paper = 2.76 ± 0.15).

We used binomial generalised linear models to predict the annual changes in the relative proportion of conservation interventions and threats, as well as the number of interventions being tested in each year. In all models, we used the total number of interventions or threats in each year as a benchmark to standardise values and obtain proportional values. Considering the limited sample size before the year 2000, we restricted all temporal analyses to the period 2000–2021 (note that data for 2021 extend only to the end of October). We validated models with the *check_model* function in the R package 'performance' version 0.7.2 (Lüdecke *et al*., 2020).

(5) To meta-analyse or not to meta-analyse?

For articles that statistically tested conservation interventions, we also collected associated statistical measures (if any) to generate a data baseline for performing future meta-analyses regarding the most effective interventions for the long-term preservation of subterranean species and habitats. However, given the low rate of statistical testing for conservation measures across the data set, we did not perform a meta-analysis. We believe the field has not yet matured sufficiently to support such an analysis because: (*i*) the number of quantitative studies regarding most conservation interventions was below a threshold of five independent studies, which we considered to be a minimum for deriving meaningful estimates; and (*ii*) even for the most intensively tested interventions (e.g. risk assessment, gating), we could not extract basic information for several studies due to inadequate reporting of results (e.g. studies reporting only *p*-values, not mentioning sample size, or omitting confidence intervals). The number of estimates potentially usable for future meta-analyses is given in Table 1.

III. OVERVIEW OF QUANTITATIVE RESULTS

(1) General summary of the literature

We identified 4,265 studies in the two initial *Web of Science* literature searches, of which 672 were deemed relevant for full-text inspection based on the screening of titles and abstracts. Of these, 438 studies satisfied our inclusion criteria. Additionally, we included a further 228 papers based on literature known to us and through cross-referencing with other literature data sets, and 42 papers through *Web of Science* email alerts. In total, 708 studies met our criteria for inclusion (Fig. 1A; Appendix S1). These papers entailed 1,954 unique conservation interventions.

Predictably, the majority of conservation interventions occurred in the Palearctic (42%) and Nearctic (22%) biogeographic regions, with few studies originating in the Afrotropical and Indomalayan regions (both 5%; Fig. 2A). The terrestrial environment – caves, show caves, and artificial systems – was the focus of most conservation interventions (59%), followed by groundwater habitats (27%) and marine cave/anchialine systems (8%); difficult-to-access fissure systems were the least studied in conservation science (1%; Fig. 2B). Arthropods (32%) and cave-roosting bats (33%) were the most studied organisms, with plants and microorganisms (bacteria, archaea, unicellular fungi, and viruses) the least studied (both 2%; Fig. 2C). Over one-third of conservation interventions for arthropods and bats were tested.

Table 1. Usable data for meta-analyses based on the sampled literature. Out of the total number of unique interventions, this table reports the percentage (%) that have been tested, the number of quantitative estimates, and the number of studies. Potential number of standardised estimates indicate the number of estimates that could be converted to Pearson's *r* using standard conversion formulae (Lajeunesse, 2013)

Intervention	Total number of estimates (% tested)	Number of quantitative estimates (number of studies)	Potential number of standardised estimates (% of total studies)
Protected area	183 (0%)	1 (1)	1 (100%)
Ex-situ conservation	10 (0%)	0 (0)	–
Gating	174 (72%)	125 (16)	71 (57%)
Legislation	95 (0%)	0 (0)	–
Regulate access	127 (43%)	55 (6)	44 (80%)
Eradication	15 (27%)	4 (1)	0 (0%)
Decontamination	54 (35%)	19 (6)	2 (11%)
Habitat creation	13 (38%)	5 (1)	4 (80%)
Habitat restoration	115 (14%)	16 (3)	15 (94%)
Reintroduction	5 (0%)	0 (0)	–
Risk assessment	465 (63%)	295 (37)	208 (71%)
Prioritisation	213 (21%)	44 (12)	10 (23%)
Education	105 (0%)	0 (0)	–
Monitoring	399 (11%)	45 (14)	20 (44%)

Pollution (24%) and visitors (19%) were the most frequently addressed, whereas climate change (2%) and overexploitation & poaching (2%) were the least studied and tested (Fig. 2D). Of all conservation interventions, protected areas (9%) and gating (9%) were the most mentioned direct interventions, while risk assessment (24%) and monitoring (20%) were the most considered indirect interventions (Fig. 2E). The frequency of different conservation interventions, whether proposed or tested, varied among the identified threats. For example, monitoring and education were suggested more or less equally in relation to all threats, regulation was mostly recommended in response to visitors, assessments were largely proposed to target pollution, and restoration interventions were mostly suggested in response to alien species & pathogens and subterranean habitat change (Fig. 3).

(2) Temporal trends

Perhaps one of the clearest findings was that only 609 out of 1,954 conservation interventions (31%) were tested using statistical techniques, despite the rapid increase in the number of publications from 2000 to October 2021 (Fig. 4A). This result implies that most of the conservation science in subterranean biology, and the resulting interventions, were not developed using quantitative evidence – the exceptions were gating and risk assessments, where 72 and 63% of cases were quantified and/or tested, respectively (Fig. 2E).

Of the conservation interventions and threats, one intervention and five threats exhibited notable temporal trends (Table 2, Fig. 4B, C). Monitoring actions were increasingly mentioned in the literature since the year 2000 (Fig. 4C). Studies focusing on alien species & pathogens have increased significantly since the year 2000 (Fig. 4B), mostly due to a recent surge in research on white-nose syndrome in North American bat populations (Blehert *et al.*, 2009). Although the effects of climate change are at the forefront of conversation regarding surface environments (Arneth *et al.*, 2020), only a relatively shallow increase in such studies was observed for subterranean environments (Fig. 4B). Indeed, discussion on the impacts of anthropogenic climate change on subterranean ecosystems has begun only recently (Mammola *et al.*, 2019b; Howarth, 2021). Finally, the three most mentioned threats in earlier research – visitors, pollution, and subterranean habitat change – all displayed a significant decrease over time. This may be due to more balanced attention applied across multiple threats or a shift in research interest in recent years (Fig. 4B).

IV. CURRENT KNOWLEDGE AND RESEARCH TRAJECTORIES FOR CONSERVATION INTERVENTIONS

As illustrated in this review, the field of subterranean conservation is still in its infancy regarding the testing of conservation interventions and their practical implementation. Despite the growing literature concerning the subterranean biome and the breadth of potential threats, reports of conservation interventions have been largely descriptive (Table 1). In this section, we provide a qualitative assessment of past and current conservation interventions and discuss potential future research trajectories. We use the six broad categories for conservation interventions defined in Section II.3 (see Fig. 1B). In Table 3, we provide examples of potential research areas and study designs that can be applied to diverse subterranean species and/or ecosystems to test conservation interventions effectively.

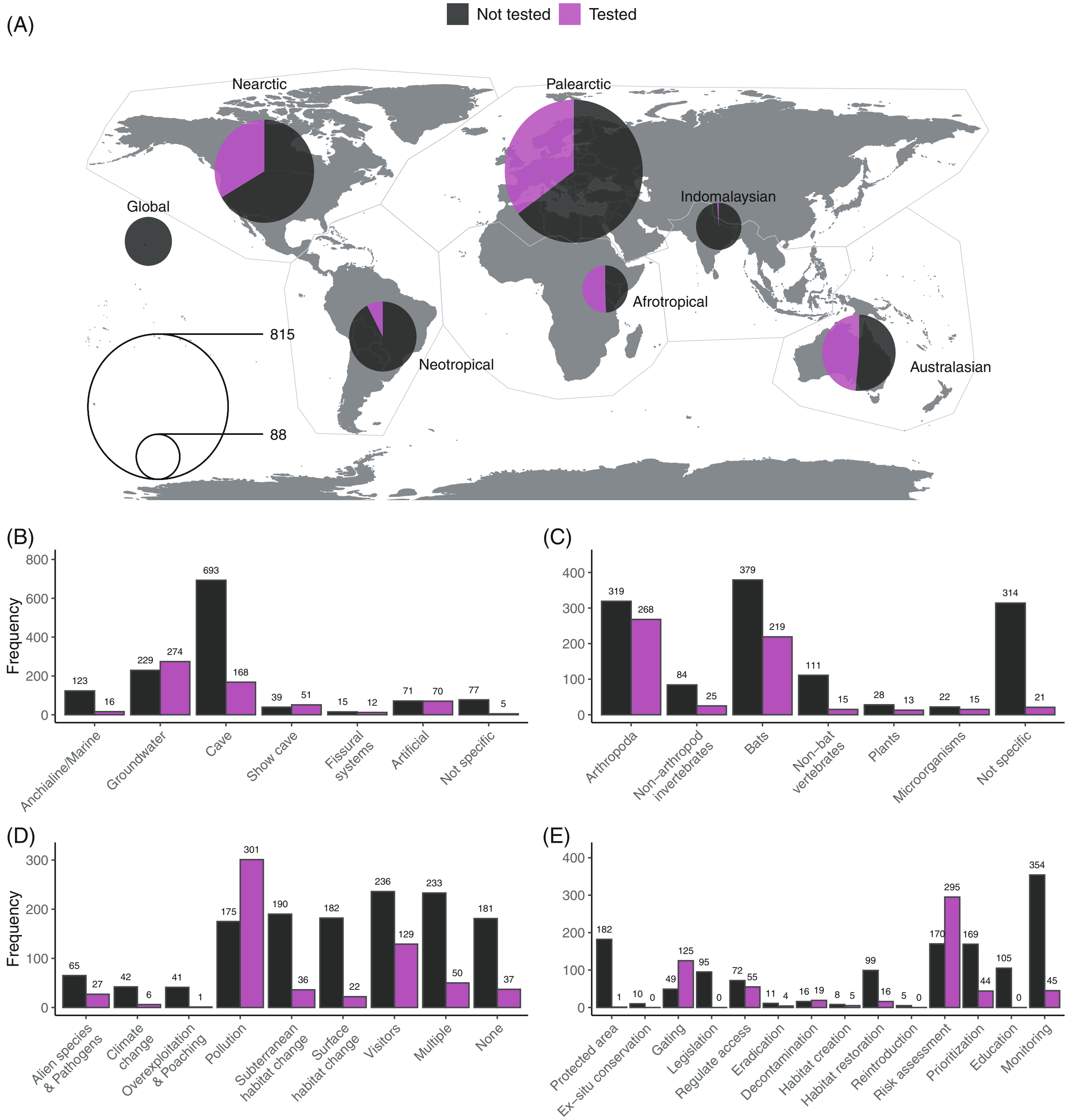

Fig. 2. Summary of the surveyed literature. Proportion of conservation interventions tested across our data set by biogeographic region (A), habitat (B), taxon (C), threat (D), and conservation intervention (E). Size of the circle in A indicates the number of conservation interventions. For definitions of subterranean habitat types used in B see Section I.2. In B and C, 'Not specific' means that the study did not refer to a specific subterranean species/system. In D, 'Multiple' means that three or more threat groups were considered. Note that total numbers in each panel within the figure may differ slightly from the overall total number of interventions (1,954), because: (*i*) data were missing for some entries in the database (i.e. we could not derive some information); (*ii*) some studies focused on multiple biogeographic regions, taxa, or habitats.

(1) Assessment

Assessment of subterranean species or ecosystems comprises two components: prioritisation and risk assessment (Fig. 1B). These actions combined represented 35% of all suggested conservation interventions (Fig. 2E), despite their effects being indirect. Prioritisation involves the identification of criteria

Fig. 3. Chord diagram showing interrelationships among conservation interventions and threats across our data set. Threats are listed in the upper portion of the diagram and conservation interventions in the lower portion. Original silhouettes by Irene Frigo.

for cost-effective conservation interventions and resource allocation. Most studies developed indices to prioritise subterranean sites for spatial conservation planning, although the proposed indices have rarely been implemented. These prioritisation exercises are often based on criteria such as the richness of specialised subterranean species, rare species, and/or the degree of endemism (Michel *et al.*, 2009; Borges *et al.*, 2012; Nitzu *et al.*, 2018; Rabelo, Souza-Silva & Ferreira, 2018; Pipan, Deharveng & Culver, 2020), but can be controversial (Moldovan & Brad, 2019; Nitzu, Meleg & Giurginca, 2019). The effectiveness of conservation planning has been tested indirectly in most cases, for example by comparing the performance of different prioritisation methods (Rabelo, Souza-Silva & Ferreira, 2018; Cardoso, Ferreira & Souza-Silva, 2021) or by conducting complementarity analyses (Michel *et al.*, 2009; Borges *et al.*, 2012). Furthermore, with a few recent exceptions (e.g. Fattorini *et al.*, 2020; Iannella *et al.*, 2021; Tanalgo, Oliveira & Hughes, 2021), prioritisation attempts have focused solely on taxonomic diversity measures. However, it is increasingly recognised that similar exercises

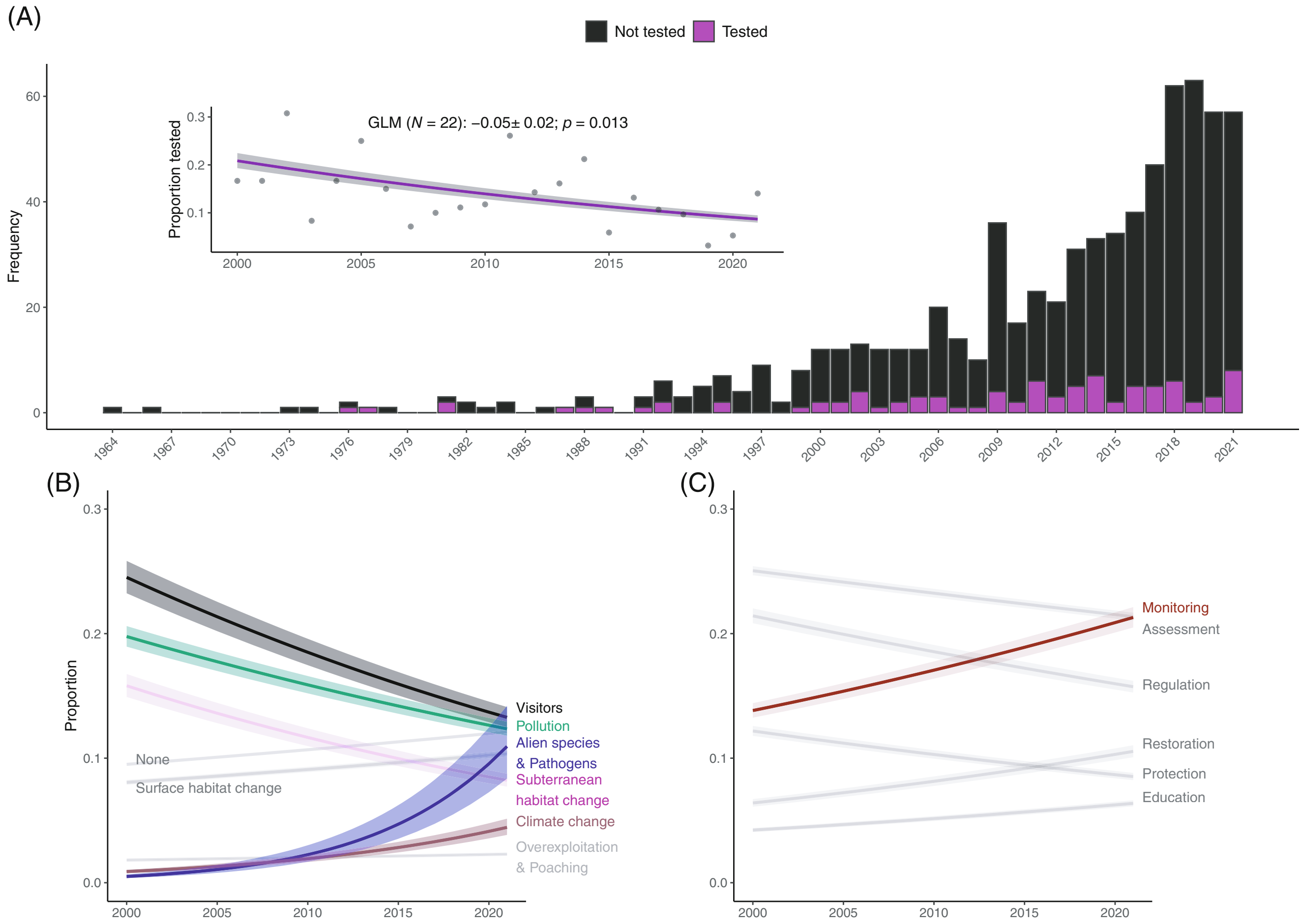

Fig. 4. Temporal trends in research on conservation measures and threats in subterranean ecosystems. (A) Proportion of conservation interventions tested across our data set by year. Inset scatterplot is the proportion of conservation interventions tested per year between 2000 and 2021 (partial data up to October for 2021), with the line fitted using a binomial generalised linear model. (B, C) Annual changes in the relative proportions of studies reporting different threats (B) and conservation interventions (C), with lines fitted using individual binomial generalised linear models. Solid lines are fitted values (slope) and shaded surfaces indicate the associated 95% confidence intervals. Bright colours highlight significant trends. Estimated regression parameters are given in Table 2.

should seek to achieve a delicate balance among multiple facets of diversity [taxonomic, phylogenetic, and functional diversity (Pollock, Thuiller & Jetz, 2017; Mazel *et al.*, 2018; Owen *et al.*, 2019b)] and other features including ecosystem services (Zhang *et al.*, 2015; Girardello *et al.*, 2019), natural resources (e.g. water; Jung *et al.*, 2021), threats (Wilson *et al.*, 2005), and species climatic niches (Hanson *et al.*, 2020). Testing multifaceted conservation planning is much needed to expand the coverage of subterranean protected areas globally (Sánchez-Fernández *et al.*, 2021), although it often remains unclear how to implement these conservation plans in practice (see Pollock *et al.*, 2020).

Risk assessment involves analyses aimed at identifying risks to species and habitats due to anthropogenic threats. Most studies in our database focused on assessing species extinction risk against International Union for Conservation of Nature (IUCN) *Red List* criteria or using other indices for assessing species imperilment (e.g. national or regional evaluations). Currently, the use of IUCN criteria can be problematic for assessing the extinction risk of most invertebrates and for specific habitats such as caves (Cardoso *et al.*, 2011). However, IUCN assessments represent one of the best measures available to evaluate extinction risks objectively and comparably across different subterranean taxa (Borges *et al.*, 2019), but the effectiveness of these assessments remains largely untested.

Finally, a large body of literature has evaluated the likelihood of harmful effects to subterranean ecosystems resulting from exposure to environmental stressors. Most assessments were conducted in groundwater systems. The main problem is that guideline-based risk scenarios for groundwater are often unrealistic because surface species (e.g. *Daphnia* spp.) are used as proxies for the sensitivity of subterranean species to pollutants (Kolar & Finizio, 2017). Proxies are used because of the shortage of ecotoxicological data concerning subterranean animals (Castaño-Sánchez, Hose & Reboleira, 2020), and

Table 2. Regression parameters for modelled temporal trends in research on conservation interventions and threats in subterranean biology shown in Fig. 4, estimated using binomial generalised linear models. For each model, sample size is equal to 22 (one observation/year between 2000 and 2021). S.E. = standard error. C.I. = 95% confidence interval

Variable	Estimated slope ± S.E.	C.I.	z	p-value	R^2
Conservation interventions					
Assessment	$-9.87e^{-03} \pm 8.79e^{-03}$	[−0.03, 0.01]	−1.12	0.26	0.07
Education	0.02 ± 0.02	[−0.01, 0.06]	1.11	0.27	0.04
Monitoring	0.02 ± 0.01	[0.01, 0.05]	2.45	0.01	0.04
Protection	−0.02 ± 0.01	[−0.04, 0.01]	−1.49	0.14	0.01
Regulation	$-0.02 \pm 9.73e^{-03}$	[−0.04, 0.01]	−1.85	0.06	0.03
Restoration	0.03 ± 0.01	[−0.01, 0.06]	1.75	0.08	0.01
Threats					
None	0.01 ± 0.01	[−0.01, 0.04]	1.01	0.31	0.06
Alien species & Pathogens	0.15 ± 0.03	[0.10, 0.21]	5.43	<0.001	0.29
Climate change	0.08 ± 0.03	[0.02, 0.14]	2.55	0.01	0.50
Overexploitation & Poaching	0.01 ± 0.03	[−0.05, 0.07]	0.38	0.71	0.58
Pollution	−0.03 ± 0.01	[−0.05, −0.01]	−2.54	0.01	0.01
Surface habitat change	0.01 ± 0.01	[−0.01, 0.04]	0.95	0.34	0.10
Subterranean habitat change	−0.04 ± 0.01	[−0.06, −0.01]	−2.92	0.004	0.07
Visitors	$-0.04 \pm 9.75e^{-03}$	[−0.05, −0.02]	−3.67	<0.001	0.01

the lack of a standard protocol to perform these trials (Di Lorenzo *et al.*, 2019). Although there have been numerous pleas for adaptation of the guidelines and for fine-tuning regulatory limits related to pollutants in subterranean environments (Di Lorenzo *et al.*, 2014, 2018, 2021; Di Marzio *et al.*, 2018), these recommendations have not been incorporated into legislation.

(2) Education

Environmental education encompasses all programs aimed at fostering environmentally related attitudes and developing awareness of biological conservation (Ardoin, Bowers & Gaillard, 2020). Moreover, education increases the success of other actions, such as citizen science-aided data collection in groundwater systems (Alther *et al.*, 2021) and reporting of poaching events in caves (Simičević, 2017). While studies have emphasised the importance of these activities to enhance the long-term preservation of subterranean biota and associated habitats, discussions on educational activities were often vague and lacked plans for practical implementation. Importantly, the effectiveness of subterranean environmental education remains untested in all cases (Fig. 2E).

Examples of concrete interventions proposed include promoting awareness through artistic representations of caves and their biota (Danielopol, 1998), the use of simple narratives to engage children in the conservation of subterranean fauna (Mammola, Frigo & Cardoso, 2022), briefings to increase visitors' awareness about sensitive taxa [e.g. for divers in marine caves (Di Franco *et al.*, 2009b; Guarnieri *et al.*, 2012)], personal contact with target audiences (Alther *et al.*, 2021), and the use of guided tours of caves to deliver an environmental education message (North & van Beynen, 2016). The latter example has received the most attention insofar as show caves represent unique windows for the general public to experience an inaccessible secluded world. Given that cave tourism can have significant ecological impacts, there remains debate as to whether we should maintain active show caves or establish new ones to achieve broad-ranging educational goals (e.g. Tičar *et al.*, 2018). The most objective way to address this sensitive topic would be to test the effectiveness of educational interventions and their long-term benefits (Table 3).

(3) Monitoring

Monitoring subterranean ecosystems entails the acquisition of knowledge used in the protection of subterranean biota (e.g. new species descriptions, cryptic species identification, natural history studies, and biological inventories) or assessing populations and ecosystems across space and time. Monitoring is often based on simple survey methods (e.g. visual census, emergence count, mark–recapture studies, trapping), the use of indirect monitoring technologies (e.g. environmental DNA, acoustic monitoring, trail cameras with infrared sensors) (Mammola *et al.*, 2021a; Saccò *et al.*, 2022), and, most recently, subterranean citizen science (Alther *et al.*, 2021). Monitoring was by far the most recommended intervention in our database (Figs 2E, 4C) despite its effects being indirect – a pattern that is not exclusive to subterranean conservation (Buxton *et al.*, 2020, 2021). This likely relates to a deficit of knowledge about subterranean ecosystems, which are notoriously difficult to explore, study, understand, and ultimately to protect (Ficetola, Canedoli & Stoch, 2019; Mammola *et al.*, 2019a, 2021a; Gerovasileiou & Bianchi, 2021). Despite their perceived importance, only 11% of the proposed monitoring plans and methods were tested. Examples include comparing the effectiveness of different sampling methods in cave systems (Wynne *et al.*, 2018, 2019) or assessing the detection probability of a given method across diverse environmental conditions (Dole-Olivier

Table 3. Examples of potential research areas and study designs that could be applied to diverse subterranean species and/or ecosystems to test conservation interventions effectively. We report examples of study designs for the effective testing of conservation interventions and anticipated timing for such tests. An expected spatial and temporal scale of the impact of the conservation intervention is also provided. We provide example references from the subterranean ecosystems literature; when not available, we provide references from the general conservation science literature

Intervention	Example of study design	Timing of testing	Expected impact	Reference
Protected areas	(1) Compare outcomes of subterranean species/ecosystems in protected sites over time *versus* control areas. (2) Monitor habitat degradation in protected *versus* non-protected areas over time. (3) Compare the status of populations of affected species in protected *versus* non-protected areas.	(1) Instantaneous (2) Years to decades (3) Years to decades	Local to regional scale. Decades.	(1) Measey, Armstrong & Hanekom (2009) (2) Moldovan *et al.* (2020a) (3) Pacheco *et al.* (2021) (1–3) Pressey *et al.* (2021)
Ex-situ conservation	(1) Check the health status of target species in captivity. (2) Test effectiveness of protocols for treating symptomatic individuals kept in captivity against controls.	(1, 2) Days to years, depending on species longevity and reproductive phenology	Local scale. Years to centuries.	(1) Gredar, Prša & Bizjak Mali (2018) (2) Lukač, Cizelj & Mutschmann (2019)
Gating	(1) Compare abundance/behaviour of animals before/after gate installation. (2) Compare community-level indicators or other abiotic parameters when installing different types of gates and fences. (3) Compare community composition of caves with and without gates within a given region, while correcting for site-level confounding factors.	(1, 2) Years to decades (3) Instantaneous	Local scale. Years to decades.	(1) Voûte & Lina (1986); Caraka *et al.* (2018) (2) Richter *et al.* (1993); Pugh & Altringham (2005) (3) Furey & Racey (2016); Phelps *et al.* (2018) (1–3) Tobin & Chambers (2017)
Legislation	(1) Compare people's behaviour before/after the enforcement of a law/conservation program. (2) Assess whether the regulations are suitable for the intended purpose by examining their success against the criteria: effectiveness, efficiency, coherence, relevance and added value.	(1–2) Years to decades	Local to regional scale. Years to decades.	(1) Infield & Namara (2001)
Regulate access	(1) Monitor species abundances/ community composition before/ after regulation. (2) Monitor species abundances during reproduction/wintering events for caves with seasonal closures. (3) Monitor species abundances/ community composition in managed *versus* unmanaged areas.	(1) Days to years (2) Years to decades (3) Instantaneous	Local scale. Years.	(1) Moldovan, Racovitza & Rajka (2003) (2) Trevelin *et al.* (2021) (3) Moldovan, Racovitza & Rajka (2003); Nicolosi *et al.* (2021); Pacheco *et al.* (2021)
Eradication	(1) Monitor the potential return(s) of alien species after eradication treatment. (2) Compare the status of native communities before/after eradication treatment.	(1) Years to decades (2) Days to years	Local to regional scale. Years to decades.	(1) Mouser *et al.* (2019) (2) Maezono & Miyashita (2004); Bergstrom *et al.* (2009)
Decontamination	(1) Quantify pathogen presence/load before and after intervention.	(1) Days to years (2) Years	Local. Years.	(1) Gabriel *et al.* (2018); Barton (2020) (2) Hoyt *et al.* (2019)

(Continues)

Table 3. *(Cont.)*

Intervention	Example of study design	Timing of testing	Expected impact	Reference
	(2) Monitor the status of species/community before/after the treatment of pathogens.			
Habitat creation	(1) Monitor arrival/long-term survival of organisms in a newly created habitat.	(1) Days to years	Local scale. Years to centuries.	(1) Turner *et al.* (2021)
Habitat restoration	(1) Monitor for potential return(s) of extirpated/extinct species after restoration event(s). (2) Compare the biological community before/after the restoration event (e.g. removal of trash, closing of artificial entrances, removal of pollutants).	(1) Years to decades (2) Days to years	Local to regional scale. Years.	(1) Manenti *et al.* (2019) (2) Tobin & Chambers (2017)
Reintroduction	(1) Monitor long-term survival of organisms after reintroduction. (2) Monitor reproduction events among the introduced individuals.	(1) Years to decades (2) One to several generations	Local scale. Years to centuries.	(1) Zhang *et al.* (2016) (2) Skalski & Word (1994)
Risk assessment	(1) Compare long-term conservation status of species that have been assessed or not against IUCN (or other local) criteria. (2) Test effectiveness of thresholds using physiological experiments. (3) Check if the response of a proposed indicator species for a given threat correlates with the response of other, non/indicator species, within the same community.	(1) Instantaneous to decades, depending on when the assessments were first performed (2, 3) Days to months	Local to regional scale. Years to decades.	(1) Betts *et al.* (2020) (2) Di Lorenzo *et al.* (2019); Pallarés *et al.* (2020b) (3) Korbel & Hose (2017); Strona *et al.* (2019); Di Lorenzo *et al.* (2020); Fattorini *et al.* (2020)
Prioritisation	(1) Compare the fraction of subterranean biodiversity captured by different prioritisation plans to identify the most optimal strategy. (2) Use optimisation algorithms to resolve/simulate different prioritisation scenarios.	(1, 2) Instantaneous	Regional scale. Years to decades.	(1) Abellán *et al.* (2005); Phelps *et al.* (2016); Rabelo, Souza-Silva & Ferreira (2018); Tanalgo & Hughes (2019); Linke *et al.* (2019) (2) Cardoso, Ferreira & Souza-Silva (2021)
Education	(1) Use questionnaires to evaluate public attitudes towards subterranean life in different countries/regions with different educational programs (e.g. guided tours, educational materials/panels) on caves and karst. (2) Use questionnaires to evaluate students' attitudes toward subterranean life before/after being exposed to an educational program.	(1) Instantaneous (2) Days	Local to regional scale. Decades to centuries.	(1) Lopez-Maldonado & Berkes (2017) (1, 2) Ardoin, Bowers & Gaillard (2020)
Monitoring	(1) Estimate detection probability achieved by different monitoring methods and/or indices. (2) Identify trigger points to activate management intervention commensurate with the observed population/habitat change. (3) Test performance and ability to detect change of different monitoring technologies and/or protocols.	(1, 3) Instantaneous to years (2) Years to decades	Local scale. Years to decades.	(1) Mouser *et al.* (2021) (3) Moldovan & Levei (2015) Trevelin *et al.* (2021) (2, 3) Lindenmayer, Piggott & Wintle (2013)

et al., 2009; Pellegrini *et al*., 2016; Korbel *et al*., 2017; Mouser *et al*., 2021; Trevelin *et al*., 2021). Given that monitoring is applied to test the effectiveness of most other conservation interventions (Table 3), we need to ensure that the performance of monitoring technologies and the reliability of monitoring protocols are comprehensively tested.

(4) Protection

While protection (protected areas or *ex-situ* conservation; Fig. 1B) was frequently recommended as a conservation intervention, virtually no studies tested its effectiveness (Fig. 2E). Currently, only 6.9% of known subterranean ecosystems overlap with protected areas globally (Sánchez-Fernández *et al*., 2021). Importantly, most of these subterranean sites are protected simply because they occur within a protected area established for surface species or ecosystems. Given that surface-focused protected areas are rarely designed to account for the vertical dimension of subterranean ecosystems (Linke *et al*., 2019; Sánchez-Fernández *et al*., 2021), including soils (Guerra *et al*., 2020), it is important to understand and test the extent to which protected areas on the surface benefit the ecosystems underneath (Canedoli *et al*., 2022).

A special case of protection is *ex-situ* conservation, that is the conservation of species outside their natural habitat. Off-site conservation is still in its infancy in subterranean biology. According to our literature survey, the only existing *ex-situ* breeding program is focused on the European olm, *Proteus anguinus* Laurenti (Amphibia: Proteidae). This emblematic subterranean salamander is often washed out of its groundwater habitats during flood events. The Tular Cave Laboratory (Kranj, Slovenia) has established an *ex-situ* breeding program for washed-out or injured olms. These individuals are rehabilitated and eventually reintroduced back to their natural habitats (Aljančič, Aljančič & Golob, 2016). One important issue associated with *ex-situ* conservation and reintroduction is that breeding should be sustainable. The health and well-being of animals kept in captivity is of vital importance both for rearing and to prevent reintroduced animals from becoming vectors of pathogens to wild populations. In the case of the European olm, there are diagnostic tools to monitor haematological parameters of animals in captivity (Gredar, Prša & Bizjak Mali, 2018) and protocols have been developed to treat symptomatic individuals (Lukač, Cizelj & Mutschmann, 2019).

(5) Regulation

Regulation encompasses all activities that aim to manage access to subterranean ecosystems and resources. These include legislation, limiting the number of visitors or seasonal closures, gating of cave entrances, and other such measures (Fig. 1B). Despite the fact that legislative actions for subterranean environments have been taken at both national and international levels (Niemiller, Taylor & Bichuette, 2018), their effectiveness in terms of implementation and enforcement has not been rigorously evaluated. Whereas at the regional and national levels many subterranean organisms enjoy protection under endangered species designation, most international legislation and multilateral agreements overlook or only allude to subterranean environments (Wynne *et al*., 2021). Policies for groundwater protection, for instance, have been implemented to protect effectively and use sustainably this resource at regional levels; however, explicit language on groundwater ecosystems is still needed to ensure such sustainability (Elshall *et al*., 2020). To our knowledge, the only multilateral agreement that explicitly considers subterranean habitats and species is the European Union's Habitats Directive (92/43/EEC); however, only a few specialised subterranean species are listed in its appendices, with *Congeria kusceri* (Bole) (Mollusca: Bivalvia), *Leptodirus hochenwartii* Schmidt (Coleoptera: Leiodidae), and *Proteus anguinus* being the most notable examples.

Of the regulation interventions identified in this review, gating of cave entrances was the most tested. These steel structures are often erected to protect cave resources by preventing human access while allowing air, water, and wildlife to pass in and out freely. However, testing the effectiveness of gating has primarily focused on the effects of the gate and its structure on the presence, abundance, and behaviour of bats and has yielded mixed results (Tobin & Chambers, 2017). Only a handful of studies tested for effects of cave gating on other ecosystem components, such as microclimate (e.g. King, 2005; Martin *et al*., 2006), and no studies have examined effects on the abundance and/or behaviour of organisms other than bats.

Regulating human access concerns interventions to mitigate the effects of all human visitors – primarily tourists, but also recreational cavers, divers, and scientists – on cave ecosystems. Understanding the impacts of regulating access could be accomplished in most situations, however only 43% of such studies tested the effectiveness of this regulatory intervention. Most of these tests were conducted in show caves because these sites allow ideal experimental designs due to the presence of a 'tourist' section of the cave, and more pristine areas not accessible to visitors that can be used as a control.

(6) Restoration

Restoration of subterranean ecosystems comprises all interventions aimed at improving and/or recovering species and ecosystems due to human-induced perturbations. These encompass habitat restoration, eradication of alien species, decontamination, reintroduction of species, and the creation of artificial habitats. There were only scattered examples of such interventions in our database, with about 14% of studies testing for effectiveness (Fig. 2E). Encouragingly, the frequency of restoration interventions has been increasing in recent years (Fig. 4C), broadly aligning with the Aichi Convention on Biological Diversity Target 15 of restoring at least 15% of degraded ecosystems by 2020.

Given that restoration is perhaps the most direct intervention, with potentially the greatest impact but generally also the most expensive, such interventions should be carefully planned, tested, and monitored. As pre-intervention pilot studies are typically performed either in the laboratory (Gabriel *et al*., 2018; Barton, 2020) or through modelling/simulation exercises, translation of their findings into practical management actions is not always straightforward. Post-intervention monitoring should include the target species and other components of the ecosystem (including temperature, relative humidity, and nutrient inputs), other relevant taxa (e.g. predators, prey and competitors), and the geological integrity of the site (Meierhofer *et al*., 2022). The few studies that quantified the effectiveness of restoration were focused solely on the target species of the intervention, disregarding the subterranean community as a whole. For example, studies examining the impact of *Pseudogymascus destructans* (the fungus that causes white-nose syndrome) only looked at bat species recovery post-intervention (Hoyt *et al*., 2019; Turner *et al*., 2021). Additionally, mitigation strategies for lampenflora (i.e. autotrophic organisms proliferating in the proximity of artificial light sources in show caves) rarely examined feedback effects on other biotic components (Meyer *et al*., 2017; Pfendler *et al*., 2018). It is possible that the creation of suitable conditions for target species may lead to the decline of populations of other taxa, as different species have disparate habitat requirements (Meierhofer *et al*., 2022). Furthermore, efforts to manage or protect biodiversity can negatively affect other resources, including damaging sensitive areas that contain archaeological, palaeontological, or geological resources.

V. FUTURE DIRECTIONS

Despite the combined effects of multiple anthropogenic stressors threatening subterranean species and ecosystems throughout the world (Mammola *et al*., 2019a; Li *et al*., 2020; Cardoso *et al*., 2020b; Jasechko & Perrone, 2021), there are reasons for optimism. 2021 was nominated the International Year of Caves and Karst (http://iyck2021.org/; later extended to 2022), to promote collective global efforts to raise awareness on subterranean ecosystems, the ecosystem services they provide, and their unique conservation challenges (Veni, 2021). Indeed, we saw several calls for action, often published in general and high-impact journals (e.g. Gladstone *et al*., 2021; Raghavan, Britz & Dahanukar, 2021; Sánchez-Fernández *et al*., 2021; Wynne *et al*., 2021; Oliveira *et al*., 2022). The International Year of Caves and Karst is thus a perfect milestone to pause and reflect on the current status of protection of subterranean ecosystems, confronting an important question: how can we make conservation efforts in subterranean biology more practical, effective, and long-lasting? Although there is no simple answer, we believe that key points include better focusing of our intellectual and funding investments by strategically identifying conservation objectives (Buxton *et al*., 2021), implementing robust study designs and increasing statistical testing (Christie *et al*., 2020), building upon current knowledge (Sutherland *et al*., 2020), and emphasising positive achievements (Balmford, 2017; Akçakaya *et al*., 2018). Here, we have built upon the current literature to provide practical recommendations to test the effectiveness of conservation interventions in subterranean ecosystems (Table 3). We view this as a starting point from which we can shift the current negative trajectory (inset in Fig. 4A), going forth with brighter lights into the darkness. Seven important points emerged from this synthesis to guide decision-makers and researchers towards evidence-based conservation of subterranean ecosystems.

(*a*) *Do not reinvent the wheel*

Modern conservation science emphasises the importance of grounding conservation practice with evidence (e.g. the Conservation Evidence database). Likewise, researchers in the field of subterranean biology should be aware of advances in conservation science not necessarily focused on subterranean ecosystems, to identify solutions and generate new ideas for subterranean issues. Under this paradigm, high-quality literature synthesis will be key to avoid repeating studies on what is already known and, most importantly, will allow us to learn from past experiences to improve current and future practice (McMahan & McFarland, 2021). We view the database associated with this publication as a baseline for building a centralised and curated corpus of literature on the effectiveness of conservation interventions for subterranean ecosystems. Further development of this database could follow the framework recently implemented by Conservation Evidence (Sutherland *et al*., 2019), whereby information is presented according to an effectiveness score for the intervention, the certainty of the evidence underlying it, and a quantification of potential harmful effects.

(*b*) *Be meticulous with study design and reporting of statistics*

The application of robust study designs for testing conservation interventions is sparse, even for well-studied taxa like birds and amphibians (Christie *et al*., 2020). Designing rigorous studies both to test conservation interventions effectively, and to allow thorough reporting of the findings is critically important in subterranean biology – a field in a constant shortage of both personnel and financial resources to conduct robust conservation studies and monitoring projects. An appropriate study design is a key factor determining the strength of the evidence resulting from applied conservation research (Salafsky *et al*., 2019). For example, non-experimental (i.e. correlational) studies produce evidence that is less robust than quasi-experimental (control–impact, or before–after control–impact) and experimental designs (randomised controlled trial). Equally important, we found that the metrics used by studies to measure effectiveness included a multitude of different variables, corroborating previous conclusions (Christie *et al*., 2020). Furthermore, the paucity of quantitative studies and the often-incomplete presentation of their results (Table 1) illustrates the need for more thorough reporting (Cichoń, 2020). Correctly reporting statistical methods, model parameters, sample sizes, and outcomes provides a foundation for other scientists to benefit from the testing of conservation interventions (e.g. using meta-analysis; Gerstner *et al.*, 2017), while ensuring reproducibility.

(*c*) *Embrace ignorance*

A lack of detailed information on subterranean biota should not stall practical conservation activities (Wilson *et al.*, 2007). As for epidemiology or medicine, conservation science is a 'crisis discipline' (Soulé, 1985; Kareiva & Marvier, 2012), often requiring us to make decisions without having all of the information (Cook, Hockings & Carter, 2010). A solid body of literature on tested actions (Sutherland *et al.*, 2019, 2020), complemented with expert opinion (Branco & Cardoso, 2020; Miličić *et al.*, 2021), will often be the best information available to make informed decisions about the most effective conservation intervention(s) for a given subterranean species, community, or ecosystem.

(*d*) *Look beyond your backyard*

We tend to view subterranean ecosystems as isolated systems. In reality, their ecology is highly dependent upon the surface, soil, and/or open-water ecosystems with which they interact (Culver & Pipan, 2014, 2019; Fišer, Pipan & Culver, 2014; Mammola, 2019). In Europe, for example, the effects of contaminated groundwater on groundwater-dependent surface ecosystems were acknowledged and incorporated into the groundwater directive (2006/118/EC). This currently unidirectional view could be elaborated upon with complementary actions to monitor how anthropogenic disturbances on the surface affect subterranean ecosystems. Specifically, it has been shown that laws that subdivide an interconnected resource can often have negative long-term implications that linger long after policy makers begin dismantling the artificial divide (Montesino Pouzols *et al.*, 2014; Arrondo *et al.*, 2018; Owen *et al.*, 2019a). Ideally, then, the best way to promote effective conservation of subterranean environments in a holistic manner is to establish dialogue with surface conservation practitioners, and to use what is known and available (Mammola *et al.*, 2019a; Wynne *et al.*, 2021). This will entail benefiting from conservation strategies and international agreements focused on habitats interconnected with subterranean environments, such as soils (Guerra *et al.*, 2021), karst mountain systems (e.g. GEO Mountains – Mountain Research Initiative), and various groundwater-dependent ecosystems (Cantonati *et al.*, 2020b).

(*e*) *Focus on the gaps*

Conservation interventions appear unevenly distributed across biogeographic regions, taxa, systems, and threats (Fig. 2). Such biases are not unique to the subterranean conservation literature (Troudet *et al.*, 2017; Christie *et al.*, 2020). Further efforts are needed to examine neglected regions properly (Wynne *et al.*, 2021), especially in the Afrotropical, Neotropical, and Indomalayan regions, to fill significant information gaps [see Asase *et al.*, 2021 for suggestions]. Taxa such as microbes and viruses play a critical role in the functioning of subterranean ecosystems (Griebler & Lueders, 2009; Griebler, Malard & Lefébure, 2014; Sánchez-Fernández *et al.*, 2021), and yet they are poorly studied. Furthermore, fissure systems, marine caves, and anchialine systems remain particularly unexplored and underprotected (Mammola *et al.*, 2016; Gerovasileiou & Bianchi, 2021). Finally, emerging global threats such as climate change require redoubled efforts to predict and prevent negative consequences to the subterranean environment (Mammola *et al.*, 2019b).

(*f*) *Be aware of constraints*

While there is an ideal goal of protecting all species and ecosystems, we are working in a deficit of funding, time, and personnel. There will be occasions when the cost of management and the likelihood of achieving conservation goals does not compare favourably with management expenditures allocated for subterranean ecosystems. Therefore, we must define conservation priorities clearly and prioritise efforts to those interventions whose cost-effectiveness has been tested and supported quantitatively.

(*g*) *Dialogue with decision-makers and stakeholders*

Protection is only effective when moving from the scientific to the societal and political arenas (Balmford *et al.*, 2021; Kadykalo *et al.*, 2021). Engaging with the public, non-governmental organisations, government conservation and environmental protection agencies, and other decision-makers is necessary but often overlooked by academics (Knight *et al.*, 2008; Arlettaz *et al.*, 2010). Furthermore, conservation recommendations that appear in the most prestigious journals often do not reach their intended targets (the decision makers). This entails establishing a dialogue with regional, national, and international initiatives, or organisations such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the IUCN. Scientists should strive to foster local initiatives for the development of conservation or recovery plans with relevant authorities, even if it requires stepping down from the academic ivory tower (Arlettaz *et al.*, 2010). Only in this way will we ensure that the visibility of the surface environments does not lead to conservation programs that fail to recognise both the scientific importance and ecosystem services provided by subterranean ecosystems.

VI. CONCLUSIONS

(1) Subterranean ecosystems are some of the most understudied ecosystems on Earth, and contain a high diversity of specialised organisms accounting for a unique fraction of the global taxonomic, phylogenetic, and

functional diversity. This biodiversity is exposed to escalating anthropogenic threats. A scientifically informed protection of subterranean biodiversity is thus a matter of the highest importance.

(2) We provide the first quantitative global assessment on subterranean ecosystem conservation, by synthesising 708 publications (1964–2021) that discussed, recommended, or implemented 1,945 conservation interventions.

(3) We documented a consistent increase in the number of studies from the 2000s; yet, the proportion of studies quantifying the impact of conservation interventions has significantly decreased in the last 20 years. Overall, the effectiveness of 31% of conservation interventions was tested statistically, although this proportion varied substantially by type of intervention, taxon, and subterranean system.

(4) There were important trends in the data that can guide future research. Most studied threats were pollution, disturbance due to tourism, and habitat change, whereas limited research was devoted to understanding climate change effects, alien species, pathogens, and overexploitation. Assessments of the effectiveness of conservation interventions were heavily biased towards indirect measures (monitoring and risk assessment), a limited sample of organisms (mostly arthropods and bats), more accessible systems (terrestrial caves), and temperate regions (Europe and North America).

(5) We provide practical suggestions for developing study designs able to test quantitatively the effectiveness of conservation interventions in subterranean ecosystems (Table 3). Our recommendations mostly build upon current literature on subterranean ecosystems, but we also draw upon ideas from research carried out on the surface.

(6) Our synthesis establishes baseline data that can be expanded in the future, enabling, for example, the ability to perform meta-analyses aimed at quantifying the effectiveness of conservation interventions. This will help generate quantitative knowledge about interventions likely to yield the greatest impacts depending upon the subterranean species and habitats of interest.

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VIII. AUTHOR CONTRIBUTIONS

S.M. conceived the idea. S.M., M.B.M., and P.C. designed the methodology. All authors (except for A.S., L.D., and M.I.) extracted data from the literature. S.M. and M.B.M. analysed data and wrote the first draft. S.M. prepared the figures. All authors contributed to the writing with suggestions and critical comments.

IX. DATA ACCESSIBILITY

The curated literature database supporting this study is available in Zenodo (doi: 10.5281/zenodo.6088818). R code to reproduce the analyses is also available on GitHub (https://github.com/StefanoMammola/Analysis_Practical-Subterranean-Conservation.git).

X. REFERENCES

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XI. Supporting information

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

Appendix S1. Full list of papers extracted from the *Web of Science*, with an indication of whether it was included in the analysis and, if not, the reasons for exclusion.

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