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Review

Shedding light on the hidden world of subterranean fauna: A transdisciplinary research approach

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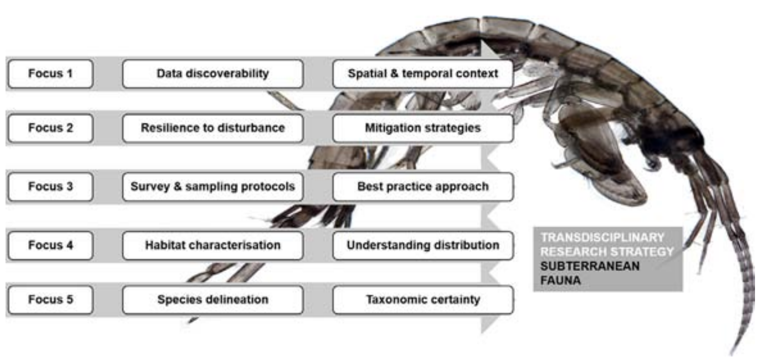
HIGHLIGHTS

- Knowledge status of subterranean fauna in the context of anthropogenic disturbances
- Consensus on key knowledge gaps that hinder environmental decision making
- Innovative, multidisciplinary research strategy to address complex questions
- Demonstration of a transdisciplinary approach that maximises benefits to end users
- Reducing uncertainty for policy makers; minimising risk to groundwater ecosystems

GRAPHICAL ABSTRACT



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ABSTRACT

Subterranean environments contain a diverse and unique obligate fauna: either aquatic living in the groundwater or terrestrial living in voids above the water table. In the arid region of the western part of the Australian continent, a particularly rich subterranean fauna coincides with a concentration of natural resource extraction operations. Since the inclusion of subterranean fauna in assessments of environmental impact in the mid-1990s, taxonomic research in Australia on this group of mainly invertebrates has grown exponentially. However, remaining knowledge gaps continue to frustrate both environmental regulators and development proponents due to high uncertainty in the decision-making process. In early 2017, the Western Australian Biodiversity Science Institute was tasked with leading the development of a research program to improve on the current state of knowledge of subterranean fauna. To balance the diverse environmental, economic and social needs of a range of stakeholders, transdisciplinary principles were applied to program development. A clear consensus on five broad focus areas to progress include: (1) data consolidation; (2) resilience to disturbance; (3) survey and sampling protocols; (4) abiotic and biotic habitat requirements; and (5) species delineation. In the context of these focus areas; we describe the research program development, reviewing the status of knowledge within each focus area, and the research initiatives to close the gaps in knowledge. We argue that, by adopting a transdisciplinary approach, the likelihood of success of the research program, as measured by the effective translation and adoption of research findings, will be maximized. This review is timely given the ever-increasing demand on

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groundwater systems for water extraction worldwide. A holistic understanding of the influence of anthropogenic activities on these ecosystems, and the functional role of organisms within them, will help to ensure that their health is not compromised.

Contents

1. Introduction

Along with its significant marine values including coral reef structures, marine invertebrates and marine megafauna, the World Heritage listed Ningaloo Coast, located along a remote section of Western Australia's East Indian Ocean, is recognised globally for its extensive karst, and the associated unique and spectacularly diverse subterranean fauna (Humphreys, 2000; UNESCO World Heritage Centre, 2018). It is also in this region that subterranean fauna were first considered in the mid-1990s in environmental impact assessments associated with natural resource development projects (EPA, 2012). Since then, research in Australia pertaining to subterranean fauna has grown exponentially with much learnt about taxonomic relationships and evolutionary history (reviewed in Humphreys, 2008 and Hose et al., 2015). However, little effort has gone into improving our knowledge of the basic biology and ecology of subterranean fauna (Humphreys, 2018), which is critical to better understanding their resilience to anthropogenic disturbances. What we do know is that certain characteristics of their distribution, such as their restricted ranges and high level of endemism, and their adaptations to a low energy environment, increases the susceptibility of this distinctive fauna to localised impacts on their habitat (Harvey et al., 2011; Hose et al., 2015; Halse, 2018).

In Australia, species diversity of both stygofauna (i.e. those residing in the groundwater) and troglofauna (i.e. those inhabiting the unsaturated zone above the water table but below the surface) is surprisingly high, particularly in the arid western part of the continent (Humphreys, 2008), with projections of >4000 species given the current rate of species discovery (Guzik et al., 2011). What largely sets them apart from their Northern Hemisphere counterparts is their habitat, with most known Australian species occupying small underground cavities (< 500 mm) distributed within suitable substrates, as opposed to cave systems (Halse, 2018). Most of the Australian diversity coincides with areas highly prospective to mining, and in Western Australia these areas have been the focus of environmental impact assessments. Mining activities, such as excavation and groundwater drawdown and reinjection, can threaten the persistence of whole populations and even entire species of subterranean fauna (Nevill et al., 2010; Stumpp and Hose, 2013; Halse, 2018). Changes to micro-climate, hydrology, water quality and nutrient inputs are added threats (Tomlinson and Boulton, 2010; Hose et al., 2015; Korbel and Hose, 2015). To this day, determining the persistence of subterranean fauna after these disturbances remains a major challenge (Hose et al., 2015).

Most of the difficulty lies in the fact that these predominantly minute invertebrates live in a hidden world. An assessment of impact requires knowledge on the distribution of individual species both within and beyond a development 'footprint'. Currently, estimates of distribution largely rely on sampling that is restricted to drill holes created for minerals exploration or water supply, which may or may not intersect suitable habitat (Halse, 2018). Consequently, the distribution of these sampling locations is also highly biased both spatially and environmentally (Mokany et al., 2019). The significant cost of establishing new drill holes usually precludes more extensive systematic surveys (Halse, 2018; Humphreys, 2018), hampering accurate estimates of distribution and broader habitat suitability. The added complexity of the third vertical dimension of subterranean environments challenges our understanding of local scale habitat availability (Ficetola et al., 2018). Species detection rates also tend to be low, meaning that many sampling events are often required to estimate the species assemblage at any single location (Eberhard et al., 2009). Species delimitation poses an additional issue for this highly cryptic group where species have evolved to the same dark, stable and low energy environment (Asmyhr and Cooper, 2012; Hose et al., 2015). These limitations to a holistic understanding of subterranean ecosystems, and the role of subterranean fauna within them, exacerbate any decision-making process whether it is for impact assessment or conservation management.

The growing frustration of environmental regulators faced with uncertain predictions of impacts, and development proponents due to associated delays in decisions, has highlighted the need for a more coordinated effort to improve the current state of knowledge of subterranean fauna and their ecosystems. A transdisciplinary approach to developing a program of research that balances the diverse needs of stakeholders is needed to maximise economic, environmental and social outcomes (Roux et al., 2010; Lang et al., 2012; Campbell et al., 2015). This approach necessitates a close collaboration between researchers and end users of the research to define the problem (or common goal), identify the knowledge gaps and formulate a strategy to close them (Roux et al., 2010; Campbell et al., 2015). Sustained discourse and engagement between all parties throughout the life of the research program is essential to ensure that research outputs are tailored to meet both the needs of end users, and they can be implemented to address real-world problems (Laurance et al., 2012; Campbell et al., 2015). According to Roux et al. (2010), the concept of 'transdisciplinarity' shifts an emphasis from research as the producer of information, to research contributing to a process of problem solving through participation and social learning.

As an independent science broker, the Western Australian Biodiversity Science Institute (WABSI) was engaged in 2017 to develop a coordinated state-wide subterranean fauna research program based on the transdisciplinary principles above. The intent is to encourage collaboration rather than duplication of research effort. The particular challenge here is to find solutions that allow the state of Western Australia to take advantage of its rich minerals resources to support its ongoing economic development, while minimising adverse impacts on the environment, in this case, subterranean fauna. Indeed, there is a growing community expectation that the resources sector adheres to sustainability practices (Hose et al., 2015). Here, we describe the research program development, review the critical knowledge gaps that were identified by end users, and outline the emerging research initiatives to address these, all in the context of a transdisciplinary research framework.

2. Methods

The research program development pathway is illustrated in Fig. 1. The Western Australian Biodiversity Science Institute and the Chamber of Minerals and Energy of Western Australia co-hosted an initial workshop attended by representatives from the minerals resources sector, policy makers, and environmental regulators and their advisors, to identify the critical gaps in knowledge about subterranean fauna that made informed decision making challenging. During this workshop, presentations on the current state of knowledge of subterranean fauna, as well as issues from a regulatory perspective, provided the context for further discussion. Participants (21 in total), were divided into five breakout groups and asked to identify major knowledge gaps that presented challenges to their respective organizations, including questions around process. Based on these responses, the key focus areas were identified collectively. Each group then ranked these in terms of need in terms of improving decision making relevant to their organization. There was a clear consensus on five broad focus areas to be progressed, ranked in order of importance: (1) data discoverability and accessibility to provide spatial and temporal context; (2) improved understanding of resilience to disturbance to inform mitigation strategies; (3) improved survey and sampling protocols to optimise effectiveness and efficiency; (4) improved understanding of habitat requirements to better define species distributions; and (5) more accurate, efficient and consistent species identification processes to increase taxonomic certainty. This workshop also confirmed a widespread agreement for developing a collaborative subterranean fauna research program.

A range of scientific specialists with knowledge on subterranean fauna (14 participants) were invited to a second workshop to scope research projects designed to address the knowledge gaps identified above. During this workshop, participants were divided into two groups. One was tasked to develop project ideas that addressed 'resilience to disturbance' and 'habitat characterisation', and the other to address 'survey and sampling protocols' and 'species delineation'. 'Data consolidation', while recognised as important, was not discussed in any detail as it was not considered a research question per se. To provide context, the specific questions raised by end users in the first workshop under each focus area, were provided to each group. In their approach, participants were asked to include: project outcomes and benefits to the end user, project outline and structure (i.e. one large project or a combination of short and long-term projects), proposed key personnel, an estimate of timeline and an indication of budget requirements if known.

A final workshop brought together the technical expertise and experience of a broad range of stakeholders from the scientific and resources sector, policy makers, potential funders, and environmental consultants (32 participants in attendance). Multiple disciplines were represented including hydrologists, geophysicists, geologists, geochemists, biologists, geneticists, taxonomists and spatial modellers. The purpose of this workshop was to review and validate components of the subterranean fauna research program emerging from the previous two workshops, and to populate outstanding components of this program not addressed in the second workshop. The definition of a 'shared vision' was also discussed. Again, contextual information was provided (though many had attended at least one of the previous workshops) before their allocation to four groups based on interests and relevant expertise. As in the second workshop, participants were asked to formulate a scope of work for each research idea specifically addressing the knowledge gaps.

3. The research program – a shared vision

The outcomes of the three workshops provided the basis for the research program plan summarised in Table 1. This should be viewed as a guiding framework to direct resources to research activities that specifically address end-user needs. The agreed shared vision was to "dramatically improve assessments of the impacts of resource developments and threat mitigation strategies on subterranean fauna by transforming our knowledge of patterns and processes in subterranean ecosystems." The sections presented below address the five broad focus areas covering the critical gaps in knowledge about subterranean fauna. Within each of these sections, a rationale for the research (i.e. what is known and unknown), associated research ideas generated during the expert workshops, and the intended outcome are outlined. While these are focused on issues within Western Australia, they are likely to be applicable more broadly, both nationally and internationally.

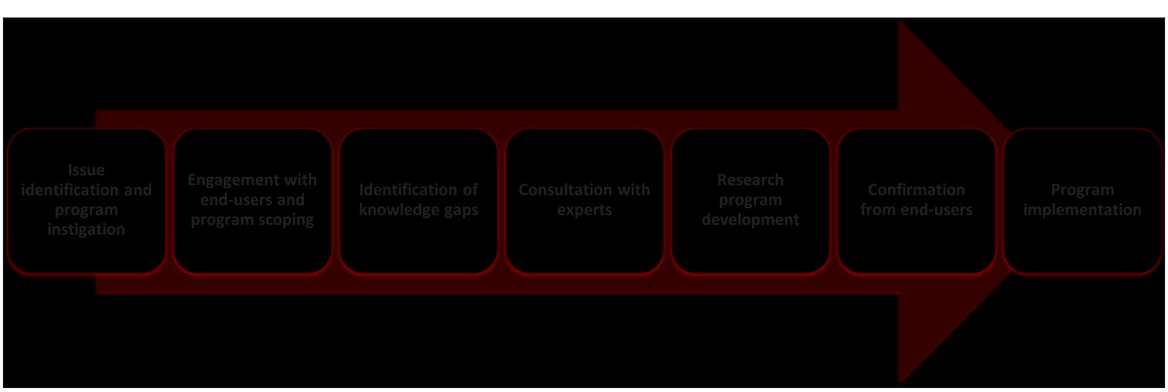

Fig. 1. Research program development pathway.

Table 1
Summary of proposed research initiatives for each focus area identified as a critical gap in knowledge and the expected end user outcome.

Focus area	End user outcome	Research direction
Data consolidation	Data associated with subterranean fauna is discoverable and accessible	• Consolidate existing subterranean fauna records and associated habitat attributes in a publicly accessible information system
Resilience to disturbance	Threat mitigation strategies are more targeted and effective	• Establish successful animal husbandry techniques in the laboratory for selected species • Review historic and newly collected monitoring data to assess the effects of disturbances on subterranean fauna • Examine experimentally the sensitivity of fauna to changes in physicochemical conditions and toxins • Examine experimentally the lateral and vertical mobility of fauna in response to water level change • Examine changes to and recovery of fauna in dewatered/-injected areas
Survey and sampling protocols	Efficiency of survey and monitoring programs are optimised	• Investigate the application of meta-barcoding and eDNA approaches • Statistically appraise historical data to better understand species detection, sampling efficiency and accuracy • Investigate and validate new sampling methods to improve species detection using an experimental framework • Establish long term monitoring sites to investigate natural variability
Habitat characterisation	Ability to map the distribution of suitable habitat is significantly advanced	• Develop a standardised approach for subterranean fauna assessment based on three-dimensional habitat characterisation • Create a validated toolkit to characterise energy and nutrient sources and trophic interactions across a range of groundwater habitats
Species delineation	Efficiency and accuracy of species identifications is significantly increased	• Develop a best practice approach for recognising species boundaries by integrating multiple lines of evidence (i.e. morphology, multiple genetic markers & environment)

3.1. Data consolidation

The inclusion of subterranean fauna in environmental impact assessments (EIA) has resulted in a proliferation of survey information. While the Western Australian Environmental Protection Authority (WA EPA) specifies that specimens, and accompanying data, collected during these surveys is to be offered to the Western Australian Museum, historically there has been no formal requirement for the wider array of data associated with the EIA process to be captured and consolidated (EPA, 2012). This data leakage represents a missed opportunity in terms of a comprehensive data asset that would provide defendable information for more informed decision making (EPA, 2012). For example, a database collating stygofauna records across the Australian state of Queensland enabled a regional review of biodiversity patterns and environmental associations to inform land use planning (Glanville et al., 2016). A further example is the PASCALIS (Protocols for the ASsessment and Conservation of Aquatic LIfe in the Subsurface) project; an integrated database with distributional information of stygofauna across six European countries (Gibert et al., 2005). This database has been used to evaluate patterns in distributions and to identify biodiversity hotspots (Deharveng et al., 2009), and to inform the establishment of a groundwater reserve network (Michel et al., 2009).

In 2017, the Western Australian Government launched the Index of Biodiversity Surveys for Assessments (IBSA; https://dwer.wa.gov.au/ibsa), the Department of Water and Environmental Regulation's online portal to access information about land-based surveys in Western Australia. The objective of IBSA is to capture and consolidate data contained in biodiversity survey reports in Western Australia to support assessments and compliance under the *Environmental Protection Act 1986* and to provide a platform to make the information publicly available. Everyone who conducts land-based biodiversity surveys to support assessment and compliance is now required to submit the survey report, associated metadata and spatially referenced raw data from the survey via the IBSA portal. This is a positive first step; however there remains a considerable volume of historical information that has not been captured via this process. An initiative to capture and consolidate historical subterranean fauna records, and associated habitat attributes, in a publicly accessible information system has been proposed. The intended outcome is that data associated with subterranean fauna are discoverable and accessible to everyone.

3.2. Resilience to disturbance

In the context of resource extraction operations, habitat removal, blasting, groundwater drawdown, inundation, salinisation, and changes to hydrology, water quality and nutrient inputs have been identified as potential threats to subterranean fauna (EPA, 2016a; Hose et al., 2015; Halse, 2018). However, determining the likely significance of these changes in habitat on the persistence of subterranean fauna after the impact remains a major challenge when undertaking environmental impact assessments (EPA, 2016a; Hose et al., 2015). Complete removal of habitat has obvious implications however the impact of groundwater extraction on stygofauna is not as clear due to a poor understanding of the vertical distribution of species and communities in the aquifer (Stumpp and Hose, 2013). For example, it is not known whether species are partitioned according to depth below the surface, whether they can migrate down the water column or if they can survive in small pockets of water remaining after drawdown (Nevill et al., 2010; Stumpp and Hose, 2013). We know that some aquifers have gradients in physicochemical properties with increasing depth, such as salinity levels, which influence the distribution of stygofauna communities (Humphreys, 2006; Humphreys et al., 2009). Niche partitioning of species according to salinity tolerance, and hence depth, is therefore likely. Hose et al. (2017) also report that the abundance of stygofauna differs according to fine scale changes in the sedimentary properties of different layers in a perched aquifer. Groundwater drawdown is also likely to have consequences for troglofauna by altering humidity (EPA, 2012); however, actual humidity thresholds are not clear. Some troglofauna have been shown to be highly sensitive to changes in temperature (Novak et al., 2014; Mammola et al., 2018).

Similarly, while it is recognised that changes to the rate and volume of groundwater moving through an aquifer can alter nutrient distribution and oxygen infiltration, the level of impact of these changes on subterranean fauna and the flow-on effects on ecosystem function have yet to be quantified (Nevill et al., 2010; Tomlinson and Boulton, 2010). There is also little evidence regarding what effect other above-ground disturbances have on subterranean fauna communities, such as the impact of vegetation removal on nutrient supply or the effects of overburden dumps on oxygen, nutrient or toxin inputs (Hancock et al., 2005; Hose et al., 2015). In a Moroccan study, El Adnani et al. (2007) suggest that their observed decrease in stygofauna richness in areas downstream of a mine tailings site compared to those upstream, was due to changes in water quality caused by mining activity.

Understanding the ability of subterranean fauna to recover from disturbances is also hindered by the lack of knowledge about life history characteristics, such as longevity, fecundity and length of development (Humphreys, 2008). European studies on stygofauna have indicated species typically have a life history adapted to a stable, low energy aquifer environment, which may be dramatically disturbed by rapid environmental change (Tomlinson and Boulton, 2010). The life history characteristics described, such as longer life cycles and lower fecundity, compared to related surface water species (Dole-Olivier et al., 2000), also have implications for recolonisation capacity following local extinction.

In stark contrast to surface water systems, there is limited knowledge on the response of stygofauna to changes in groundwater quality (Hose et al., 2015). There is emerging evidence that stygofauna themselves play a role in maintaining groundwater quality (e.g. Smith et al., 2016; Griebler et al., 2019) and the hydraulic properties of the groundwater (Hose and Stumpp, 2019). Leaks or leaching from tailings and waste water, and introduction of toxins, can result in alterations to ground water chemistry and quality (El Adnani et al., 2007). Intrusion of saline water into freshwater aquifers may also have a toxic effect on stygofauna (Hancock et al., 2005; Hose et al., 2015). Although this is likely to be region dependent, since some species are known to occur in highly saline habitats such as the anchialine systems along the Western Australian coast (Humphreys, 2008), and the greenstones and calcretes of the southern Yilgarn region in Western Australia (Humphreys et al., 2009; Karanovic et al., 2013).

To inform mitigation strategies to ameliorate possible threats, both laboratory and field studies that better quantify tolerances of subterranean fauna to changes in habitat condition have been proposed. This includes establishing successful animal husbandry techniques in the laboratory, as well as reviewing historic and newly collected data to assess the effects of disturbances on subterranean habitats and the species they support. For example, where the WA EPA has concluded that there are significant residual impacts to subterranean fauna as a result of a development, conditions are likely to be imposed to reduce or mitigate these impacts. If ongoing monitoring has been stipulated as a condition, the data collected once mining has commenced, are a potential source of important information. Laboratory experiments are also likely to be useful for examining sensitivity of fauna to changes in physicochemical conditions and toxins, and lateral and vertical mobility in response to water level change (e.g. Stumpp and Hose, 2013; Hose and Stumpp, 2019). Field experiments designed to incorporate stratification according to depth (e.g. discrete interval sampling), such as the use of nested bores or by deploying packers to isolate sections of the bore (Sorensen et al., 2013), are proposed to examine the lateral and vertical movement of fauna in response to changes in groundwater level.

3.3. Survey and sampling protocols

Adequate survey is integral to understanding both the species present within a given area and to determine their distribution. Several studies have described sampling methodologies for stygofauna (e.g. Allford et al., 2008; Eberhard et al., 2009; Halse et al., 2014) and troglofauna (e.g. Halse and Pearson, 2014) when accessed via bores (drill holes or wells). The most common sampling method entails hauling a phreatobiological net through the water column or using baited traps for troglofauna (Humphreys, 2018). The WA EPA also provides technical guidance to development proponents on the minimum requirements for subterranean fauna survey for the purpose of environmental assessments (EPA 2016b & c). However, due to the generally low capture rate of individuals, and the restricted sampling access via bore holes established for other purposes such as minerals exploration, survey strategies to date have proved relatively inefficient, with many species only detected in a single bore (Eberhard et al., 2009). There can also be a high level of false absences, whereby a species is not detected even though it is present, resulting in the underestimation of distribution (Eberhard et al., 2009; Zagmajster et al., 2018).

While it is recognised that some level of repeated sampling is required to adequately detect a significant proportion of the species occurring at a site (Eberhard et al., 2009, 2016; Zagmajster et al., 2018), there are uncertainties regarding the actual level of survey effort required to reach a predetermined threshold. Typically, it is the relatively rare species, and those that have geographically restricted ranges, that are of most conservation concern, and their detection often requires many more sampling events than the more common and widespread species. This is a particular issue for subterranean fauna given the high level of short-range endemism, with range sizes of troglofauna tending to be an order of magnitude smaller than those of stygofauna species (Eberhard et al., 2009; Halse et al., 2014). Some studies have indicated that the level of effort recommended by the WA EPA technical guidance for subterranean fauna is inadequate (Karanovic et al., 2013; Eberhard et al., 2016), and that the survey design needs to consider spatial and temporal influences on habitat suitability (Dole-Olivier et al., 2009; Karanovic et al., 2013).

Detecting a change in species abundance provides an additional challenge, as the survey effort required is considerable (Eberhard et al., 2009). There is also uncertainty regarding the setting of thresholds to determine 'impact', as opposed to natural fluctuations in abundance over time. The approach of detecting the presence of DNA in the environment (eDNA), such as in soil and water, that has been shed from an organism, has been shown to be effective in both marine and aquatic environments (Thomsen and Willerslev, 2015). Without the need to capture the organisms, this approach may be a means of improving the accuracy and efficiency of subterranean fauna survey and monitoring. Recent advances in the area of next generation sequencing (NGS) metabarcoding mean that only trace amounts of DNA are required, thereby facilitating the detection of rare taxa (e.g. Ficetola et al., 2015; Valentini et al., 2016). Preliminary results from a recently completed proof- of-concept project indicated that the eDNA approach is a viable option for holistic surveys of subterranean fauna (White et al., 2018). Environmental DNA has also successfully been used to detect target species of both subterranean invertebrates (e.g. Niemiller et al., 2018) and vertebrates (e.g. Gorički et al., 2017).

With a clear end-user need to refine survey and sampling protocols to ensure contemporary approaches are efficient, repeatable and effective, research has been proposed to: 1) investigate the utility of eDNA and metabarcoding techniques for sampling and monitoring subterranean fauna, 2) review historical survey data to better understand sampling efficiency and accuracy using existing approaches, 3) using a combination of field, laboratory and modelling inputs, investigate and validate new sampling methods to improve species detection using an experimental framework, and 4) establish long term monitoring sites (multiple bores) to investigate natural variability. The intended outcome is a best practice approach to subterranean fauna survey and monitoring to inform environmental management.

3.4. Habitat characterisation

Understanding the habitat preferences of subterranean fauna is critical to making realistic predictions of the extent of suitable habitat. In the context of assessing likely impacts of proposed developments, this extent needs to be estimated both within the development area but also in the surrounding region. Due to the difficulty in detecting subterranean fauna species, the WA EPA moved towards a more risk-based approach whereby habitat surrogates can be used to infer the likely presence of a species beyond the area surveyed (EPA, 2016b), but the efficacy of this approach remains untested.

Regarding abiotic characteristics, it appears that hydrological connectivity (including to the surface), salinity and dissolved oxygen levels, and geological setting (karst, alluvium and colluvium, or fractured rock) influence the occurrence of stygofauna (Dole-Olivier et al., 2009; Halse et al., 2014; Hose and Stumpp, 2019). However, there remains limited understanding of their micro-habitat requirements, such as the size, degree and distribution of interconnected void spaces within geological formations which determine the transmissivity of an aquifer (Korbel and Hose, 2015). There is also a poor understanding of the fine-scale variation in suitable habitat over spatial and vertical scales, and the degree of habitat connectivity is particularly difficult to determine (Bradford et al., 2013). Habitat requirements of troglofauna are even less understood apart from a general association with weathered iron ore deposits (Halse, 2018) and, karst and pseudokarst landscapes (Humphreys, 2017). Recent studies examining two-dimensional spatial patterns of subterranean fauna, have highlighted the challenges inherent in both the species data (i.e. poor taxonomic resolution, incomplete sampling and spatial bias) and sourcing relevant environmental data layers to use in predictive models (Christman et al., 2016; Mammola et al., 2018; Zagmajster et al., 2018; Mokany et al., 2019). Mokany et al. (2019) used a community-level approach to address some of these issues.

A poor understanding of ecosystem function, including trophic relationships, means that there is also a lack of knowledge of the biotic factors that influence the occurrence of subterranean fauna (Tomlinson and Boulton, 2010; Saccò et al., 2019). If we are to truly maintain ecological integrity (EPA, 2016a) in the face of anthropogenic disturbances, research into how subterranean ecosystems function is fundamental (Tomlinson and Boulton, 2010). We know that the food web is truncated and lacks primary photosynthesising producers, and so the main food source, organic matter, filters down from surface environments; chemoautotrophy being a notable exception (Gibert and Deharveng, 2002). There is also a general assumption that because of the scarcity of food, tropic specialisation is lacking (Gibert and Deharveng, 2002). However, more recent studies involving the application of stable isotope techniques have revealed greater potential complexity in the food web (e.g. Bradford et al., 2014; Francois et al., 2016; Hutchins et al., 2016).

To advance our understanding of preferred habitat for subterranean fauna, two primary areas of research are proposed based on multidisciplinary and innovative approaches. The first area aims to develop, test and apply a standardised approach for characterising subterranean fauna habitat in three dimensions. Three-dimensional models of the sub-surface can already be produced by integrating geophysical data collected for minerals exploration, along with other information (e.g. https://www.leapfrog3d.com/). Similar approaches are also likely to be applicable to 3D-modelling of subterranean fauna habitat. The second area is the creation of a toolkit to characterise energy and nutrient sources, and trophic interactions, across a range of groundwater habitats using a combination of DNA metabarcoding and compound-specific stable isotope analyses to characterise food webs and ecosystem function (see Saccò et al., 2019). By transforming our understanding of abiotic and biotic characteristics of subterranean ecosystems, the outcome is a clearer understanding of distributional patterns and ecosystem function.

3.5. Species delineation

The recognition of a species within a given area is the first step in a determining potential environmental impact of any development proposal. However, traditional species delineation based on morphological characteristics is often problematic for subterranean fauna. Adapting to a stable, nutrient-poor and dark environment has led to convergent evolution among isolated populations, and as such, a high proportion of species are morphologically cryptic (Finston et al., 2007; Hose et al., 2015). To add to the confusion, there is also considerable morphological variation within some genera, blurring species boundaries (Finston et al., 2004; Karanovic and Bláha, 2019). With emerging molecular genetic tools, DNA barcoding has become a useful approach to distinguish between cryptic species (e.g. Asmyhr and Cooper, 2012; Framenau et al., 2018). However, due to the limited capacity of subterranean fauna to disperse, problems at the molecular level arise from the fact that there is often a high level of genetic structuring within populations, and intraspecific genetic variation is high (Harms et al., 2018). For example, there are cases where a large sequence divergence is observed between two populations yet there is no evidence of long-term geological barriers (e.g. Asmyhr et al., 2014). As the degree of sequence divergence between species tends to vary among taxonomic groups, it is also important to determine the level of variation within each group when comparing across multiple taxonomic groups (Halse, 2018). Practically, it can also be difficult to extract DNA from these tiny organisms which have delicate exoskeletons that often degrade relatively quickly (Perina et al., 2018). Given these complexities, many taxonomists have approached the challenge by integrating multiple lines of evidence such as key morphological characters (including geometric morphometrics), the use of multiple genetic markers in molecular analyses, and environmental information (e.g. Javidkar et al., 2016; Karanovic et al., 2016; Eme et al., 2018; Perina et al., 2018; Karanovic and Bláha, 2019).

The current high rate of species discovery in Australia (Guzik et al., 2011), and the considerable proportion of subterranean fauna species yet to be formally described (Harms et al., 2018), means that without an adequate taxonomic framework, assessments of environmental impact are likely to become significantly more difficult. For example, of the estimated 4000 species in arid Western Australia, only 10% has formal descriptions (Guzik et al., 2011). Research activity to increase taxonomic certainty by developing a standardised best practice approach for recognising species boundaries has been proposed. Using an integrated approach described above, the idea is to initially target an exemplar taxonomic group to build a rapid identification ‘toolkit’ and then test the generality of the approach by applying it to other closely related groups. The scope of work includes an audit of existing specimens, building a multi-gene DNA barcode reference library, establishing a procedure for sequencing old and degraded samples, guidance for the collection of samples specifically for molecular analyses, and morphological descriptions. The intended outcome is to significantly increase the efficiency and accuracy of species identifications.

4. A transdisciplinary approach

As the scope of the research program described is large, sources of funding are uncertain, and the nature of individual components varies widely, a strategic approach to implementation will be necessary. The successful delivery of the program will depend on sustained engagement between end users and researchers to update priorities, ensure research outcomes are meeting end-user needs and to identify funding opportunities (Laurance et al., 2012). An appropriate governance structure to guide this process is likely to be fundamental. In this case, a steering committee that represents the strategic interests of all partners including end users, researchers and policy makers has been established to meet this need. Starting with ‘early win’ short-term projects to demonstrate achievement and build trust also makes sense strategically. Early successes can then be leveraged to commence addressing the more complex, long-term and resource demanding issues. An end-user driven approach also encourages investment, as has been the case here, with early projects solely funded by stakeholders.

As the program is implemented, one measure of success is the extent to which research outcomes are adopted (Campbell et al., 2015). Effective translation of outcomes using appropriate forms of delivery is required to facilitate the uptake of the new knowledge (Lang et al., 2012). For example, while it is recognised that peer-reviewed journal articles are one important form of information dissemination, particularly from a scientist's perspective, few development proponents, environmental practitioners or policy makers are likely to read them. As such, other forms of communicating research results, such as technical guidance statements, will also be important. As a science broker, WABSI has a key role to encourage knowledge exchange and sharing between end users and researchers. By collaboratively defining the common goal, knowledge gaps and research objectives from the very beginning of program development, ownership of research outputs by the various stakeholders is encouraged (Campbell et al., 2015).

Success of the research program is also contingent on a sound understanding of the benefits it will provide to all stakeholders, particularly in times of constrained research funding. While not explicitly addressed in this paper, a complementary analysis identified several major benefits. In summary, environmental regulators directly benefit by having access to new knowledge to support robust and timely decisions based on scientific rigour, and to guide policy setting. Conservation agencies benefit in relation to land use planning, and a better understanding of both the conservation status of subterranean species and communities, and mitigation strategies to promote species persistence. Major benefits to industry are primarily related to more efficient decisions regarding development proposals and a stronger social licence to operate given the increased community trust in environmental decisions. Social values are broad ranging but are centred on the promotion of sustainable developments that balance economic growth and adequate protection of environmental values, and the ecosystems services subterranean fauna provide (Griebler and Avramov, 2014).

5. Conclusions

This paper describes the development of a collaborative research program specific to the needs of Western Australians; however, it also represents a case study that has broad applicability both nationally and internationally. Firstly, a poor understanding of the three-dimensional complexity of subterranean ecosystems both at the local and landscape scale poses an issue world-wide, particularly in relation to confounding conservation and land use planning decisions (Ficetola et al., 2018) and managing valuable groundwater ecosystems (Humphreys, 2011; Griebler et al., 2019). This paper is timely given the increasing significant demand on groundwater systems and the consequent considerable pressure on them (Richey et al., 2015; Griebler et al., 2019). Better understanding the influence of anthropogenic activities on groundwater ecosystems, and the functional role of organisms within them, will help to ensure that their health is not compromised. Secondly, there is a growing trend of using transdisciplinary research approaches to address complex environmental problems (Roux et al., 2010), an approach that has become a core element of global sustainability science (Cundill et al., 2015). The value the Australian government places on transdisciplinary approaches is evident in their funding of multi-million-dollar programs such as the National Environmental Science Programme (NESP), whereby a proportion of the budget is dedicated to knowledge brokering, stakeholder engagement and communication strategies (Campbell et al., 2015). The application of such approaches to bridging the gap between science and policy is also of considerable international interest (Reyers et al., 2010; Hering, 2018). This participatory approach to science delivery will bring a step-change in the environmental management of a unique and diverse fauna, and thereby provide a benefit to multiple stakeholders that far outweigh the cost.

CRediT authorship contribution statement

Lesley Gibson: Conceptualization, Methodology, Writing - original draft, Visualization. **William F. Humphreys:** Conceptualization, Validation, Writing - review & editing. **Mark Harvey:** Conceptualization, Validation, Writing - review & editing. **Bridget Hyder:** Conceptualization, Writing - review & editing. **Andrew Winzer:** Conceptualization, Writing - review & editing.

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Lesley Gibson: Conceptualization, Methodology, Writing - original draft, Visualization. **William F. Humphreys:** Conceptualization, Validation, Writing - review & editing. **Mark Harvey:** Conceptualization, Validation, Writing - review & editing. **Bridget Hyder:** Conceptualization, Writing - review & editing. **Andrew Winzer:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

Authors have no competing interests to declare.

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