



Towards invasion ecology for subterranean ecosystems

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Abstract

Invasive alien species (IAS) are widely recognized as a major threat to ecosystems globally. Despite the growing interest and research effort on biological invasions, the impact of IAS on both terrestrial and aquatic subterranean habitats remains considerably understudied in comparison to other environments. The Convention on Biological Diversity (CBD) has established global targets to mitigate the impacts of IAS, emphasizing the need for countries, organizations, and the scientific community to identify gaps in knowledge, monitoring, and management strategies for IAS. To this end, we mapped knowledge gaps in biological invasions of subterranean habitats that emerged from the first systematic surveys of the available information. We suggest that there are five main gaps restricting our ability to understand and tackle biological invasions in subterranean ecosystems. Given the vulnerability of subterranean ecosystems and the lack of attention they have received in conservation policies, it is crucial to increase research emphasis on IAS. This opinion paper aims to stimulate such efforts and contribute to the preservation of these ecosystems.

Keywords Invasive alien species · Subterranean biology · Caves · Conservation · Biological invasions · Research gaps

Introduction

Subterranean ecosystems are among the most widespread environments on Earth, constituting one of the five core realms of the biosphere and encompassing transitional ecosystems with the freshwater and marine realms (Keith et al. 2022). They include a diverse

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range of aphotic, resource-poor environments such as aerobic, anchialine and marine caves, endolithic systems and groundwater. Within these environments thrives a plethora of specialized organisms, contributing substantially to global taxonomic, phylogenetic, and functional diversity (Culver and Pipan 2019). Nevertheless, despite their significance, our comprehension of their biodiversity remains constrained. This deficiency in understanding is exacerbated by mounting anthropogenic threats that jeopardize these fragile ecosystems (Mammola et al. 2022).

Invasive alien species (IAS) are widely acknowledged as a significant global threat to ecosystems (Pyšek et al. 2020) and subterranean ecosystems are no exception (Mammola et al. 2020). A recent manifesto by Wynne et al. (2021) underlined the urgent need to address the issue of biological invasions in these ecosystems. However, the study of biological invasions in both terrestrial and aquatic subterranean habitats lags behind that of other environments. Existing literature on the subject is fragmented, and the vulnerability of these ecosystems to IAS impacts remains largely unexplored (Nicolosi et al. 2023). This is exacerbated by the intrinsic inaccessibility of subterranean ecosystems (Ficetola et al. 2019), their high individuality (Gerovasileiou and Bianchi 2021), and numerous impediments that make research in these environments particularly challenging (Mammola et al. 2021).

In line with the Convention on Biological Diversity (CBD) and its global targets to mitigate the impacts of IAS (UNEP 2022), there is a pressing need for countries, organizations, and the scientific community to identify knowledge gaps, improve monitoring efforts, and enhance management strategies.

Taking prompt conservation action concerning subterranean ecosystems is essential to safeguard these fragile and confined environments, which are relatively more vulnerable than other ecosystems. Preserving the highly specialized organisms residing in these habitats, often geographically restricted and scarce in numbers, becomes crucial to safeguard them from even minor disturbances (Culver and Pipan 2019).

Drawing upon recent attempts to synthesize information on alien species (also known as non-indigenous) in subterranean habitats (Gerovasileiou et al. 2022; Nicolosi et al. 2023; see Table S1), we have identified certain notable gaps related to biological invasions in subterranean ecosystems, including (1) limited data sharing, (2) lack of knowledge, (3) limited monitoring activities, (4) lack of funding and resources, (5) deficiencies in conservation policy, awareness, and education (Fig. 1). Our aim is to highlight key gaps in understanding and to propose potential solutions and directions for future research.

Limited data sharing

Significant progress has been made in the availability and accessibility of global data on alien organisms and their distribution (Pyšek et al. 2020), thanks especially to the numerous national and international databases such as the Global Invasive Species Database (GISP, <http://www.issg.org/database>), the Global Register of Introduced and Invasive Alien Species (GRIIS, www.griis.org; Pagad et al. 2018), the World Register of Introduced Marine Species (WRiMS, <https://www.marinespecies.org/introduced/>; Costello et al. 2021), NEMESIS (<https://invasions.si.edu/nemesis/>) and alien species inventories for Europe (e.g., AquaNIS 2015, EASIN: Katsanevakis et al. 2015; Tsiamis et al. 2019).



Fig. 1 Diagram showing five gaps in invasion ecology regarding subterranean ecosystems along with potential solutions to address them

Nonetheless, information concerning new introductions into subterranean habitats often remains inadequate, as existing databases do not consistently document details regarding habitat type. Moreover, relying solely on geographic coordinates may not adequately address this issue. Subterranean ecosystems are frequently overlooked as a separate habitat, thereby denying a comprehensive global knowledge of the phenomena, which could lead to further insights and understanding. To the best of our knowledge, only one thematic database focusing on marine caves, the World Register for Marine Cave Species (WoRCS, Gerovasileiou et al. 2016a, 2024), lists alien taxa from aquatic subterranean habitats, mostly based on recent findings from the Mediterranean Sea. Being largely scattered in the literature, information is often not available in an appropriate format to enable scientists and governments to take prompt action on the conservation of subterranean ecosystems.

To address this gap effectively, establishing a network of experts and leveraging existing data-sharing platforms is paramount. This could involve developing a centralized database specifically on subterranean habitats or the utilization of existing databases to consolidate pertinent information on alien species within these habitats.

By ensuring the data is findable, accessible, interoperable and reusable (FAIR), integration with existing global and thematic databases (e.g., GISP, GRIIS, WRiMS) and data infrastructures (e.g., the Global Biodiversity Information Facility, GBIF) can be achieved, facilitating access to relevant data for researchers, policymakers, and conservationists (Weigand et al. 2022). Furthermore, by specifically integrating and making data on subterranean habitats available, incorporating these species into IAS databases could enhance them significantly, and in this way contribute to better-informed conservation efforts.

To ensure that the data collected on subterranean habitats and their associated alien species are useful and comparable, data collection should be standardized. This can be achieved by developing guidelines for collecting data on alien species, which should include information as to the species taxonomy, abundance and distribution in the cave habitats (i.e., cave zone), and traits data on alien subterranean species such as trophic guilds and dispersal pathways, among other aspects.

Lack of knowledge

Research on pathways and mechanisms of introduction of alien species is crucial for understanding and tackling the invasion process. It represents a key step in implementing measures to manage pathways, thereby preventing the introduction and establishment of alien species (Pyšek et al. 2011). Despite research efforts to understand pathways of biological invasions (Meyerson and Mooney 2007), information on subterranean species is scarce. A thorough understanding of the key mechanisms through which alien species become invasive within subterranean habitats would also be pivotal for effectively mitigating their impacts in the new environment (Kumschick et al. 2015).

The overall impacts of IAS in subterranean habitats remain largely unknown (Gerasileiou et al. 2022; Nicolosi et al. 2023). However, negative effects such as competition, predation, and disease transmission, have frequently been observed. Notably, species such as *Procambarus clarkii* (Girard, 1852) and *Solenopsis invicta* Buren, 1972 have demonstrated their ability to outcompete native species, while rats [*Rattus rattus* (Linnaeus, 1758)], pose serious threats to cave-dwelling species and ecosystems. These species are invasive in surface habitats and as well possess the capability to invade subterranean environments.

The lack of historical data concerning the past ecological state of subterranean habitats leads to an underestimate of the impacts of IAS (Gerasileiou et al. 2016b; Seebens et al. 2017). Moreover, empirical studies on the ecological interactions among IAS and native cave dwellers are generally rare (Mammola et al. 2022).

To address these challenges, scientists must improve their understanding of the primary mechanisms by which IAS invade and impact subterranean habitats. Utilizing standardized methods to assess the magnitude of their environmental impacts (Blackburn et al. 2014) and employing diverse horizon-scanning approaches can aid in prioritizing the threat posed by potentially new IAS (Roy et al. 2019).

To systematically collect data on the ecological impacts of IAS, a standardized and quantitative framework is needed (e.g., Hawkins et al. 2015; Vimercati et al. 2022). This framework should encompass standardized indicators, such as changes in species richness, abundance, diversity, ecosystem functioning (e.g., ecosystem-based indices), and ratios between alien and native cave species. Data on these indicators should be collected through

a combination of field surveys, experimental and modeling approaches. This would allow for a comprehensive assessment of the ecological impacts of invasive species and provide valuable and comparable information to guide management and conservation efforts.

Limited monitoring activities

Effective conservation and management of biodiversity measures are restricted because of a lack of critical knowledge on species' distributions and abundances (Cardoso et al. 2011). This issue is particularly exacerbated for species living in fragmented habitats that are difficult to access or survey, such as terrestrial and aquatic subterranean habitats (Mammola et al. 2021; Navarro-Barranco et al. 2023).

It is essential to establish long-term monitoring programmes with tailored protocols for subterranean habitats and their fauna to track population trends and responses to environmental changes.

To address this challenge, scientists in the field of subterranean biology should prioritize early detection and monitoring of alien species, considering both species-specific indicators and those emerging as by-products of community assessments. One approach is to actively report the presence of alien species during species inventories in caves, in addition to considering the existence of endemism and rarity (Nicolosi et al. 2023). Integrating subterranean habitats into existing monitoring networks (e.g., national networks of the European Union's member countries in the framework of the Marine Strategy Framework Directive - Descriptor 2 "Non-indigenous species", and Contracting Parties of the Barcelona Convention in the framework of the Integrated Monitoring and Assessment Programme - Ecological Objective 2 "Non-indigenous species") would greatly enhance our understanding of biological invasions and their impacts on these habitats.

Emerging non-invasive survey methods such as environmental DNA (eDNA) monitoring represent a revolutionary new tool for the detection and monitoring of biodiversity that occurs in such habitats (Saccò et al. 2022; Weigand et al. 2022).

Further assets could be represented by involving local communities, especially individuals who frequently explore caves for recreation, such as cavers and divers. Volunteers in surveillance and monitoring efforts can provide valuable contributions (Roy et al. 2015; Groom et al. 2019). Their regular presence in caves for leisure aligns with a shared interest in safeguarding and enhancing the natural heritage (Weigand et al. 2022). Recruiting and training volunteers, also by establishing citizen science projects, would greatly increase early detection ability and also aid in recording the spread and location of alien species, improving the coverage and efficiency of monitoring efforts.

Lack of funding and human resources

As in surface habitats, our knowledge of biological invasion in subterranean habitats is geographically and taxonomically biased toward high-income regions. Conversely, regions such as Asia, Africa, and South America are under-studied, which can be linked to their lower economic prosperity (Leimu and Koricheva 2005; Pyšek et al. 2008). This strong geographical and taxonomic bias hampers a balanced understanding of alien species in sub-

terranean ecosystems and how they affect the subterranean biota. Compounding this issue is the decline in the number of taxonomists, reducing the capacity to accurately identify these species (Löbl et al. 2023). Consequently, cave biologists involved in monitoring may be unaware of the presence of alien taxa in subterranean environments.

The achievement of international projects that include distinct geographic areas and support intercontinental cooperation may help to overcome geographical biases within specific continents (Pyšek et al. 2008), including subterranean environments.

Adequate allocation of funds for monitoring and conservation is also essential to ensure comprehensive coverage of subterranean environments and their biodiversity, thereby contributing to regional and global conservation targets (e.g., Hermoso et al. 2017; Mammola et al. 2019). Furthermore, research efforts should focus on the Afrotropical, Neotropical, and Indo-Malayan regions to fill significant information gaps (Wynne et al. 2021).

Regarding the taxonomic bias, there is a need for increased attention and training of taxonomists in the study of small-sized inconspicuous taxa (e.g., macroinvertebrates) and microbiota (e.g., microbes and fungi) in subterranean ecosystems. These taxa have been poorly investigated despite their significant role in subterranean ecosystems (Gerovasileiou and Bianchi 2021; Mammola et al. 2022). Moreover, in future biodiversity monitoring, it is crucial to regard the community as a whole, encompassing the extensive range of cave-dwelling biota, including seasonally cave-dwelling and epigeal animal taxa, along with microorganisms (Weigand et al. 2022).

Allocating research funding specifically towards the identification, study, and understanding of the role and impact of these taxa in subterranean ecosystems is an essential step in the search for solutions to address this bias.

Deficiencies in conservation policy, awareness, and education

Apart from marginal considerations in Recommendation No. 36 of the Bern Convention (1992), the European Union's Habitat Directive, the Barcelona Convention for the protection of the Mediterranean Sea, the Federal Cave Resources Protection Act of 1988 (FCRPA) in the United States or the Environment Protection and Biodiversity Conservation Act 1999 (the EPBC Act) in Australia, there is a general lack of conservation policies and multilateral agreements at regional and national levels aimed at protecting subterranean habitats (Mammola et al. 2020; Sánchez-Fernández et al. 2021; Navarro-Barranco et al. 2023; Saccò et al. 2023).

For the better protection of subterranean diversity and the improvement of restoration measures focused on subterranean habitats and biodiversity, these ecosystems need to be explicitly included in conservation policies (Wynne et al. 2021). This may involve creating national cave protection acts, state-level legislation, or regional regulations to address the conservation needs of these unique environments. These measures should address the presence of alien species rather than merely emphasize native biodiversity (Mačić et al. 2018).

To effectively restore and conserve subterranean habitats against IAS, it is crucial to develop specific regulations that encompass prevention, monitoring, control, and, where necessary, removal strategies. These regulations should also provide guidelines for managing accidental introductions of such species while recognizing the unique characteristics

of subterranean ecosystems. Adopting a multidisciplinary approach that integrates science, governance, and society is essential in tackling biological invasions (Vaz et al. 2017).

Additionally, prioritizing the development of educational programmes focused on subterranean habitats (Mammola et al. 2022) and engagement with the public, non-governmental organizations, government conservation, and environmental protection agencies (Arlettaz et al. 2010; Groom et al. 2019) is necessary for the protection of subterranean ecosystems. An initial crucial step involves revisiting Recommendation No. 36 (Bern Convention 1992), in order both to reinstate criteria for identifying biologically valuable subterranean habitats and to suggest procedures for their protection and management. This would establish a shared foundation for future cave monitoring endeavours.

Conclusion

We are currently facing a global escalation of IAS, driven by our interconnected world and growing human population. This pervasive issue demands greater attention than it has received in the past, particularly in vulnerable ecosystems such as subterranean habitats that are relatively more sensitive to human threats. Unfortunately, these habitats are often neglected in conservation policies. It is essential to address the gaps in protecting subterranean ecosystems, specifically concerning invasive species, in order to meet the global targets set by the CBD. By incorporating subterranean ecosystems in the CBD's agenda and implementing targeted policies and actions, we can make a significant contribution to the conservation and sustainable management of these unique habitats which are all too frequently overlooked.

Hopefully this paper, through raising general awareness on this issue, will stimulate increased research emphasis on IAS, particularly in subterranean habitats.

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Declarations

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