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Global overview on groundwater fauna

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Abstract

Groundwater is an important global resource, providing water for irrigation, industry, geothermal uses and potable water. Moreover, groundwater contains the world's largest terrestrial freshwater biome with ecosystems, inhabited mainly by invertebrates (stygofauna) and microbes, undertaking important services including water purification, as well as nutrient and carbon cycling. Despite investigations on the spatial and temporal variations of groundwater fauna and the influence of environmental parameters on these organisms, in parts of the world, even the most basic knowledge of these ecosystems is still lacking. The aims of this study are to provide an overview on groundwater fauna (stygofauna) research, including the historical evolution of research topics and the development of sampling methods and secondly to identify the global distribution of groundwater fauna research and resulting data gaps. To achieve this, an extensive review of accessible groundwater fauna data was conducted by analysing 859 studies. It was evident that over time, there has been an exponential increase in the number of groundwater fauna studies together with changing paradigms in the research focus, particularly as sampling methods have developed from using simple nets, substrate samples and hand-pumps in the beginning to recent molecular analyses (e.g. eDNA). As application of molecular methods becomes more common, knowledge on groundwater diversity and functional ecology is expected to increase. Studies on groundwater fauna are spatially uneven and are dominated by research in Europe and Australia, with few studies in Africa, Asia and the Americas. This presently biased view on groundwater biota hinders the identification of biodiversity patterns and ecosystem functions on a wider geographic and climatic scale. In the future, a more evenly distributed stygofauna sampling effort in currently underrepresented areas of the globe is necessary to ensure a more comprehensive perspective on stygofauna biodiversity, roles and functional significances. This is increasingly important with the accumulating knowledge of the sensitivities of these ecosystems to anthropogenic activities, including climate change, and is fundamental to effective management of these ecosystems.

KEYWORDS
biodiversity, climate change, groundwater biodiversity, groundwater ecology, groundwater fauna, stygofauna

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1 | INTRODUCTION

Groundwater is an important source of freshwater, drinking water and service water for irrigation, industrial and geothermal uses (Job, 2022; Siebert et al., 2010; Stauffer et al., 2013). Moreover, groundwater is the largest terrestrial freshwater biome of the world (Griebler, Malard, & Lefébure, 2014) and is considered as a species-rich habitat (>100,000 species) with many taxa displaying high endemism (Culver & Holsinger, 1992; Martinez et al., 2018). Groundwater communities consist of a highly diverse biota, including bacteria and archaea, viruses, protozoans, fungi, invertebrates, salamanders and fish (Marmonier et al., 2023). Fauna populating groundwater, known as stygofauna, comprise stygobiotic species (exclusively inhabiting groundwaters), stygophilic species (affiliated with both ground and surface waters) and stygoxenic fauna (accidentally or occasional groundwater inhabitants) (Gibert et al., 1994; Hahn, 2006).

Within groundwater communities, microorganisms play essential roles in water purification through biogeochemical cycling (Griebler & Avramov, 2015) and form biofilms, on which stygofauna feed. Stygofauna have roles in promoting microbial growth (Edler & Dodds, 1996; Mermillod-Blondin et al., 2002), enhancing aquifer water transmission (Hose & Stumpp, 2019; Stumpp & Hose, 2017), organic matter processing (Kinsey et al., 2007; Simon & Benfield, 2001) and contribute to the subterranean food web (Saccò, Blyth, Venarsky, & Humphreys, 2022). Combined, these species provide several functions sustaining groundwater ecosystems, aiding groundwater health and water quality (Mermillod-Blondin et al., 2023).

Globally, groundwater and groundwater fauna are facing common threats, including abstraction (Wada et al., 2014), contamination (see Burri et al., 2019) and climate change (Amanambu et al., 2020), all of which place multiple stresses on groundwater ecosystems. Groundwater abstraction for irrigation, potable water and mining activities (Danielopol et al., 2003; Hancock et al., 2005) alter groundwater levels, with duration and rate of abstraction known to strand particular stygobiotic biota, causing desiccation and death (Korbel et al., 2019; Patel et al., 2020). These pressures are particularly prevalent in Africa, Asia and South America (Wada et al., 2010) and are associated with demographic increases (Vörösmarty et al., 2000). Groundwater contamination is another frequent threat to stygofauna, with common pollutants derived from agriculture (di Lorenzo, Fiasca, di Cicco, & Galassi, 2020; di Lorenzo & Galassi, 2013; Korbel, Greenfield, & Hose, 2022), heavy industry (Hose et al., 2014), urbanisation (Hallam et al., 2008), surface waters (Danielopol et al., 2003; Kristensen et al., 2018) and thermal pollution (Menberg et al., 2013; Taylor & Stefan, 2009; Tissen et al., 2019; Zhu et al., 2010). Additionally, anthropogenic climate change poses a significant threat to groundwater ecosystems and biogeochemical processes (Griebler et al., 2016) due to altered recharge events, increased evapotranspiration, increased temperatures (Figura et al., 2011; Menberg et al., 2014; Tissen et al., 2019) and increased groundwater extraction caused by drying rivers. Climate change threats are most severe in areas with semi-arid to arid climate, humid areas of the Northern Hemisphere and (sub-) tropical areas (humid monsoonal countries) (Danielopol et al., 2003).

The multiple stressors that humans have placed on groundwaters globally (Becher et al., 2022) have the potential to alter groundwater community structure (e.g. Korbel, Greenfield, & Hose, 2022) and compromise ecosystem functions, resulting in the deterioration of groundwater health (Hancock, 2002; Hancock et al., 2005). Furthermore, these stressors can impact biodiversity and alter surface water groundwater connectivity, leading to species extinction and shift in the community composition as ubiquitous surface water species outcompete and replace groundwater species (Danielopol et al., 2003). Such changes to groundwater regimes, connectivity and biota can have implications for terrestrial vegetation and fauna (Eamus & Froend, 2006), freshwater ecosystems (Hancock et al., 2005; Korbel, Rutlidge, et al., 2022) and estuarine and near-shore marine ecosystems (Moore, 1999) due to the ubiquity of groundwater dependence in terrestrial ecosystems (Hancock et al., 2005). These impacts highlight the need for increased knowledge on subterranean ecosystems, their assessment and protection (Griebler, Malard, & Lefébure, 2014).

However, investigations on groundwater fauna and the impacts of humans on these ecosystems are still rare (Dole-Olivier et al., 2009; Gibert & Culver, 2009; Martinez et al., 2018). A pioneering study of the global diversity of subterranean fauna, 'Stygofauna mundi', highlighted the biodiversity values of these ecosystems identifying 6,634 species of aquatic subterranean dwellers, from a variety of groundwater habitats (Botosaneanu, 1986; Malard et al., 2009). Later studies indicated over 7,800 subterranean species (Juberthie, 2000), with the most recent knowledge of global biodiversity synthesised in the revised edition of Groundwater Ecology and Evolution (Marmonier et al., 2023). As groundwater ecosystem diversity, functions and processes differ across landscapes (Korbel, Hancock, et al., 2013; Zagmajster et al., 2023), knowledge of these ecosystems must be drawn globally from a variety of bioregions and climatic zones in order to implement effective management. Attempts have been made to improve knowledge of stygofauna diversity patterns in various regions of the world (e.g. Gibert et al., 2009: European PASCALIS-project) with broad-scale studies synthesising current knowledge of groundwater biological and habitat diversity in Europe (Cornu et al., 2013), Thailand and Vietnam in South-East Asia (Brancelj et al., 2013) and Australia (Hose et al., 2015). Despite these studies, there is a notable absence of an overall analysis of spatial and temporal distribution and research into groundwater fauna on a global scale.

The aim of this study is to provide a global overview on groundwater fauna (stygofauna) research. Hence, we conduct an extensive review of accessible groundwater fauna data by analysing data from national and international publications in journals, national reports, doctoral theses, historical writings, books, consisting online databases and others in various languages. In the following, we provide an overview of (i) the historical evolution of stygofauna research, (ii) stygofauna sampling methodologies and (iii) an analysis of the global spatial and temporal distribution of groundwater fauna research and knowledge gaps, with regional summaries. It is envisaged that by encapsulating such data, we can start to build a common knowledge basis for increased understanding, assessment and conservation of groundwater biodiversity on a larger scale. Moreover, we can identify where data is lacking, which has important implications for the implementation of environmental policies for sustainable groundwater management (Danielopol et al., 2003; Tomlinson et al., 2007).

2 | HISTORICAL EVOLUTION OF GROUNDWATER FAUNA RESEARCH

According to Griebler, Malard and Lefébure (2014), groundwater ecology is a relatively young discipline with research and knowledge lagging behind that of surface ecosystems such as streams and lakes. Historically, data were collected both opportunistically and sporadically; however, more recent awareness of the importance of groundwater ecosystem processes and services (Mermillod-Blondin et al., 2023) has seen the increase in well-designed ecological research and monitoring programs. Much of this research has broadened the knowledge on the biological distribution of stygofauna (Marmonier et al., 2023) as well as efforts to conserve this biota (see Boulton et al., 2023). This review analyses over 800 publications published prior to 2022 (Table S4.1), providing an overview of the evolution of this research as well as temporal and spatial analysis of research sites, with as summary provided in Figure 1.

2.1 | Early research phase

The earliest written observation in groundwater ecology dates back to 1537 with a sporadic observation in a cave (Figure 1) (Mylroie, 2004). The 17th century saw increased research on groundwater fauna and microbiology, with the first stygobiotic species identified in scientific writing, namely a cave salamander in Slovenia (Culver & Pipan, 2013; von Valvasor & Weichard, 1689). Early research focused on groundwater fauna, while groundwater microbiology research became established in the second half of the 19th century (Griebler, Malard, & Lefébure, 2014). Likewise, early research concentrated on cave ecosystems (Figure 1, red phase), due to the accessibility of this habitat. During the second half of the 19th century, other subsurface habitats (e.g. aquifers) became more accessible, leading to the discovery of organisms previously unknown to science (Danielopol & Griebler, 2008) and the emergence of groundwater ecology as a research field.

2.2 | Pre-ecological research phase

In the 18th and 19th centuries, during the so-called ‘Pre-ecological phase’ of groundwater research (Danielopol & Griebler, 2008), the emphasis of research was on cataloguing new species, their habitats and their biogeographical origin (Danielopol & Griebler, 2008)

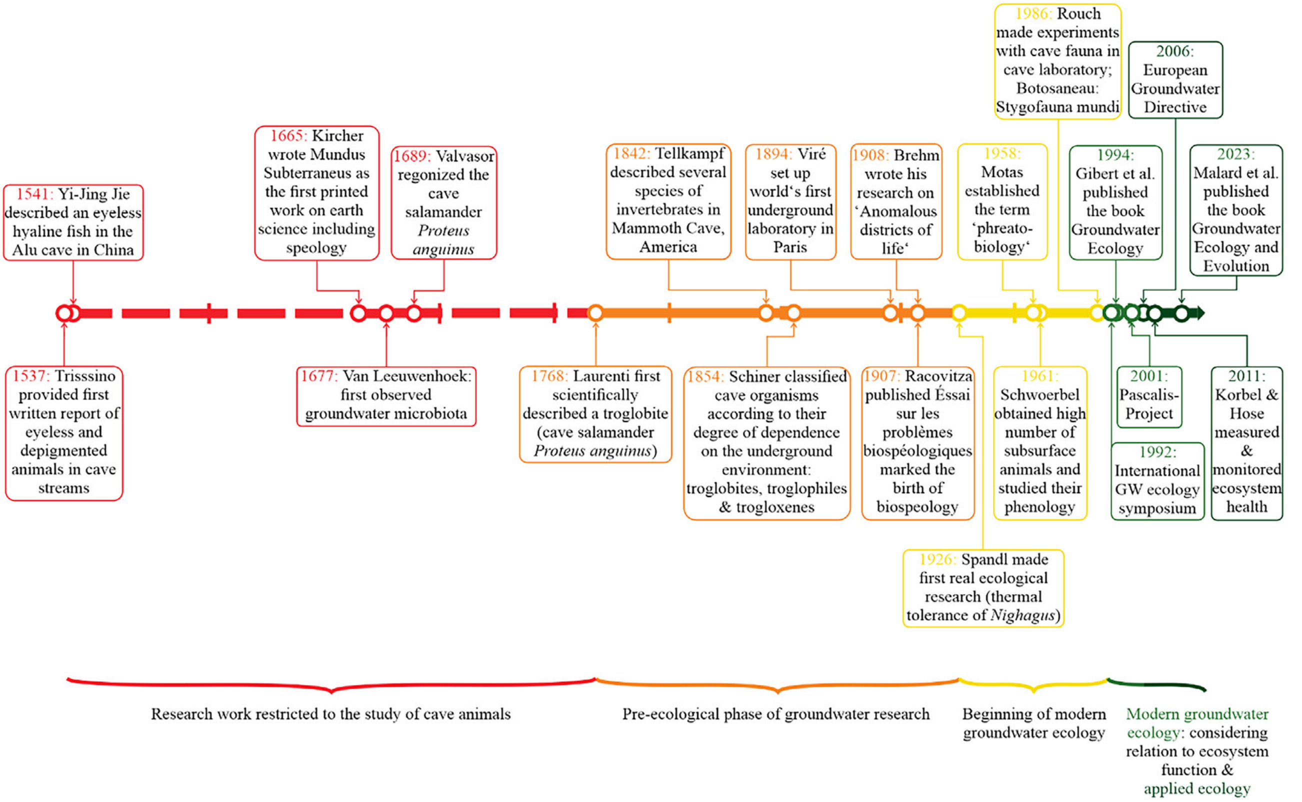

FIGURE 1 Chronology and milestones of groundwater fauna research and chronological overview over the change of research topics. The colouring points out the four phases of groundwater research.

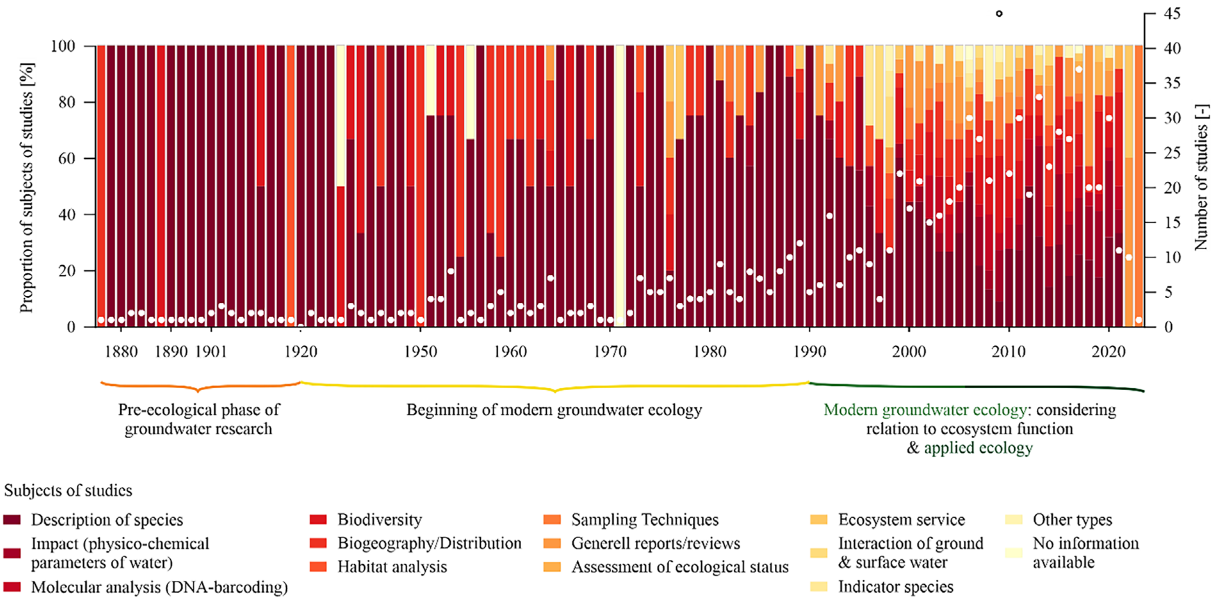

FIGURE 2 Proportion of the different subjects of all considered studies over time (first y-axis) and number of studies over time as white dots (second y-axis).

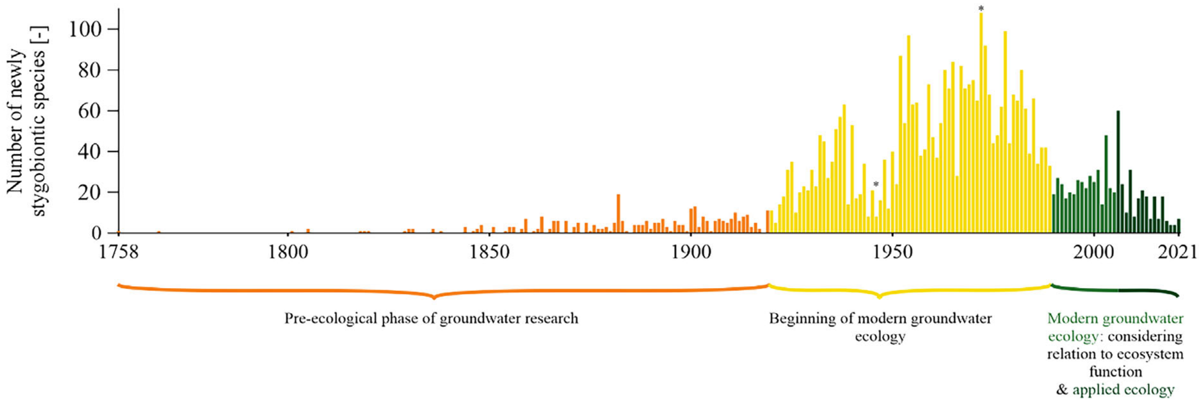

FIGURE 3 Number of newly discovered stygobiotic species mentioned in all considered studies. The colouring points out the four phases of groundwater research (Figure 1) and the * marked important years. A list with all 859 used studies is provided in Table S4.1.

(Figure 2, orange phase). The term 'biospeology' was proposed by Racovitza (1907) and characterised the research activities at this time (Hancock et al., 2005).

2.3 | Modern ecology research phase

The beginning of the 'modern groundwater ecology phase' (Figure 3, yellow phase) began in the 1920s, with a significant increase in the number of studies, sampling events (Figure S2.1) and, consequently, a sharp increase in the reporting of newly discovered stygobiotic species. In this context, the year 1971 is striking. No information on published studies was found for this year; however, many new stygobiotic species were found in this and the following years. One reason for this could be a time delay between the conduction of studies and the actual publication of results. The number of reported new stygobiotic species saw a dip around the early to mid-1940s (coinciding with global unrest), then peaked in 1972 and has shown a general declining trend since this time (Figure 3). During this period, the awareness of groundwater fauna increased and paved the way for modern groundwater research with the development of new integrated concepts, sampling methods and knowledge of ecology.

The 'modern groundwater ecology phase' of research saw the emergence of studies on the ecology of unconsolidated sediments (Hancock et al., 2005), sampling of wells and tap water (Brehm, 1930) as well as the ecology of alluvial aquifers and karst systems. Arguably, this began with Spandl (1926) (Hancock et al., 2005), who conducted the first true ecological research of groundwater fauna in his study of the thermal tolerance of the genus *Niphargus* in 1926 (see Figure 1). The term 'phreatobiology' was introduced by Motas (1958) to describe the research on the biology of groundwater organisms living in porous, unconsolidated sediments (Danielopol & Marmonier, 1992; Hancock et al., 2005; Motas, 1958). Other important innovations in this period included the description of groundwater and hyporheic fauna in relation to subsurface water chemistry (Danielopol & Marmonier, 1992) and the beginning of groundwater phenology studies (Danielopol & Griebler, 2008) in the 1960s (Schwoerbel, 1961). Moreover, the first experimental studies under conditions in the cave laboratory 'Laboratoire Souterrain du C.N.R.S' in Moulis were conducted (Rouch, 1986). Besides the influx of new species discovered in this era, for the first time, studies began to concentrate on the ecosystem functions, e.g. studies on whole subsurface karstic drainage system (Danielopol & Marmonier, 1992).

The early 1990s saw the development of a novel view on biodiversity of subterranean aquatic organisms in relation to ecosystem functioning and services (Danielopol & Griebler, 2008) (Figure 3, green phase). The subject of studies shifted from the description of newly discovered species (i.e. descriptive typological approach) towards an ecosystemic and holistic view with research incorporating the whole of ecosystem functioning (Danielopol & Marmonier, 1992) (Figure 2). The growing interest on groundwater fauna research is reflected in the exponential increase in the number of studies over time since the 1920s, which peaked in 2009 (Figure 2). The importance of ecosystem function and functional traits of groundwater fauna continues to be recognised (Griebler & Avramov, 2015; Hose et al., 2022; Saccò et al., 2021).

Alongside the increased interest in groundwater fauna and ecology developing in the late 1990s, technological advances allowed the usage of DNA methods for the identification of biota. Initially, the use of DNA centred on groundwater microbial studies (Barton et al., 2004; Hebert et al., 2003), with a focus on contamination and remediation (Alfreider et al., 2002; Geets et al., 2001; Ross et al., 2001). The emergence of molecular methods for stygofauna first saw DNA used to study stygofauna phylogeny, which added to our understanding of groundwater species and their evolutionary pathways (Cooper et al., 2002; Lefébure et al., 2006; Leys et al., 2003). Molecular methods were then pioneered for groundwater fauna studies in groundwater karst systems, utilising environmental DNA (eDNA) for the targeted detection of threatened subterranean species which was followed by the use of eDNA for studies in stygofauna biodiversity, ecosystems and routine ecosystem monitoring (Korbel & Hose, 2017). The continued shift in focus towards ecosystem functioning and whole-of-ecosystem analysis (occurring in the late 1990s and early 2000s) followed the path taken in surface ecology research and is likely aided by the emergence of molecular analysis and eDNA allowing the identification of unprecedented numbers of potentially new species.

2.4 | Applied ecology research phase

During the late 1990s, the responses of fauna to external influences, such as chemical and thermal alterations, anthropogenic and natural and changes in habitat structure on groundwater ecosystems received more attention. By the late 20th century, scientists began to investigate the use of stygofauna as bioindicators, describing the sensitivities of these species to both natural and anthropogenic factors with research on human impacts on groundwater fauna rising in prominence (Mösslacher & Notenboom, 1999). As scientists continued to discover the functions and roles of stygofauna, and the important biodiversity that groundwater hosts, a new research topic began to emerge and a new sub-phase of groundwater research began—the 'applied ecology phase' (Figure 3, dark green).

With increased social and political recognition of the importance of groundwater, the topics of conservation and groundwater management began to emerge as a focus of ecological research (Boulton, Dole-Olivier, & Marmonier, 2003; Danielopol et al., 2003). However, due to limited knowledge of stygofauna biodiversity and spatial range, these early studies were largely unrecognised by governments worldwide. Accordingly, the development of new assessment schemes for the monitoring of ecological status or health of groundwater ecosystem received more attention in the 21st century. By 2010, the increased interest in bioindicator species and studies investigating natural and anthropogenic influences on groundwater fauna distributions (Danielopol et al., 2000; Goldscheider et al., 2006; Griebler, 2001; Griebler et al., 2002; Humphreys, 2006; Malard et al., 1994; Marmonier et al., 2000; Mösslacher et al., 2001; Mösslacher & Notenboom, 1999; Notenboom et al., 1995; Sinclair et al., 1993) had paved the way for the first studies attempting to monitor groundwater health and diversity using bioindicator. Groundwater scientists began to apply the notion of 'health' (which had recently been applied globally in environmental policies) to groundwater ecosystems; with connotations to human health, it is deemed an easy way for non-scientists and water managers to understand environmental conditions.

A milestone and driver for groundwater ecosystem management and research in Europe was the European Groundwater Directive 2006, which attempted to incorporate ecological knowledge into schemes for environmental planning and policies (Griebler et al., 2023; Steube et al., 2009). This directive saw the emergence of studies to assess groundwater ecosystems: Hahn (2006) utilising abiotic indicators and detritus, predictive methods (Stoch et al., 2009) to assess groundwater diversity, and Steube et al. (2009) suggesting the combination of both abiotic and biotic factors. Griebler et al. (2010) provided alternate methods for groundwater ecosystem assessments, suggesting the use of natural reference conditions for aquifers of differing typology. At this same time, other countries were also developing policies to conserve and protect groundwater quality and groundwater-dependent ecosystems (GDE). In Australia, groundwater initiatives began to gain momentum in the mid-2000s with the emergence of national policies to monitor groundwater ecosystems' health and stress (Griebler et al., 2023; NGC, 2004); however, the lack of scientific methods to implement such policies was recognised (Boulton, Humphreys, & Eberhard, 2003; Hatton & Evans, 1998). The first attempt to assess, measure and monitor ecosystem health, using a two-tiered framework consisting of a multi-metric suite of biotic and abiotic indicators, was in Australia in 2011 (Korbel & Hose, 2011). The development of this ‘Groundwater Health Index’ (GHI) framework was triggered by Australian water management policies and the heavy reliance on groundwater from irrigation-based industries. Methods to measure groundwater health and monitor groundwater ecosystems continue to be refined and developed (di Lorenzo, Fiasca, di Camillo, et al., 2020; Fillinger et al., 2019; Griebler, Stein, et al., 2014; Koch et al., 2021; Korbel & Hose, 2017), with these management tools being used by governments to monitor groundwater health (e.g. report Korbel, Greenfield, & Hose, 2022). Integral to these management tools is flexibility with emerging technologies, such as eDNA (Korbel, McKnight, et al., 2022; Saccò, Guzik, Van der Heyde, et al., 2022) able to be integrated into frameworks which allow for the integration of most recent science to inform management decisions.

Other important research areas emerging in the ‘applied ecology’ phase include attempts to better understand the links between groundwaters and adjoining ecosystems (Boulton et al., 1998; Danielopol & Marmonier, 1992; Hahn, 2006; Hancock et al., 2005; Korbel, McKnight, et al., 2022; Korbel, Rutlidge, et al., 2022). Such studies holistically investigated interconnectivity between ecosystem and the dynamic of exchange between the surface, hyporheic and subsurface zones. Again, these studies have been mainly prompted by management decisions and directives, for example understanding the mechanisms behind the loss of river baseflow due to over-extraction of groundwater is required for water allocations and management. As a last milestone, Malard et al. (2023) published the second edition of the book ‘Groundwater Ecology and Evolution’. This updated edition synthesises the current state of knowledge on groundwater ecology and evolution and highlights the opportunities and challenges for conserving and managing groundwater ecosystems.

Furthermore, groundwater research has begun to include multidisciplinary approaches combining experts from various fields to refine subterranean ecological patterns (Saccò et al., 2021). It is becoming more common for studies to combine skills of hydrogeology, geomorphology, hydrochemistry, molecular science, ecology and biology to answer complex questions (Burrows et al., 2017; Korbel, Rutlidge, et al., 2022). Some other approaches have combined techniques, using isotopes, radiocarbon analysis (^{14}C) and DNA methods for the analyses of environmental samples (Hartland et al., 2011; Saccò et al., 2019). Such multidisciplinary techniques allow for more sophisticated ecological studies including the identification of energy flows and food web structure and biological and water exchanges between connected ecosystems (Hartland et al., 2011).

3 | SAMPLING GROUNDWATER FAUNA

Traditionally, environmental sampling involves accessing numerous sites within a limited time frame, ideally with a representative spatial distribution of samples for the area under investigation (Hahn &

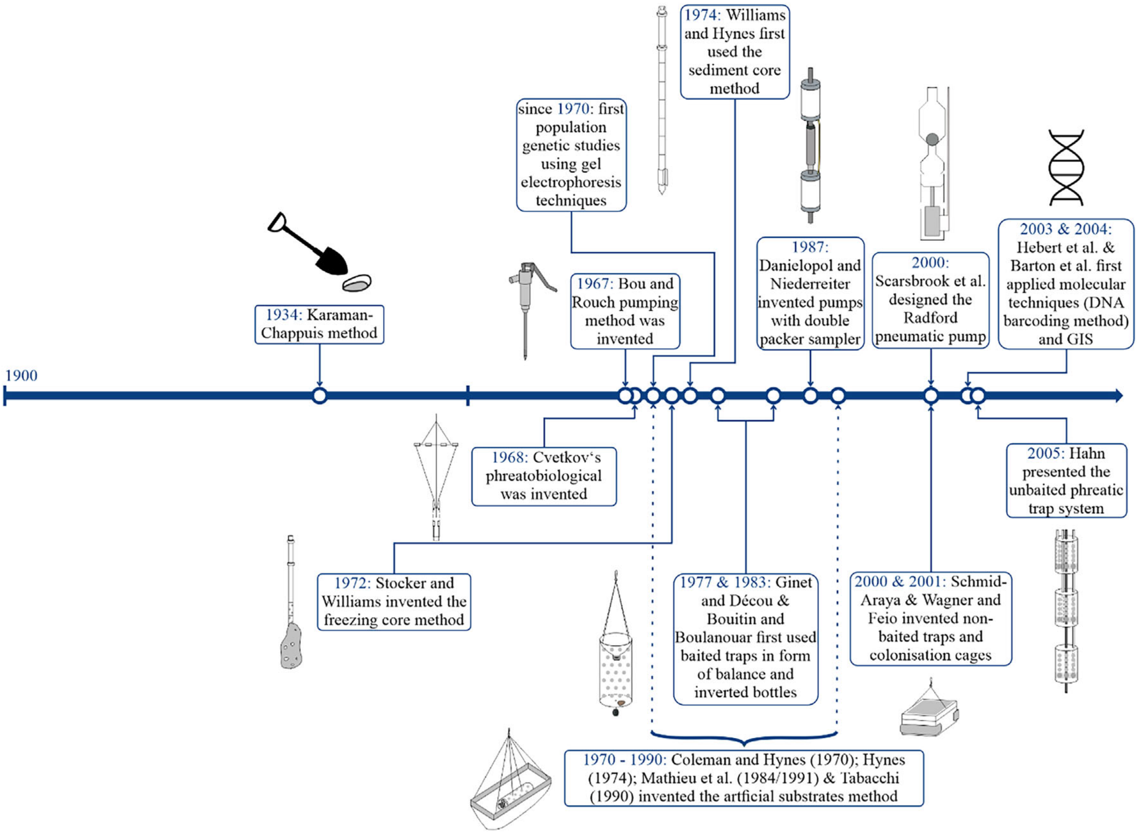

FIGURE 4 Temporal development of sampling methods with sketches of the invention (for more information, see Figure S1.1).

Matzke, 2005). In the case of groundwater fauna sampling, this represents a great challenge because the living space, i.e. the aquifer, is hard to access (Korbel et al., 2017; Steube et al., 2009). Access points to springs, caves and sediments from the hyporheic zone of rivers are rare and selective (Maurice, 2009), and groundwater wells accessing aquifers are expensive to establish. Moreover, different technical requirements for sampling are required for differing aquifer types (Hahn, 2002; Thulin & Hahn, 2008). Besides access, the patchy distribution and high endemism of groundwater fauna require a larger number of sampling points to obtain representative results (Gibert & Deharveng, 2002; Hahn & Matzke, 2005; Mösslacher, 1998; Thulin & Hahn, 2008). Additionally, the small and sensitive anatomy of stygobiotic species complicates the intact extraction of samples for morphological identification and representative aquifer sampling (Hahn, 2002). Over time several novel methods, described in detail in the Supporting Information (Chapter S1), were developed to account for these challenges (Figure 4).

3.1 | Temporal development of sampling methods

As expected, the number of different sampling methods has increased with the number of studies and with the emergence of more advanced methods from the 1960s onwards (Figure 5). Hancock et al. (2005) and Danielopol and Griebler (2008) provide a short summary of the historical and technical background of sampling and analysis methods for groundwater ecology including microbiology and fauna. Our study highlights the different types of stygofauna methods used in each period of time, as a proportion of the studies completed (Figure 5).

Before and during the ‘pre-ecological phase’ of groundwater research simple nets, substrate samples and hand-pumps were used to sample fauna of wells, caves and springs. More complex methods were developed from 1934 onwards, in particular the rapid and qualitative Karaman–Chappuis method (Karaman, 1933) (Figure 4) and the Bou–Rouch method (Bou & Rouch, 1967), which allows pumping of animals living in sandy and gravel sediments and consequently led to discovering more diverse meio- and macro-organismal assemblages (Danielopol & Griebler, 2008). Nevertheless, this method is not strictly representative of in situ conditions as faunal diversity and density are not expressed per volume of sediment and larger species such as amphipods and isopods can be damaged (Malard et al., 2002; Pospisil, 1992).

Sampling methods were further developed between the mid-1960s and 1990 in the beginning of ‘modern groundwater ecology phase’, with specific traps and pumps offering increased quantitative data (Danielopol & Griebler, 2008). However, issues still exist with such sampling methods, for example the commonly used balance and inverted bottle traps (Boutin & Boulanouar, 1983; Ginet & Decou, 1977) are species-selective, such that representative sampling requires a combination with other methods such as nets. Table 1 summarised the most important dis- and advantages and fields of applications of the sampling methods for groundwater fauna.

Recent sampling of stygofauna (‘modern groundwater ecology’ era) is still dominated by sampling well waters (Figure 5), with pumping and filtering animals the most common and well-established method for stygofauna studies (Hahn, 2002; Thulin & Hahn, 2008). Additionally, pumping well water enables a simultaneous sampling of fauna, sediment and water (Hahn, 2002) and is easy to standardise by extracting a defined volume of water (Hahn, 2002). However, pumping is considered as a selective sampling method, because of filtering effects and a resistance against the suction of pump. Hence, large, sessile or more active species can be underrepresented in the samples (Allford et al., 2008). The net sampler or phreatobiological net is a valuable alternative to pumping devices with respect to obtained numbers of taxa and community composition (Hahn & Matzke, 2005;

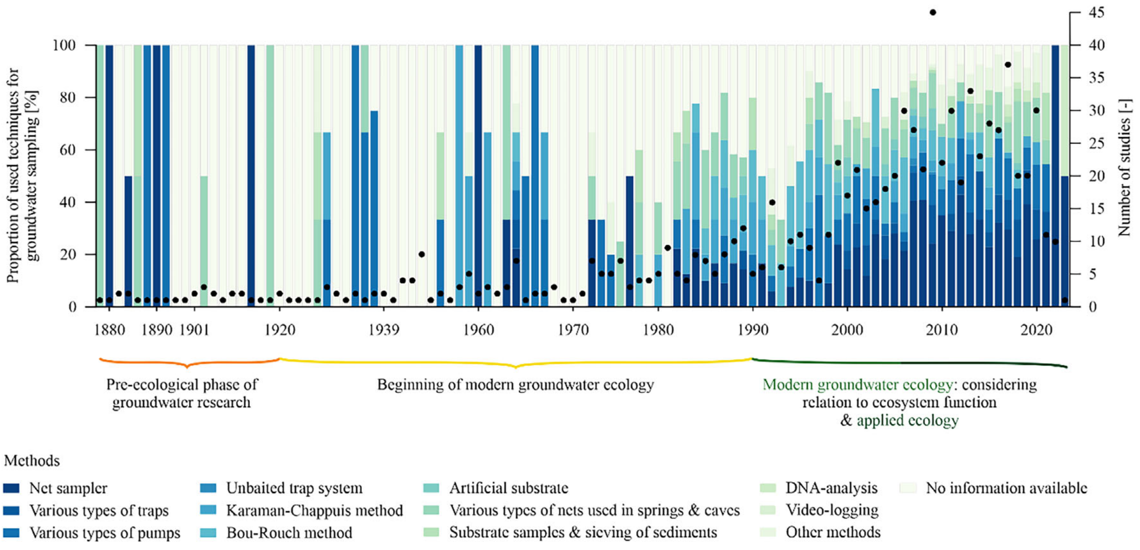

FIGURE 5 Proportion of applied methods for groundwater sampling and number of considered studies over time as black dots (secondary y-axis).

TABLE 1 Comparison of several methods for groundwater fauna sampling (++ = very good; + = good; o = moderate; − = negative; −− = very negative; NA = information not available) in order of their temporal development (Figure 3).

Sampling method		Feasibility	Expenditure of time		Expenditure of costs	Condition of fauna sample	Efficiency	Potential animal findings	Habitat
			Sampling duration	Sample preparation					
Karaman–Chappuis method		++	+	++[1]	++	++	+	Free swimming fauna of interstitial water[1]	Riverbed sediments (subterranean rivers, lakes)[1], groundwater
Bou and Rouch technique		++[1,2]	+[12]	++	+/o[12]	+[12]	+	Diverse meio- and macro-organisms[3]; swimming organisms & species linked to sand particles[1]	Sandy sediments and gravel of rivers, lakes & shallow groundwater[1], max. depth 6 m^2
Phreatobiological net		++[13]	++[7,13]	++[13]	++[7,13]	++[13]	+[13,14]	Fauna of well water & in the bottom sediments of the well[1]	Large diameter wells[1] in alluvial sediments
Traps	Baited traps	++	−−[1]	++	++[8]	++	+[8,14]	Limited to isopods, amphipods, planarians[1]	Wells, lakes, caves (siphons, pools)[1]
	Non-baited traps	++	−	++	++[8]	++	+[8,14]	NA	Manly used for the hyporpheos[1], upper part of groundwater body[15]
	Phreatic trap system	o	−[7]	++	+[7]	++	+	NA	Wells
Freezing core method		−−[4]	+	−−	−−[2]	++	++[2]	Interstitial fauna[14]	Stony streambeds[11]; restricted to superficial sediments[14]
Artificial substrates		+	−−[1,10]	++	++	++	+[1]	Meiofauna[1]	Caves, along subterranean rivers & streams[1]
Sediment core		++	+	++	++	+	+	NA	In uniform & mixed gravels up to 10 mm in diameter[5] (coarse substrates of stony streams[4])
Pump	Centrifugal pump	+	o[8]	++	o	−−[9]	NA	Small animals (mites & copepods), larger animals as fragments[9]	Wells, aquifers, hyporheic zones; up to 50-m depth
	Double packer pump	+	o[8]	++	−[7]	NA	+	Small, less tenacious animals & larger animals[13]	
	Pneumatic pump	+	o[8]	++	−[9,14]	++[8,9]	+[14]	Small animals & larger amphipods, isopods[9] and syncarids	
Molecular techniques		o/+	++	−/o	+/o[8]	NA	o[8]	All, including cryptic species[16,17]	Water & sediment[16]

TABLE 1 (Continued)

Sampling method	Feasibility	Expenditure of time		Expenditure of costs	Condition of fauna sample	Efficiency	Potential animal findings	Habitat
		Sampling duration	Sample preparation					
Video-logging	+	NA	NA	NA	–	NA	Very low abundance taxa	Wells in sandy & silty environments[6]

[1] Malard et al., 2002.
[2] Pospisil, 1992.
[3] Danielopol & Griebler, 2008.
[4] Boxshall et al., 2016.
[5] Williams & Hynes, 1974.
[6] Datry et al., 2003.
[7] Hahn, 2005.
[8] Hose & Lategan, 2012.
[9] Scarsbrook et al., 2000.
[10] Sket, 2018.
[11] Stocker & Williams, 1972.
[12] Stubbington et al., 2016.
[13] Allford et al., 2008.
[14] Hahn, 2002.
[15] Thulin & Hahn, 2008.
[16] Saccò, Blyth, Douglas, et al., 2022.
[17] Trontelj et al., 2009.

Malard et al., 2002; Thulin & Hahn, 2008) and can be used for large-scale faunal surveys (Allford et al., 2008) and wells up to 100-m depth (Hahn, 2002); however, like well sampling from pump, there are issues with these sampling methods collecting representative samples of stygofauna communities.

3.2 | Discussion of efficiency and representativity

The issue of representative sampling is complicated for stygofauna, with sampling regimes needing to consider the inclusion or exclusion of purged well water in sample design, the volume of water sampled and the extraction rate of pumped waters (see Korbel, McKnight, et al., 2022). Groundwater wells typically provide an artificial environment, in which there is a large column of water that may be atypical of the surrounding aquifer (particularly in alluvial aquifers) and may be enriched in oxygen organic matter (Hahn & Matzke, 2005). Due to these factors, wells often contain a larger abundance of stygofauna than the surrounding aquifer (Hahn & Matzke, 2005; Roudnew et al., 2014; Sorensen et al., 2013) and may favour taxa that prefer the open water column provided by well casings, thus purging wells prior to sampling becomes important for any study looking at richness and abundance measures (Korbel et al., 2017). However, studies have indicated that there are compositional differences in pre-purged and purged samples (Korbel et al., 2017; Korbel, McKnight, et al., 2022). To date, only 29 studies sample fauna exclusively by pumping aquifer water through purged wells, with Australia playing a leading role (13 studies: Castaño-Sánchez et al., 2020b; Cook et al., 2012; Hartland et al., 2011; Korbel & Hose, 2011, 2015, 2017; Korbel et al., 2019; Sorensen et al., 2013; Terramin, 2018). The issues of purging wells and sample volumes need to be considered in the aims and objectives of monitoring programs, in order to ensure that stygofauna communities are accurately represented (Korbel, McKnight, et al., 2022).

3.3 | The evolution of molecular methods for groundwater sampling

A methodological milestone that altered the view on the diversity of groundwater fauna was the application of molecular tools on individual specimens and water samples (see Boulton et al., 2023; Danielopol & Griebler, 2008). Initially, molecular methods for stygofauna were primarily used to identify new species and identify evolutionary processes (e.g. Cooper et al., 2002), which was followed by the adoption of environmental DNA (eDNA) techniques to detect threatened subterranean species (Gorički et al., 2017; Niemiller et al., 2018). However, eDNA promises more than just the identification of single species and their linages; it offers a powerful tool for the rapid, non-invasive assessment of stygofauna within groundwaters, providing information on biodiversity, ecosystem functioning, phylogenetics and trophic interactions from a single sample (see Boulton et al., 2023). This can be seen in the most recent uses of eDNA metabarcoding to identify multiple species within the same environmental sample to characterise stygofauna communities, functions and biodiversity (Korbel, McKnight, et al., 2022) and their trophic interactions (Saccò et al., 2021; Saccò, Blyth, Venarsky, & Humphreys, 2022).

Environmental DNA/RNA (ribonucleic acid) methods are based on the concept that organisms shed DNA/RNA in groundwater either while they are alive (e.g. exoskeleton shedding) or leaving DNA when they die. As DNA lasts much longer than RNA (which degrades very quickly), eDNA indicates animals that have either lived, been transient or died in groundwater, with eRNA indicating the animals that are functionally present at the time of sampling. Recent studies have indicated that, due to the low presence of RNA within groundwater, presumably due to low biotic abundances, eDNA is a more viable method for biodiversity studies than eRNA (Korbel, Rutlidge, et al., 2022). Both eDNA and eRNA analyses in groundwater follow a conventional workflow (see Boulton et al., 2023) whereby groundwater and/or sediment samples (e.g. from springs, caves and wells) are filtered and membranes frozen (Korbel, Rutlidge, et al., 2022). DNA is extracted from the membrane and PCR (polymerase chain reaction) is conducted, samples are then sequenced and results are interpreted using bioinformatics (see Saccò, Guzik, Van der Heyde, et al., 2022).

Environmental DNA analysis has several benefits over traditional sampling techniques (see Boulton et al., 2023). This molecular method has increased our knowledge of the breadth of taxa within groundwater ecosystems, as it is able to detect very small protozoans as well as cryptic species (Sbordoni et al., 2000), clarifying genetic difference between morphologically similar specimens and allowing the study of entire phylogenetic lineages (Zakšek et al., 2007). In addition, this method does not require the removal of animals from their habitat, and as such provides a non-intrusive method for monitoring rare and endangered species (Niemiller et al., 2018). Furthermore, eDNA methods allow for the characterisation of entire communities (prokaryotic and eukaryotic) and their functional roles and can elude to potential interactions between taxa (Deiner et al., 2017). Molecular methods are still rare for groundwater stygofauna studies (Fenwick et al., 2021; Korbel et al., 2017; Korbel, Rutlidge, et al., 2022; Lennon, 2019; Saccò, Guzik, Van der Heyde, et al., 2022; Vörös et al., 2017; West et al., 2020), although they show great potential for their ability to identify new species and metabolic functions of groundwater biota (Boulton et al., 2023; Korbel et al., 2017) with improvement in these methods for the detection of stygofauna promising (e.g. van der Heyde et al., 2023).

However, eDNA methods do not come without limitations. A lack of reference sequence databases (Korbel, Rutlidge, et al., 2022) often results in large numbers of unidentified taxa in the bioinformatic processing of sequences (Lennon, 2019; Saccò, Guzik, Van der Heyde, et al., 2022), which is compounded by a lack of taxonomic keys for stygofauna in many parts of the world. There are also several knowledge gaps surrounding the use of eDNA within groundwaters, many of which involve the detection of crustacea, a dominant stygofauna taxa. Additional research on primers, the fate and transportation of DNA within aquifers and research on stygofauna DNA shedding capacity (Korbel, Rutlidge, et al., 2022; Trimbos et al., 2021) is required before this method can replace traditional sampling (Korbel, McKnight, et al., 2022; Saccò, Guzik, Van der Heyde, et al., 2022).

In summary, net sampling and pumping well water are the dominating sampling methods worldwide. Nevertheless, each of the described methods has its limitations. Hence, a combination of methods, such as net sampling together with pumping and/or DNA-analysis, is recommended (Korbel et al., 2017; Saccò, Blyth, Douglas, et al., 2022).

4 | GLOBAL GROUNDWATER FAUNA RESEARCH

The investigation of the global distribution of groundwater fauna sampling sites, both temporally and spatially, is one of the main aims of this paper. Our analysis revealed the scale of the uneven spatial distribution of sampling events and the number of studies over the world (Table S4.1 and Figure 6). Most research in the northern hemisphere is concentrated in Europe, Northern America and Northern Africa. In the southern hemisphere, groundwater fauna research is focused on Australia, with New Zealand researchers increasingly contributing to the knowledge of stygofauna. A lack of temporal sampling in many parts of the world was noted, with repeated sampling over many years mainly occurring in regions of Europe, Australia and America. This lack of replicated sampling has limited the understanding of basic biology and ecology of many species until now. Below a more detailed analysis on stygofauna studies is presented, by geographic region, on the spatial and temporal distribution of studies (Figure 6), topic of studies (Figure 7a) and sample methods employed (Figure 7b).

4.1 | Africa

Africa, as a whole continent, is one of the least-studied regions of the world in terms of stygobiotic organisms (Tuekam Kayo et al., 2012). We identified a total of 155 studies, 749 sampling sites and 1,505 individual samplings (i.e. individual sampling events at one site, including repeated measurements). Studies concentrated in the Maghreb (Northwest Africa), particularly in Algeria (24 studies, 223 sampling sites, 816 samplings) and Morocco (44; 266; 347), with limited studies in South Africa (9; 20; 20) and Madagascar (4; 9; 11). For the remaining continent, only a few studies and very limited sampling sites exist (Table S3.1). Some apparently un-sampled regions of Africa, especially the Sahara, can be explained by the absence, or at least the low occurrence, of shallow groundwater, as can be seen by the light colours indicating a low groundwater recharge in Figure S2.2. Also, worth mentioning is the number of studies (13) with no information about the exact location of the sampling sites (star symbol in Figure 6), which is due to the age of these studies (>30 years old), which were incompletely available in secondary literature. Similar observations regarding the lack of specific locations of species findings in Africa have been made previously (Tuekam Kayo et al., 2012).

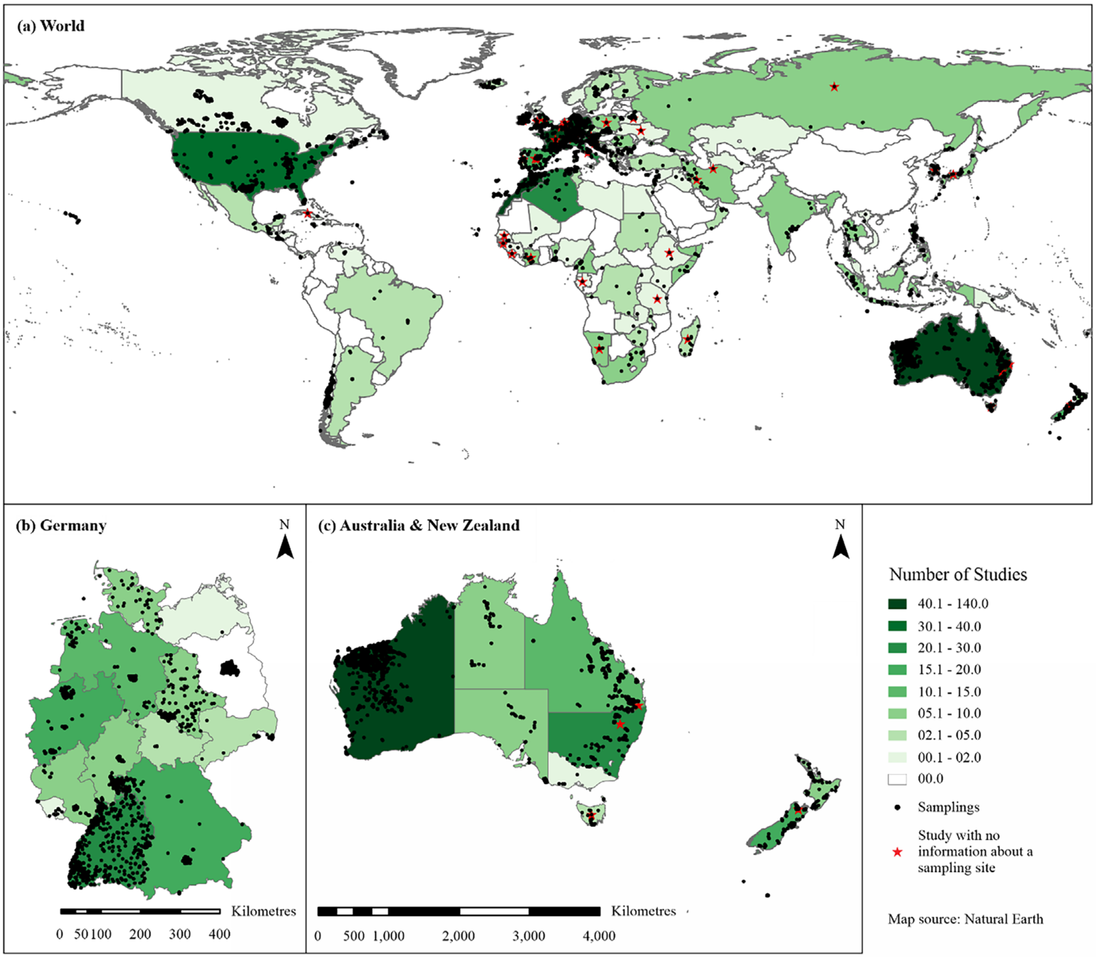

FIGURE 6 Overview of groundwater fauna samplings and number of studies (a) worldwide, (b) within Germany and (c) within Australia. Data sourced from 859 studies (Table S4.1).

More detailed evaluation of the reviewed studies revealed that 70% of studies in Africa concentrated on the description of newly discovered groundwater fauna (Figure 7a). Nevertheless, more than a dozen of studies in Algeria and Morocco conducted eco-toxicological investigations, revealing that faunal richness in some urban and mining areas is linked with groundwater quality and stygofauna abundance decreases with pollution (Aidaoui, 2019; Boughrous, 2007; Boughrous et al., 2007; Boulaassafer et al., 2021; Boulal et al., 2017; Boutin et al., 1995; Boutin & Idbennacer, 1989; El Adnani et al., 2006, 2007; el Moustaine et al., 2013, 2014; Hallam et al., 2008; Hichem et al., 2019; Laid & Zouheir, 2018; Merzoug et al., 2011, 2014; Ramzi et al., 2020) with authors proposing the use of stygofauna as bioindicators of water quality (Merzoug et al., 2011, 2014). Boulaassafer et al. (2021) study on evolutionary processes considerably expanded the knowledge of diversity and geographic range of a freshwater snail genus, and information on endemism and biogeographical distribution of stygobiotic crustacean species of Africa and Madagascar has been recorded (Tuekam Kayo et al., 2012). Additional findings of a new Nematode species in deep (3.6 km) fractured aquifers of South Africa expanded the global knowledge of the understanding of life under extreme conditions such as high temperatures (41°C), high pressures (1.3 to 6.8 kPa) or low dissolved oxygen concentrations (13 to 72 μM) and food shortages (Borgonie et al., 2011). Other research topics on the African continent such as biodiversity, biogeography and ecosystem service and ecological status are missing so far, as is any concerted effort from governments to monitor ecosystem health and biodiversity. Moreover, groundwater fauna of Africa is mainly sampled by using net samplers (in 25% of the considered studies) or traps (14%). In only 3% of the considered studies pumps are used (Figure 7b).

In Africa, there is very limited information about stygofauna distribution, ecosystem services and ecological status. Hence, more research effort should be directed to evaluate groundwater ecosystems to gain an understanding of their functions and roles in providing ecosystem services. Furthermore, an updated, comprehensive and broad overview of the geographical spread of groundwater fauna including associated trends over time is missing. Thus, more information is required from this continent to understand the full extent of faunal diversity and how to effectively manage these resources.

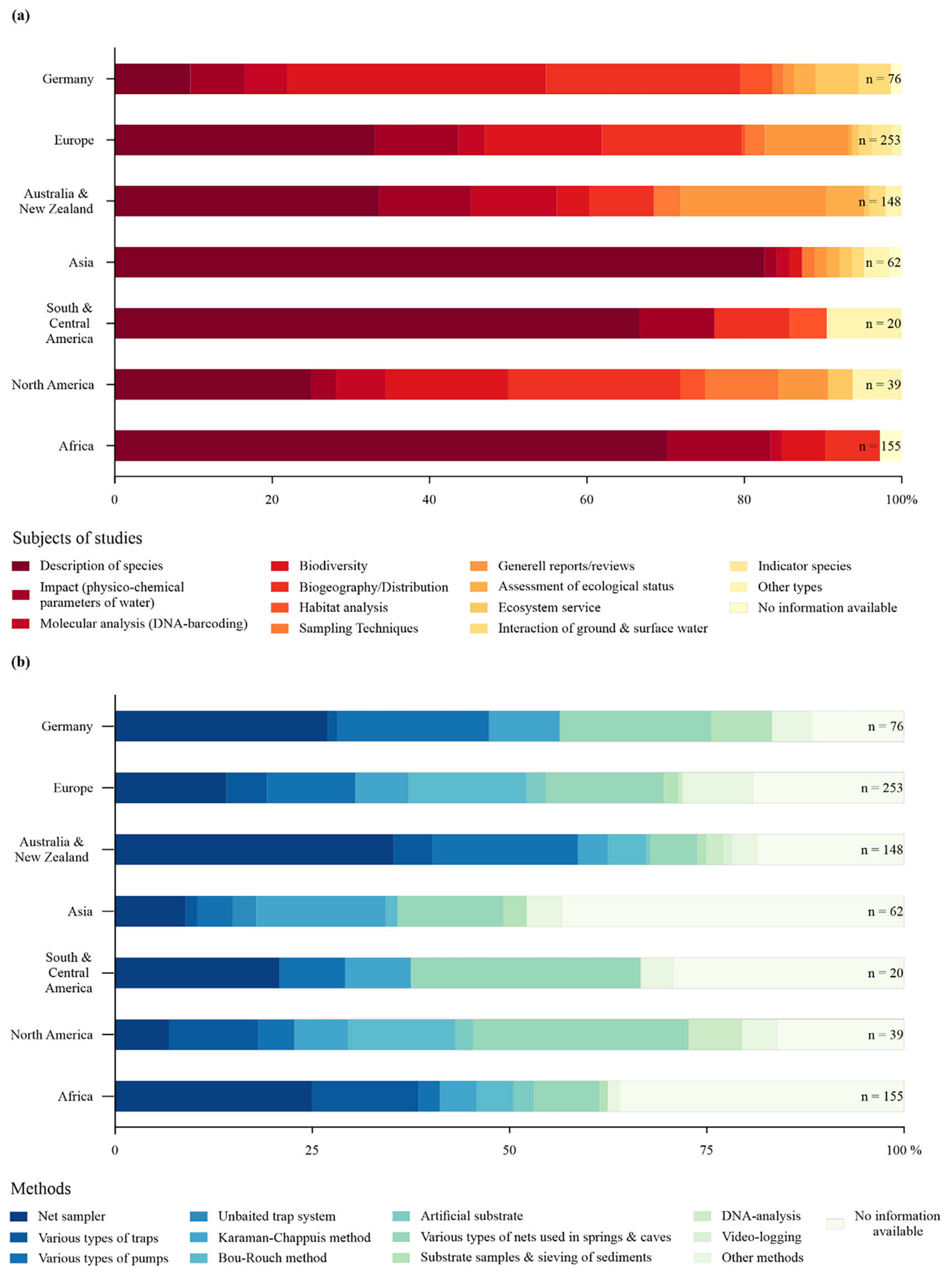

FIGURE 7 (a) Proportion of the different subjects of studies and (b) proportion of main techniques for sampling groundwater fauna for each continent and Germany (*n* = number of studies).

4.2 | Americas

Combined, the Americas have a total of 57 studies focusing on groundwater fauna, showing a lack of research in this field, given the size of the continents. The distribution of studies is unevenly distributed across the Americas (Figure 6). In the United States, the first groundwater fauna research was conducted in 1842 in the Mammoth Cave by Tellkampf (Romero, 2001). Broader investigation started in the 1960s and 1970s, for example conducted by Culver and Holsinger (Culver & Holsinger, 1992; Holsinger & Longley, 1980). As can be seen in Figure 6, research is patchy and focussed on the federal state Texas (7 studies, 248 samplings) and the east coast, with the federal states New York (5; 23), Florida (4; 384), West Virginia (3; 443), the District of Columbia (2; 87) and Alabama (1; 1,529), contributing

29 groundwater fauna studies with a comparably large number of 3,368 individual samplings. In contrast to other continents, groundwater fauna is mostly sampled in caves, springs and the interstitial of rivers and is also linked to a limited use of net samplers (only 7% of all studies; Figure 7b). The topic of most studies here is the description of newly discovered species including their traits (e.g. Wilhelm et al., 2006), followed by biogeographical analyses of groundwater fauna. In this context, studies on the influence of the last glaciation event on the present biogeographical distribution of stygobionts have to be emphasised. It is assumed that stygobionts are infrequent north of the glacial border and that more specialised species are unable to migrate into previously glaciated regions. Only less specialised species have invaded groundwater from surface after glacial retreat (Lewis & Reid, 2007; Strayer et al., 1995). Discussions on ecosystem service and biomonitoring on this continent are lacking.

As in North America, the main research focus in Central and South America are the description of newly discovered species (67% of studies) and biogeographical analyses of groundwater fauna (10%). In Central America, 14 studies were carried out at 128 sites, with the most studies conducted in Mexico (3 studies, 48 sampling sites). A similar number of studies (10) and samplings (235) were identified in South America, with a distinct lack of spatial distribution of studies across the continent (Figure 6). Groundwater research was conducted in both Argentina and Brazil, with studies concentrating on the impacts of land use and hydrogeological characteristics on groundwater invertebrate (Centurião et al., 2020; Tione et al., 2016).

In summary, North America groundwater fauna studies predominantly provide insight into newly discovered species and biogeographical analyses including factors influencing biogeographical distribution of stygobionts (e.g. glaciation), whereas Central and South America studies typically also concentrated on the discovery of new species and anthropogenic influences on these taxa. There were limited studies in porous aquifers, with groundwater fauna being also mostly sampled in caves, springs and the interstitial of rivers. Studies on the influence of aquifer types, climates, aquifer types and human disturbances on stygofauna are in their infancy, with very limited discussions on ecosystem service up to now.

4.3 | Asia and the Middle East

Although it boasts one of the oldest records of cave fauna (a cave fish identified in China in 1537), studies on groundwater fauna in Asia are limited and unevenly distributed. Overall, 63 studies and 1,286 samplings were recorded in Asia on 745 sampling sites (excluding Russia, Turkey and Cyprus, which are counted as European). The main focus of groundwater fauna studies was the description of newly discovered species (83%), with 119 new species and seven new genera described in the available studies. Similar to North America, groundwater fauna is mostly sampled in caves, springs and the interstitial of rivers, with the Karaman–Chappuis method and the usage of various types of nets being the dominating sampling methods.

In Eastern Asia, Japan and South Korea dominated the sampling effort (9; 237), with seven and nine groundwater fauna studies, respectively. In 1916, the first groundwater animal of Japan was described, while the first comprehensive and large-scaled study on faunal distribution was published in 1976 (Matsumoto, 1976), with the presence (or absence) of groundwater fauna revealing their potential as bioindicators (Matsumoto, 1976). Recent studies in Japan and South Korea have focused on the understanding of the subclass Copepoda, especially on the origin, relationship and distribution patterns of different species by analysing morphological micro-characters and phylogenetic relationships using modern techniques like scanning electron microscopy and molecular techniques (Karanovic, 2020; Karanovic et al., 2012; Karanovic et al., 2013; Karanovic et al., 2015; Karanovic & Lee, 2012). Berkhoff et al. (2003) was the first groundwater fauna research in South Korea in 2003 and related the distribution of fauna to land use (Berkhoff et al., 2003).

In the eastern part of India, seven studies with 43 samplings have been identified. The description of newly discovered species is the subject of all studies, while two recent studies have applied phylogenetic analyses to examine evolutionary relationships (Bandari et al., 2017; Karanovic & Ranga Ready, 2004). The research project ‘Biodiversity of subterranean groundwater fauna of India, with special reference to Copepoda and Bathynellacea’ from 2008 to 2013 increased the number of stygobiotic cyclopoid species of India from three to 11 (Totakura & Reddy, 2015). In all, one genus and 17 species have been described.

Within South-east Asia, there have been a total of 25 studies in the following three countries: Indonesia (9 studies; 51 samplings), Philippines (10; 139) and Thailand (6; 637). Descriptions and temporal analyses of species are the subject matter of all these studies, with research on caves dominating (e.g. Culver et al., 2006; Watiroyram et al., 2017). However, Husana and Yamamuro (2013) have attempted to identify several factors impacting stygofauna distributions. According to Brancelj et al. (2013), 122 stygofauna species have been described within South-East Asia, with 24 species described after this review. Additionally, an extensive study on ecosystem health and monitoring in the Philippines is currently underway (Magbanua, 2022).

A larger number of groundwater fauna studies (27 studies with 129 samplings) can be found in the Middle and Near East. However, 37% of the studies and 33% of the samplings were conducted in Iran. Research on groundwater fauna, focused on the amphipod genus *Niphargus*, has been conducted in Iran (Esmaeili-Rineh et al., 2015). Morphological characters and phylogenetic analyses resulted in the identification of 17 new stygofauna species in 2018, along with studies comparing Iranian amphipods with European nipargids (Bargrizaneh et al., 2021; Esmaeili-Rineh et al., 2015, 2016, 2018; Esmaeili-Rineh, Mirghaffari, & Sharifi, 2017; Esmaeili-Rineh, Sari, et al., 2017; Hekmatara et al., 2013; Mamaghani-Shishvan & Esmaeili-Rineh, 2019). Other studies in Iran used molecular techniques to investigate the distributional ranges of amphipods, revealing that ‘there is no evidence to consider that groundwater species are geographically more restricted than surface species’

(Esmaeili-Rineh et al., 2020), thus adding to the global understanding stygofauna distribution.

Our findings reveal that in Asia and the Middle East, most studies are still focused on the description of newly discovered species, with limited studies investigating the origin, functioning and distribution of stygofauna or groundwater ecology. Spatially, studies are concentrated in Japan, South Korea, India and Iran. In relation to the large area of this continent, Asia is poorly investigated and more information is required to effectively describe the biodiversity of stygofauna in this region.

4.4 | Australia and New Zealand

With 133 studies, 4,014 sampling sites and 5,826 samplings in total, extensive research on stygofauna and groundwater ecology is still conducted in different regions across Australia. Studies by Charles Chilton between 1882 and 1925 placed Australia at the forefront of groundwater fauna research in the late 19th and early 20th centuries. Much of the early focus of research on groundwater fauna was on discovery, species descriptions and biogeographic and evolutionary processes (Goater, 2009), with early studies on the origin and evolutions of groundwater biota occurring in western and central Australia (Bradford et al., 2010; Cooper et al., 2002; Leys et al., 2003). In the mid-late 1990s, groundwater fauna research saw a resurgence, as ecological analyses became a requirement for some environmental impact assessment (e.g. in Western Australia in 1998), with specific species gaining legislative protection (e.g. the crustacean *Lasionectes exleyi*). Government policies developed throughout the late 1990s to the early 2000s, aimed at protecting groundwater and their related ecosystems (Goater, 2009; Humphreys, 2006; Playford, 2001).

The close links between groundwater fauna research, water management policies and extractive industries (Hose et al., 2015) have seen sampling efforts unevenly distributed throughout the continent. Studies are focused in areas of intensive mining activities (Hose et al., 2015) and in the Murray Darling Basin, an area heavily reliant on groundwater for agriculture and potable water (Figure 6). As a result, the majority of groundwater fauna studies have been conducted in Western Australia (WA), New South Wales (NSW) and Queensland (QLD) (78, 23 and 15 studies, respectively), with notable descriptions of the stygofauna inhabiting Tasmanian cave systems (Eberhard, 1992, 2001) and research in South Australia that have contributed to knowledge stygofauna distribution and ecosystem functioning (e.g. Smith et al., 2016; Zeidler, 1985). Due to legislative requirements for sampling, groundwater fauna research has mainly focused on wells, using net and pump collection methods, with recent government initiatives investigating the effectiveness of sampling methods and eDNA for stygofauna monitoring (Korbel, McKnight, et al., 2022).

In WA, research has focused on the description of new species (28) and phylogenetics (12), with more recent studies looking at stygofauna diversity (5 studies). Most sampling events in WA have been conducted in the iron-ore-rich areas of the Pilbara region (2,020 of 3,742 samplings). Early studies from the Pilbara unveiled one of the richest stygofauna diversities in the world (Eberhard et al., 2004; Eberhard et al., 2005; Humphreys, 2001), with descriptions of Amphipods (Bradbury & Eberhard, 2000), Isopods, Ostracods (Karanovic, 2006; Karanovic & Marmonier, 2003), Spelaeogriphaceans (Poore & Humphreys, 1998) and Copepods (De Laurentiis et al., 1999). The biodiversity of the areas was further uncovered in 2004 with extensive surveying detecting stygofauna in 71% of sampled wells, with an average of 3.8 taxa and 23.3 individuals per sample (Eberhard et al., 2004). The Yilgarn region of WA has also seen a concentration of stygofauna genetics and evolution research, with 979 samplings in its numerous isolated calcrete aquifers, leading to suggestions of evolution within individual calcretes following independent colonisation by their epigean ancestors ('subterranean island hypothesis') (Allford et al., 2008; Cooper et al., 2007). West of the Pilbara region, the first discoveries of groundwater fauna occurred in the Cape Range and Barrow Island, with research here continuing (e.g. Saccò, Humphreys, Stevens, et al., 2022). The Cape Range Province in the Gascoyne region is globally recognised for its subterranean fauna and karst systems (Goater, 2009). Research in calcrete aquifers has added to the global understanding of stygofauna distribution patterns (Humphreys, 2001; Saccò et al., 2020). In the Perth region, with 30 samplings, studies focused on Copepods from basins and craton aquifers (De Laurentiis et al., 2001). Other surveys were the result of legislative requirement on coal and iron ore projects, e.g. surveys in the Enneaba region which resulted in the discovery of an undescribed Bathynellidid (see Hose et al., 2015). More recently, functional ecology (Bradford et al., 2010; Bradford et al., 2013; Saccò et al., 2019) and investigations into the use of eDNA techniques for stygofauna (e.g. van der Heyde et al., 2023) have become the object of stygofauna studies in WA. Such studies are contributing greatly to the worldwide understanding of ecosystem functioning, processes and stygofauna distribution.

Sampling in the Eastern states of Australia (QLD, NSW, VIC) is again linked with mining and agricultural groundwater dependencies. NSW is represented by 23 studies, 255 sampling sites and 794 samplings. The Hunter Valley contains over 20 of the world's largest coal mines, which resulted in numerous ecological surveys investigating stygofauna (including microbiota). Early work in the Hunter region improved the ecological knowledge of stygofauna, identifying the importance of organic matter supply for stygofauna richness (Hancock & Boulton, 2008), and leading to the discovery of the first stygobiotic beetle in eastern Australia (Watts et al., 2007). Other early work focused on biodiversity within karst ecosystems (e.g. Eberhard & Spate, 1995). However, most sampling sites in NSW (225) are located in the arid to semi-arid regions of the Murray Darling Basin, where industries extracting groundwater dominate (e.g. mining, agriculture). Here, groundwater studies have focused on the ecology of the alluvial deposits of the Namoi and Gwydir River catchments, improving knowledge of the environmental and human influences on stygofauna distribution (Eberhard et al., 2017; Menció et al., 2014), their connectivity with surface waters (e.g. Korbel, Rutlidge, et al., 2022), then using this information to develop frameworks for the assessment of groundwater ecosystem health (Korbel et al., 2017, 2019; Korbel, Greenfield, & Hose, 2022; Korbel, Hancock, et al., 2013; Korbel & Hose, 2011, 2015, 2017; Korbel, Lim, & Hose, 2013). Several of these Australian studies have been amongst the first to investigate the use of eDNA as a method for assessing biodiversity (e.g. Asmyhr & Cooper, 2012) and ecosystem functional processes in groundwaters. Others have been conducted in the alluvial aquifers of the Murray, Murrumbidgee, Lachlan and Macquarie catchments (Lennon, 2019; MacDonald, 2017; Nelson, 2020). Moreover, a review by Saccò, Blyth, Douglas, et al. (2022) on coastal groundwater ecosystems in Australia points out the importance of stygofaunal communities in coastal aquifers and the threats to them caused by size-reduction of the aquifer, salinization from seawater intrusion, land clearing, anthropogenic contamination and impacts of mining and industry.

In 2011, Korbel and Hose suggested a tiered multi-metric framework for assessing ecosystem health in groundwater, resulting in the Groundwater Health Index (see Section 2.4). This framework was first applied in the Gwydir River catchment, demonstrating differences in groundwater fauna and water quality under different land uses and allowing a numerical health ranking (Korbel & Hose, 2011, 2017). The GHI was improved in 2017 (Korbel & Hose, 2017) where its use was expanded into the Namoi and Macquarie catchment (Korbel & Hose, 2017) and is currently being utilised by the NSW government to monitor groundwater health in several of the Murray Darling subcatchments (NSW Department of Planning and Environment, 2022) and has been adapted for Europe (e.g. di Lorenzo, Fiasca, di Camillo, et al., 2020) and the Philippines (Magbanua, 2022).

In Queensland, sampling of stygofauna is geographically patchy and sparse (15 studies, 1,077 samplings), with many areas of the north and west un-sampled (Glanville et al., 2016). The spatial distribution is clustered around locations with extractive industry and intensive groundwater use (Glanville et al., 2016), for example in the Bowen (188 samplings) and Surat Basins (373 samplings), where Australia's largest known proven coal seam gas reserves are located (Hose et al., 2015). In the Surat Basin, consultant reports (Subterranean Ecology, 2012) fauna diversity in the Horse Creek alluvium and Walloon coal measures near Wandoan were described (Hose et al., 2015). The knowledge of stygofauna biogeography and biodiversity in Queensland has been contributed to by several studies (e.g. Little et al., 2016; Schulz et al., 2013) and is described in Glanville et al. (2016). A special feature of the state is the Queensland Subterranean Aquatic Fauna Database, which contains data from 755 samples of 582 sites provided by the Queensland Government and industry. In recent times, work describing groundwater species has occurred in the Northern Territory (Oberprieler et al., 2021; Rees et al., 2020).

Also, of note in this global region is the stygofauna research conducted in NZ, with 23 studies covering 305 sites. The first research on subterranean fauna in New Zealand was conducted by Charles Chilton (1882) who described the first amphipods. This study focused on range extensions and intraspecific variations, from the southern hemisphere in the alluvial groundwaters of the Canterbury Plains. An extensive sampling effort in the 1970s was mounted by Kuschel in the Waimea Plains, producing a collection of insects, crustaceans and molluscs (Fenwick, 2001). These early studies were followed by assessments of stygofauna distribution patterns (Fenwick & Scarsbrook, 2004; Scarsbrook & Fenwick, 2003; Wilson & Fenwick, 1999), hyporheic fauna (Boulton et al., 1997) and potential human impacts (Sinton, 1984). Such studies were succeeded by investigations into groundwater fauna ecology (Fenwick et al., 2021), interconnected hyporheic zones (Larned et al., 2007), human impacts on stygofauna (Hartland et al., 2011) and ecosystem functioning, including microbial studies (Close et al., 2008; Weaver et al., 2016). Alongside the ecological studies, there have been significant collections of stygofauna in the BioHertitage Project, funded by the National Institute of Water and Atmospheric Research (NIWA), where reference databases from 65 wells were collected with the aim to develop invertebrate indicators of groundwater health (Greenwood & Fenwick, 2019).

Overall research within the Australasian region has aided the global knowledge of stygofauna and their functions. It has been stated that 'Australia is considered world leading in its recognition of the need to protect groundwater resource and their dependent ecosystems through water resource policy' (Goater, 2009). Australia is regarded as a pioneer in the field of stygofauna monitoring programs but has also contributed greatly to the global understanding of stygofauna evolution, distribution, sampling methods, ecosystem functions and processes as well as anthropogenic impacts on these ecosystems (e.g. Bradford et al., 2010; Hose & Stumpp, 2019; Humphreys, 2001; Korbel et al., 2019; Korbel, Greenfield, & Hose, 2022; Leys et al., 2010; Murphy et al., 2009; Saccò et al., 2021). Due to the emergence of policies and legislation based on groundwater-dependent ecosystems in this region, researchers have been at the forefront in incorporating global knowledge on groundwater species, ecology and responses to disturbance to lead in the development of applied ecological research. This research is being used by governments to monitor, evaluate and report on groundwater health.

4.5 | Europe

Groundwater fauna research in Europe dates back to the 17th century, with pioneering work in France (Hertzog, 1933; Moniez, 1889), Italy (Pesce, 1980), Austria (Spandl, 1926), Germany (Kiefer, 1957; Noll, 1939), Slovenia (Sket, 1999; von Valvasor & Weichard, 1689), Switzerland (Graeter & Chappuis, 1913; Schnitter & Chappuis, 1914) and Spain (Camacho, 1989; Notenboom & Meijers, 1985). In total, there are 358 studies in Europe, covering 12,524 sites. As in all continents, early groundwater fauna research in Europe began with descriptions of species and taxonomy as well as the development of more complex sampling methods (e.g. the Karaman–Chappuis method [1933] and the Bou and Rouch [1967]). The application of diverse sampling methods (net sampler, various types of pumps and nets and Bou-Rouch method), particularly in Germany, has led to groundwater fauna research over numerous stygofauna habitats, including interstitial and hyporheic zone of rivers, cave and springs (Figure 7b).

Spatial analysis of fauna sampling sites in Europe is concentrated near the latitude of 45°N, along the Pyrenees in the west to the Dinaric Karst of Slovenia, Serbia, Montenegro and Croatia in the east. At this latitude, richness of aquatic and terrestrial species is high, resulting in the preferential examination of these fauna hotspots in many groundwater studies (Rapoport's rule [Rapoport, 1982]) (Culver et al., 2006; Pipan et al., 2020; Zagmajster et al., 2014). Additionally, as many of these 'hotspots' are located in Europe's vast cave system, some of which have special legislative protection (e.g. Vjetrenica in Bosnia Herzegovina), there has been a concentration of studies in these regions. For example, the Postojna–Planina Cave System (PPCS) in Slovenia is one of the most-studied caves globally, with more known stygobiotic species than any other cave or subterranean location in the world (Culver & Sket, 2000). In addition to research on new species, ecological and species distribution studies have been conducted in these karst environments, highlighting the potential use of copepods as natural tracers of complex water movements in epikarst (Pipan & Culver, 2007). Contrastingly, northern Europe has had a low frequency of sampling, with studies here indicating stygofauna consist mainly of a few old stygobiotic species and ubiquists (Särkkä & Mäkelä, 1998; Thulin & Hahn, 2008).

European studies on groundwater fauna have produced much of the global knowledge on the impact of natural events (e.g. glaciation, earthquakes) on stygofauna distribution and patterns of endemism (Särkkä et al., 1998; Thulin & Hahn, 2008). Due to its status as an island and its glaciation during the last ice age, the United Kingdom (UK) is also interesting for groundwater fauna research; however, there is a distinct lack of research into groundwater ecology in this region with only 10 stygobiotic species, three of them endemic to Ireland or England, having been identified. Moreover, most groundwater taxa in England have been collected in cave systems (Maurice, 2009), with the known distribution of most stygobiotic taxa restricted to an area south of the maximum limit of the Devensian glaciation (Proudlove et al., 2003). Additional knowledge of the impacts of natural events on stygofauna endemism and distribution were uncovered after the 2009 earthquake in L'Aquila, Italy, with authors who observed a decrease in subterranean copepod species abundance as a result of the earthquake-induced aquifer strain and a consequential flushing of fauna (Galassi et al., 2014).

As in Australia, European groundwater ecology research has been advanced through policies and legislative requirements in the 1990s. Particularly worthy of mention is the importance of the Swiss Water Protection Ordinance in groundwater research, which was one of the first international authorities to include monitoring of both water quality (physical–chemical water standards) and ecological criteria for groundwater systems (Danielopol & Griebler, 2008). In 2006, the European Groundwater Directive also triggered groundwater ecological research by stating the importance of protecting groundwater ecosystems, noting 'research should be conducted in order to provide better criteria for ensuring groundwater ecosystem quality' (European Union, 2006).

These government initiatives precipitated the PASCALIS project, which was the first project to investigate groundwater biodiversity and endemism patterns across several countries (Gibert & Culver, 2009). PASCALIS not only introduced a standardised sampling technique but also uncovered the spatial distribution of stygofauna (locating 214 species new to six European regions) and 112 species new to science (Gibert & Culver, 2009). This project was important for a global understanding of the importance of hydrological connectivity on biotic distribution within groundwaters. Additional research in Europe during this time also contributed to the global understanding of stygofauna with suggestions that altitude, hydrogeology, palaeographical factors and human activities in a region can interact in complex ways to influence species diversity and compositions (Dole-Olivier et al., 2009; Gibert & Culver, 2009).

Other research around the 1990s focused on the human impacts, ecotoxicology as well as functional roles of groundwater fauna (Avramov et al., 2013; Becher et al., 2022; Castaño-Sánchez et al., 2020a; di Lorenzo et al., 2019; Reboleira et al., 2013) leading to the development of bioindicators, which were utilised in more recent applications of ecology into groundwater monitoring frameworks. These studies along with studies indicating stygofauna habitat tolerances and distribution patterns (e.g. Dole-Olivier et al., 2009) and human impacts on stygofauna (e.g. di Lorenzo et al., 2015; di Lorenzo, Fiasca, di Cicco, & Galassi, 2020; di Lorenzo & Galassi, 2013) have indicated that groundwater organisms can be used as tools of landscape changes with the absence or presence of communities reflecting the impact of changes in regional groundwater quality (Marmonier et al., 1993). Adding to this research, studies investigated the agricultural impact in alluvial aquifers on groundwater communities, producing threshold values for nitrate, and produced faunal indicators of human impacts and thus groundwater health. Additional studies in Italy building on the Australian groundwater health index (Korbel & Hose, 2017) developed a European-based monitoring framework specific to nitrate (di Lorenzo, Fiasca, di Camillo, et al., 2020). Castaño-Sánchez et al. (2020a) reviewed existing ecotoxicological studies and presented a database containing experimentally derived species' tolerance data for 28 contaminants and temperature for 46 terrestrial and groundwater species.

Due to the breadth of stygofauna studies in Europe, this region has been at the forefront of developing bioindicators of groundwater condition (e.g. Malard et al., 1996; Marmonier et al., 2018; Mösslacher & Notenboom, 1999). Early attempts to use stygofauna as indicators for monitoring formed in Europe (e.g. Hahn, 2006; Steube et al., 2009; Stoch et al., 2009). Other more recent studies in Germany (see below section) have resulted in the development of ecological assessment frameworks (Fillinger et al., 2019; Griebler, Stein, et al., 2014). Marmonier et al. (2018) used two combined methodological approaches to assess the ecological status of groundwater ecosystems in two alluvial plains in France. Composition analysis showed that the species richness, abundance and assemblage composition significantly changed with agricultural land use or urbanisation around the wells, and in wells with low oxygen and high nitrate concentrations, the Ecophysiological Index (EPI) decreased.

The understanding of subterranean biodiversity and human impacts on this ecosystem is a necessary step for incorporating current biological concepts within the framework of groundwater management (Danielopol et al., 2004). Along with Australia, the majority of research on groundwater ecology and applications for management and monitoring frameworks was conducted in Europe (Fillinger et al., 2019; Griebler et al., 2010; Griebler, Stein, et al., 2014; Hahn, 2006; Koch et al., 2021; Stoch et al., 2009). As can be seen, much of the current research on European groundwater health frameworks has been conducted in Germany and Italy (di Lorenzo, Fiasca, di Camillo, et al., 2020; Stoch et al., 2009) with collaborations between German, Italian and Australian researchers a noted development (Castaño-Sánchez et al., 2020a, 2020b; Danielopol et al., 2003; Di Lorenzo et al., 2019; Galassi et al., 2009; Korbel, Rutlidge, et al., 2022; Stumpp & Hose, 2013).

4.5.1 | A focus on Germany

Our study indicates that research on groundwater fauna began in Germany in 1876. Since then, there are records of 76 studies, 2,378 sampling sites and 4,232 samplings (sampling density: 1.18×10^{-2} [samplings/km^2]) (Figure 8a). Although comparable high sampling densities can be found in Slovenia (4.59×10^{-2} [samplings/km^2]), Luxemburg (2.48×10^{-2}), Austria (1.78×10^{-2}) and Belgium (1.46×10^{-2}), these countries are spatially smaller and have less than half the number of studies and samplings than Germany. The high density and frequency of sampling in Germany have placed Germany at the forefront of stygofauna research.

Much of the sampling effort in Germany has occurred since 2000, with sampling concentrated in the state of Baden-Württemberg (Figure 8a). Fauna samplings are dominated by net and pump sampling (wells) and nets (caves and springs) (Figure 8b). Sampling methods vary due to aquifer type, for example netting method dominates studies in fractured chalk rock springs of the Baumberge area (Beyer, 1932). Nevertheless, most German research has occurred in unconsolidated aquifers (Figure 8c).

In the state of Baden-Württemberg, there have been 28 studies, at 950 sample sites with 2,026 samplings, at a density of 5.6×10^{-2} samplings per square kilometre (area: 35,751 km^2), one of the highest worldwide (Table S3.1). By the early 2000s, 105 taxa, 60 of them stygobionts, had been found in Baden-Württemberg, with studies covering diverse hydrogeology, including karst, quaternary sediments, crystalline and sedimentary rocks (see Figure S2.2). As such, this region has contributed to the global understanding of stygofauna distribution, including the identification of relationships between subterranean fauna distribution and hydrogeological aquifer type (Hahn & Fuchs, 2009). The temporal resolution of data in Baden-Württemberg is also remarkable, with 44 sites sampled annually or bi-annually between 2002 and 2020. Such frequent sampling has enabled the temporal analysis of groundwater fauna assemblages, with results indicating that abiotic, microbiological and faunistic parameters displayed limited changes between 2002 and 2014 (Stein et al., 2015).

Colonisation of groundwater by fauna has been a main topic of study within Europe. Stygofauna have surface water origins, with numerous theories surrounding their colonisation of groundwaters (Cooper et al., 2023), resulting in a high degree of endemism, many relict species ('living fossils') and a truncated food web consisting of few predators (Gibert & Deharveng, 2002). Another characteristic of groundwater is the scarcity of stygobiotic species so that often only half of all stygobiotic species in any given region are found at less than 5% of sites (Castellarini et al., 2004; Hahn, 2015; Martin et al., 2009).

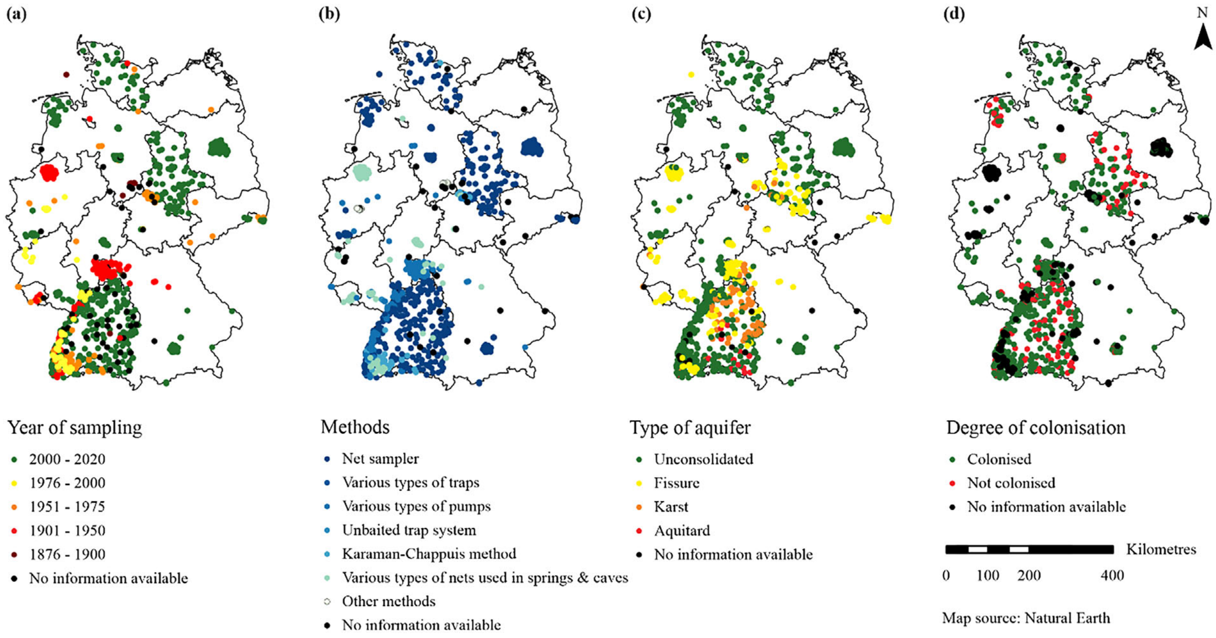

FIGURE 8 Overview over the (a) year of sampling; (b) used main techniques for groundwater sampling; (c) type of the aquifer and (d) the degree of colonisation of every sampling in Germany.

Distribution patterns within Europe are particularly impacted by glaciation (Stein, 2012; Stoch & Galassi, 2010). Our survey revealed that stygofauna were found in 63% (2,662 samples) of samples in Germany. However, in 27% of these samples, no information on the colonisation status was available, potentially due to the clustered results of older studies (early–mid-1900s), where results of individual measurements were not resolved on a site-specific level but interpreted as an overall result for a wider research area (Figure 8d).

The volume of data collected in Germany has resulted in the ability to investigate stygofauna distribution. Studies within Germany have indicated differences in distribution patterns of stygofauna spatially, with investigations of 'stygoregions' (Gibert et al., 2009) used to explain differences in distribution patterns explained by geological events (Hahn, 2009; Stein, 2012), such studies have been completed elsewhere in Europe (e.g. Stoch & Galassi, 2010). Studies have indicated that the degree of colonisation varies spatially within Germany, e.g. groundwater fauna is reported to be nearly absent in the Northern Lowlands, because of fine sediments and low oxygen concentrations (Stein et al., 2012). Yet, our analysis shows that 37% (161 samples) of the samples in this region contained fauna. Nevertheless, the number of samples with no available information is still high (226 samples; 52%). Additionally, there has been important research conducted on the impacts of geology and water chemistry on stygofauna, with studies investigating the impacts of oxygen concentrations (Stein, 2012) and physical habitat characteristics (e.g. aquifer and pore sizes; Hahn and Matzke (2005); Hahn, 2006; Hahn & Fuchs, 2009; Stein, 2012) on stygofauna distribution.

Interestingly, there is a clear difference in the main subjects studied between Germany and the rest of Europe. Within Germany, stygofauna biodiversity (33%) and biogeography (25%) are a distinct focus of research, with only 10% of the studies in our literature review focused on the description of species. This differs from the European context, where 33% of studies focused on taxonomy and species descriptions and 18% on biogeographic distribution and evolutionary processes.

Besides the focus on biodiversity and ecology issues, Germany has seen itself at the forefront of applying ecological research to address groundwater management and monitoring requirements. Early approaches for monitoring groundwater ecosystems began in Germany (see Section 2.4). Hahn (2006) introduced early frameworks, and Stoch et al. (2009) developed a predictive model for assessing groundwater ecosystems. Further, Steube et al. (2009), supported by the German Federal Environment Agency, suggested the use of biotic and abiotic indicators in groundwater ecosystem assessment and acknowledged difficulties in establishing reference conditions and the need to test proposed methods. Additionally, Griebler et al. (2010) proposed groundwater assessment methods utilising aquifer typology. These significant early developments paved the way for the development of the groundwater health frameworks (Korbel & Hose, 2011, 2017) and, for Griebler, Stein, et al. (2014), ecologically-based assessment scheme for groundwater ecosystems. Much of this work has been aimed to support the European Union Water Framework Directive (EC-WFD 2000). An assessment scheme using microbial indicators has since been developed the microbial Density-Activity-Carbon index (Fillinger et al., 2019), and Germany-based assessment schemes have been applied in numerous studies (Berkhoff, 2010; Gutjahr et al., 2014; Hahn et al., 2020; Koch et al., 2021; Spengler, 2017).

5 | CONCLUSION

This study has provided a global perspective on groundwater fauna research including its historical and technical development and spatial distribution.

The main findings of the current study are as follows:

- a continuing, exponential increase in the number of studies on groundwater fauna over the last 10 decades,
- changing research paradigms from the description of newly discovered species and their evolution towards ecosystemic and more holistic analyses of fauna and their functions to the application of ecological management and monitoring programs,
- a change in sampling methods from simple nets and hand pumps to more complex methods,
- the recent emergence of molecular technologies, such as eDNA, which offer the potential to ease sampling and enable vast data collection,
- large gaps in the spatial and temporal distribution of groundwater fauna remain, particularly in Africa, Asia and the Americas,
- due to spatial biases, the knowledge on groundwater biota and their potential functions may be biased towards the intensively sampled aquifers studied in Europe, Australia and New Zealand.

As such, a comprehensive and broad overview of the global geographical distribution of groundwater fauna in diverse climatic zones, aquifer types and associated trends over time is still required. In the future, a shift from local studies to a global perspective is essential in order to provide a common knowledge basis for understanding, assessment, monitoring and conservation of groundwater biodiversity. A worldwide effort to collect information on groundwater ecosystems, functional roles and human impacts on them is required to implement stronger policies and monitoring requirements for groundwater fauna so as to ensure these ecosystems are maintained and preserved into the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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