Biodiversity decline in aquatic ecosystems – is groundwater fauna at particular risk?

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The terrestrial subsurface harbours the largest available freshwater reserves on our planet: In particular, shallow aquifers are home to a vast but insufficiently explored biodiversity. Whilst biodiversity research gained a strong momentum in the past decades, threats to groundwater ecosystems increased as well and we may lose species before their discovery and formal description. Negative impacts to groundwater fauna mainly encompass groundwater pollution, warming, and habitat loss. Given their peculiar adaptation to the usually dark and energy poor environment including a slow metabolism and low reproduction rates, as well as further special characteristics of groundwater fauna like their fragmented distribution, and high number of endemic species, groundwater invertebrates seem to be specifically at risk. We firmly propose to establish ecological measures in routine groundwater monitoring and to take action in the development of biodiversity conservation strategies and groundwater ecosystem protection.

Englisch C, Zittra C, Griebler C (2024) Rückgang der biologischen Vielfalt in aquatischen Ökosystemen – ist die Grundwasserfauna besonders gefährdet?
Der terrestrische Untergrund beherbergt das weltweit größte Reservoir an verfügbarem Süßwasser. Zudem sind oberflächennahe Grundwasserökosysteme Lebensraum einer großen, bisher aber unzureichend erforschten Biodiversität an wirbellosen Tieren, der sogenannten Stygofauna. Während die Erforschung dieser verborgenen Vielfalt an Evertebraten in den letzten Jahrzehnten gehörig Fahrt aufnahm, stiegen gleichzeitig auch die negativen Einflüsse auf das Grundwasser, weshalb die Möglichkeit besteht, dass Grundwasserarten aussterben, noch bevor sie entdeckt und formal beschrieben werden. Negative Einflüsse auf die Lebensgemeinschaften umfassen chemische Verunreinigungen, Erwärmung und Übernutzung der Grundwasservorkommen. Wegen der besonderen Anpassungen der Grundwassertiere an den lichtlosen und energiearmen Lebensraum, wie etwa niedriger Stoffwechsel oder geringe Reproduktionsraten, sowie weiterer spezieller Merkmale wie sehr fragmentierte, räumliche Verteilung der Organismen, und einer großen Anzahl an endemischen Arten, scheint die Grundwasserfauna ganz besonders gefährdet. In diesem Überblicksartikel wird eingefordert ein ökologisches Monitoring für Grundwasserlebensräume zu etablieren und Strategien für die Ausweisung von Schutzgebieten und Maßnahmen zur Erhaltung der Biodiversität zu entwickeln.

Keywords: groundwater, stygofauna, threats, monitoring, protection.

Introduction

Groundwater ecosystems harbour hidden hotspots of biodiversity. Fauna in groundwater habitats are particularly adapted to the dark and generally energy-poor environment. In the following, we identify the most important threats to groundwater biodiversity and summarize its risk status. Moreover, we outline measures that could be adopted for a better protection and conservation of groundwater ecosystems and important ecosystem services they supply. Thereby, we hope to foster political and societal action and demand that groundwater ecosystems are considered in water legislation already today, for a prosperous tomorrow.

Groundwater fauna and its habitats – a brief Intro

Groundwater systems are extraordinary aquatic ecosystems that exceed all surface inland waters in their overall spatial dimension and volume. While lakes, rivers and wetlands contain only about 3 % of the world's available (unfrozen) freshwater, groundwater comprises 97 % (Danielopol et al. 2003). Groundwater ecosystems are dark and typically limited in space, energy- and resource poor environments that select for very specific morphological, and physiological adaptations (Gibert & Deharveng 2002). Groundwater animals usually lack pigmentation, have reduced or no eyes, and their bodies are small and elongated for better mobility in the interstitial space (Botosaneanu 1986; Gibert et al. 1994; Culver et al. 2023). Compared to their surface water congeners, metabolic rates of groundwater taxa are low, which enables them to tolerate oxygen- and nutrient-deficiencies over extended periods of time. Furthermore, groundwater fauna, which is also called stygofauna, has a longer life expectancy than their epigean relatives. To give one example, surface water isopods rarely live longer than two years, but groundwater isopods may live up to >20 years (Carpenter 2021). For the cave olm (*Proteus anguinus*), specimens with an age of more than 60 years have been recorded, and it is even estimated that they may live longer than 100 years (Voituron et al. 2010). Comparably little is known about dispersal and migration, reproduction rates, food web interactions and feeding behavior of stygofauna, a consequence of their secluded habitats (Mammola et al. 2020). For a long time, groundwater systems were erroneously considered a "biological desert", thought to harbor little to no life. Contrary, groundwater ecosystems are places of surprisingly high biodiversity. For instance, in Austrian groundwater, amphipods comprise at least 2–3 times more species than known from surface waters – a picture that is mirrored in many regions of the world. The high proportion of endemic species and the high cryptic diversity point at groundwaters as hotspots of a very specialized biodiversity that also consists to a considerable degree of relic forms whose present distribution reflects old river basins (e.g. of the Danube), the extent of primordial seas (e.g. the ancient Mediterranean Sea Tethys), or the glaciation during the ice ages (e.g. Würm ice age) (Galassi et al. 2009; Stoch & Galassi 2010; Robertson et al. 2023). While living in groundwater ecosystems seems to be quite challenging, the fact that environmental conditions are comparably constant is advantageous as it allows to optimize adaptation. According to the ecological K-strategy, Gibert et al. (1994) discusses the A-strategy to be realized with animals in groundwater habitats, a strategy that usually occurs in physically predictable, but ecologically unfavorable, environments. Naturally, extreme hydrological events and/or fast changes in temperature are the exception. It is assumed that the high stability of conditions in groundwater systems is one reason why epigean organisms regularly enter subterranean aquatic habitats, possibly to seek refuge from adverse conditions at the surface, and in many cases lastingly colonize it (Zagmajster et al. 2014; Robertson et al. 2023).

Stygofauna living permanently and throughout their life cycle in groundwater habitats are termed stygobionts, while those that only spend parts of their life cycle in these environments are considered stygophiles. Stygoxenes are surface water species accidentally and usually fatally trapped in groundwater ecosystems (Gibert et al. 1994; Culver et al. 2023). First observations of stygobionts and stygophiles were made in caves and springs, comprising mainly invertebrates, with few, very regional species of cave fish and amphibians. The most common taxonomic groups of stygofauna are crustaceans. These are Ostracoda, Copepoda, Amphipoda, and Isopoda that can be typical stygobionts and stygophiles. The group of Syncarida, that includes the order Bathynellacea, are stygobionts exclusively. Besides, groundwater habitats are populated by Cnidaria, Rotifera, Gastrotricha, Platyhelminthes, Annelida (Oligochaeta and Polychaeta), Gastropoda, Bivalvia, Nematoda, Tardigrada, Acari and Insecta (e.g. Coleoptera, Plecoptera, Trichoptera) (Fig. 1). The majority of these forms are meiofauna (< 1 mm), but body sizes range from ≤ 100 µm (e.g. Rotifera or small nematodes) to ≥ 1 cm (e.g. large amphipods or insect larvae) with only a few very large forms (i.e., several centimeters to decimeters in large oligochaetes or cave fish and salamander) (Marmonier et al. 2023).

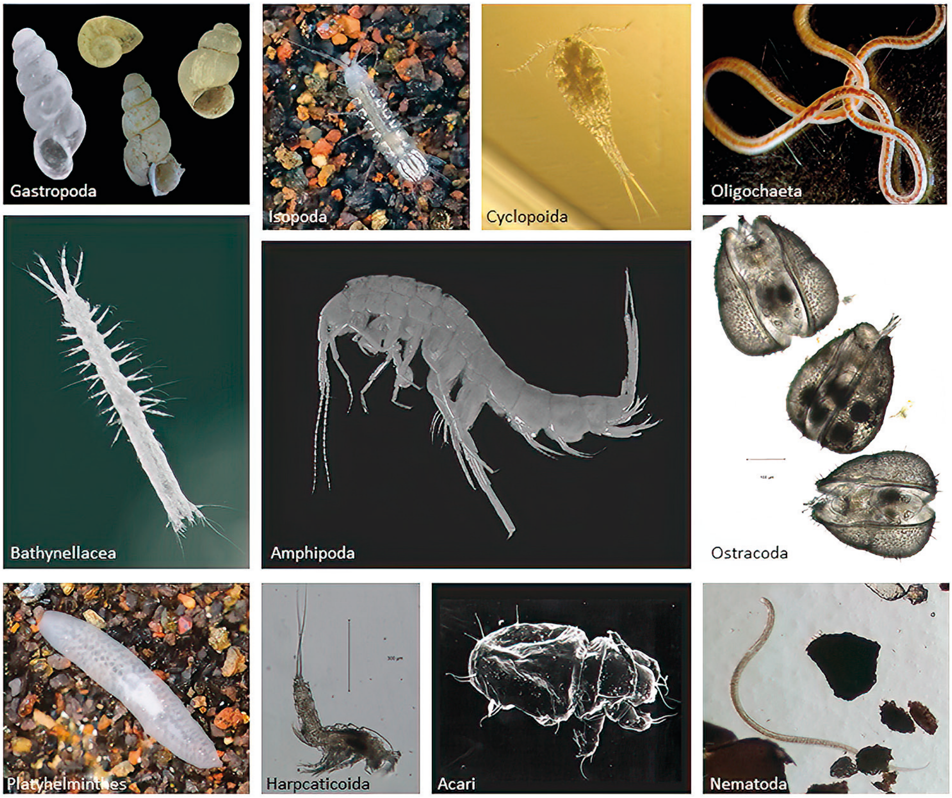

Fig. 1: Examples of some of the most common fauna groups in groundwater ecosystems. Sizes are not true to scale. Photos: Gastropoda & Amphipoda – Constanze Englisch; Isopoda, Oligochaeta & Platyhelminthes – Günther Teichmann; Cyclopoida – Günther Teichmann & Maria Avramov; Bathynellacea – Erhard Christian; Ostracoda & Harpacticoida – Santiago Gaviria; Acari – Peter Pospisil & Dan L. Danielopol; Nematoda – Florian Scharhauser. – Abb. 1: Beispiele für einige der häufigsten Tiergruppen in Grundwasserökosystemen. Die Größenangaben sind nicht maßstabsgetreu. Fotos: Gastropoda & Amphipoda – Constanze Englisch; Isopoda, Oligochaeta & Platyhelminthes – Günther Teichmann; Cyclopoida – Günther Teichmann & Maria Avramov; Bathynellacea – Erhard Christian; Ostracoda & Harpacticoida – Santiago Gaviria; Acari – Peter Pospisil & Dan L. Danielopol; Nematoda – Florian Scharhauser.

So far, about 2,000 groundwater animals have been described at species level from Europe (Mösslacher & Hahn 2003), but new taxa are continuously being discovered. In fact, the global maximum estimate for subterranean metazoan richness is about 100,000 species, of which about a third is assumed to be aquatic (Culver & Holsinger 1992; Malard et al. 2023a). Knowledge on the distribution of groundwater metazoans is limited and indicates the existence of patchy biodiversity hotspots (Iannella et al. 2020), but lacks clear-cut spatial patterns. This is likely related to the very heterogenous groundwater environments that enforce highly variable biodiversity patterns at regional scales by modulating local species pools. At larger scales, biogeographical patterns crystallize. In Europe, a latitudinal cave and groundwater fauna "biodiversity ridge" has been observed between approx. 42° N and 47° N, where both metazoan biodiversity and the number of known biodiversity hotspots is comparatively high (Culver & Sket 2000; Culver et al. 2006; Deharveng et al. 2009; Eme et al. 2017; Pipan et al. 2021; Zagmajster et al. 2023). This pattern reflects the maximum extent of glaciations during the last ice ages (Riss/Würm ice age), during which most aquatic species living in glaciated areas either became extinct, sought refuge in groundwater habitats or migrated southwards (Thienemann 1950; Culver et al. 2006). Regions that were fully glaciated during the ice ages therefore hold little groundwater biodiversity at low abundances, even after re-colonisation, but harbour relic species (Deharveng et al. 2009; Martin et al. 2009). This pattern is partly also related to the structure of groundwater habitats. While glacier activities in low altitudes grinded coarse rock and sediment material into fine sediments with little pore space and slow water flow velocities as well as typically hypoxic to anoxic conditions, in the high biodiversity belt we find extended karst systems such as the Dinaric karst, the Alps and the Pyrenees. Austria´s groundwater fauna reflects these general patterns of European subterranean biodiversity, as the maximum extent of the Würm/Riss glaciations was partially located here, making it a border region to the high biodiversity ridge (Fig. 2). The exact position in the northern slope of the biodiversity ridge, however, is so far not well defined since large areas of Austria's subsurface have not yet been explored in detail.

Large scale biogeographic patterns are also present in the eastern United States with higher taxonomic richness of stygobionts between the borders of Pleistocene glaciation and the coastal plain, than within/along the respective limits (Strayer et al. 1995; Marmonier et al. 2023). For most continents we currently lack the data basis to extract such clear large-scale groundwater biodiversity patterns.

Differences in spatial patterns of species richness at varying spatial scales suggest that they are influenced, besides historic climate events and structural properties (habitat availability, opportunity for dispersal) by current climate conditions (precipitation and groundwater recharge) and surface productivity (Zagmajster et al. 2023), among others. Groundwater fauna depends on a minimum supply of dissolved oxygen. In consequence, fauna in groundwater is found in large quantities close to the groundwater table and in the vicinity of surface waters. Where oxygen penetrates deeply, e.g. in karstified rock and highly permeable and energy poor alluvial aquifers, fauna may occasionally conquer deeper zones with a lower boundary in distribution of approximately 2,000–4,000 meters, mainly controlled by oxygen, temperature, and pressure (Borgonie et al. 2011; Sendra & Reboleira 2012; Fišer et al. 2014).

Several additional environmental factors driving groundwater biodiversity, usually acting together, were identified (by e.g. Deharveng et al. 2009; Malard et al. 2009). The size of

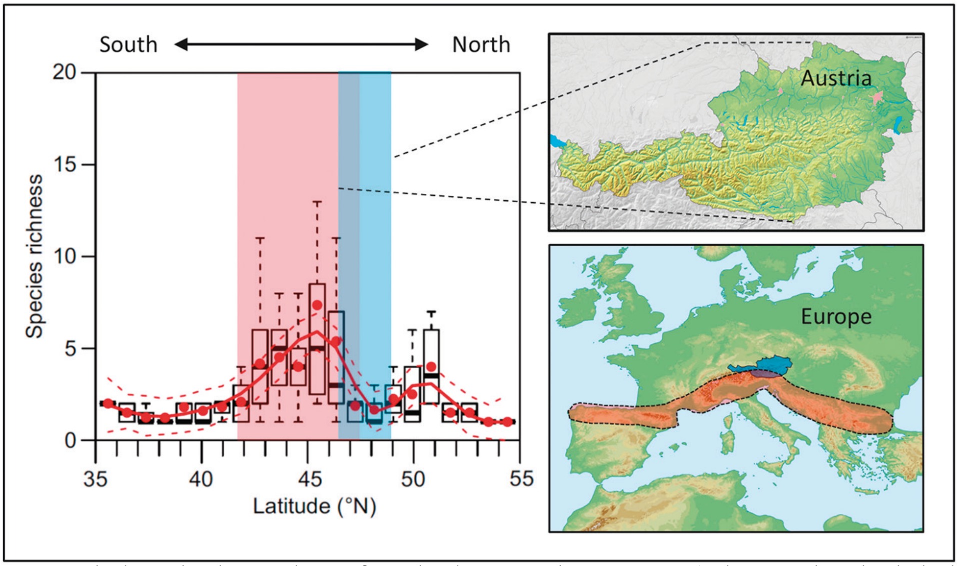

Fig. 2: The latitudinal groundwater fauna biodiversity ridge in Europe (red area within the dashed line). Left figure was modified from Eme et al. (2017); right upper map is from https://de.wikipedia.org/wiki/Datei:Austria_topographic _map.png; © User: Reinim19; right lower map is from https://en.m.wikipedia.org/wiki/File:Western%20_Europe_DEMIS_topographic_map.svg; © User: Pethrus. – Abb. 2: Das latitudinale Biodiversitätsband der europäischen Grundwasserfauna (roter Bereich innerhalb der gestrichelten Linie). Die linke Abbildung wurde verändert aus Eme et al. (2017), übernommen; die rechte obere Karte stammt von https://de.wikipedia.org/wiki/Datei:Austria_topographic _map.png; © User: Reinim19; die rechte untere Karte stammt aus https://en.m.wikipedia.org/wiki/File:Western%20_Europe_DEMIS_topographic_map.svg; © User: Pethrus.

void space in the aquifer appears an important property as well as connectivity of interstitial space and the degree of hydrological connectivity to the surface. Co-acting, these habitat properties steer the availability of dissolved oxygen and organic matter as key resources for stygofauna (Dole-Olivier et al. 2009; Johns et al. 2015; Korbel & Hose 2015). Other properties known to modulate stygofauna biodiversity and community composition are the altitude and the depth of the groundwater table, *i.e.* stygofauna abundances generally decrease with an increasing distance between land surface and groundwater table, and highest taxonomic richness in Europe was found at mid altitudes between 200 and 500 m.a.s.l. (Dole-Olivier et al. 2009). With respect to temperature, a vast portion of stygobionts is sensitive to a rapid and pronounced temperature increase (Brielmann et al. 2011; Griebler et al. 2016; Spengler & Hahn 2018; Di Lorenzo & Reboleira 2022; Di Lorenzo et al. 2023), yet, with individual species being more resilient to temperature changes than previously thought (Di Cicco et al. 2023). On the other hand, no clear patterns with respect to groundwater composition and hydrochemistry have yet been observed, but long-term exposure to, e.g. high salinity may increase stygofauna mortality (Castaño-Sánchez et al. 2020; Becher et al. 2022).

Major threats to groundwater ecosystems and fauna biodiversity

Groundwater and as such all subterranean aquatic ecosystems experience serious pressures. On a global scale, there are three major critical threats to groundwater resources and consequently to groundwater biodiversity and ecosystem functioning. These are (1) contamination with priority pollutants (e.g. petroleum hydrocarbons, chlorinated solvents), anthropogenic chemicals (e.g. pesticides, pharmaceuticals), and nutrients (e.g. nitrate), (2) overuse of groundwater, as well as (3) heat and climate change effects (Griebler et al. 2019; Mammola et al. 2019). Increasing land use change for urbanization and agricultural activities are pressures integrating more than one of the threats mentioned above (Burri et al. 2019; Kretschmer et al. 2023).

Intense agriculture is a key driver of negative impacts to groundwater ecosystems through the import of nutrients, organic and inorganic contaminants into aquifers, changes in groundwater recharge due to deforestation, monocultures and soil compaction, and groundwater abstraction for irrigation (Marmonier et al. 2018; Tweed et al. 2018; Rohde et al. 2021). Urbanization comes along with groundwater contamination from leaking sewage pipelines, surface run-off and a reduced groundwater recharge through extensive surface sealing. Additionally, urbanization favors groundwater warming, the evolution of subsurface heat islands and reducing conditions in the aquifer(s) (McDonough et al. 2020; Becher et al. 2022). New pressures to urban groundwater ecosystems include active heat discharge, i.e. from the use of groundwater as cooling agent in industry and for air conditioning of buildings (Menberg et al. 2013; Blum et al. 2021). Sources of contamination are landfills and infiltration of contaminated surface waters (Uhl et al. 2022). Intervention in the morphology and hydrology of surface waters via bank stabilization and the construction of dams disconnect the vital surface water-groundwater interface (Piégay et al. 2009). Threats from industry include, besides the improper storage of waste and direct release of contaminants, underground and surface mining activities (Mammola et al. 2019; Li et al. 2021). Increasing demands for drinking water supply may additionally drive overexploitation of groundwater resources. Climate change with its increase in air temperature, in evapotranspiration, and extreme weather events such as long-lasting droughts, accelerates water needs for irrigation and promotes groundwater overexploitation (Scanlon et al. 2012; Kretschmer et al. 2023; Benz et al. 2024).

In conclusion, there are many factors caused by human activities that directly or indirectly impact groundwater quantity and quality with a potential negative effect to groundwater fauna biodiversity (Castaño-Sánchez et al. 2020; Becher et al. 2022; Kretschmer et al. 2023). Intensification of these activities and threats is expected in the near future.

Is groundwater fauna currently at risk?

A solid assessment of the risk status of groundwater fauna, e.g. species richness and size of populations, is extremely difficult since only a fraction of the subsurface habitats has been explored and long-term monitoring data are almost completely absent. There are serious knowledge gaps regarding overall taxonomic richness, species-specific biogeographic ranges, vertical extent and live-limiting conditions, autecology, and ecological niches, as well as food web interactions and the ecological roles of fauna (Mammola et al. 2020; Griebler et al. 2023a; Marmonier et al. 2023). While groundwater is by far the largest freshwater biome, it is not easily accessible, which is one reason why exploration of groundwater fauna produces rather patchy patterns. Moreover, stygofauna comprises high proportions of cryptic, rare, and endemic species as well as relic species, which makes generalisations with respect to ecological prerequisites and risk assessment of stygofauna difficult to achieve (Malard et al. 2023b). At present, it is estimated that about 50 % of the global groundwater biodiversity is not known yet, therefore if we consider a biodiversity loss occurring in groundwater habitats similar to what is observed for surface aquatic and terrestrial ecosystems (Dudgeon et al. 2006; Newbold et al. 2015; Leclère et al. 2020; Albert et al. 2021), extinction rates among still unknown groundwater species may be suspected to be high (Niemiller et al. 2013; Griebler et al. 2023a). To put it in a nutshell, it's possible that we try to 'count the books while the library burns', as stated by Lindenmayer et al. (2013).

While risk assessment of groundwater fauna and biodiversity is difficult, there is clear evidence for the high sensitivity of groundwater organisms and high vulnerability of groundwater ecosystems to disturbance once it occurs. First, stygofauna has adapted to its specific habitat over thousands of years to successfully thrive in these comparably stable and energy-deprived environments (Fišer et al. 2023), providing it with a limited potential to tolerate and adapt to short- and mid-term changes in key living conditions. Due to highly fragmented populations, low dispersal capacities, and low reproduction rates, the integrity and resilience of groundwater fauna communities is furthermore susceptible to rapid disturbances (Di Lorenzo et al. 2023). Second, the resistance of an ecosystem to disturbance is to some extent related to its energetical status and productivity. Groundwater ecosystems, typically being energy-poor and oligotrophic (low productivity) environments, are as such particularly vulnerable to disturbance (Kovarik 2015; Hose et al. 2022). Two examples are briefly highlighted in the following.

(1) Groundwater ecosystems do have a natural capacity to purify incoming water from organic matter and nutrients, including organic and inorganic contaminants. This ecosystem service is based on a sensitive balance between the low microbial biomass and activity in aquifers, the flux of matter to the aquifer, the comparatively long residence time of compounds introduced, as well as the large dimensions of aquifers (Griebler et al. 2019). Groundwater ecosystems can buffer inputs of dissolved organic carbon and nutrients to a certain degree by increasing microbial biomass and activity (Fillinger et al. 2023). This is particularly the case at the boundary of the saturated and unsaturated zones, as well as in the hyporheic zones. However, an overload with organic carbon, nutrients and contaminants can readily exceed the ecosystem's capacity for "natural attenuation". Frequent consequences are the accumulation of contaminants (as occasionally seen for nitrate, pesticides, heavy metals, and heat) as well as the shift to reducing conditions (Stenger et al. 2008; Stuart et al. 2012; Benz et al. 2018b; Vesper 2019). Both constitute a serious threat to groundwater fauna richness and abundance (Castaño-Sánchez et al. 2020; Di Lorenzo et al. 2023).

(2) The sealing of surfaces, the construction of urban subsurface infrastructure like underground parking lots, sewage pipelines, district heating networks, subway tunnels, as well as the use of geothermal energy, lead to excessive warming of groundwater below cities (Huang et al. 2009; Menberg et al. 2013; Benz et al. 2018b; Hemmerle et al. 2019). However, groundwater temperature is not only rising steadily in urban aquifers. With some delay, climate warming is reaching down into the subsurface (Benz et al. 2016, 2018a; Epting et al. 2021; Noethen et al. 2023; Benz et al. 2024). Since an increase in temperature stimulates metabolic activities, groundwater warming accelerates the energy require-

ments of stygofauna (as well as microbes) in a typically energy-poor environment. Higher metabolism is linked to faster consumption of available oxygen. Additionally, solubility of oxygen is negatively correlated to groundwater temperature. Moreover, many groundwater invertebrates are cold-stenothermic with low tolerance to chronically elevated water temperatures (Brielmann et al. 2011; Becher et al. 2022; Di Lorenzo et al. 2023). Consequently, in oligotrophic groundwater ecosystems warming can lead to a loss of biodiversity via starvation, heat stress, and oxygen deficiency.

A wide range of environmental factors and habitat properties shape groundwater fauna. The significance of individual factors for a condition should however be interpreted critically, as several influencing factors typically overlap. Indeed, experience from laboratory experiments testing the toxicity of selected chemicals and tolerance of individual taxa must be interpreted with caution (Di Lorenzo et al. 2023) for the following reasons: In their natural environment, organisms are typically exposed to a multitude of limitations, mixtures of contaminants, and combinations of stressors that amplify each other, i.e. increased groundwater temperature, eutrophication, and the presence of toxic contaminants. Under laboratory conditions, however, only a small selection of species that are abundant and resilient enough for laboratory testing can be tested for a limited number of stressors at a time. Testing biases like excluded or added negative as well as positive cumulating effects (e.g. food supply under laboratory conditions: more regular/higher availability could benefit productivity and increase resilience, or starvation could falsify sensitivity thresholds and decrease resilience) can hardly be prevented. Therefore, it is challenging to gain a realistic, holistic impression of impacting factors on groundwater ecosystems or fauna populations.

Various studies have addressed the negative effects of intensive agricultural land use on groundwater fauna biodiversity and density (Korbel et al. 2013a, 2013b; Marmonier et al. 2018). Also, the locally fast warming of groundwater and the overall ongoing contamination of aquifers in cities clearly put groundwater fauna diversity at risk (Becher et al. 2022). A fact that seriously impacts groundwater fauna biodiversity is the overexploitation of groundwater. Abstraction of groundwater from many aquifers worldwide by far exceeds the natural renewal rate (Gleeson et al. 2012). Regional declines of groundwater levels by several meters over the past years to decades are very common in many regions of the world (Mammola et al. 2019). At many sites, groundwater drawdown exceeds dozens of meters (Konikow & Kendy 2005). In comparison to other pressures, the ecological consequences of groundwater abstraction for fauna have received little attention. Lowering of groundwater levels first and foremost is habitat loss to groundwater fauna (Di Lorenzo & Galassi 2013; Stumpp & Hose 2013), which in consequence also means a loss of populations, species, and ecosystem functions and services (Larned 2012). In fact, an increasing distance between land surface and groundwater table correlates negatively with the abundance and richness of groundwater fauna, which can be explained by a progressive scarcity of food and oxygen (Danielopol et al. 2000; Datry et al. 2005; Hancock et al. 2008; Stumpp & Hose 2013). Groundwater overuse in karstic areas may lead to disappearance of cave drip-pools, larger standing water bodies and subterranean rivers with its related invertebrate communities (Brancelj & Stoch 2022; Pipan & Culver 2022). In addition, lowering of groundwater levels can lead to salt water intrusion in coastal areas and the disconnection between (freshwater) surface waters and aquifers, with detrimental consequences for groundwater quality (Uhl et al. 2022).

Tab. 1: Cause-Effect matrix for key groundwater ecosystem pressures, environmental conditions, and biodiversity/density of groundwater fauna. GW = groundwater; SW = surface water. – Tab. 1: Ursache-Wirkungs-Matrix für die wichtigsten Belastungen des Grundwasser-Ökosystems, Umweltbedingungen und Artenvielfalt/Dichte der Grundwasserfauna. GW = Grundwasser; SW = Oberflächenwasser.

	Habitat availability/loss	Deterioration of GW quality	Warming of GW	Reduction in GW fauna abundance	Loss in GW fauna biodiversity
GW Contamination	no	strong	moderate	strong	strong
GW Overuse	strong	minor	no	moderate	moderate
Urbanization	strong	strong	strong	strong	strong
Conventional agriculture	strong	strong	minor	strong	strong
Mining activities	strong	strong	No studies available	strong	strong
Climate change	moderate	minor	moderate	No studies available	No studies available
SW contamination	minor	strong	no	minor	minor
Invasive species	No studies available	no	no	No studies available	No studies available

strong	
moderate	
minor	
no	
No studies available	

Measures for the protection of groundwater ecosystems and conservation of groundwater fauna

Existing laws and directives for the protection of groundwater are mostly resource-focused with no intentional consideration of biotic communities and their importance for the maintenance of essential ecosystem functions (Tomlinson et al. 2007; Griebler et al. 2010; Mammola et al. 2022b; Griebler et al. 2023a). This is in contrast to current regulations dedicated to surface waters, such as the European Water Framework Directive (EU-WFD 2000). Groundwater ecosystems and fauna are highly vulnerable to environmental changes and disturbance and therefore require similar consideration and protection (Hose et al. 2022; Griebler et al. 2023a). Fortunately, there are some positive developments. There are good examples of the protection of cave habitats and subterranean fauna at international and national level. Several European countries located at the subterranean biodiversity ridge (i.e. Slovenia, France or Croatia) already protect selected cave systems and established Red Lists including stygobionts (Baillie et al. 1996; Allanic 2012). A particular good-practice example is the Croatian Red Book of Cave Fauna which is the first Red List dealing with nearly 200 subterranean species. Here, about one third of all listed species are considered "Critically Endangered" (Ozimec 2011). The long Austrian tradition in speleology has led to the implementation of the Natural Caves Law (Naturhöhlengesetz 2013) that protects groundwater habitats in natural caves and therefore plays an indirect role (by not protecting species themselves, but rather their habitats) in the conservation of cave fauna, including stygobionts. Apart from caves, other groundwater ecosystems receive protection only indirectly, via protection of drinking water resources and the protection of surface terrestrial and aquatic ecosystems, i.e., in National Parks. In Austria, only a handful of groundwater species are covered by existing legislation (e.g., through the Habitats Directive or the Species Protection Ordinance). The Austrian Red List contains only a few groundwater/spring snails (Reischütz & Reischütz 2007).

Similar to surface ecosystems, groundwater habitats face increasing pressures and groundwater fauna is, globally as well as on the Austrian scale, at risk. One may argue that groundwater fauna, due to the protective features of soils and sediments covering aquifers, is less exposed to negative threats when compared to surface aquatic communities. As already mentioned above, because of the scarcity of available autecological and ecotoxicological information of groundwater fauna and associated difficulties in systematic risk assessment, we are unable to provide a final clue. Worth highlighting, the achievement of protection statuses for groundwater species, e.g. to be listed on IUCN Red Lists (IUCN 1948), is extremely challenging. In this context, the Red List criteria and thresholds for the admission of invertebrate species has been repeatedly criticized to be inappropriate (Cardoso et al. 2011, 2012) and so far, no major changes in the Red List assessment system were implemented to specifically target groundwater fauna.

Effective steps towards the protection of groundwater ecosystems and conservation of (aquatic) subterranean fauna require equal treatment by law of all kinds of aquatic and terrestrial ecosystems (Hahn et al. 2018). Groundwater ecosystems provide essential services (Griebler and Avramov 2015) and deserve targeted protection. Protection and conservation of groundwater fauna must be implemented by water directives and regulations that define clear targets as well as sustainable management strategies for groundwater use. Such legal actions need to be accompanied by monitoring programs as well as measures to build awareness regarding the role of groundwaters in supplying vital ecosystem services but also as hotspots for biodiversity. In the best case, groundwater ecosystem protection targets large, interconnected areas. Furthermore, ideally landscape and surface waters are encompassed as well, since these habitats are primary links to the groundwater systems. Besides, international, national and regional regulations for the protection on bigger spatial scales such as the Convention on Biological Diversity (CBD 1993), the Convention on Wetlands of International Importance (Ramsar 1975), the World Heritage Convention (WHC 1975), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 1975), or the currently being developed IUCN Red List of Ecosystems (RLE) (Keith et al. 2015) are or may become dedicated tools to tackle conservation of groundwater biodiversity (Niemiller et al. 2018). Indeed, nature conservation areas have already proven to be effective in sustaining biodiversity, ecosystem functioning and ecosystem services in several surface areas as well as a few subterranean cases (Ozimec 2011; Tanalgo et al. 2022; Griebler et al. 2023b).

A key motivation for groundwater protection and conservation is that groundwaters provide vital ecosystem services like water purification that depend on healthy groundwater communities (Griebler & Avramov 2015), and any negative feedback on groundwater quality and availability through groundwater biodiversity loss will have direct and dramatic consequences for human well-being (e.g. provision of drinking water). To build a strong foundation for the establishment of effective conservation measures and policies, further research is necessary that should focus on closing knowledge gaps in stygofauna species identification, distribution and limiting conditions (e.g. through a combination of experimental and explorative in-situ research). Use should be made of modern methods (e.g. eDNA, species distribution modelling) to characterize stygofauna biodiversity patterns and their susceptibility to human impact (Mammola et al. 2021; Griebler et al. 2023a). In parallel, species extinction risk should be assessed and threshold values for anthropogenic stressors defined to provide guidelines for the sustainable use of groundwater. Finally, an integrative groundwater management strategy should be implemented based on biological and ecological criteria and anchored in national and international legal frameworks (Wynne et al. 2021; Griebler et al. 2023a). This should specifically include standardized monitoring and sampling methods and guidelines for sustainable groundwater use (Ferreira et al. 2022).

As stated by Griebler et al. (2023a), "a direct dialogue with policymakers and stakeholders aiming to achieve legal protection and recognition for the biological component of groundwater ecosystems is necessary. Concretely, it would be important to obtain: (i) legal equality for groundwater and surface water ecosystems; (ii) explicit implementation of the terms 'groundwater ecosystems' and 'groundwater ecological status' in the laws pertaining to water and to conservation inclusive impact regulation; (iii) definition and legal consideration of biological references, indicator parameters and threshold values for the monitoring of groundwater ecosystems, (iv) implementation of these ecological criteria and thresholds into groundwater management plans". Recommendations and tools for the application of such integrative groundwater management strategies that incorporate biological properties into groundwater assessments have already been formulated and await broad application and testing (Hahn 2006; Korbel & Hose 2017; Fillinger et al. 2019; Hose et al. 2023). But not only policy-makers and stakeholders need to be aware of the societal relevance of groundwaters. Generally, the public awareness about groundwater habitats and species should be increased through popular science events, the involvement of the public through citizen science, art projects to visualize groundwater organisms, guided cave tours, or workshops targeted at the general public, starting with children's school education (Danielopol 1998; North & van Beynen 2016; Alther et al. 2021; Mammola et al. 2022a).

Summary and Conclusion

Groundwater ecosystems are fascinating hidden habitats for a large variety of organisms. Groundwater fauna has adapted to the demanding, energy-poor but usually stable environment for thousands of years and has in this process developed highly diverse communities that largely consist of cryptic, endemic, and relic species (Deharveng et al. 2009; Fišer et al. 2023). Our current knowledge about distribution patterns and drivers of groundwater fauna biodiversity as well as community structures, living conditions or vulnerability to stressors/changes is steadily increasing (Di Lorenzo et al. 2023; Zagmajster et al. 2023). Still there are serious knowledge gaps that need to be filled (Mammola et al. 2020). Limited access to the groundwater environment and difficulties of studying stygofauna under laboratory conditions result in a fragmented picture, leading to challenges in defining conservation measures. These challenges are presumably also a reason that groundwater fauna biodiversity on the large scale appears to be very heterogenous, showing rather patchy biodiversity hotspots than clear patterns (Deharveng et al. 2009; Malard et al. 2009).

Factors that have shown to play a role in groundwater fauna biodiversity distribution, besides historic events (e.g. former extent of glaciation during last ice age or former extent of surface water like the Tethys), are sediment void size, the interconnectedness, the hydrological exchange with surface water, the availability of dissolved oxygen and organic matter, and the thermal stability (Thienemann 1950; Marmonier et al. 2023). Regularly, altitude as well as the depth of the groundwater table have appeared to be drivers of richness and density (Dole-Olivier et al. 2009). The majority of the mentioned factors are strongly impacted by anthropogenic actions that pose a potential threat to groundwater biodiversity. The exploitation of groundwater as a resource with disregard to its biological properties and ecological health of the ecosystem as well as the numerous negative aspects that accompany consistently advancing land use changes including urbanization, deforestation, agriculture, and industrialization put groundwater fauna biodiversity at serious risk (Castaño-Sánchez et al. 2020; Rohde et al. 2021; Becher et al. 2022).

Protection and conservation measures of groundwater fauna and habitats are mostly lacking (e.g. severe underrepresentation of groundwater species on Red Lists like the IUCN, absence of actions for the protection of groundwater ecosystems in legal frameworks, etc.), even though they are urgently needed. Therefore, it is vital that actions are taken to close knowledge gaps, spread awareness of the importance of the biological groundwater properties not only with stakeholder and policy makers but including the general public, with the aim to create guidelines for the sustainable use of groundwater resources and implement the use of integrative groundwater management strategies as a standard practice. Ultimately, we all depend on a healthy groundwater ecosystem and should therefore protect it not less than we already protect surface waters (Griebler et al. 2023a).

Acknowledgments

We are grateful to the reviewers, Wolfram Graf and Gabriel Singer, for their critical and constructive contribution to this manuscript. Work on this review was funded by the Vienna Science and Technology Fund (WWTF) [10.47379/ESR20040], and by Biodiversa+, the European Biodiversity Partnership under the 2021-2022 BiodivProtect joint call for research proposals, i.e. the project 'DarCo', co-funded by the European Commission (GA N°101052342) and the Austrian Fonds zur Förderung der Wissenschaftlichen Forschung (I 6371-B). Finally, support was granted to CG in the frame of the project Stygofauna Austriaca funded by the biodiversity funds of the Austrian Federal Ministry of Climate Action, Environment, Energy, Mobility, Innovation and Technology.

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Received: 2023 11 11

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