Groundwater is a hidden global keystone ecosystem

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August 17, 2023

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Preface

Groundwater is a vital ecosystem of the global water cycle, hosting unique biodiversity and providing essential ecosystem services to societies. Despite being the largest unfrozen freshwater resource, in a period of depletion by extraction and pollution, groundwater environments have been repeatedly overlooked in global biodiversity conservation agendas. Disregarding the importance of groundwater as an ecosystem ignores its critical role in preserving surface biomes. To foster timely global conservation of groundwater, we propose elevating the concept of keystone species into the realm of ecosystems, claiming groundwater as a keystone ecosystem that influences the integrity of many dependent ecosystems. Our global analysis shows that over half of land surface areas (52.6%) has a medium-to-high interaction with groundwater, reaching up to 75% when deserts and high mountains are excluded. We postulate that the intrinsic transboundary features of groundwater are critical for shifting perspectives toward more holistic approaches in aquatic ecology and beyond. Furthermore, we propose eight key themes to develop a science-policy integrated groundwater conservation agenda. Given ecosystems above and below the ground intersect at many levels, considering groundwater as an essential component of planetary health it is pivotal to the reduction of biodiversity loss and buffering against climate change.

Introduction

Groundwater is the most extensive unfrozen continental reserve of freshwater on Earth[1,2]. From deep karstic aquifers to shallow alluvial sediments, groundwater is globally ubiquitous and functionally connected to surficial aquatic and terrestrial groundwater-dependent ecosystems (GDEs). Groundwater interacts with the five global surface aquatic biomes (Fig. 1) and, together with oceans and the atmosphere, is the backbone of the global water cycle[3]. While often exclusively regarded as an economic resource, providing drinking water and water for irrigation and industrial uses[4], groundwater is also an ecosystem. It hosts a vast diversity of microbial and metazoan species sustaining essential functions and processes[5,6], many of which are endemic and highly specialised to a life in permanent darkness[7]. Together, these specialised organisms account for a unique share of the global taxonomic, phylogenetic, and functional diversity[8], with recent research estimating that more than 25,000 aquatic metazoan species exist in freshwater and saline groundwaters worldwide[9].

The groundwater ecosystem is facing mounting anthropogenic pressure[10]. Water depletion driven by urbanisation, industry, agriculture, and exacerbated by climate change, has been documented on both regional and global scales[11]. According to estimations, nearly 50% of the world’s urban population depends on groundwater resources[4], with the human demand currently being about 3.5 times the actual volume of aquifers[12]. Predictably, this situation is likely to further deteriorate. As the intensification of drought and flood events induced by climate and land use change increases, the demand and dependence on groundwater for human consumption, agricultural irrigation, and environmental water needs will also escalate[13,14]. Furthermore, salinization and contamination of groundwaters by persistent organic pollutants such as nitrate, heavy metals, oil, and microplastics is a major threat to diverse subterranean ecosystems and, in turn, to the integrity of the global water cycle[10]. Subterranean waters are often old: once meteoric waters enter subterranean systems, it may take months, years, and sometimes millennia before they resurface[15]. Hence, there is often a generational lag between contamination event and effect, and even major conservation efforts might take an epoch before these ecosystems recover if groundwater quality deterioration is not urgently considered. Ultimately, we risk compromising the insurance policy of life on Earth: the largest body of liquid freshwater.

Despite growing concerns over global groundwater depletion and degradation, and the feedback effect on diverse surface ecosystems, subterranean ecosystems remain the dark exotic siblings of surface water bodies when it comes to conservation[7]. Indeed, groundwaters have so far been largely overlooked in global conservation policies, and biodiversity and climate change agendas for water resources[16,17,18]. For example, as many as 85% of protected areas with GDEs have groundwater-sheds (or catchments) that are unprotected[19]. Foremost, this is because of the still incomplete knowledge about the spatial distribution, biodiversity, vulnerability, and biochemical processes and services of groundwater ecosystems[17,20,21]. While divers can physically explore submerged caves and cenotes, the vast majority of subterranean water bodies are inaccessible to humans unless by indirect means[22,23,24]. Indeed, access to groundwater organisms is often restricted to caves, wells, and springs that serve as windows to the subterranean world[8]. The real extent of groundwater ecosystems is therefore roughly estimated (between 22.6 and 23.6 million km^3 in the upper 2 km of continental crust[1,2]) and we have only a partial understanding of their three-dimensionality and verticality—i.e., structural diversity[25]. Furthermore, as the adage "*out of sight, out of mind*" goes, there is generally poor awareness about the importance of the groundwater biodiversity and ecosystem services across policymakers, stakeholders, and the general public alike (Supplementary Section 1). This lack of awareness reflects the conservation status of groundwaters: in many areas of the world, groundwater ecosystem protection is confined to aquifers with economic value or the unplanned overlap between valuable groundwater ecosystems and protected areas established for surface ecosystems[16,26].

As a result, a global approach to policy that incorporates the value of groundwater ecosystems and their services is required to protect these precious resources. With this in mind, we propose the application of the keystone ecosystem concept to groundwater, as this approach has proven to be extremely valuable in nature conservation[27]. By mapping predicted groundwater biodiversity and its overlap with surface biodiversity at global scale, we provide both conceptual and empirical evidence that this focus is scientifically sound, timely, and beneficial for the broader context of groundwater conservation. Following the GDEs categorization proposed by Eamus et al.[28], we focus on the ecological and functional links between groundwater ecosystems (e.g., aquifers and caves where aquatic subterranean biota reside; GDE class I) and GDEs requiring the surface expression of groundwater (e.g., wetlands and rivers; GDE class II) or GDEs dependent on groundwater availability for their biodiversity, growth and productivity (e.g., forests, GDE class III).

With the goal of taking a step further towards inter-realm approaches, we also highlight eight directions – spanning from biomonitoring to transboundary policies – to advance conservation of groundwater and groundwater-dependent ecosystems over two interlinked axes of science and policy. A much stronger focus on groundwater conservation is needed in the face of accelerating global climate change and uncontrolled biodiversity loss, and we advocate that such a change in perspective and management strategies will consistently increase the efficacy of our global conservation strategies.

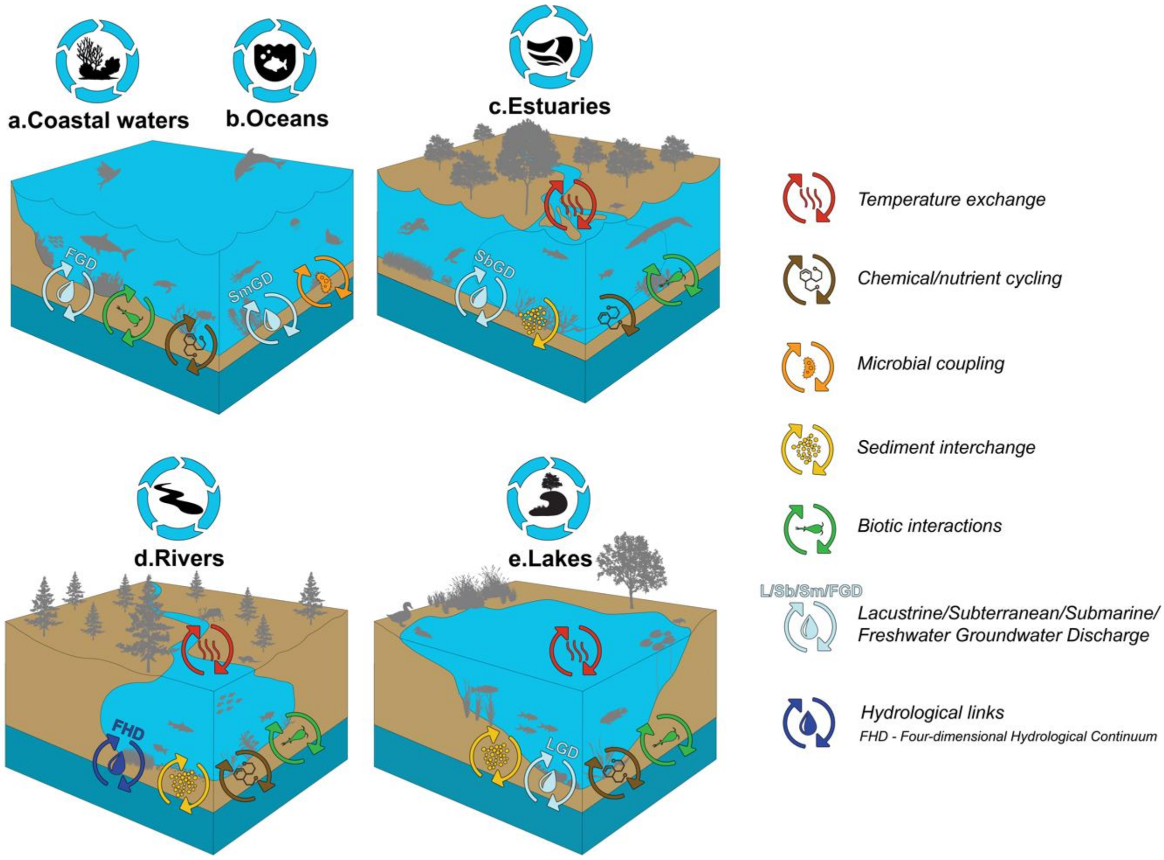

Fig. 1|Schematic representation of interactions and functional links of groundwater ecosystems (in dark blue) with the five unfrozen surface water biomes (marine and freshwater) composing the global water cycle (in light blue). See Supplementary Section 2 for a detailed description of the ecological and hydrological connections between them. For conciseness, anthropogenic impacts are not illustrated; gaps between groundwater environments and the five unfrozen surface water biomes have been added for illustrative purposes.

1. Current conservation efforts of groundwater ecosystems: the challenge of protecting the “unknown”

Comprehensive protection of groundwaters, whether direct or indirect *via* conservation of GDEs, is lacking or not implemented in most regions[29,30]. Globally, there are only a few examples of direct conservation measures for subterranean habitats or groundwater species[30]. Global treaties on biodiversity or conservation frequently fail to recognise groundwaters[7,31] or are hindered by the limited taxonomic description of most groundwater biota[30]. The application of direct conservation measures is complicated by inconsistencies between conservation and natural resource legislation[32] and often the boundaries of aquifers transcend those of jurisdictions or surface catchments that are the typical focus of land and water management[19].

Until recently, direct protection and conservation measures for groundwater ecosystems have focused on protecting rare, iconic species or habitats[21,30,33], being generally informed by habitat mapping[34] and species-occurrence databases[35]. This focus has enabled the conservation of globally significant areas[32,36], but is ineffective in areas where the knowledge of habitats is limited and biota are unknown or undescribed[37,38]. Phylogenetic or functional diversity can be used to prioritise conservation sites when taxonomic information is lacking[39]; conservation biogeography and species distribution modelling approaches also have potential as management tools[40] but are challenged by a lack of robust theoretical models to explain the distribution of biota at relevant spatial and temporal scales[30] and the high endemism typical of groundwater fauna[40].

The sustainable management of groundwater resources has been insufficient in protecting groundwater ecosystems, partly because its primary focus is the availability of water for humans rather than the ecological needs of the organisms therein. Although limiting groundwater allocations indirectly benefits groundwater ecosystems, this anthropocentric focus often ignores the quality and quantity of water needed for maintaining ecosystem processes[41,42]. Groundwater vulnerability mapping[43] has promise as a means for assessing and managing risks to groundwaters but is generally more focused on a single resource protection than ecosystem protection. This is problematic because only through the preservation of healthy groundwater biota, including both microbes and metazoans, can we ensure the maintenance of key ecological processes and the functional links with surface water ecosystems (Fig. 1).

Ultimately, groundwater and connected GDEs should be managed and conserved together, under a “one water” framework[44,45]. However, human needs often triumph over environmental water needs where knowledge is limited[46], rendering this an unrealistic option for conservation. As a result, other approaches must be explored and implemented to ensure the preservation of a healthy groundwater ecosystem. Like climate change more broadly, current inaction (“too little”) is not only generating increased contamination, habitat fragmentation, and higher rates of biodiversity loss, but also risks compromising the efficacy of our future actions (“too late”) because they will be implemented on already deteriorated groundwater ecosystems.

2. Shaping groundwater as a keystone ecosystem

Assessment, monitoring and management of biodiversity frequently relies on the use of community representatives such as flagship, umbrella and keystone species, whose protection effectively preserves many other species[47]. While all these proxy species approaches are constantly constrained by their intrinsic metaphorical nature[48], the emphasis of the keystone species on links among species has been raised as an "appropriate target for management", given the implementation of this approach can provide a good compromise between species-oriented and ecosystem function-oriented conservation strategies[49].

Initially coined by Robert T. Paine (1933–2016), the term "keystone species" was intended for species of high trophic status, whose activities exert disproportionate influence on the structure and function of biological communities[50,51]. This concept argues that a single top predator indirectly controls resource-use at lower trophic levels. Upon its removal, one species would monopolize resources, exclude competitor species, and cause a decline of biodiversity[52]. The use of keystone or any other proxy species in nature conservation is frequently advocated for systems where the number of species being protected or monitored is uncertain[53], such as groundwater[54]. However, while keystone species appear to be a promising approach for protection and monitoring of groundwater ecosystems, its implementation is hindered by conceptual and applied issues (Box 1).

BOX 1: Keystone species in groundwater ecosystems: an impossible task?

There are many obstacles to the implementation of the concept of keystone species in groundwater ecosystems, emphasizing the need to adopt a “keystone ecosystem” approach. The first, main challenge lies in the identification of appropriate keystone species. The term “keystone” has been broadly debated[55,56] and refined such that it could apply to all species from any trophic level. The ultimate recognition of keystone species, however, remains a two-step procedure that first applies operational criteria to identify keystone candidates, and then empirically tests how their removal impacts species diversity in a community[56]. Nonetheless, the application of this procedure to groundwater is theoretically questionable and technically challenging because a clear picture of trophic structure for all GDEs is missing. For example, until recently, groundwater was considered a bottom-truncated ecosystem, with no primary producers and few specialized top predators[57]. Since then, some evidence for trophic specialization within trophic levels has been identified[58,59,60], as well as for multiple trophic levels within species-rich groundwater communities[61,62,63,64] making it difficult to identify suitable keystone species in most cases.

Second, there is a remarkably high frequency of narrow range endemics among groundwater species[65]. High spatial turnover in groundwater species composition at larger geographical scales emerges as a consequence of the dominance of species with small distributional ranges[66,67]. Identifying keystone species on a scale of some ten kilometres is often an impossible task.

Third, the vertical dimension of groundwater exacerbates the aforementioned issues. Groundwater is not a homogenous habitat, but an array of interconnected habitats[68,69]. In groundwater ecosystems, life has evolved to use space in three dimensions. In karstic massifs alone, at the same geographic point, species from fissure systems in the unsaturated zone live under different environmental conditions to species from the permanently flooded zone[70], leading to vertically stratified communities. Such vertically distributed communities may be only weakly connected functionally, with predators in lower zones hardly influencing dynamics in upper zones.

The extension of the keystone concept to communities or ecosystems[71] is a plausible area to explore for easing some of the current roadblocks in groundwater conservation efforts (Supplementary Section 1). Since the early 1990s, conservation strategies across the globe have shifted their focus from species- to habitat/ecosystem-level[72]. Complementarity between both approaches has been recognized as beneficial[72], but overall, the increased cost-effectiveness and elaboration of more effective management guidelines are reported for the ecosystem-level focus[73], as well as reducing funding bias[74]. The value of this approach is enhanced when applied to groundwater habitats, where biodiversity is still mostly spared from macro-organismal invasive species possibly due to the selective conditions and isolation of these environments[75]. As a result, compared to other surface counterparts such as rivers and lakes, groundwaters can be broadly considered less biologically degraded (even if still mostly unprotected worldwide) ecosystems, a common prerogative for conservational purposes through keystone ecosystems approaches[71].

Concurrently, recent investigations into GDEs (class II and III according to Eamus et al.[28]) indicate that they are widely distributed in dry climate zones (accounting for almost a third of the total global surface area[76]), and groundwater supports riparian and floodplain vegetation in tropical and temperate zones[77]. Globally, groundwater has strong physical/ecological relationships with surface water (e.g., intermittent streams), and the presence of surface water in some geographic areas is highly related (at least in some periods of the year) to groundwater level (e.g., groundwater-fed streams in semi-arid areas)[28]. For instance, shallow groundwater influences 22 to 32% of global land area, and 15% of groundwater-fed surface water features and plant rooting zones[78].

Similar to the transition from species- to ecosystem-level conservation agendas, the shift from local to regional and continental studies in groundwater ecology has been undoubtedly enabled by the increased availability of data, combined with the enhanced awareness of the importance of groundwater at global scale[19]. As a result of all these observations, groundwater provides a uniquely valid conceptual candidate to be a keystone ecosystem, defined as ecological structures "*providing resources, shelter or 'goods and services' crucial for other species*"[27].

Partially due to the lack of groundwater accessibility and the resultant lack of subterranean spatial analysis, data sources for environmental parameters driving groundwater biodiversity patterns on a global scale are currently limited to estimates of water quantity (e.g., groundwater recharge and water table depth). To evaluate the potential of groundwater ecosystems as keystone ecosystems, we modelled available data to map the biodiversity of groundwater ecosystems in combination with groundwater interaction with the surface (Fig. 2). This analysis is based on an indicator composed by four proxies: three proxies that are positively associated with groundwater ecosystem biodiversity, (i) groundwater recharge[79], proxy for high biodiversity because groundwater recharge regimes are associated with the inflow of nutrients, replenishment of water, and oxygen regeneration; (ii) existence of karst[80], proxy for habitat availability and connectivity (iii) interaction between groundwater and surface water[81], another proxy for high biodiversity being a key factor in enriching oligotrophic groundwater environments with carbon loads and fresher water resources; and (iv) groundwater water table depth as negatively associated proxy to the same biodiversity factor[78] (see Supplementary Section 3 for further information).

Globally, 7.1% of the land area shows a high degree of groundwater biodiversity (90th percentile globally) and high interconnectivity to surface water bodies (90th percentile globally). 52.6% of global areas have medium to high interactions, independent to the modelled groundwater biodiversity considered. In almost a third of the global area (29.8%) there is only low (10th percentile) predicted subsurface biodiversity coupled with groundwater - surface water interaction. Within this category, a vast portion is occupied by deserts (e.g., Sahara Desert covering 8% of total global area) and high mountains, regions where the water table can be very deep (e.g., Andes), the recharge rates are very low (e.g., Arabian Desert), and/or surface environments host low biodiversity (e.g., Kalahari Desert). Once those areas with modelled low biodiversity and low interactions are removed from the global analysis, the proportion of areas with medium to high interactions jumps to 75%. Nonetheless, within these broad regions categorised as low biodiverse, important pockets of groundwater biodiversity do exist. For instance, the Pilbara in Australia is considered a major subterranean biodiversity hotspot globally[82], and the seemingly inhospitable Sahara Desert hosts endemic species of copepods in its groundwater ecosystems[83]. An in-depth global analysis on these "*islands under the desert*"[84] would shed further light on the understanding of functional groundwater-surface water interactions, and will only be possible once further data is gathered.

Having mapped where groundwater biodiversity is potentially high and connected to the surface, we incorporated the occurrence of surface ecosystems into the analysis (Fig. 3a-b). We combined the previous map (Fig. 2) with an indicator for surface ecosystem biodiversity (consisting of the integration of four proxies: soil bacteria, plant diversity, macrophyte occurrence and riverine species richness; Supplementary Section 3). Our goal was to estimate the overlaps and interdependence between groundwater and surficial ecosystems' biodiversity patterns. Therefore, we excluded higher-order biodiversity indicators such as avian or mammalian diversity, given that these taxa are not necessarily associated with the interlinked groundwater-surface ecosystems at a global scale. Indeed, an analysis involving groups such as marine animals[85] or reptiles[86], and modelling their degree of direct or indirect dependency/functional links with groundwater resources could be of much interest, but it lies outside of the scope of current work.

Globally, for 10.1% of the land area there is an overlap between predicted high groundwater biodiversity and interactions (90th percentile globally), and predicted high surface biodiversity (90th percentile globally). Half of global surficial area (50.0%) has high biodiversity with some extent of groundwater interactions, reaching up to 71.7% when groundwater-sheds[19] are considered (see Supplementary Section 3). For all the three surface biodiversity categories (low, medium and high), the areas with the lowest groundwater biodiversity and interactions (10th percentiles) were the most abundant (8.4%, 32.1% and 23.9%, respectively). However, the choice of aggregation of Fig. 2 (compare Fig. S11) influences this outcome towards more areas with low biodiversity and interaction.

Overall, our findings suggest that global groundwater biodiversity and interactions can be considered as a first order estimator for surface biodiversity (Fig. 3a). For example, when we focussed into the Po (North Italy) (Fig. 2b and Fig. S14b) and Mekong (Southeast Asia) (Fig. 2c and Fig. S16b) river basins, two areas that in 2022 experienced the worst droughts in 70 years[87,88], distinctive patterns emerged. The Po basin shows a high groundwater ecosystem biodiversity close to the Alps and the Mediterranean Sea with medium interconnectivity to surface waters compared to other global systems (Supplementary Section 3). On the other hand, the Mekong shows a high groundwater ecosystem biodiversity and interconnection between groundwater and surface water. When surface biodiversity is incorporated in the modelling, the Po basin (Fig. S14b) shows hotspots of groundwater ecosystem biodiversity and surface ecosystem biodiversity closer to the delta and the pre-Alp areas. In contrast, hotspots of interconnectivity remain as in Fig. 2b. The Mekong shows extensive areas of high surface and subsurface ecosystem biodiversity together with a highly interconnected system (Fig. S16).

Groundwater and surface systems are often inter-connected, and focusing only on one, limits the effectiveness of conservation efforts. Only a holistic view that includes groundwater ecosystems will enable us to understand how excessive groundwater extraction will also affect surface ecosystems[89] and how land cover changes, e.g., deforestation, agricultural use or effect of river incision, will affect the groundwater quantity and quality and, in turn, the connected ecosystems. Without further research, the global role of groundwater in the carbon cycle remains unclear. When prioritizing areas for biodiversity conservation, integrating surface and groundwater biodiversity is more effective[90]. Combined protection of surface and subsurface areas is most efficient in terms of costs, available space, and societal awareness. Recognizing groundwater as a keystone ecosystem highlights the cascading effects that would be triggered if we further contaminate and/or deplete groundwater. While some authors have already discussed the hydrological transboundary role of groundwater at global scale[91], to the best of our knowledge, this is the first ecological quantification of groundwater ecosystems' relevance for the Earth system.

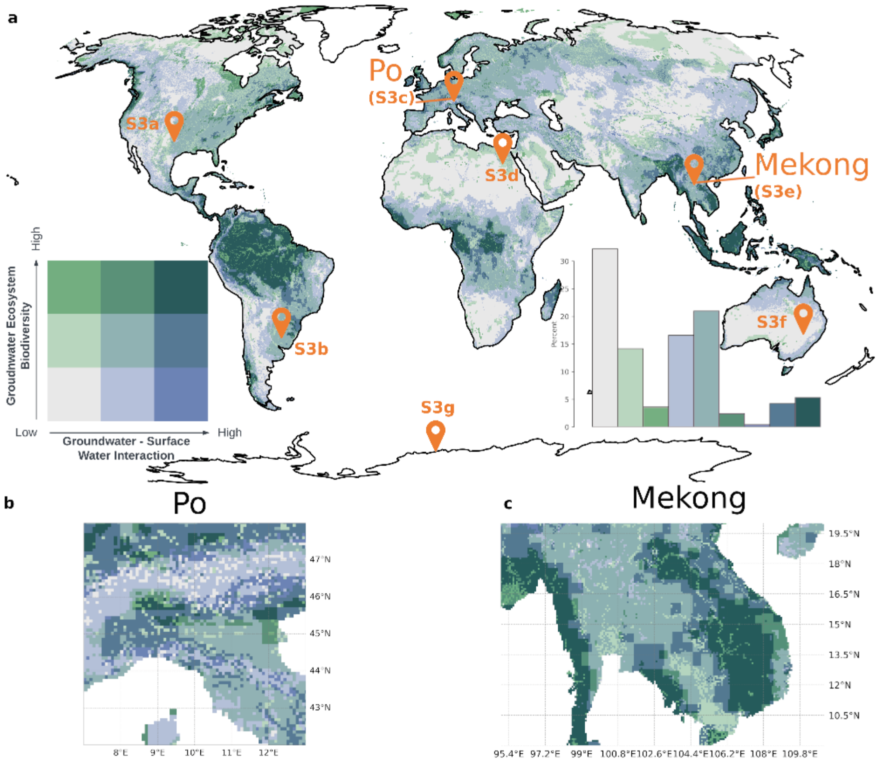

Fig. 2|Linkages between predicted groundwater ecosystem biodiversity and groundwater-surface water exchange fluxes. Dark green areas indicate a high groundwater ecosystem biodiversity and a high interaction between groundwater and surface water. Light green indicates areas with high groundwater biodiversity but low interactions, blue indicates high interactions (in both directions) between surface water and groundwater but low groundwater biodiversity. Groundwater ecosystem biodiversity is approximated by groundwater recharge, karst and water table depth. The interactions between groundwater and surface water are based on a global groundwater model. The categories of biodiversity and exchange fluxes are based on quantiles of normalized data. Orange markers identify focus regions used to evaluate the map. (See Supplementary Section 3 for an in-depth development and discussion of this figure).

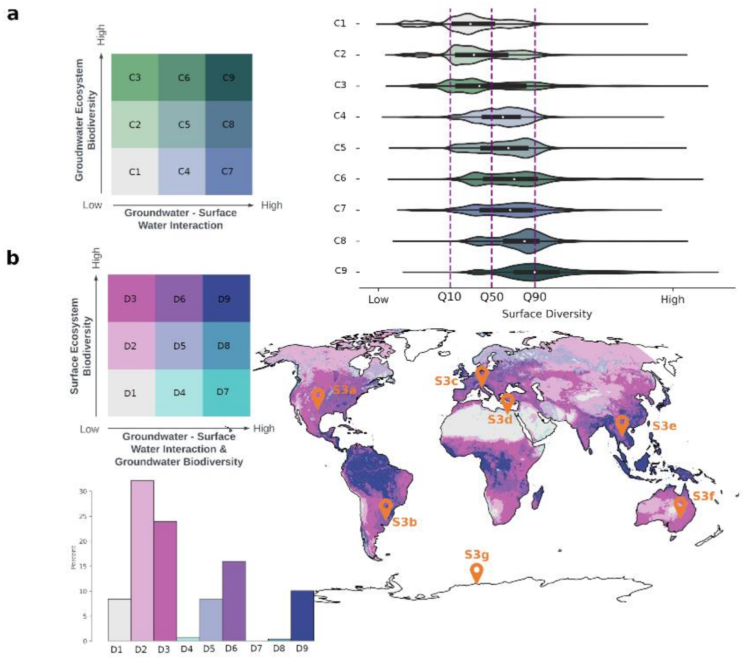

Fig. 3|Linkages between predicted surface ecosystem biodiversity and connected groundwater biodiversity. Here we show how categories of groundwater biodiversity and interaction (Fig. 2) relate to surface ecosystem biodiversity. With higher groundwater ecosystem biodiversity and interaction (C1 = lowest; C9 = highest), surface ecosystem biodiversity increases as well a). This relationship is mapped into nine new categories of surface ecosystem biodiversity and groundwater ecosystem biodiversity and interaction (D1 = lowest; D9 = highest) shown on a global map b). Dark blue in b) indicates areas of high ecosystem biodiversity, high groundwater ecosystem biodiversity, and high interactions between groundwater and surface water. Pink areas indicate only a high surface biodiversity, and turquoise, areas without large surface ecosystem biodiversity. Groundwater-surface interactions and groundwater ecosystem biodiversity are based on Figure 2. Surface ecosystem biodiversity is based on soil bacteria, fish diversity, macrophyte diversity, and vascular plant diversity, and the biodiversity categories are based on normalized data quantiles (see Supplementary Section 3).

3. Setting the ground(water) for a more effective protection of aquatic subterranean ecosystems

The success of groundwater conservation in the 21st century will be contingent on our ability to limit climate change[92], minimize contamination[4], and reduce overexploitation of natural resources[93]. However, the magnitude of the challenge ahead is in stark contrast with ongoing conservation inaction[16,21,37]. Amidst an increasingly unpredictable climate, widespread aridification, and scattered rainfall events[94], many rivers and lakes are transitioning from permanent to intermittent[95], glaciers and snowfields are melting away, and thus two major freshwater sources are rapidly disappearing across several regions[96]. As a result, the reliance of surficial watersheds on aquifers is increasing, with aquifers providing the only permanent (if replenished) freshwater resource available for many areas worldwide. Given the uneven distribution of global groundwater[97], inequitable access, and the limited replenishment of ancient global groundwater reserves, shifts in the dependence of ecosystems from surface to groundwater will be spatially variable[98]. Therefore, effective groundwater governance will be a crucial aspect to mitigate the impact of droughts on economies, societies, and diverse environments[99].

Recent research has demonstrated that groundwater ecosystems and their biota actively assimilate terrigenous carbon[100], acting as carbon sinks[101] analogous to freshwater wetlands. Hence, maintaining the carbon assimilation capacity of groundwater ecosystems is essential to maximise the terrestrial carbon sink and minimise climate change effects. Aquifers are also crucial for maintaining surface environments[102], including their biodiversity, within natural and anthropogenic contexts[103] (Fig. 4). However, current lack of implementation of effective groundwater management strategies is hindering also the preservation of associated GDEs. The development of biodiversity indices for groundwater ecosystems, similarly to biodiversity variables proposed to monitor biodiversity at global levels[104,105] and for discrete targeted purposes[106], could provide a solution to overcome this roadblock. By initially targeting well-studied regions with comprehensive diversity datasets (e.g., the Krim region in Slovenia[107] or the Pilbara in Western Australia[89]) regional biodiversity indices can be designed, with the goal to expand the foci as groundwater biodiversity data from less studied systems become available.

Overall, our analysis emphasizes the high interconnectedness between groundwater and surface systems, and demonstrates how focusing only on one compartment limits the effectiveness, scope, and comprehensiveness of conservation efforts. To achieve more holistic conservation strategies, we will need to find effective strategies able to overcome the surface-subterranean divide. With this in mind, we advocate for a two-tiered approach for the conservation of groundwaters, composed by science and policy, and we propose eight key focal areas to develop an effective global strategy.

(i) Create standardized global datasets. Global dataset’s record information on groundwater fauna is abundant, but generally scattered across myriad databases, publications, and personal datasets, often not openly accessible and lacking inter-operability due to different data standards and vocabularies. Two ongoing ambitious projects, the World Register for marine Cave Species (WoRCS)[108] and *Stygofauna Mundi*[9], aim to create a centralized, openly available, and comprehensive taxonomic and ecological database of all groundwater organisms. If successful, this will break a major barrier hampering conservation, offering much-needed data for accurate assessments of global groundwater biodiversity and providing information for evidence-based conservation[21]. Similar to rivers and lakes, integration of this information with available hydrogeological data will directly enhance the quality of groundwater environmental assessments. At transboundary ecosystem levels, published global data on the distribution of GDEs are not available to date. However, successful initiatives such as the Australian GDE Atlas[109] provide a promising initial step towards the creation of a scientifically sound global GDE map. Like in other disciplines, application of FAIR Data Principles[110] to all global groundwater-based generated data should be ensured, assuring effective findability, accessibility, interoperability, and reuse of these digital assets.

(ii) Test and apply novel biomonitoring approaches. Novel biomonitoring of groundwater and its typical biota is a crucial aspect of environmental management, as many ecosystem services are dependent on a healthy environment and diversity of species that, despite being almost invariably overlooked, are irreplaceable[5]. While monitoring of physical-chemical properties or chemical pollutants in groundwater is a regular practice across the world, the biota are often overlooked if not in connection with pollutant contamination. Therefore, novel tools are required to monitor these ecosystems. Particularly promising is the use of DNA extracted from environmental samples (environmental DNA or eDNA)[111] to assess diversity of, and map the distributions of, species[112]. First applications of eDNA to groundwater systems have been promising, recovering vast biodiversity hitherto mostly undocumented[113,114,115,116]. For selected taxa such as subterranean salamanders and cavefish, bioacoustics, the study of animal sounds, can be used to not only detect species, but also inform on their welfare and behaviour [117,118].

(iii) Advance science to better understand ecosystem function. Capturing the entire diversity of subterranean species is currently not logistically feasible. For instance, it is estimated that 80% of the world's biggest subterranean biodiversity hotspot region, Western Australia, is undescribed[119]. Therefore, traditional diversity metrics may not provide a mechanistic understanding of disturbance effects[120]. To circumvent this, the use of trait-based (functional) methods is gaining ground in recent ecological studies. This approach highlights how functional traits (intended, in a broad sense, as morphological, ecological, physiological, behavioural features measured at the species level[121]) mediate a species' ability to respond to changes in their environment[122,123]. However, functional studies targeting groundwater ecosystems are still rare[89,124]. At a global level, an in-depth and groundwater-specific functional characterisation proposed by Keith et al.[125] could be informative. Microbes and aquatic invertebrates are essential for subterranean ecosystem functioning, contributing to nutrient cycling, energy flow, water filtration, and biodiversity[8,126,127]. Therefore, targeting these components of underground aquatic ecosystems unveils crucial aspects of functioning and resilience.

(iv) Involve interdisciplinary approaches: A cross-pollination of ideas among researchers from different scientific backgrounds — e.g., hydrologists, hydrogeologists, climatologists, geochemists, ecologists and taxonomists — and operating both above and below the ground would enhance the implementation of conservation interventions able to embrace the entirety of the surface-subterranean continuum. Some possible ways forward to break the artificial divide between surface- and subterranean-based scientists and foster cooperation could include: a) limiting discipline-specific jargon in communication[128]; b) broadening reading habits outside one's own niche expertise; c) seeking active collaboration by exposing oneself to different scientific cultures (e.g., by attending scientific meeting outside one's own expertise) and d) fostering open data policies to ensure data exchange among researchers, groups, and companies as well as data availability for future generations.

(v) Implement global policies to protect transboundary waters. Conservation of biodiversity often requires operating across country boundaries[129], an endeavour often complicated by bureaucracy and geopolitical instability[130,131]. Worldwide, 468 transboundary aquifers (namely aquifers crossing multiple states[132]) have been delineated[133], several of which are subject to mounting human pressure[134]. However, there is currently no specific global convention or law for the management of transboundary aquifers. Today, transboundary aquifers are still governed by the 1997 UN Watercourses Convention which applies to groundwater systems, "[…] *but only to the extent that an aquifer is connected hydrologically to a system of surface waters, parts of which are situated in different States*"[135]. Transboundary aquifers cooperation is still lagging as it is directly related to the capacity of the States to understand and value the groundwater systems and associated ecosystems they depend upon. Efforts should be made on valuing groundwater as a shared resource beyond frontiers—e.g., by reporting evidence of anthropogenic impact on transboundary groundwater ecosystems to showcase and boost transboundary aquifers' cooperation[136].

(vi) Improve water management and governance. It is essential to achieve a more balanced effort (both financial and conservational) to the management of the different components of the hydrosphere and biosphere. The historical focus on surface water in freshwater management[93], in part reflects knowledge deficits on the role of groundwater ecosystems at the time when the main freshwater policies were set up[137] and the lack of ability in updating and adjusting strategies as scientific research progresses[138] (Supplementary Section 1). Now, thirty years after the publication of the cornerstone book "The Freshwater imperative"[139], inter-realm monitoring and management are more imperative than ever[140]. It is just a matter of treasure lessons learned, expanding views, and being ambitious[141]. Most ecosystems will benefit from this timely (almost overdue) shift in perspectives.

<u>(vii) Develop restoration and monitoring programs.</u> Hydrogeological restoration of aquifers[142] and surface-groundwater interactions[143] have been the focus of extensive research over the last three decades, yet studies on the ecological restoration of groundwater ecosystems are still rare[144]. As data on groundwater biodiversity and resilience to contamination and climate change are gathered, integration of comprehensive biotic-driven restoration guidelines is essential for the effective management of groundwater pollution both in natural and anthropogenic contexts[3].

<u>(viii) Encourage participatory approaches.</u> The value of a natural resource is only acknowledged when citizens are involved[145]. Alther et al.[113] and Raghavan et al.[146] employed participatory approaches to raise awareness on the importance of aquatic subterranean fauna, in projects that also led to the discovery of new species (amphipod genus *Niphargus* and catfish *Horaglanis populi*). Extension and upscaling of such an initiative to other regions, countries, and continents can provide a highly effective tool to increase societal awareness and advance science. Concurrently, the incorporation of local indigenous knowledge into ecological science harbours enormous potential to increase the efficacy of conservation and management strategies[147]. For instance, by harnessing the power of local knowledge through participatory science programs, the opportunity exists to build up a database of active and inactive global spring locations[148]. Such community-led monitoring programs could also provide information about groundwater quality (levels of eutrophication and contamination) and provide the catalyst to building a groundswell of support for rehabilitating and restoration of inactive springs to benefit surface and subsurface biodiversity.

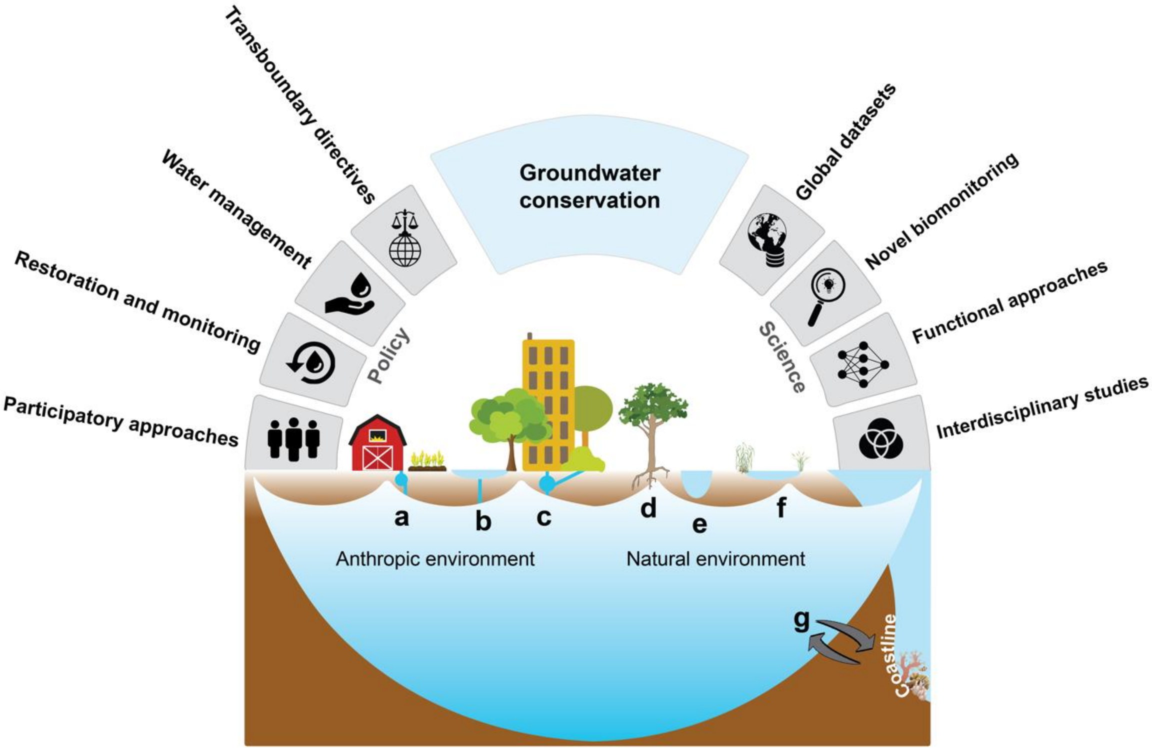

Fig. 4|Examples of groundwater ecosystem services within anthropic (a, b, c) and natural (d, e, f, g) frameworks and recommended guidelines for groundwater conservation in terms of scientific advancements (top right) and policy developments (top left). Anthropic environment: a, clean groundwater plays a key role in maintaining the agrobiodiversity[149]; b, interchanges between urban wetlands and groundwater can maintain the diversity of aquatic species and the functional integrity of urban wetlands[150]; c, water for urbanisation can also supply a key resource for the maintenance of urban vegetation[151]; natural environment: d, terrestrial vegetation groundwater dependent ecosystem (GDE)[152]; e, lotic GDE[153]; f, lentic GDE[154]; g, coastal GDE[155].

Conclusions

Water is the basis of life on Earth: by overlooking the ecological integrity of groundwater, we are threatening the long-term prospects of entire ecosystems and ultimately of humanity itself. Too often, current conservation efforts consider groundwater as disjoint from the rest of the components of the global water cycle, despite the multiple functional interlinks between the subterranean, surface and atmospheric realms. The application of the keystone ecosystem concept to groundwater would enable breaking the conceptual and mechanistic barriers still existing in water science and policy. We provide evidence that most habitable global areas

(75%) have a medium to high level of ecological interactions with groundwater. We also provide the first indication that groundwater biodiversity and interconnections can represent an ecological estimator for global surface biodiversity patterns. Given this foundation, conservation and water resource policies are pivotal to assure the maintenance of the essential ecosystem services provided by groundwater ecosystems worldwide. We argue that the overall benefits of this approach extend beyond the dark underworld, allowing the preservation of diverse terrestrial and aquatic ecosystems. This is urgent for wise water management plans within the current climate change scenario, considering that many regions across the globe are already experiencing a water crisis.

Acknowledgments

The authors would like to acknowledge the broader groundwater ecology community for its persistence in raising awareness of the importance of groundwater ecosystems for life on Earth.

Author contributions

This study was conceived by M.S., S.M. and R.R. The methods were developed by M.S. and R.R.

Analysis was performed by R.R. Figures were developed by M.S. and R.R. Paper writing was led by M.S. with input from all authors. All authors discussed the results and edited the paper at multiple stages.

Competing interests

The authors declare no competing interests.

Data availability

This study uses data from multiple open-access datasets. Source data are documented in Supplementary Section 2 and can be downloaded from the persistent web-links provided. Data produced in this study have been deposited on Zenodo at the address doi: 10.5281/zenodo.7924816.

Funding

This project received support from BHP-Curtin alliance within the framework of the “eDNA for Global Environment Studies (eDGES)” programme, and Biodiversa+, the European Biodiversity Partnership under the 2021-2022 BiodivProtect joint call for research proposals, co-funded by the European Commission (GA N°101052342) and with the funding organisations Ministry of Universities and Research (Italy), Agencia Estatal de Investigación – Fundación Biodiversidad (Spain), Fundo Regional para a Ciência e Tecnologia (Portugal), Suomen Akatemia – Ministry of the Environment (Finland), Belgian Science Policy Office (Belgium), Agence Nationale de la Recherche (France), Deutsche Forschungsgemeinschaft e.V. – BMBF-VDI/VDE INNOVATION + TECHNIK GMBH (Germany), Schweizerischer Nationalfonds zur Forderung der Wissenschaftlichen Forschung (Switzerland), Fonds zur Förderung der Wissenschaftlichen Forschung (Austria), Ministry of Higher Education, Science and Innovation (Slovenia), and the Executive Agency for Higher Education, Research, Development and Innovation Funding (Romania). S.M. and T.D.L. acknowledge the support of NBFC to CNR, funded by the Italian Ministry of University and Research, P.N.R.R., Missione 4 Componente 2, "Dalla ricerca all'impresa", Investimento 1.4, Project CN00000033. S.M. was further supported by the PRIN DEEP CHANGE (2022MJSYF8), funded by the Italian Ministry of Education, University and Research. A.S.P.S.R was supported by the VILLUM FONDEN (research grant 15471) and by Portuguese National Funds through "Fundação para a Ciência e a Tecnologia" (FCT) within the cE3c Unit funding UIDB/00329/2020. A.B. was supported by national Slovenian program P1-0255 financed by the Slovenian Research Agency (ARRS). F.A. has been funded by the University of Zurich Research Priority Programme on Global Change and Biodiversity and the Swiss National Science Foundation Grant. Š.B., M.Z. and C.F. were funded by Slovenian Research Agency through core program P1-0184 and project J1-2464. R.L.F. was supported by the CNPq (National Council for Scientific and Technological Development, grant n. 302925/2022-8). E.L. was funded by the Water Development and Partnership Programme of the Dutch Ministry of Foreign Affairs. K.K. was supported by Australian Research Council (ARC) grant LP190100927. S.J.B.C., M.T.G. and W.F.H. were funded by ARC grants LP190100555, DP180103851 and DP230100731. F.M. was supported by the French National Research Agency projects CONVERGENOMICS (ANR-15-CE32-0005) and EUR H20'Lyon project (ANR-17-EURE-0018).

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