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REVIEW

Groundwater is a hidden global keystone ecosystem

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Abstract

Groundwater is a vital ecosystem of the global water cycle, hosting unique biodiversity and providing essential 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 74.9% when deserts and high mountains are excluded. We postulate that the intrinsic transboundary features of groundwater are critical for shifting perspectives towards more holistic approaches in aquatic ecology and beyond. Furthermore, we

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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 is pivotal to reduce biodiversity loss and buffer against climate change.

KEYWORDS
biodiversity, biomes, climate change, conservation, ecology, ecosystems, groundwater-dependent ecosystem, subterranean, water cycle

1 | INTRODUCTION

Groundwater is the most extensive unfrozen continental reserve of freshwater on Earth (Ferguson et al., 2021; Gleeson et al., 2016). 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 (Figure 1) and, together with oceans and the atmosphere, is the backbone of the global water cycle (Scanlon et al., 2023). While often exclusively regarded as an economic resource, providing drinking water and water for irrigation and industrial uses (United Nations, 2022), groundwater is also an ecosystem. It hosts a vast diversity of microbial and metazoan species sustaining essential functions and

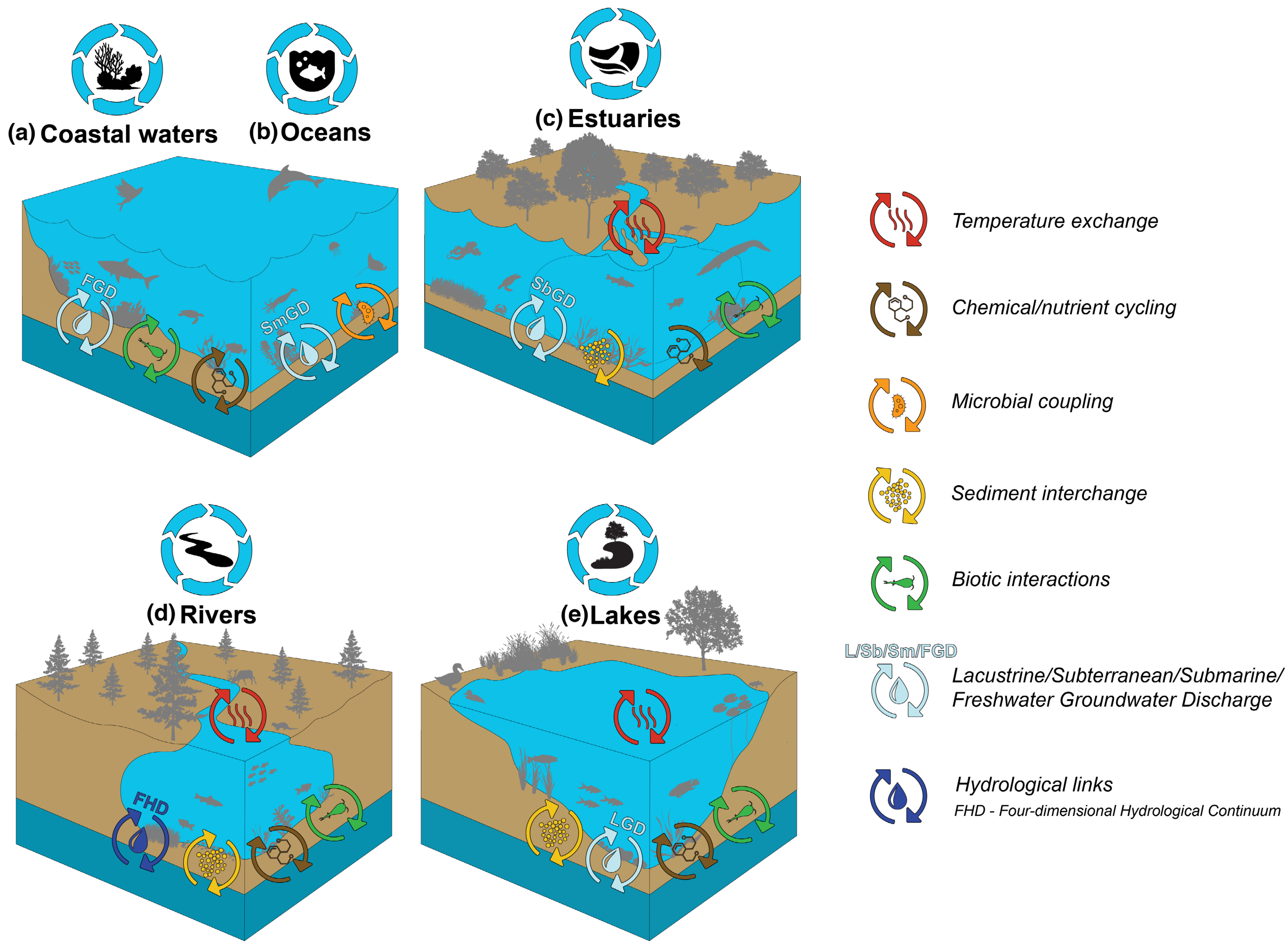

FIGURE 1 Schematic representation of interactions and functional links of groundwater ecosystems (in dark blue) with the five unfrozen surface water biomes (marine and freshwater) composing the global water cycle (in light blue: (a) coastal waters, (b) oceans, (c) estuaries, (d) rivers and (e) lakes). See Supporting Information 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.

processes (Canedoli et al., 2022; Griebler & Avramov, 2015), many of which are endemic and highly specialized to a life in permanent darkness (Howarth & Moldovan, 2018). Altogether, these specialized organisms account for a unique share of the global taxonomic, phylogenetic and functional diversity (Malard et al., 2023), with recent research estimating that more than 25,000 aquatic metazoan species exist in freshwater and saline groundwaters worldwide (Martinez et al., 2018).

The groundwater ecosystem is facing mounting anthropogenic pressure (Castaño-Sánchez et al., 2020; Mammola et al., 2019; Vaccarelli et al., 2023). Water depletion driven by urbanization, industry, agriculture and exacerbated by climate change, has been documented on both regional and global scales (Wada et al., 2010). According to estimations, nearly 50% of the world's urban population depends on groundwater resources (United Nations, 2022), with the human demand currently being about 3.5 times the actual volume of aquifers (Gleeson et al., 2012). 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 (Condon et al., 2020; Wu, Lo, et al., 2020). 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 (Castaño-Sánchez et al., 2020). Subterranean waters are often old: once meteoric waters enter subterranean systems, it may take months, years and sometimes millennia before they resurface (Jasechko et al., 2014). 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. 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 (Griebler et al., 2023). Indeed, groundwaters have so far been largely overlooked in global conservation policies, and biodiversity and climate change agendas for water resources (Fišer et al., 2022; Sánchez-Fernández et al., 2021; Vaccarelli et al., 2023; Wynne et al., 2021). For example, as many as 85% of protected areas with GDEs have groundwater sheds (or catchments) that are unprotected (Huggins et al., 2023). Foremost, this is because of the still incomplete knowledge about the spatial distribution, biodiversity, vulnerability and biochemical processes and services of groundwater ecosystems (Gerovasileiou & Bianchi, 2021; Mammola et al., 2022; Wynne et al., 2021). While divers can physically explore submerged caves and cenotes, the vast majority of subterranean water bodies are inaccessible to humans unless by indirect means (Ficetola et al., 2019; Navarro-Barranco et al., 2023; Saccò, Blyth, Douglas, et al., 2022). Indeed, access to groundwater organisms is often restricted to caves, wells and springs that serve as windows to the subterranean world (Malard et al., 2023). 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, see Ferguson et al. (2021) and Gleeson et al. (2016)) and we have only a partial understanding of their three-dimensionality and verticality—that is, structural diversity (Fei et al., 2023). 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 (Supporting Information 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 (Giakoumi et al., 2013; Sánchez-Fernández et al., 2021).

As a result, a global approach to policy that incorporates the value of groundwater ecosystems and their services is required urgently. 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 (Tews et al., 2004). 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 and Froend (2006), 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.

2 | 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 (Boulton et al., 2023; Famiglietti, 2014). Globally, there are only a few examples of direct conservation measures for subterranean habitats or groundwater species (Boulton et al., 2023). Global treaties on biodiversity or conservation frequently fail to recognize groundwaters (Iannella et al., 2021) or are hindered by the limited taxonomic description of most groundwater biota (Boulton et al., 2023). The application of direct conservation measures is complicated by inconsistencies between conservation and natural resource legislation (Devitt et al., 2019) and often the boundaries of aquifers transcend those of jurisdictions or surface catchments that are the typical focus of land and water management (Huggins et al., 2023).

Until recently, direct protection and conservation measures for groundwater ecosystems have focused on protecting rare, iconic species or habitats (Boulton et al., 2023; Griebler et al., 2023; Mammola et al., 2022; Moldovan, 2019), being generally informed by habitat mapping (Cornu et al., 2013) and species-occurrence databases (Zagmajster et al., 2014). This focus has enabled the conservation of globally significant areas (Devitt et al., 2019; Iannella et al., 2020), but is ineffective in areas where the knowledge of habitats is limited and biota are unknown or undescribed (Mammola et al., 2019; Raghavan et al., 2021). Phylogenetic or functional diversity can be used to prioritize conservation sites when taxonomic information is lacking (Asmyhr et al., 2014); conservation biogeography and species distribution modelling approaches also have potential as management tools (Mammola & Leroy, 2018), but are challenged by a lack of robust theoretical models to explain the distribution of biota at relevant spatial and temporal scales (Boulton et al., 2023) and the high endemism typical of groundwater fauna (Mammola & Leroy, 2018).

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 (Howard et al., 2023; Korbel & Hose, 2011). Groundwater vulnerability mapping (Machiwal et al., 2018) 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 (Figure 1).

Ultimately, groundwater and connected GDEs should be managed and conserved together, under a 'one water' framework (Linke et al., 2019; McNutt, 2014). However, human needs often triumph over environmental water needs where knowledge is limited (Rohde et al., 2017), 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.

3 | 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 benefits many other species in different ways (Caro, 2010; Lundberg & Arponen, 2022; Verissimo et al., 2011). While all these proxy species approaches are constantly constrained by their intrinsic metaphorical nature (Barua, 2011), 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 (Simberloff, 1998).

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 (Paine, 1969a, 1969b). 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 (Paine, 1966). 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 (Wiens et al., 2008), such as groundwater (Larned, 2012). 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).

The extension of the keystone concept to communities or ecosystems (Mouquet et al., 2013) is a plausible area to explore for easing some of the current roadblocks in groundwater conservation efforts (Suppoting Information Section 1). Since the early 1990s, conservation strategies across the globe have shifted their focus from species to habitat/ecosystem level (Lindenmayer et al., 2007). Complementarity between both approaches has been recognized as beneficial (Lindenmayer et al., 2007), but overall, the increased cost-effectiveness and elaboration of more effective management guidelines are reported for the ecosystem-level focus (Walker & Salt, 2012), as well as reducing funding bias (Adamo et al., 2022). 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 (Nicolosi et al., 2023). 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 ecosystem approaches (Mouquet et al., 2013).

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 (Davic, 2003; Mills et al., 1993) 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 (Davic, 2003). 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 (Gibert & Deharveng, 2002). Since then, some evidence for trophic specialization within trophic levels has been identified (Ercoli et al., 2019; Francois et al., 2016, 2020; Saccò, Blyth, Humphreys, Karasiewicz, et al., 2020; Saccò, Humphreys, et al., 2022), including the discovery of autotrophic systems based on chemoautotrophic bacteria that serve as primary producers (Sarbu et al., 1996). These aspects, together with existing multiple trophic levels within species-rich groundwater communities (Hutchins et al., 2016; Premate et al., 2021; Saccò, Blyth, Humphreys, et al., 2019; Saccò, Blyth, Humphreys, Cooper, et al., 2020) and the frequent dependency on surface carbon sources in biodiverse shallow groundwater ecosystems (Saccò et al., 2021; Saccò, Campbell, et al., 2022; Simon et al., 2003), make it difficult to identify suitable keystone species in most cases.

Second, there is a remarkably high frequency of narrow range endemics among groundwater species (Malard et al., 2009). High spatial turnover in groundwater species composition at larger geographical scales emerges as a consequence of the dominance of species with small distributional ranges (Bregović et al., 2019; Trontelj et al., 2009). Identifying keystone species on a scale of some 10km 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 (Culver & Pipan, 2014; Fišer et al., 2014). In groundwater ecosystems, life has evolved to use space in three dimensions. In karstic massifs alone, at the same geographical point, species from fissure systems in the unsaturated zone live under different environmental conditions to species from the permanently flooded zone (Culver & Pipan, 2019), 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.

Concurrently, recent investigations into GDEs [class II and III according to Eamus & Froend, 2006] indicate that they are widely distributed in dry climate zones [accounting for almost a third of the total global surface area, Salem, 1989], and groundwater supports riparian and floodplain vegetation in tropical and temperate zones (Glanville et al., 2023). Globally, groundwater has strong physical/ecological relationships with surface water (e.g. intermittent streams), and the presence of surface water in some geographical areas is highly related (at least in some periods of the year) to groundwater level [e.g. groundwater-fed streams in semi-arid areas, Eamus & Froend, 2006]. For instance, shallow groundwater influences 22%–32% of global land area, and 15% of groundwater-fed surface water features and plant rooting zones (Fan et al., 2013).

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 (Huggins et al., 2023). 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*' (Tews et al., 2004).

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 (Figure 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 (e.g. Reinecke et al., 2021), 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 (e.g. Zagmajster et al., 2018), proxy for habitat availability and connectivity; (iii) interaction between groundwater and surface water (e.g. Hancock et al., 2005), 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 (e.g. Fan et al., 2013) (see Supporting Information Section 3 for further information and limitations of these assumptions; de Graaf et al., 2015; Fan et al., 2013; Reinecke et al., 2019; Verkaik et al., 2022).

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

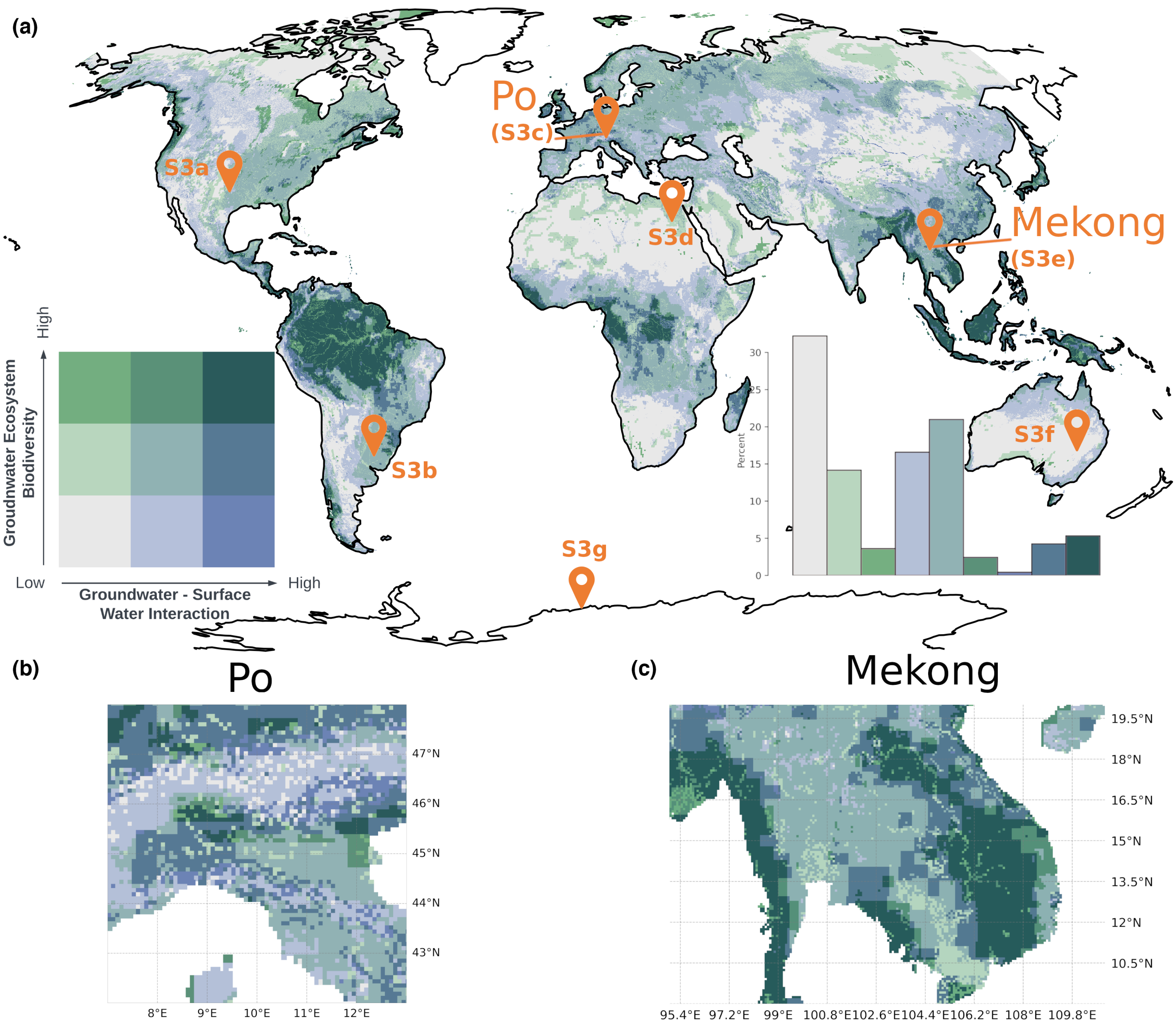

FIGURE 2 Linkages between predicted groundwater ecosystem biodiversity and groundwater-surface water exchange fluxes. Dark green areas in (a–c) indicate a high groundwater ecosystem biodiversity and a high interaction between groundwater and surface water. Light green in (a–c) indicates areas with high 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 in (a) identify focus regions used to evaluate the map, and (b, c) show zoom-ins on the Po and Mekong river basins, respectively (See Supporting Information Section 3 for an in-depth development and discussion of this figure). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(e.g. Sahara Desert covering 8% of total global area) and high mountains, regions where the water table can be very deep (e.g. certain areas in the 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 74.9%. Nonetheless, within these broad regions categorized as low biodiverse, important pockets of groundwater biodiversity do exist. For instance, the Pilbara in Australia is considered a major subterranean biodiversity hotspot globally (Saccò, Blyth, Bateman, et al., 2019), and the seemingly inhospitable Sahara Desert hosts endemic species of copepods in its groundwater ecosystems (Brancelj, 2015). An in-depth global analysis on these *'islands under the desert'* (Cooper et al., 2002) would shed further light on the understanding of functional groundwater–surface water interactions, and will only be possible once further data are gathered.

Having mapped where groundwater biodiversity is potentially high and connected to the surface, we incorporated the occurrence of surface ecosystems into the analysis (Figure 3a,b). We combined

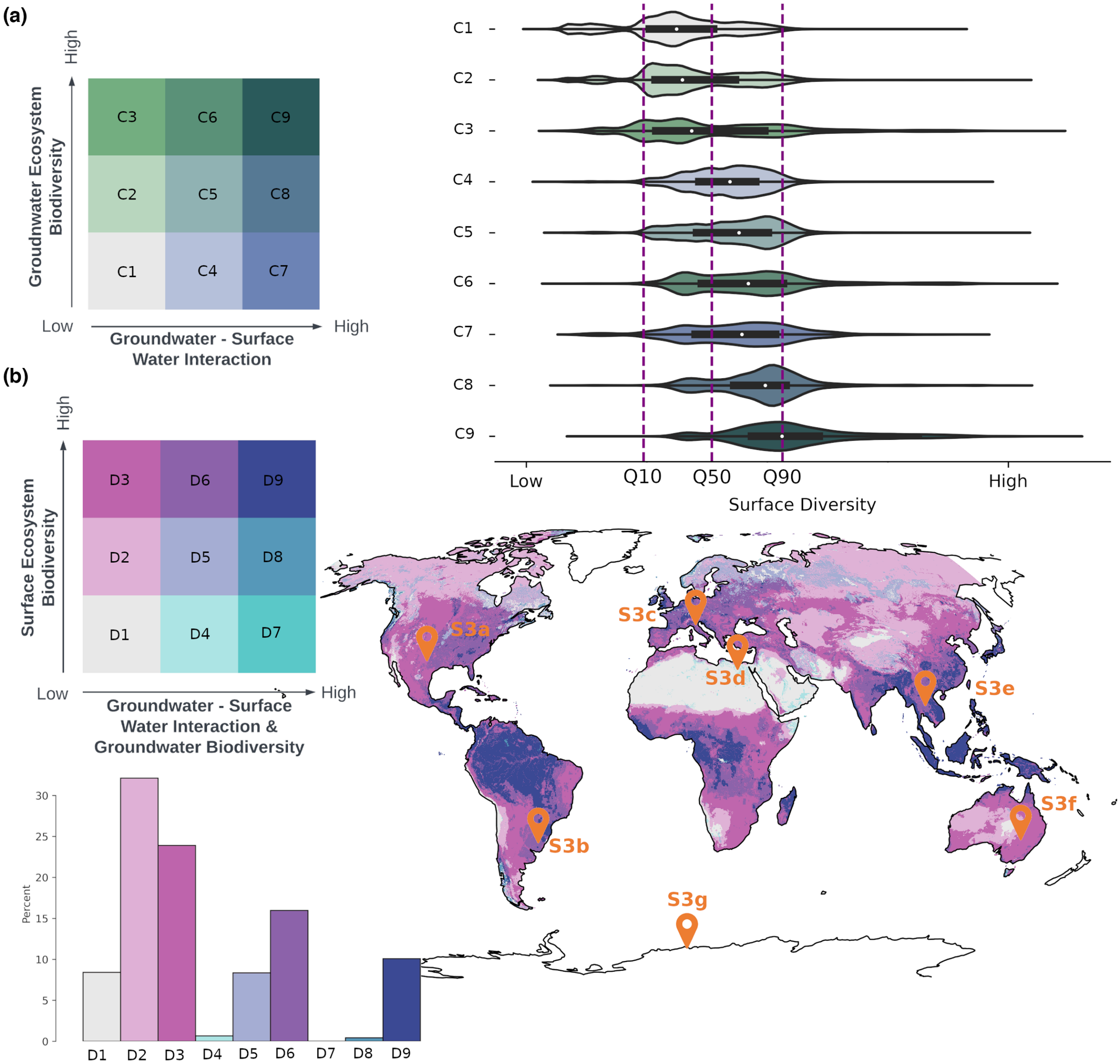

FIGURE 3 Linkages between predicted surface ecosystem biodiversity and connected groundwater biodiversity. Here we show how categories of groundwater biodiversity and interaction (Figure 2) relate to surface ecosystem biodiversity. With higher groundwater ecosystem biodiversity and interaction (C1 = 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 water interactions and groundwater ecosystem biodiversity are based on Figure 2. Surface ecosystem biodiversity is based on soil bacteria, riverine fish diversity, macrophyte diversity and vascular plant diversity, and the biodiversity categories are based on normalized data quantiles (see Supporting Information Section 3). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

the previous map (Figure 2) with an indicator for surface ecosystem biodiversity (consisting of the integration of four proxies: soil bacteria, plant diversity, macrophyte occurrence and riverine fish species richness; Supporting information 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 (Lecher & Mackey, 2018) or reptiles (Bateman & Merritt, 2020), 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 (Huggins et al., 2023) are considered (see Supporting Information 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 Figure 2 (compare Figure 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 (Figure 3a). For example, when we focussed into the Po (North Italy; Figure 2b; Figure S13b) and Mekong (Southeast Asia; Figure 2c; Figure S15b) river basins, two areas that in 2022 experienced the worst droughts in 70 years (Bonaldo et al., 2023; Kang et al., 2022), 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 (Supporting Information 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 (Figure S13b) 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 Figure 2b. The Mekong shows extensive areas of high surface and subsurface ecosystem biodiversity together with a highly interconnected system (Figure S15).

Groundwater and surface systems are often interconnected, 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 (Uhl et al., 2022) and how land cover changes, for example, 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 (Rohde et al., 2019). 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 (Gleeson et al., 2020), to the best of our knowledge, this is the first ecological quantification of groundwater ecosystems' relevance for the Earth system.

4 | 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 (Amanambu et al., 2020), minimize contamination (United Nations, 2022) and reduce overexploitation of natural resources (Foster et al., 2013). However, the magnitude of the challenge ahead is in stark contrast with ongoing conservation inaction (Mammola et al., 2019, 2022; Sánchez-Fernández et al., 2021). Amidst an increasingly unpredictable climate, widespread aridification and scattered rainfall events (IPCC, 2022), many rivers and lakes are transitioning from permanent to intermittent (Messager et al., 2021), glaciers and snowfields are melting away, and thus two major freshwater sources are rapidly disappearing across several regions (Peterson et al., 2021). As a result, the reliance of surficial watersheds on aquifers is increasing, with groundwater providing the only permanent (if replenished) freshwater resource available for many areas worldwide. Given the uneven distribution of global groundwater (Kretschmer et al., 2023), 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 (Link et al., 2023; López-Corona et al., 2013). Therefore, effective groundwater governance will be a crucial aspect to mitigate the impact of droughts on economies, societies and diverse environments (Petersen-Perlman et al., 2022).

Recent research has demonstrated that groundwater ecosystems and their biota actively assimilate terrigenous carbon (Hartland et al., 2011), acting as carbon sinks (Chen et al., 2023) analogous to freshwater wetlands. Hence, maintaining the carbon assimilation capacity of groundwater ecosystems is essential to maximize the terrestrial carbon sink and minimize climate change effects. Aquifers are also crucial for maintaining surface environments (Boulton et al., 2010), including their biodiversity, within natural and anthropogenic contexts (Becher et al., 2022; Figure 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 (Jetz et al., 2019; Pereira et al., 2013) and for discrete targeted purposes (Guerra et al., 2021), 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 (Sket et al., 2004) or the Pilbara in Western Australia (Saccò, Blyth, Douglas, et al., 2022)] regional biodiversity indices can be designed, with the goal to expand the foci as groundwater biodiversity data from less studied systems become available.

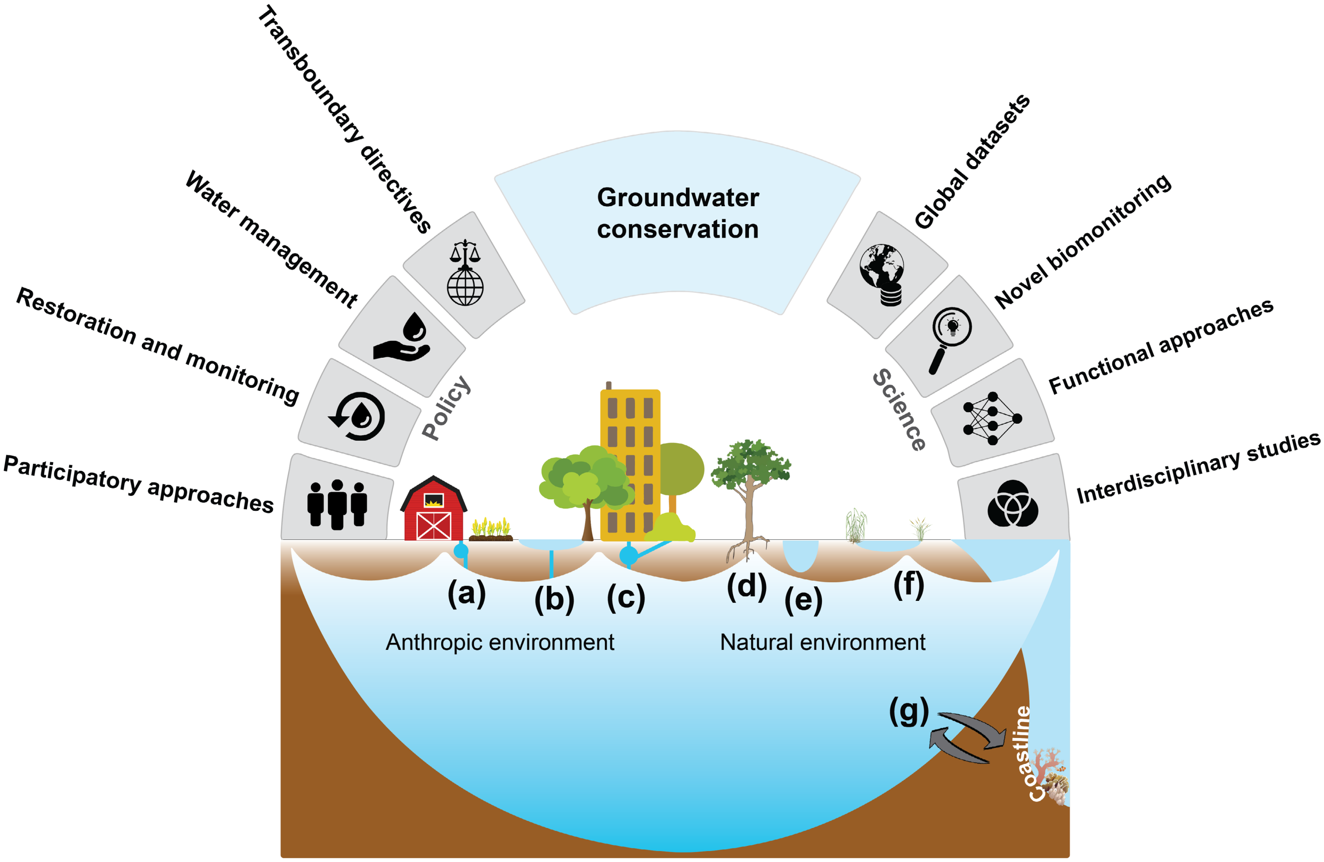

FIGURE 4 Examples of groundwater ecosystem services within anthropic (a, b, c) and natural (d, e, f, g) frameworks and recommended guidelines for groundwater conservation in terms of scientific advancements (top right) and policy developments (top left). Anthropic environment: (a) clean groundwater plays a key role in maintaining the agrobiodiversity (Trajkova et al., 2021); (b) interchanges between urban wetlands and groundwater can maintain the diversity of aquatic species and the functional integrity of urban wetlands (Ameli & Creed, 2019); (c) water for urbanization can also supply a key resource for the maintenance of urban vegetation (Marchionni et al., 2020); natural environment: (d) terrestrial vegetation groundwater-dependent ecosystem (GDE; Shukla et al., 2022); (e) lotic GDE (Erostate et al., 2020); (f) lentic GDE (Wu, Ma, et al., 2020); (g) coastal GDE (Santos et al., 2021).

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 on-going ambitious projects, the World Register for marine Cave Species (WoRCS; Gerovasileiou et al., 2016) and *Stygofauna Mundi* (Martinez et al., 2018), aim to create centralized, openly available and comprehensive taxonomic and ecological databases 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 (Mammola et al., 2022). 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 (Doody et al., 2017) provide a promising initial step towards the creation of a scientifically sound global GDE map. Like in other disciplines, application of FAIR Data Principles (Wilkinson, 2016) 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 (Griebler & Avramov, 2015). 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, Pawlowski et al. (2020)) to assess diversity of, and map the distributions of, species (Takahashi et al., 2023). First applications of eDNA to groundwater systems have been promising, recovering vast biodiversity hitherto mostly undocumented (Alther et al., 2021; Couton, Hürlemann, et al., 2023; Couton, Studer, et al., 2023; Saccò, Guzik, et al., 2022; van der Heyde et al., 2023). 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 (Hyacinthe et al., 2019; Mcloughlin et al., 2019).

(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 (Guzik et al., 2011). Therefore, traditional diversity metrics may not provide a mechanistic understanding of disturbance effects (Li et al., 2021). 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, see Toussaint et al., 2021) mediate a species' ability to respond to changes in their environment (Green et al., 2022; Palacio et al., 2022). However, functional studies targeting groundwater ecosystems are still rare (Hose et al., 2022). At a global level, an in-depth and groundwater-specific functional characterization proposed by Keith et al. (2022) could be informative. Microbes and aquatic invertebrates are essential for subterranean ecosystem functioning, contributing to nutrient cycling, energy flow, water filtration and biodiversity (Malard et al., 2023; Saccò, Blyth, Humphreys, Middleton, et al., 2020; Saccò, Blyth, Venarsky, et al., 2022; Venarsky et al., 2023). 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—for example, 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 (Martínez & Mammola, 2021); (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 (Liu et al., 2020), an endeavour often complicated by bureaucracy and geopolitical instability (Allan et al., 2019; Sousa et al., 2022). Worldwide, 468 transboundary aquifers (namely aquifers crossing multiple states, Stephan, 2009) have been delineated (IGRAC, 2021), several of which are subject to mounting human pressure (Wada & Heinrich, 2013). 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*' (United Nations, 1997). 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—for example, by reporting evidence of anthropogenic impact on transboundary groundwater ecosystems to showcase and boost transboundary aquifers' cooperation (Brancelj et al., 2020).

(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 (Foster et al., 2013), in part reflects knowledge deficits on the role of groundwater ecosystems at the time when the main freshwater policies were set up (EC-GWD, 2006) and the lack of ability in updating and adjusting strategies as scientific research progresses (Backhaus, 2023; Supporting Information Section 1). Now, 30 years after the publication of the cornerstone book 'The Freshwater imperative' (Naiman et al., 1995), inter-realm monitoring and management are more imperative than ever (Bugnot et al., 2019). It is just a matter of treasure lessons learned, expanding views and being ambitious (Saito et al., 2021). Most ecosystems will benefit from this timely (almost overdue) shift in perspectives.

(vii) *Develop restoration and monitoring programs.* Hydrogeological restoration of aquifers (Kresic, 2009) and surface–groundwater interactions (Kasahara et al., 2009) have been the focus of extensive research over the last three decades, yet studies on the ecological restoration of groundwater ecosystems are still rare (Liu & Mou, 2016). 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 (Scanlon et al., 2023).

(viii) *Encourage participatory approaches*. The value of a natural resource is only acknowledged when citizens and key stakeholders are involved (Kobori et al., 2016). This is true for subterranean ecosystems, where the success of conservation campaigns often rests on the involvement of multiple actors—from conservation scientists, to the media, the public and decision-makers (Gavish-Regev et al., 2023). For example, Alther et al. (2021), Couton, Studer, et al. (2023) and Raghavan et al. (2023) employed participatory approaches to raise awareness on aquatic subterranean fauna, in projects that also led to the discovery of new species (amphipod genus *Niphargus* and catfish *Horaglanis populi*) and new information on the distribution and abundance of subterranean species. 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 (Ban et al., 2018). 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 (Goodall, 2008). 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.

5 | 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, 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 almost two thirds of habitable global areas (74.9%) 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.

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The authors declare no competing interests.

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DATA AVAILABILITY STATEMENT

This study uses data from multiple open-access datasets. Source data are documented in Supporting Information Section 2 and can be downloaded from the persistent web-links provided. The data that support the findings of this study are openly available on Zenodo at https://doi.org/10.5281/zenodo.7924816.

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REFERENCES

Adamo, M., Sousa, R., Wipf, S., Correia, R. A., Lumia, A., Mucciarelli, M., & Mammola, S. (2022). Dimension and impact of biases in funding for species and habitat conservation. *Biological Conservation*, *272*, 109636.

Allan, J. R., Levin, N., Jones, K. R., Abdullah, S., Hongoh, J., Hermoso, V., & Kark, S. (2019). Navigating the complexities of coordinated conservation along the river Nile. *Science Advances*, *5*(4), eaau7668.

Alther, R., Bongni, N., Borko, Š., Fišer, C., & Altermatt, F. (2021). Citizen science approach reveals groundwater fauna in Switzerland and a new species of Niphargus (Amphipoda, Niphargidae). *Subterranean Biology*, *39*, 1–31.

Amanambu, A. C., Obarein, O. A., Mossa, J., Li, L., Ayeni, S. S., Balogun, O., Oyebamiji, A., & Ochege, F. U. (2020). Groundwater system and climate change: Present status and future considerations. *Journal of Hydrology*, *589*, 125163.

Ameli, A. A., & Creed, I. F. (2019). Groundwaters at risk: Wetland loss changes sources, lengthens pathways, and decelerates rejuvenation of groundwater resources. *JAWRA Journal of the American Water Resources Association*, *55*(2), 294–306.

Asmyhr, M. G., Linke, S., Hose, G., & Nipperess, D. A. (2014). Systematic conservation planning for groundwater ecosystems using phylogenetic diversity. *PLoS One*, *9*(12), e115132.

Backhaus, T. (2023). Commentary on the EU Commission's proposal for amending the water framework directive, the groundwater directive, and the directive on environmental quality standards. *Environmental Sciences Europe*, *35*(1), 1–7.

Ban, N. C., Frid, A., Reid, M., Edgar, B., Shaw, D., & Siwallace, P. (2018). Incorporate indigenous perspectives for impactful research and effective management. *Nature Ecology & Evolution*, *2*(11), 1680–1683.

Barua, M. (2011). Mobilizing metaphors: The popular use of keystone, flagship and umbrella species concepts. *Biodiversity and Conservation*, *20*, 1427–1440.

Bateman, H. L., & Merritt, D. M. (2020). Complex riparian habitats predict reptile and amphibian diversity. *Global Ecology and Conservation*, *22*, e00957.

Becher, J., Englisch, C., Griebler, C., & Bayer, P. (2022). Groundwater fauna downtown–Drivers, impacts and implications for subsurface ecosystems in urban areas. *Journal of Contaminant Hydrology*, *248*, 104021.

Bonaldo, D., Bellafiore, D., Ferrarin, C., Ferretti, R., Ricchi, A., Sangelantoni, L., & Vitelletti, M. L. (2023). The summer 2022 drought: A taste of future climate for the Po valley (Italy)? *Regional Environmental Change*, *23*, 1.

Boulton, A. J., Bichuette, M. E., Korbel, K., Stoch, F., Niemiller, M. L., Hose, G. C., & Linke, S. (2023). Recent concepts and approaches for conserving groundwater biodiversity. In F. Malard, C. Griebler, & S. Retaux (Eds.), *Groundwater ecology and evolution* (2nd ed., pp. 525–550). Elsevier.

Boulton, A. J., Datry, T., Kasahara, T., Mutz, M., & Stanford, J. A. (2010). Ecology and management of the hyporheic zone: Stream–groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society*, *29*(1), 26–40.

Brancelj, A. (2015). Two new stygobiotic copepod species from the Tibesti area (Northern Chad) and a re-description of *Pilocamptus schroederi* (van Douwe, 1915). *Zootaxa*, *3994*(4), 531–555.

Brancelj, A., Mori, N., Treu, F., & Stoch, F. (2020). The groundwater fauna of the Classical Karst: Hydrogeological indicators and descriptors. *Aquatic Ecology*, *54*, 205–224.

Bregović, P., Fišer, C., & Zagmajster, M. (2019). Contribution of rare and common species to subterranean species richness patterns. *Ecology and Evolution*, *9*(20), 11606–11618.

Bugnot, A. B., Hose, G. C., Walsh, C. J., Floerl, O., French, K., Dafforn, K. A., Hanford, J., Lowe, E. C., & Hahs, A. K. (2019). Urban impacts across realms: Making the case for inter-realm monitoring and management. *Science of the Total Environment*, *648*, 711–719.

Canedoli, C., Ficetola, G. F., Corengia, D., Tognini, P., Ferrario, A., & Padoa-Schioppa, E. (2022). Integrating landscape ecology and the assessment of ecosystem services in the study of karst areas. *Landscape Ecology*, *37*, 1–19.

Caro, T. (2010). *Conservation by proxy: Indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press.

Castaño-Sánchez, A., Hose, G. C., & Reboleira, A. S. P. (2020). Ecotoxicological effects of anthropogenic stressors in subterranean organisms: A review. *Chemosphere*, *244*, 125422.

Chen, L., Tan, L., Zhao, M., Sinha, A., Wang, T., & Gao, Y. (2023). Karst carbon sink processes and effects: A review. *Quaternary International*, *652*, 63–73.

Condon, L. E., Atchley, A. L., & Maxwell, R. M. (2020). Evapotranspiration depletes groundwater under warming over the contiguous United States. *Nature Communications*, *11*(1), 873.

Cooper, S. J. B., Hinze, S., Leys, R., Watts, C. H. S., & Humphreys, W. F. (2002). Islands under the desert: Molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics*, *16*(4), 589–590.

Cornu, J. F., Eme, D., & Malard, F. (2013). The distribution of groundwater habitats in Europe. *Hydrogeology Journal*, *21*(5), 949–960.

Couton, M., Hürlemann, S., Studer, A., Alther, R., & Altermatt, F. (2023). Groundwater environmental DNA metabarcoding reveals hidden diversity and reflects land-use and geology. *Molecular Ecology*, *32*, 3497–3512.

Couton, M., Studer, A., Hürlemann, S., Locher, N., Knüsel, M., Alther, R., & Altermatt, F. (2023). Integrating citizen science and environmental DNA metabarcoding to study biodiversity of groundwater amphipods in Switzerland. *Scientific Reports*, *13*(1), 18097.

Culver, D. C., & Pipan, T. (2014). *Shallow subterranean habitats: Ecology, evolution, and conservation*. Oxford University Press.

Culver, D. C., & Pipan, T. (2019). *The biology of caves and other subterranean habitats*. Oxford University Press.

Davic, R. D. (2003). Linking keystone species and functional groups: A new operational definition of the keystone species concept. *Conservation Ecology*, *7*(1), r11.

de Graaf, I. D., Sutanudjaja, E. H., Van Beek, L. P. H., & Bierkens, M. F. P. (2015). A high-resolution global-scale groundwater model. *Hydrology and Earth System Sciences*, *19*(2), 823–837.

Devitt, T. J., Wright, A. M., Cannatella, D. C., & Hillis, D. M. (2019). Species delimitation in endangered groundwater salamanders: Implications for aquifer management and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(7), 2624–2633.

Doody, T. M., Barron, O. V., Dowsley, K., Emelyanova, I., Fawcett, J., Overton, I. C., Pritchard, J. L., Van Dijk, A. I. J. M., & Warren, G. (2017). Continental mapping of groundwater dependent ecosystems: A methodological framework to integrate diverse data and expert opinion. *Journal of Hydrology: Regional Studies*, *10*, 61–81.

Eamus, D., & Froend, R. (2006). Groundwater-dependent ecosystems: The where, what and why of GDEs. *Australian Journal of Botany*, *54*(2), 91–96.

EC-GWD. (2006). Directive 2006/118/EC of the European Parliament and of the Council of 12 December 2006 on the protection of groundwater against pollution and deterioration. *Official Journal of the European Union*, *L 372*(19).

Ercoli, F., Lefebvre, F., Delangle, M., Godé, N., Caillon, M., Raimond, R., & Souty-Grosset, C. (2019). Differing trophic niches of three French stygobionts and their implications for conservation of endemic stygofauna. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(12), 2193–2203.

Erostate, M., Huneau, F., Garel, E., Ghiotti, S., Vystavna, Y., Garrido, M., & Pasqualini, V. (2020). Groundwater dependent ecosystems in coastal Mediterranean regions: Characterization, challenges and management for their protection. *Water Research*, *172*, 115461.

Famiglietti, J. S. (2014). The global groundwater crisis. *Nature Climate Change*, *4*(11), 945–948.

Fan, Y., Li, H., & Miguez-Macho, G. (2013). Global patterns of groundwater table depth. *Science*, *339*(6122), 940–943.

Fei, S., LaRue, E. A., Hardiman, B. S., & Dahlin, K. M. (2023). Structural diversity: A digital revolution. *Frontiers in Ecology and the Environment*, *21*(1), 3.

Ferguson, G., McIntosh, J. C., Warr, O., Sherwood Lollar, B., Ballentine, C. J., Famiglietti, J. S., Kim, J.-H., Michalski, J. R., Mustard, J. F., Tarnas, J., & McDonnell, J. J. (2021). Crustal groundwater volumes greater than previously thought. *Geophysical Research Letters*, *48*(16), e2021GL093549.

Ficetola, G. F., Canedoli, C., & Stoch, F. (2019). The Racovitzan impediment and the hidden biodiversity of unexplored environments. *Conservation Biology*, *33*(1), 214–216.

Fišer, C., Borko, Š., Delić, T., Kos, A., Premate, E., Zagmajster, M., Zakšek, V., & Altermatt, F. (2022). The European green deal misses Europe's subterranean biodiversity hotspots. *Nature Ecology & Evolution*, *6*(10), 1403–1404.

Fišer, C., Pipan, T., & Culver, D. C. (2014). The vertical extent of groundwater metazoans: An ecological and evolutionary perspective. *Bioscience*, *64*(11), 971–979.

Foster, S., Chilton, J., Nijsten, G. J., & Richts, A. (2013). Groundwater—A global focus on the 'local resource'. *Current Opinion in Environmental Sustainability*, *5*(6), 685–695.

Francois, C. M., Mermillod-Blondin, F., Malard, F., Fourel, F., Lécuyer, C., Douady, C. J., & Simon, L. (2016). Trophic ecology of groundwater species reveals specialization in a low-productivity environment. *Functional Ecology*, *30*(2), 262–273.

Francois, C. M., Simon, L., Malard, F., Lefébure, T., Douady, C. J., & Mermillod-Blondin, F. (2020). Trophic selectivity in aquatic isopods increases with the availability of resources. *Functional Ecology*, *34*(5), 1078–1090.

Gavish-Regev, E., Frumkin, A., Na'aman, I., Langford, B., Aharon, S., Ya'aran, S., Kolodny, O., & Mammola, S. (2023). *The power of academic and public opinion in conservation: The case of Ayyalon Cave, Israel*. Integrative Conservation.

Gerovasileiou, V., & Bianchi, C. N. (2021). Mediterranean marine caves: A synthesis of current knowledge. *Oceanography and Marine Biology: An Annual Review*, *59*, 1–88.

Gerovasileiou, V., Martínez, A., Álvarez, F., Boxshall, G., Humphreys, W. F., Jaume, D., Becking, L. E., Muricy, G., van Hengstum, P. J., Dekeyzer, S., Decock, W., Vanhoorne, B., Vandepitte, L., Bailly, N., & Iliffe, T. M. (2016). World Register of marine Cave Species (WoRCS): A new Thematic Species Database for marine and anchialine cave biodiversity. *Research Ideas and Outcomes*, *2*, e10451.

Giakoumi, S., Sini, M., Gerovasileiou, V., Mazor, T., Beher, J., Possingham, H. P., Abdulla, A., Çinar, M. E., Dendrinos, P., Cemal Gucu, A., Karamanlidis, A. A., Rodic, P., Panayotidis, P., Taskin, E., Jaklin, A., Voultsiadou, E., Webster, C., Zenetos, A., & Katsanevakis, S. (2013). Ecoregion-based conservation planning in the Mediterranean: Dealing with large-scale heterogeneity. *PLoS One*, *8*(10), e76449.

Gibert, J., & Deharveng, L. (2002). Subterranean ecosystems: A truncated functional biodiversity. *Bioscience*, *52*, 473.

Glanville, K., Sheldon, F., Butler, D., & Capon, S. (2023). Effects and significance of groundwater for vegetation: A systematic review. *Science of the Total Environment*, *875*, 162577.

Gleeson, T., Befus, K. M., Jasechko, S., Luijendijk, E., & Cardenas, M. B. (2016). The global volume and distribution of modern groundwater. *Nature Geoscience*, *9*(2), 161–167.

Gleeson, T., Cuthbert, M., Ferguson, G., & Perrone, D. (2020). Global groundwater sustainability, resources, and systems in the Anthropocene. *Annual Review of Earth and Planetary Sciences*, *48*, 431–463.

Gleeson, T., Wada, Y., Bierkens, M. F., & Van Beek, L. P. (2012). Water balance of global aquifers revealed by groundwater footprint. *Nature*, *488*(7410), 197–200.

Goodall, H. (2008). Riding the tide: Indigenous knowledge, history and water in a changing Australia. *Environment and History*, *14*(3), 355–384.

Green, S. J., Brookson, C. B., Hardy, N. A., & Crowder, L. B. (2022). Trait-based approaches to global change ecology: Moving from description to prediction. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1971), 20220071.

Griebler, C., & Avramov, M. (2015). Groundwater ecosystem services: A review. *Freshwater Science*, *34*(1), 355–367.

Griebler, C., Hahn, H. J., Mammola, S., Niemiller, M. L., Weaver, L., Saccò, M., Bichuette, M. E., & Hose, G. C. (2023). Legal frameworks for the conservation and sustainable management of groundwater ecosystems. In F. Malard, C. Griebler, & S. Retaux (Eds.), *Groundwater ecology and evolution* (2nd ed., pp. 551–571). Elsevier.

Guerra, C. A., Bardgett, R. D., Caon, L., Crowther, T. W., Delgado-Baquerizo, M., Montanarella, L., Navarro, L. M., Orgiazzi, A., Singh, B. K., Tedersoo, L., Vargas-Rojas, R., Briones, M. J. I., Buscot, F., Cameron, E. K., Cesarz, S., Chatzinotas, A., Cowan, D. A., Djukic, I., van den Hoogen, J., … Eisenhauer, N. (2021). Tracking, targeting, and conserving soil biodiversity. *Science*, *371*(6526), 239–241.

Guzik, M. T., Austin, A. D., Cooper, S. J., Harvey, M. S., Humphreys, W. F., Bradford, T., Eberhard, S. M., King, R. A., Leys, R., Muirhead, K. A., & Tomlinson, M. (2011). Is the Australian subterranean fauna uniquely diverse? *Invertebrate Systematics*, *24*(5), 407–418.

Hancock, P. J., Boulton, A. J., & Humphreys, W. F. (2005). Aquifers and hyporheic zones: Towards an ecological understanding of groundwater. *Hydrogeology Journal*, *13*, 98–111.

Hartland, A., Fenwick, G. D., & Bury, S. J. (2011). Tracing sewage-derived organic matter into a shallow groundwater food web using stable isotope and fluorescence signatures. *Marine and Freshwater Research*, *62*(2), 119–129.

Hose, G. C., Chariton, A., Daam, M. A., Di Lorenzo, T., Galassi, D. M. P., Halse, S. A., Reboleira, A. S., Robertson, A. L., Schmidt, S. I., & Korbel, K. L. (2022). Invertebrate traits, diversity and the vulnerability of groundwater ecosystems. *Functional Ecology*, *36*(9), 2200–2214.

Howard, J. K., Dooley, K., Brauman, K. A., Klausmeyer, K. R., & Rohde, M. M. (2023). Ecosystem services produced by groundwater dependent ecosystems: A framework and case study in California. *Frontiers in Water*, *5*, 1115416.

Howarth, F. G., & Moldovan, O. T. (2018). In O. T. Moldovan, L. Kováč, & S. Halse (Eds.), The ecological classification of cave animals and their adaptations. In *Cave ecology* (pp. 41–67). Springer.

Huggins, X., Gleeson, T., Serrano, D., Zipper, S., Jehn, F., Rohde, M. M., Abell, R., Vigerstol, K., & Hartmann, A. (2023). Overlooked risks and opportunities in groundwatersheds of the world's protected areas. *Nature Sustainability*, *6*, 1–10.

Hutchins, B. T., Engel, A. S., Nowlin, W. H., & Schwartz, B. F. (2016). Chemolithoautotrophy supports macroinvertebrate food webs and affects diversity and stability in groundwater communities. *Ecology*, *97*(6), 1530–1542.

Hyacinthe, C., Attia, J., & Rétaux, S. (2019). Evolution of acoustic communication in blind cavefish. *Nature Communications*, *10*(1), 4231.

Iannella, M., Fiasca, B., Di Lorenzo, T., Biondi, M., Di Cicco, M., & Galassi, D. M. (2020). Jumping into the grids: Mapping biodiversity hotspots in groundwater habitat types across Europe. *Ecography*, *43*(12), 1825–1841.

Iannella, M., Fiasca, B., Di Lorenzo, T., Di Cicco, M., Biondi, M., Mammola, S., & Galassi, D. M. (2021). Getting the 'most out of the hotspot' for practical conservation of groundwater biodiversity. *Global Ecology and Conservation*, *31*, e01844.

IGRAC. (2021). Transboundary Aquifers of the World, Update 2021, Scale 1:50000000.

IPCC. (2022). Climate change 2022: Mitigation of climate change. *Contribution of Working Group III to the sixth assessment report of the Intergovernmental Panel on Climate Change* [P.R. Shukla, J. Skea, R. Slade, A. Al Khourdajie, R. van Diemen, D. McCollum, M. Pathak, S. Some, P. Vyas, R. Fradera, M. Belkacemi, A. Hasija, G. Lisboa, S. Luz,

& J. Malley, (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA.
Jasechko, S., Birks, S. J., Gleeson, T., Wada, Y., Fawcett, P. J., Sharp, Z. D., McDonnell, J. J., & Welker, J. M. (2014). The pronounced seasonality of global groundwater recharge. *Water Resources Research*, *50*(11), 8845–8867.
Jetz, W., McGeoch, M. A., Guralnick, R., Ferrier, S., Beck, J., Costello, M. J., Fernandez, M., Geller, G. N., Keil, P., Merwo, C., Meyer, C., Muller-Karger, F. E., Pereira, H. M., Regan, E. C., Schmeller, D. S., & Turak, E. (2019). Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology & Evolution*, *3*(4), 539–551.
Kang, H., Sridhar, V., & Ali, S. A. (2022). Climate change impacts on conventional and flash droughts in the Mekong River Basin. *Science of the Total Environment*, *838*, 155845.
Kasahara, T., Datry, T., Mutz, M., & Boulton, A. J. (2009). Treating causes not symptoms: Restoration of surface–groundwater interactions in rivers. *Marine and Freshwater Research*, *60*(9), 976–981.
Keith, D. A., Ferrer-Paris, J. R., Nicholson, E., Bishop, M. J., Polidoro, B. A., Ramirez-Llodra, E., Tozer, M. G., Nel, J. L., Mac Nally, R., Gregr, E. J., Watermeyer, K. E., Essl, F., Faber-Langendoen, D., Franklin, J., Lehmann, C. E. R., Etter, A., Roux, D. J., Stark, J. S., Rowland, J. A., & Kingsford, R. T. (2022). A function-based typology for Earth's ecosystems. *Nature*, *610*(7932), 513–518.
Kobori, H., Dickinson, J. L., Washitani, I., Sakurai, R., Amano, T., Komatsu, N., Kitamura, W., Takagawa, S., Koyama, K., Ogawara, T., & Miller-Rushing, A. J. (2016). Citizen science: A new approach to advance ecology, education, and conservation. *Ecological Research*, *31*, 1–19.
Korbel, K. L., & Hose, G. C. (2011). A tiered framework for assessing groundwater ecosystem health. *Hydrobiologia*, *661*, 329–349.
Kresic, N. (2009). *Groundwater resources: Sustainability, management, and restoration*. McGraw-Hill Education.
Kretschmer, D., Wachholz, A., & Reinecke, R. (2023). Global groundwater in the Anthropocene. In F. Malard, C. Griebler, & S. Retaux (Eds.), *Groundwater ecology and evolution* (2nd ed., pp. 483–500). Academic Press.
Larned, S. T. (2012). Phreatic groundwater ecosystems: Research frontiers for freshwater ecology. *Freshwater Biology*, *57*(5), 885–906.
Lecher, A. L., & Mackey, K. R. (2018). Synthesizing the effects of submarine groundwater discharge on marine biota. *Hydrology*, *5*(4), 60.
Li, W., He, S., Cheng, X., & Zhang, M. (2021). Functional diversity outperforms taxonomic diversity in revealing short-term trampling effects. *Scientific Reports*, *11*(1), 18889.
Lindenmayer, D., Fischer, J., Felton, A., Montague-Drake, R., Manning, A. D., Simberloff, D., Youngentob, K., Saunders, D., Wilson, D., Felton, A. M., Blackmore, C., Lowe, A., Bond, S., Munro, N., & Elliott, C. P. (2007). The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos*, *116*(7), 1220–1226.
Link, A., El-Hokayem, L., Usman, M., Conrad, C., Reinecke, R., Berger, M., Wada, Y., Coroama, V., & Finkbeiner, M. (2023). Groundwater-dependent ecosystems at risk–global hotspot analysis and implications. *Environmental Research Letters*, *18*(9), 094026.
Linke, S., Turak, E., Asmyhr, M. G., & Hose, G. (2019). 3D conservation planning: Including aquifer protection in freshwater plans refines priorities without much additional effort. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(7), 1063–1072.
Liu, J., Yong, D. L., Choi, C. Y., & Gibson, L. (2020). Transboundary frontiers: An emerging priority for biodiversity conservation. *Trends in Ecology & Evolution*, *35*(8), 679–690.
Liu, Q., & Mou, X. (2016). Interactions between surface water and groundwater: Key processes in ecological restoration of degraded coastal wetlands caused by reclamation. *Wetlands*, *36*, 95–102.
López-Corona, O., Padilla, P., Escolero, O., Armas, F., García-Arrazola, R., & Esparza, R. (2013). Playing with models and optimization to overcome the tragedy of the commons in groundwater. *Complexity*, *19*(1), 9–21.
Lundberg, P., & Arponen, A. (2022). An overview of reviews of conservation flagships: Evaluating fundraising ability and surrogate power. *Nature Conservation*, *49*, 153–188.
Machiwal, D., Jha, M. K., Singh, V. P., & Mohan, C. (2018). Assessment and mapping of groundwater vulnerability to pollution: Current status and challenges. *Earth-Science Reviews*, *185*, 901–927.
Malard, F., Boutin, C., Camacho, A. I., Ferreira, D., Michel, G., Sket, B., & Stoch, F. (2009). Diversity patterns of stygobiotic crustaceans across multiple spatial scales in Europe. *Freshwater Biology*, *54*(4), 756–776.
Malard, F., Griebler, C., & Retaux, S. (Eds.). (2023). *Groundwater ecology and evolution: An introduction* (2nd ed.). Elsevier.
Mammola, S., Cardoso, P., Culver, D. C., Deharveng, L., Ferreira, R. L., Fišer, C., Galassi, D. M. P., Griebler, C., Halse, S., Humphreys, W. F., Isaia, M., Malard, F., Martinez, A., Moldovan, O. T., Niemiller, M. L., Pavlek, M., Reboleira, A. S. P. S., Souza-Silva, M., Teeling, E. C., … Zagmajster, M. (2019). Scientists' warning on the conservation of subterranean ecosystems. *BioScience*, *69*(8), 641–650.
Mammola, S., & Leroy, B. (2018). Applying species distribution models to caves and other subterranean habitats. *Ecography*, *41*(7), 1194–1208.
Mammola, S., Meierhofer, M. B., Borges, P. A., Colado, R., Culver, D. C., Deharveng, L., Delić, T., Di Lorenzo, T., Dražina, T., Ferreira, R. L., Fiasca, B., Fišer, C., Galassi, D. M. P., Garzoli, L., Gerovasileious, V., Griebler, C., Halse, S., Howarth, F. G., Isaia, M., & Cardoso, P. (2022). Towards evidence-based conservation of subterranean ecosystems. *Biological Reviews*, *97*(4), 1476–1510.
Marchionni, V., Daly, E., Manoli, G., Tapper, N. J., Walker, J. P., & Fatichi, S. (2020). Groundwater buffers drought effects and climate variability in urban reserves. *Water Resources Research*, *56*(5), e2019WR026192.
Martinez, A., Anicic, N., Calvaruso, S., Sanchez, N., Puppieni, L., Sforzi, T., Zaupa, S., Alvarez, F., Brankovits, D., Gasiorowski, L., Gerovasileiou, V., Gonzalez, B. C., Humphreys, W. F., Iliffe, T. M., Worsaae, K., Bailly, N., & Fontaneto, D. (2018). A new insight into the Stygofauna Mundi: Assembling a global dataset for aquatic fauna in subterranean environments. In *ARPHA conference abstracts* (Vol. *1*, p. e29514). Pensoft Publishers.
Martínez, A., & Mammola, S. (2021). Specialized terminology reduces the number of citations of scientific papers. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1948), 20202581.
Mcloughlin, M. P., Stewart, R., & McElligott, A. G. (2019). Automated bioacoustics: Methods in ecology and conservation and their potential for animal welfare monitoring. *Journal of the Royal Society Interface*, *16*(155), 20190225.
McNutt, M. (2014). The drought you can't see. *Science*, *345*(6204), 1543.
Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391–397.
Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience*, *43*(4), 219–224.
Moldovan, O. T. (2019). Cave protection in Romania. In G. M. Ponta & B. P. Onac (Eds.), *Cave and Karst systems of Romania* (pp. 537–541). Springer.
Mouquet, N., Gravel, D., Massol, F., & Calcagno, V. (2013). Extending the concept of keystone species to communities and ecosystems. *Ecology Letters*, *16*(1), 1–8.
Naiman, R. J., Magnuson, J. J., McKnight, D. M., & Stanford, J. A. (1995). *The freshwater imperative*. Island Press.
Navarro-Barranco, C., Ambroso, S., Gerovasileiou, V., Gómez-Gras, D., Grinyó, J., Montseny, M., & Santín, A. (2023). Conservation of dark habitats. In F. Espinosa (Ed.), *Coastal habitat conservation* (pp. 147–170). Academic Press.
Nicolosi, G., Mammola, S., Verbrugge, L., & Isaia, M. (2023). Aliens in caves: The global dimension of biological invasions in subterranean ecosystems. *Biological Reviews*, *98*(3), 849–867.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65–75.

Paine, R. T. (1969a). A note on trophic complexity and community stability. *The American Naturalist*, *103*(929), 91–93.

Paine, R. T. (1969b). The Pisaster-Tegula interaction: Prey patches, predator food preference, and intertidal community structure. *Ecology*, *50*(6), 950–961.

Palacio, F. X., Callaghan, C. T., Cardoso, P., Hudgins, E. J., Jarzyna, M. A., Ottaviani, G., Riva, F., Graco-Roza, C., Shirey, V., & Mammola, S. (2022). A protocol for reproducible functional diversity analyses. *Ecography*, *2022*(11), e06287.

Pawlowski, J., Apothéloz-Perret-Gentil, L., & Altermatt, F. (2020). Environmental DNA: What's behind the term? Clarifying the terminology and recommendations for its future use in biomonitoring. *Molecular Ecology*, *29*(22), 4258–4264.

Pereira, H. M., Ferrier, S., Walters, M., Geller, G. N., Jongman, R. H., Scholes, R. J., Bruford, M. W., Brumitt, N., Butchart, S. H. M., Cardoso, A. C., Coops, N. C., Dulloo, E., Faith, D. P., Freyhof, J., Gregory, R. D., Heip, C., Hoft, R., Hurtt, G., Jetz, W., & Wegmann, M. (2013). Essential biodiversity variables. *Science*, *339*(6117), 277–278.

Petersen-Perlman, J. D., Aguilar-Barajas, I., & Megdal, S. B. (2022). Drought and groundwater management: Interconnections, challenges, and policyresponses. *Current Opinion in Environmental Science & Health*, *28*, 100364.

Peterson, T. J., Saft, M., Peel, M. C., & John, A. (2021). Watersheds may not recover from drought. *Science*, *372*(6543), 745–749.

Premate, E., Borko, Š., Delić, T., Malard, F., Simon, L., & Fišer, C. (2021). Cave amphipods reveal co-variation between morphology and trophic niche in a low-productivity environment. *Freshwater Biology*, *66*(10), 1876–1888.

Raghavan, R., Britz, R., & Dahanukar, N. (2021). Poor groundwater governance threatens ancient subterranean fishes. *Trends in Ecology & Evolution*, *36*(10), 875–878.

Raghavan, R., Sundar, R. L., Arjun, C. P., Britz, R., & Dahanukar, N. (2023). Evolution in the dark: Unexpected genetic diversity and morphological stasis in the blind, aquifer-dwelling catfish Horaglanis. *Vertebrate Zoology*, *73*, 57–74.

Reinecke, R., Foglia, L., Mehl, S., Trautmann, T., Cáceres, D., & Döll, P. (2019). Challenges in developing a global gradient-based groundwater model (G 3 M v1. 0) for the integration into a global hydrological model. *Geoscientific Model Development*, *12*(6), 2401–2418.

Reinecke, R., Müller Schmied, H., Trautmann, T., Andersen, L. S., Burek, P., Flörke, M., Gosling, S. N., Grillakis, M., Hanasaki, N., Koutroulis, A., Pkhrel, Y., Thiery, W., Wada, Y., Yusuke, S., & Döll, P. (2021). Uncertainty of simulated groundwater recharge at different global warming levels: A global-scale multi-model ensemble study. *Hydrology and Earth System Sciences*, *25*(2), 787–810.

Rohde, M. M., Froend, R., & Howard, J. (2017). A global synthesis of managing groundwater dependent ecosystems under sustainable groundwater policy. *Groundwater*, *55*(3), 293–301.

Rohde, M. M., Sweet, S. B., Ulrich, C., & Howard, J. (2019). A transdisciplinary approach to characterize hydrological controls on groundwater-dependent ecosystem health. *Frontiers in Environmental Science*, *7*, 175.

Saccò, M., Blyth, A., Bateman, P. W., Hua, Q., Mazumder, D., White, N., Humphreys, W. F., Laini, A., Griebler, C., & Grice, K. (2019b). New light in the dark-a proposed multidisciplinary framework for studying functional ecology of groundwater fauna. *Science of the Total Environment*, *662*, 963–977.

Saccò, M., Blyth, A. J., Douglas, G., Humphreys, W. F., Hose, G. C., Davis, J., Guzik, M. T., Martinez, A., Eberhard, S. M., & Halse, S. A. (2022a). Stygofaunal diversity and ecological sustainability of coastal groundwater ecosystems in a changing climate: The Australian paradigm. *Freshwater Biology*, *67*(12), 2007–2023.

Saccò, M., Blyth, A. J., Humphreys, W. F., Cooper, S. J., Austin, A. D., Hyde, J., Mazumder, D., Hua, Q., White, N. E., & Grice, K. (2020b). Refining trophic dynamics through multi-factor Bayesian mixing models: A case study of subterranean beetles. *Ecology and Evolution*, *10*(16), 8815–8826.

Saccò, M., Blyth, A. J., Humphreys, W. F., Cooper, S. J., White, N. E., Campbell, M., … Grice, K. (2021). Rainfall as a trigger of ecological cascade effects in an Australian groundwater ecosystem. *Scientific Reports*, *11*(1), 3694.

Saccò, M., Blyth, A. J., Humphreys, W. F., Karasiewicz, S., Meredith, K. T., Laini, A., Cooper, S. J. B., Bateman, P. W., & Grice, K. (2020a). Stygofaunal community trends along varied rainfall conditions: Deciphering ecological niche dynamics of a shallow calcrete in Western Australia. *Ecohydrology*, *13*(1), e2150.

Saccò, M., Blyth, A. J., Humphreys, W. F., Kuhl, A., Mazumder, D., Smith, C., & Grice, K. (2019). Elucidating stygofaunal trophic web interactions via isotopic ecology. *PLoS One*, *14*(10), e0223982.

Saccò, M., Blyth, A. J., Humphreys, W. F., Middleton, J. A., White, N. E., Campbell, M., Mousavi-Derazmahalleh, M., Laini, A., Hua, Q., Meredith, K., Cooper, S. J. B., Griebler, C., Allard, S., Grierson, P., & Grice, K. (2020c). Tracking down carbon inputs underground from an arid zone Australian calcrete. *PLoS One*, *15*(8), e0237730.

Saccò, M., Blyth, A. J., Venarsky, M., & Humphreys, W. F. (2022). Trophic interactions in subterranean environments. In T. Mehner & K. Tockner (Eds.), *Encyclopedia of inland waters* (2nd ed., pp. 537–547). Elsevier.

Saccò, M., Campbell, M. A., Nevill, P., Humphreys, W. F., Blyth, A. J., Grierson, P. F., & White, N. E. (2022). Getting to the root of organic inputs in groundwaters: Stygofaunal plant consumption in a calcrete aquifer. *Frontiers in Ecology and Evolution*, *10*, 854591.

Saccò, M., Guzik, M. T., van der Heyde, M., Nevill, P., Cooper, S. J., Austin, A. D., Coates, P. J., Allentoft, M. E., & White, N. E. (2022d). eDNA in subterranean ecosystems: Applications, technical aspects, and future prospects. *Science of the Total Environment*, *820*, 153223.

Saccò, M., Humphreys, W. F., Stevens, N., Jones, M. R., Taukulis, F., Thomas, E., & Blyth, A. J. (2022). Subterranean carbon flows from source to stygofauna: A case study on the atyid shrimp *Stygiocaris stylifera* (Holthuis, 1960) from Barrow Island (WA). *Isotopes in Environmental and Health Studies*, *58*(3), 247–257.

Saito, L., Christian, B., Diffley, J., Richter, H., Rohde, M. M., & Morrison, S. A. (2021). Managing groundwater to ensure ecosystem function. *Groundwater*, *59*(3), 322–333.

Salem, B. B. (1989). *Arid zone forestry: A guide for field technicians (No. 20)*. Food and Agriculture Organization (FAO).

Sánchez-Fernández, D., Galassi, D. M., Wynne, J. J., Cardoso, P., & Mammola, S. (2021). Don't forget subterranean ecosystems in climate change agendas. *Nature Climate Change*, *11*(6), 458–459.

Santos, I. R., Chen, X., Lecher, A. L., Sawyer, A. H., Moosdorf, N., Rodellas, V., Tamborski, J., Cho, H.-M., Dimova, N., Sugimoto, R., Bonaglia, S., Li, H., Hajati, M.-C., & Li, L. (2021). Submarine groundwater discharge impacts on coastal nutrient biogeochemistry. *Nature Reviews Earth and Environment*, *2*(5), 307–323.

Sarbu, S. M., Kane, T. C., & Kinkle, B. K. (1996). A chemoautotrophically based cave ecosystem. *Science*, *272*(5270), 1953–1955.

Scanlon, B. R., Fakhreddine, S., Rateb, A., de Graaf, I., Famiglietti, J., Gleeson, T., Grafton, R. Q., Jobbagy, E., Kebede, S., Kolusu, S. R., Konikow, L. F., Long, D., Mekonnen, M., Müller Schmied, H., Mukherjee, A., MacDonald, A., Reedy, R. C., Shamsudduha, M., Simmons, C. T., & Zheng, C. (2023). Global water resources and the role of groundwater in a resilient water future. *Nature Reviews Earth and Environment*, *4*(2), 87–101.

Shukla, J., Dhyani, S., Pujari, P., & Verma, P. (2022). Groundwater-dependent vegetation to address the loss of ecosystems dependent on groundwater resources. In M. Kumar, S. Dhyani, & N. Kalra (Eds.), *Forest dynamics and conservation: Science, innovations and policies* (pp. 263–278). Springer Nature Singapore.

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation*, *83*(3), 247–257.

Simon, K. S., Benfield, E. F., & Macko, S. A. (2003). Food web structure and the role of epilithic biofilms in cave streams. *Ecology*, *84*(9), 2395–2406.

Sket, B., Paragamian, K., & Trontelj, P. (2004). A census of the obligate subterranean fauna of the Balkan Peninsula. In H. I. Griffiths, B. Kryštufek, & J. M. Reed (Eds.), *Balkan biodiversity: Pattern and process in the European hotspot* (pp. 309–322). Springer Netherlands.

Sousa, R. G., Silva, J. P. D., Douda, K., & Mammola, S. (2022). The cost of war for biodiversity: A potential ecocide in Ukraine. *Frontiers in Ecology and the Environment*, *20*(7), 394–396.

Stephan, R. M. (2009). *Transboundary aquifers: Managing a vital resource: The UNILC draft articles on the law of transboundary aquifers*. UNESCO.

Takahashi, M., Saccò, M., Kestel, J. H., Nester, G., Campbell, M. A., Van Der Heyde, M., Heydenrych, M. J., Juszkiewicz, D. J., Nevill, P., Dawkins, K. L., Bessey, C., Fernandes, K., Miller, H., Power, M., Mousavi-Derazmahalleh, M., Newton, J. P., White, N. E., Richards, Z. T., & Allentoft, M. E. (2023). Aquatic environmental DNA: A review of the macro-organismal biomonitoring revolution. *Science of the Total Environment*, *873*, 162322.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92.

Toussaint, A., Brosse, S., Bueno, C. G., Pärtel, M., Tamme, R., & Carmona, C. P. (2021). Extinction of threatened vertebrates will lead to idiosyncratic changes in functional diversity across the world. *Nature Communications*, *12*(1), 5162.

Trajkova, F., Arsov, S., & Gudeva, L. K. (2021). The role and importance of agrobiodiversity for agriculture. *Journal of Agriculture and Plant Sciences*, *19*(2), 47–64.

Trontelj, P., Douady, C. J., Fišer, C., Gibert, J., Gorički, Š., Lefébure, T., Sket, B., & Zakšek, V. (2009). A molecular test for cryptic diversity in ground water: How large are the ranges of macro-stygobionts? *Freshwater Biology*, *54*(4), 727–744.

Uhl, A., Hahn, H. J., Jäger, A., Luftensteiner, T., Siemensmeyer, T., Döll, P., Noack, M., Schwenk, K., Berkhoff, S., Weiler, M., Karwautz, C., & Griebler, C. (2022). Making waves: Pulling the plug—Climate change effects will turn gaining into losing streams with detrimental effects on groundwater quality. *Water Research*, *220*, 118649.

United Nations. (1997). Convention on the law of the non-navigational uses of international watercourses.

United Nations. (2022). *The United Nations World Water Development Report 2022: groundwater: Making the invisible visible*. UNESCO.

Vaccarelli, I., Colado, R., Pallarés, S., Galassi, D. M., Sánchez-Fernández, D., Di Cicco, M., Meierhofer, M. B., Piano, E., Di Lorenzo, T., & Mammola, S. (2023). A global meta-analysis reveals multilevel and context-dependent effects of climate change on subterranean ecosystems. *One Earth*, *6*, 1510–1522.

van der Heyde, M., White, N. E., Nevill, P., Austin, A. D., Stevens, N., Jones, M., & Guzik, M. T. (2023). Taking eDNA underground: Factors affecting eDNA detection of subterranean fauna in groundwater. *Molecular Ecology Resources*, *23*, 1257–1274.

Venarsky, M., Simon, K. S., Saccò, M., François, C., Simon, L., & Griebler, C. (2023). Groundwater food webs. In F. Malard, C. Griebler, & S. Retaux (Eds.), *Groundwater ecology and evolution* (2nd ed., pp. 241–261). Academic Press.

Verissimo, D., MacMillan, D. C., & Smith, R. J. (2011). Toward a systematic approach for identifying conservation flagships. *Conservation Letters*, *4*(1), 1–8.

Verkaik, J., Sutanudjaja, E. H., Oude Essink, G. H., Lin, H. X., & Bierkens, M. F. (2022). GLOBGM v1. 0: A parallel implementation of a 30 arcsec PCR-GLOBWB-MODFLOW global-scale groundwater model. *Geoscientific Model Development Discussions*, *2022*, 1–27.

Wada, Y., & Heinrich, L. (2013). Assessment of transboundary aquifers of the world—Vulnerability arising from human water use. *Environmental Research Letters*, *8*(2), 024003.

Wada, Y., Van Beek, L. P., Van Kempen, C. M., Reckman, J. W., Vasak, S., & Bierkens, M. F. (2010). Global depletion of groundwater resources. *Geophysical Research Letters*, *37*(20), L20402.

Walker, B., & Salt, D. (2012). *Resilience thinking: Sustaining ecosystems and people in a changing world*. Island Press.

Wiens, J. A., Hayward, G. D., Holthausen, R. S., & Wisdom, M. J. (2008). Using surrogate species and groups for conservation planning and management. *Bioscience*, *58*(3), 241–252.

Wilkinson, M. D. (2016). The FAIR guiding principles for scientific data management and stewardship. *Scientific Data*, *3*, 1–9.

Wu, W. Y., Lo, M. H., Wada, Y., Famiglietti, J. S., Reager, J. T., Yeh, P. J. F., Ducharne, A., & Yang, Z. L. (2020a). Divergent effects of climate change on future groundwater availability in key mid-latitude aquifers. *Nature Communications*, *11*(1), 3710.

Wu, X., Ma, T., & Wang, Y. (2020). Surface water and groundwater interactions in wetlands. *Journal of Earth Science*, *31*, 1016–1028.

Wynne, J. J., Howarth, F. G., Mammola, S., Ferreira, R. L., Cardoso, P., Di Lorenzo, T., Galassi, D. M. P., Medellin, R. A., Miller, B. W., Sánchez-Fernández, D., Bichuette, M. E., Biswas, J., BlackEagle, C. W., Boonyanusith, C., Amorim, I. R., Vieira Borges, P. A., Boston, P. J., Cal, R. N., Naowarat, C., & Zhao, Y. (2021). A conservation roadmap for the subterranean biome. *Conservation Letters*, *14*(5), e12834.

Zagmajster, M., Eme, D., Fišer, C., Galassi, D., Marmonier, P., Stoch, F., Cornu, J.-F., & Malard, F. (2014). Geographic variation in range size and beta diversity of groundwater crustaceans: Insights from habitats with low thermal seasonality. *Global Ecology and Biogeography*, *23*(10), 1135–1145.

Zagmajster, M., Malard, F., Eme, D., & Culver, D. C. (2018). Subterranean biodiversity patterns from global to regional scales. In O. T. Moldovan, L. Kováč, & S. Halse (Eds.), *Cave ecology* (pp. 195–227). Springer.

DATA SOURCES

Abbott, B. W., Bishop, K., Zarnetske, J. P., Minaudo, C., Chapin, F. S., III, Krause, S., Hannah, D. M., Conner, L., Ellison, D., Godsey, S. E., Plont, S., Marçais, J., Kolbe, T., Huebner, A., Frei, R. J., Hampton, T., Gu, S., Buhman, M., Sara Sayedi, S., … Pinay, G. (2019). Human domination of the global water cycle absent from depictions and perceptions. *Nature Geoscience*, *12*, 533–540.

Abdelahad, N., Bolpagni, R., Jona Lasinio, G., Vis, M. L., Amadio, C., Laini, A., & Keil, E. J. (2015). Distribution, morphology and ecological niche of *Batrachospermum* and *Sheathia* species (Batrachospermales, Rhodophyta) in the fontanili of the Po plain (northern Italy). *European Journal of Phycology*, *50*, 318–329.

Abou Rafee, S. A., Uvo, C. B., Martins, J. A., Domingues, L. M., Rudke, A. P., Fujita, T., & Freitas, E. D. (2019). Large-scale hydrological modelling of the Upper Paraná River Basin. *Water*, *11*, 882.

ABS 1301.0 Year Book Australia, 2009–10. (2010). Australian Bureau of Statistics. www.abs.gov.au/AUSSTATS/

Adamson, P. T., Rutherfurd, I. D., Peel, M. C., & Conlan, I. A. (2009). Chapter 4 – The hydrology of the Mekong River. In I. C. Campbell (Ed.), *The Mekong, aquatic ecology* (pp. 53–76). Academic Press.

Agostinho, A. A., Costa Bonecker, C., & Gomes, L. G. (2009). Effects of water quantity on connectivity: the case of the upper Paraná River floodplain. *Ecohydrology & Hydrobiology*, *9*, 99–113.

Agostinho, A. A., Thomaz, S. M., Minte-Vera, C. V., & Winemiller, K. O. (2000). Biodiversity in the high Paraná River floodplain. In B. Gopal, W. J. Junk, & J. A. Davis (Eds.), *Biodiversity in wetlands: Assessment, function and conservation* (pp. 89–118). The Netherlands Backhuys Publishers.

Agostinho, A. A., Vazzoler, A. E. A. M., & Thomaz, S. M. (1995). The high river Paran'a basin: Limnological and ichthyological aspects. In J. G. Tundisi, C. E. M. Bicudo, & T. Matsumura Tundisi (Eds.), *Limnology in Brazil 59–103*. Brazilian Academy of Sciences/Brazilian Limnological Society.

Allan, J. R., Levin, N., Jones, K. R., Abdullah, S., Hongoh, J., Hermoso, V., & Kark, S. (2019). Navigating the complexities of coordinated conservation along the river Nile. *Science Advances*, *5*, eaau7668.

Andersen, M. S., & Acworth, R. I. (2009). Stream-aquifer interactions in the Maules creek catchment, Namoi valley, New South Wales, Australia. *Hydrogeology Journal*, *17*, 2005–2021.

Arias, M. E., Cochrane, T. A., Norton, D., Killeen, T. J., & Khon, P. (2013). The flood pulse as the underlying driver of vegetation in the largest wetland and fishery of the Mekong Basin. *Ambio*, *42*, 864–876.

Balestrini, R., Delconte, C. A., Sacchi, E., & Buffagni, A. (2021). Groundwater-dependent ecosystems as transfer vectors of nitrogen from the aquifer to surface waters in agricultural basins: The fontanili of the Po Plain (Italy). *Science of the Total Environment*, *753*, 141995.

Barbarossa, V., Bosmans, J., Wanders, N., King, H., Bierkens, M. F. P., Huijbregts, M. A. J., & Schipper, A. M. (2021). Threats of global warming to the world's freshwater fishes. *Nature Communications*, *12*, 1701.

Barnett, S., Harrington, N., Cook, P., & Simmons, C. T. (2020). Groundwater in Australia: Occurrence and management issues. In *Sustainable groundwater management: A comparative analysis of french and australian policies and implications to other countries* (pp. 109–127). Springer.

Bartoli, M., Racchetti, E., Delconte, C. A., Sacchi, E., Soana, E., Laini, A., Longhi, D., & Viaroli, P. (2012). Nitrogen balance and fate in a heavily impacted watershed (Oglio River, Northern Italy): In quest of the missing sources and sinks. *Biogeosciences*, *9*, 361–373.

Bickel, S., Chen, X., Papritz, A., & Or, D. (2019). A hierarchy of environmental covariates control the global biogeography of soil bacterial richness. *Scientific Reports*, *9*, 12129.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J. W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & de Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*, 30–59.

Bolpagni, R., Racchetti, E., & Laini, A. (2016). Fragmentation and groundwater supply as major drivers of algal and plant diversity and relative cover dynamics along a highly modified lowland river. *Science of the Total Environment*, *568*, 875–884.

Boulton, A. J., Humphreys, W. F., & Eberhard, S. M. (2003). Imperilled subsurface waters in Australia: Biodiversity, threatening processes and conservation. *Aquatic Ecosystem Health & Management*, *6*, 41–54.

Bucior, A., Rippey, B., McElarney, Y., & Douglas, R. (2021). Evaluating macrophytes as indicators of anthropogenic pressures in rivers in Ireland. *Hydrobiologia*, *848*, 1087–1099.

Campbell, I. C. (2012). Biodiversity of the Mekong Delta. In F. G. Renaud & C. Kuenzer (Eds.), *The Mekong Delta System: Interdisciplinary analyses of a River Delta* (pp. 293–313). Springer Environmental Science and Engineering. Springer Netherlands.

Campen, R., Kowalski, J., Lyons, W. B., Tulaczyk, S., Dachwald, B., Pettit, E., Welch, K. A., & Mikucki, J. A. (2019). Microbial diversity of an Antarctic subglacial community and high-resolution replicate sampling inform hydrological connectivity in a polar desert. *Environmental Microbiology*, *21*, 2290–2306.

Chen, C. C., Gillig, D., & McCarl, B. A. (2001). Effects of climate change on a water dependent regional economy: A study of the Texas Edwards Aquifer. *Climatic Change*, *49*, 397–409.

Chen, Z., Auler, A. S., & Bakalowicz, M. (2017). The world karst aquifer mapping project: Concept, mapping procedure and map of Europe.

Collins, R. (2002). *The Nile*. Yale Univ. Press.

Commonwealth of Australia. (2014). Ecological and hydrogeological survey of the Great Artesian Basin springs - Springsure, Eulo, Bourke and Bogan River supergroups. Volume 1: history, ecology and hydrogeology, Knowledge report, prepared by UniQuest for the Department of the Environment, Commonwealth of Australia.

Costa, P. F., & Schulz, U. H. (2010). The fish community as an indicator of biotic integrity of the streams in the Sinos River basin, Brazil. *Brazilian Journal of Biology*, *70*, 1195–1205.

Culver, D. C., Pipan, T., & Schneider, K. (2009). Vicariance, dispersal and scale in the aquatic subterranean fauna of karst regions. *Freshwater Biology*, *54*, 918–929.

Dabovic, J., Dobbs, L., Byrne, G., & Raine, A. (2019). A new approach to prioritising groundwater dependent vegetation communities to inform groundwater management in New South Wales, Australia. *Australian Journal of Botany*, *67*, 397–413.

Danielopol, D. L., Pospisil, P., & Rouch, R. (2000). Biodiversity in groundwater: A large-scale view. *Trends in Ecology & Evolution*, *15*, 223–224.

David, A., & Noel, M. (2006). Aquifer and watercourse interaction in the Murray Darling Basin elucidated using electrical conductivity imaging. *ASEG Extended Abstracts*, *1*, 1–7.

de Graaf, I. D., Sutanudjaja, E. H., van Beek, L. P. H., & Bierkens, M. F. P. (2015). A high-resolution global-scale groundwater model. *Hydrology and Earth System Sciences*, *19*, 823–837.

Delgado, J. M., Merz, B., & Apel, H. (2012). A climate-flood link for the lower Mekong River. *Hydrology and Earth System Sciences*, *16*, 1533–1541.

Di Cicco, M., Di Lorenzo, T., Iannella, M., Vaccarelli, I., Galassi, D. M. P., & Fiasca, B. (2021). Linking hydrogeology and ecology in karst landscapes: The response of Epigean and obligate groundwater copepods (Crustacea: Copepoda). *Water*, *13*, 2106.

Döll, P., & Fiedler, K. (2008). Global-scale modeling of groundwater recharge. *Hydrology and Earth System Sciences*, *12*, 863–885.

Dugan, H. A., Doran, P. T., Grombacher, D., Auken, E., Bording, T., Foged, N., Foley, N., Mikucki, J., Virginia, R. A., & Tulaczyk, S. (2022). The hidden labyrinth: Deep groundwater in Wright Valley, Antarctica. *The Cryosphere*, *16*, 4977–4983.

Eamus, D., Froend, R., Loombes, R., Hose, G. C., & Murray, B. R. (2006). A functional methodology for determining the groundwater regime needed to maintain health of groundwater dependent ecosystems. *Australian Journal of Botany*, *54*, 97–114.

Edwards Aquifer Authority. (2018). Edwards aquifer authority recharge 2017 groundwater recharge report: San Antonio, Texas. *Edwards Aquifer Authority*, *7*.

Elsawwaf, M., Feyen, J., Batelaan, O., & Bakr, M. (2014). Groundwater–surface water interaction in Lake Nasser, Southern Egypt. *Hydrological Processes*, *28*, 414–430.

Evans, S. E., & Wallenstein, M. D. (2014). Climate change alters ecological strategies of soil bacteria. *Ecology Letters*, *17*, 155–164.

Fan, Y., Li, H., & Miguez-Macho, G. (2013). Global patterns of groundwater table depth. *Science*, *339*, 940–943.

Ferrill, D. A., Morris, A. P., & McGinnis, R. N. (2019). Geologic structure of the Edwards (Balcones Fault Zone) Aquifer. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 171–188). Geological Society of America Memoir 215.

Filip, Z. (2002). International approach to assessing soil quality by ecologically-related biological parameters. *Agriculture, Ecosystems & Environment*, *88*, 169–174.

Formetta, G., Tootle, G., & Therrell, M. (2022). Regional reconstruction of Po River Basin (Italy) streamflow. *Hydrology*, *9*, 163.

Gibson, J. R., Harden, S. J., & Fries, J. N. (2008). Survey and distribution of invertebrates from selected springs of the Edwards Aquifer in Comal and Hays counties, Texas. *The Southwestern Naturalist*, *53*, 74–84.

Gnann, S., Reinecke, R., Stein, L., Wada, Y., Thiery, W., Müller Schmied, H., Satoh, Y., Pokhrel, Y., Ostberg, S., Koutroulis, A., Hanasaki, N., Grillakis, M., Gosling, S., Burek, P., Bierkens, M., & Wagener, T. (2022). Functional relationships reveal differences in the water cycle representation of global water models.

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities—Approaches, patterns and prospects. *Biological Reviews*, *87*, 111–127.

Guareschi, S., Laini, A., Viaroli, P., & Bolpagni, R. (2020). Integrating habitat-and species-based perspectives for wetland conservation in lowland agricultural landscapes. *Biodiversity and Conservation*, *29*, 153–171.

Gustafson, C. D., Key, K., Siegfried, M. R., Winberry, J. P., Fricker, H. A., Venturelli, R. A., & Michaud, A. B. (2022). A dynamic saline groundwater system mapped beneath an Antarctic ice stream. *Science*, *376*, 640–644.

Hancock, P. J., Boulton, A. J., & Humphreys, W. F. (2005). Aquifers and hyporheic zones: Towards an ecological understanding of groundwater. *Hydrogeology Journal*, *13*, 98–111.

Hart, B., Walker, G., Katupitiya, A., & Doolan, J. (2020). Salinity Management in the Murray–Darling Basin, Australia. *Water*, *12*(6), 1829.

Hecht, J. S., Lacombe, G., Arias, M. E., Dang, T. D., & Piman, T. (2019). Hydropower dams of the Mekong River basin: A review of their hydrological impacts. *Journal of Hydrology*, *568*, 285–300.

Hinojosa, J., Green, J., Estrada, F., Herrera, J., Mata, T., Phan, D., Pasha, A. B. M. T., Matta, A., Johnson, D., & Kapoor, V. (2020). Determining the primary sources of fecal pollution using microbial source tracking assays combined with land-use information in the Edwards Aquifer. *Water Resources*, *184*, 116211.

Holland, R. A., Darwall, W. R. T., & Smith, K. G. (2012). Conservation priorities for freshwater biodiversity: The key biodiversity area approach refined and tested for continental Africa. *Biological Conservation*, *148*, 167–179.

Hose, G. C., Dabovic, J., Nelson, T., Pollitt, L., & Korbel, K. L. (2022). Groundwater dependent aquatic and terrestrial ecosystems. In T. Mehner & K. Tockner (Eds.), *Encyclopedia of inland waters* (2nd ed., pp. 339–347). Elsevier.

Hose, G. C., Sreekanth, J., Barron, O., & Pollino, C. (2015). Stygofauna in Australian groundwater systems: Extent of knowledge. Report to Australian Coal Association Research Program. Macquarie University and CSIRO.

Huggins, X., Gleeson, T., Serrano, D., Zipper, S., Jehn, F., Rohde, M. M., Abell, R., Vigerstol, K., & Hartmann, A. (2023). Overlooked risks and opportunities in groundwatersheds of the world's protected areas. *Nature Sustainability*, *6*, 855–864.

Hutchins, B. T., Gibson, J. R., Diaz, P. H., & Schwartz, B. F. (2021). Stygobiont diversity in the San Marcos artesian well and Edwards Aquifer groundwater ecosystem, Texas, USA. *Diversity*, *13*, 234.

Johnson, S., & Schindel, G. (2015). Tracing groundwater flowpaths in Kinney County, Texas: Dec. 2015: Edwards Aquifer Authority Report 12, 132.

Kaijser, W., Hering, D., & Lorenz, A. W. (2022). Reach hydromorphology: A crucial environmental variable for the occurrence of riverine macrophytes. *Hydrobiologia*, *849*, 4273–4285.

Kennard, M. J., Arthington, A. H., Pusey, B. J., & Harch, B. D. (2005). Are alien fish a reliable indicator of river health? *Freshwater Biology*, *50*, 174–193.

Keshavarzi, M., Baker, A., Bryce, F., Kelly, J., & Andersen, M. S. (2017). River-groundwater connectivity in a karst system, Wellington, New South Wales, Australia. *Hydrogeology Journal*, *25*, 557–574.

Korbel, K., & Hose, G. C. (2011). A tiered framework for assessing groundwater ecosystem health. *Hydrobiologia*, *661*, 329–349.

Korbel, K. L., Greenfield, P., & Hose, G. C. (2022a). Agricultural practices linked to shifts in groundwater microbial structure and denitrifying bacteria. *Science of the Total Environment*, *807*, 150870.

Korbel, K. L., Rutlidge, H., Hose, G. C., Eberhard, S., & Andersen, M. A. (2022b). Dynamics of microbiotic patterns reveal surface water groundwater interactions in intermittent and perennial streams. *Science of the Total Environment*, *811*, 152380.

Korbel, K., Chariton, A., Stephenson, S., Greenfield, P., & Hose, G. C. (2017). Wells provide a distorted view of life in the aquifer: Implications for sampling, monitoring and assessment of groundwater ecosystems. *Scientific Reports*, *7*, 40702.

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 5925–5930.

Krejca, J., & Reddell, J. (2019). Biology and ecology of the Edwards Aquifer. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 159–170). Geological Society of America Memoir 215.

Kristjánsson, B. K., & Svavarsson, J. (2007). Subglacial refugia in Iceland enabled groundwater amphipods to survive glaciations. *The American Naturalist*, *170*, 292–296.

Laini, A., Bartoli, M., Lamastra, L., Capri, E., Balderacchi, M., & Trevisan, M. (2012). Herbicide contamination and dispersion pattern in lowland springs. *Science of the Total Environment*, *438*, 312–318.

Lamontagne, S., Taylor, A. R., Cook, P. G., Crosbie, R. S., Brownbill, R., Williams, R. M., & Brunner, P. (2014). Field assessment of surface water–groundwater connectivity in a semi-arid river basin (Murray–Darling, Australia). *Hydrological Processes*, *28*, 1561–1572.

Lasne, E., Bergerot, B., Lek, S., & Laffaille, P. (2007). Fish zonation and indicator species for the evaluation of the ecological status of rivers: Example of the Loire basin (France). *River Research and Applications*, *23*, 877–890.

Loaiciga, H. A., & Schofield, M. (2019). Climate variability, climate change, and Edwards Aquifer water fluxes. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 223–238). Geological Society of America Memoir 215.

Lohani, S., Dilts, T. E., Weisberg, P. J., Null, S. E., & Hogan, Z. S. (2020). Rapidly accelerating deforestation in Cambodia's Mekong River Basin: A comparative analysis of spatial patterns and drivers. *Water*, *12*, 2191.

Lyons, W. B., Welch, K. A., Carey, A. E., Doran, P. T., Wall, D. H., Virginia, R. A., Fountain, A. G., Csathó, B. M., & Tremper, C. M. (2005). Groundwater seeps in Taylor Valley Antarctica: An example of a subsurface melt event. *Annals of Glaciology*, *40*, 200–206.

Mace, R. E. (2019). The use of water from the Edwards Aquifers, Texas. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 207–212). Geological Society of America Memoir 215.

Maclay, R. W., & Small, T. A. (1984). Carbonate geology and hydrology of the Edwards Aquifer in the San Antonio area, Texas. U.S. Geological Survey Open-File Report OFR 83-537, 72.

Menció, A., Korbel, K. L., & Hose, G. C. (2014). River–aquifer interactions and their relationship to stygofauna assemblages: A case study of the Gwydir River alluvial aquifer (New South Wales, Australia). *Science of the Total Environment*, *479*, 292–305.

Moeck, C., Grech-Cumbo, N., Podgorski, J., Bretzler, A., Gurdak, J. J., Berg, M., & Schirmer, M. (2020). A global-scale dataset of direct natural groundwater recharge rates: A review of variables, processes and relationships. *Science of the Total Environment*, *717*, 137042.

Montanari, A. (2012). Hydrology of the Po River: Looking for changing patterns in river discharge. *Hydrology and Earth System Sciences*, *16*, 3739–3747.

PRBA (Po River Basin Authority). (2007). Introduction of Po River Basin Authority. www.abdpo.it

Rau, G. C., Halloran, L. J. S., Cuthbert, M. O., Andersen, M. S., Acworth, R. I., & Tellam, J. H. (2017). Characterising the dynamics of surface water-groundwater interactions in intermittent and ephemeral streams using streambed thermal signatures. *Advances in Water Resources*, *107*, 354–369.

Rebouças, A. D. C. (1999). Groundwater resources in South America. *Episodes: Journal of International Geoscience*, *22*, 232–237.

Reinecke, R., Foglia, L., Mehl, S., Trautmann, T., Cáceres, D., & Döll, P. (2019). Challenges in developing a global gradient-based groundwater model (G 3 M v1. 0) for the integration into a global hydrological model. *Geoscientific Model Development*, *12*, 2401–2418.

Reiss, J., Perkins, D. M., Fussmann, K. E., Krause, S., Canhoto, C., Romeijn, P., & Robertson, A. L. (2019). Groundwater flooding: Ecosystem structure following an extreme recharge event. *Science of the Total Environment*, *652*, 1252–1260.

Reytar, K., Stolle, F., & Anderson, W. (2019). Deforestation threatens the Mekong, but new trees are growing in surprising places.

Rossetti, G., Pieri, V., & Martens, K. (2005). Recent ostracods (Crustacea, Ostracoda) found in lowland springs of the provinces of Piacenza and Parma (Northern Italy). *Hydrobiologia*, *542*, 287–296.

Rudke, A. P., Xavier, A. C. F., Martins, L. D., Freitas, E. D., Uvo, C. B., Hallak, R., Souza, R. A. F., Andreoli, R. V., de Almeida Albuquerque, T. T., & Martins, J. A. (2022). Landscape changes over 30 years of intense economic activity in the upper Paraná River basin. *Ecological Informatics*, *72*, 101882.

Rundel, P. W. (2009). Chapter 7 – Vegetation in the Mekong Basin. In I. C. Campbell (Ed.), *The Mekong, aquatic ecology* (pp. 43–160). Academic Press.

Sacchi, E., Acutis, M., Bartoli, M., Brenna, S., Delconte, C. A., Laini, A., & Pennisi, M. (2013). Origin and fate of nitrates in groundwater from the central Po plain: Insights from isotopic investigations. *Applied Geochemistry*, *34*, 164–180.

Saccò, M., Blyth, A. J., Humphreys, W. F., Cooper, S. J., White, N. E., Campbell, M., Mousavi-Derazmahalleh, M., Hua, Q., Mazumder, D., Smith, C., Griebler, C., & Grice, K. (2021). Rainfall as a trigger of ecological cascade effects in an Australian groundwater ecosystem. *Scientific Reports*, *11*(1), 3694.

Schindel, G. M. (2019). Genesis of the Edwards (Balcones Fault Zone) Aquifer. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 9–18). Geological Society of America Memoir 215.

Schulz, C., Steward, A. L., & Prior, A. (2013). Stygofauna presence within fresh and highly saline aquifers of the border rivers region in southern Queensland. *Proceedings of the Royal Society of Queensland*, *118*, 27–35.

Sharp, J. M., Green, R. T., & Schindel, G. M. (2019). Introduction. In J. M. Sharp, R. T. Green, & G. M. Schindel (Eds.), *The Edwards Aquifer: The past, present, and future of a vital water resource* (pp. 1–7). Geological Society of America Memoir 215.

Siddig, A. A., Ellison, A. M., Ochs, A., Villar-Leeman, C., & Lau, M. K. (2016). How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in ecological indicators. *Ecological Indicators*, *60*, 223–230.

Smith, B. A., Hunt, B. B., & Schindel, G. M. (2005). Groundwater flow in the Edwards Aquifer: Comparison of groundwater modeling and dye trace results. In *Sinkholes and the engineering and environmental impacts of karst* (pp. 131–141). ASCE (American Society of Civil Engineers).

Søndergaard, M., Johansson, L. S., Lauridsen, T. L., Jørgensen, T. B., Liboriussen, L., & Jeppesen, E. (2010). Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biology*, *55*, 893–908.

Soukhaphon, A., Baird, I. G., & Hogan, Z. S. (2021). The impacts of hydropower dams in the Mekong River Basin: A review. *Water*, *13*, 265.

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., Pletterbauer, F., & Hering, D. (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: A review. *Hydrobiologia*, *696*, 1–28.

Thomaz, S. M., Lansac-Tôha, F. A., Roberto, M. C., Esteves, F. A., & Lima, A. F. (1992). Seasonal variation of some limnological factors of Lagoa do Guaraná, a várzea lake of the high rio Paraná, state of Mato Grosso do Sul, Brazil. *Revue d'hydrobiologie Tropicale*, *25*, 269–276.

Turco, R. F., Kennedy, A. C., & Jawson, M. D. (1994). Microbial indicators of soil quality. In *Defining soil quality for a sustainable environment* (Vol. *35*, pp. 73–90). Wiley.

Uemura, T., Taniguchi, M., & Shibuya, K. (2011). Submarine groundwater discharge in Lützow-Holm Bay, Antarctica. *Geophysical Research Letters*, *38*, L08402.
Verkaik, J., Sutanudjaja, E. H., Oude Essink, G. H. P., Lin, H. X., & Bierkens, M. F. P. (2022). GLOBGM v1. 0: A parallel implementation of a 30 arcsec PCR-GLOBWB-MODFLOW global-scale groundwater model. *Geoscientific Model Development Discussions*, 1–27.
Viaroli, P., Soana, E., Pecora, S., Laini, A., Naldi, M., Fano, E. A., & Nizzoli, D. (2018). Space and time variations of watershed N and P budgets and their relationships with reactive N and P loadings in a heavily impacted river basin (Po River, Northern Italy). *Science of the Total Environment*, *639*, 1574–1587.
Wang, S., Zhang, L., She, D., Wang, G., & Zhang, Q. (2021). Future projections of flooding characteristics in the Lancang-Mekong River Basin under climate change. *Journal of Hydrology*, *602*, 126778.
World Wide Fund. (2021). Magical Mekong: New species discoveries. https://greatermekong.panda.org/discovering_the_greater_mekong/species/new_species/magical_mekong/
Zagmajster, M., Malard, F., Eme, D., & Culver, D. C. (2018). Subterranean biodiversity patterns from global to regional scales. In *Cave ecology* (pp. 195–227). Springer.

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